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Original Article

Utilizing thermal imaging drones to investigate sleeping site selection in an arboreal primate

Eva Gazagne[a,*], Chiara Goldblatt[a], Vỹ Trần Nguyễn[b], Fany Brotcorne[a] and Alain Hambuckers[a]

[a]Unit of Research SPHERES, University of Liège, Quai van Beneden, 22, Liège 4020, Belgium
[b]Institute of Tropical Biology, Vietnam Academy of Science and Technology, 9/621 Hanoi Highway, Ho Chi Minh City, Vietnam

[*]Address correspondence to Eva Gazagne. E-mail: evagazagne@live.fr.
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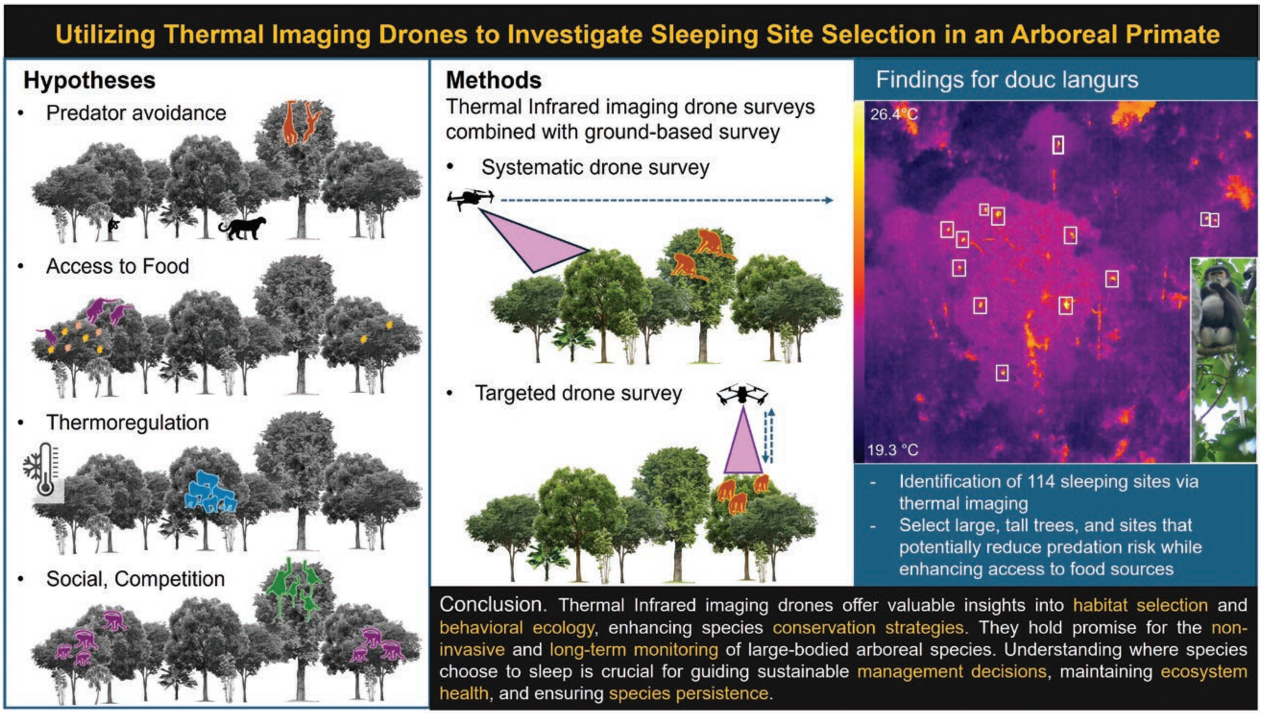
Abstract

Sleeping site selection is essential for understanding primate behavioral ecology and survival. Identifying where species sleep helps determine priority areas and critical resources for targeted conservation efforts. However, observing sleeping sites at night is challenging, especially for species sensitive to human disturbance. Thermal infrared imaging (TIR) with drones is increasingly used for detecting and counting primates, yet it has not been utilized to investigate ecological strategies. This study investigates the sleeping site selection of the Critically Endangered black-shanked douc langur (*Pygathrix nigripes*) in Cát Tiên National Park, Vietnam. Our aim is to assess the feasibility of using a TIR drone to test sleeping site selection strategies in non-nesting primates, specifically examining hypotheses related to predation avoidance and food proximity. Between January and April 2023, we conducted 120 drone flights along 22 transects (~1-km long) and identified 114 sleeping sites via thermal imaging. We established 116 forest structure plots along 29 transects in non-selected sites and 65 plots within douc langur sleeping sites. Our observations reveal that douc langurs selected tall and large trees that may provide protection against predators. Additionally, they selected sleeping sites with increased access to food, such as *Afzelia xylocarpa*, which serves as a preferred food source during the dry season. These results highlight the effective use of TIR drones for studying douc langur sleeping site selection with minimal disturbance. Besides offering valuable insights into habitat selection and behavioral ecology for conservation, TIR drones hold great promise for the noninvasive and long-term monitoring of large-bodied arboreal species.

Key words: noninvasive monitoring, primate conservation, *Pygathrix nigripes*, sleeping site selection, thermal infrared imaging drones.

Graphical Abstract



- Identification of 114 sleeping sites via thermal imaging
- Select large, tall trees, and sites that potentially reduce predation risk while enhancing access to food sources

Conclusion. Thermal Infrared imaging drones offer valuable insights into habitat selection and behavioral ecology, enhancing species conservation strategies. They hold promise for the non-invasive and long-term monitoring of large-bodied arboreal species. Understanding where species choose to sleep is crucial for guiding sustainable management decisions, maintaining ecosystem health, and ensuring species persistence.

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The selection of sleeping sites by primates is a fundamental aspect of their behavioral ecology, providing valuable insights into their environmental adaptation and survival (Anderson 1998). It holds multifaceted implications for primate biology, encompassing predator avoidance strategies, proximity to food sources, social dynamics, competition, parasite avoidance, physical comfort, and thermoregulation (Di Bitetti et al. 2000; Teichroeb et al. 2012; Savagian and Fernandez-Duque 2017; Mekonnen et al. 2021).

One prominent hypothesis regarding sleeping site selection posits that primates choose sleeping sites to minimize the risk of predation during their vulnerable sleeping hours, that is, the predator avoidance hypothesis. This hypothesis suggests that primates may select sleeping sites that are less accessible to potential predators, reduce primate detection from predators, and enhance primates' detection of predators (Di Bitetti et al. 2000; Albert et al. 2011; Fei et al. 2017). For example, sleeping high in trees with dense foliage can reduce ground-based predators' access to sleeping primates (Fan and Jiang 2008; Teichroeb et al. 2012; Mills and al. 2021). Another critical factor influencing sleeping site selection in primates is access to food resources, that is, the food proximity hypothesis. Primates may prefer sleeping in or close to food sources to enhance foraging efficiency by minimizing travel costs (i.e., reducing the energy expenditure) while maximizing food access (von Hippel 1998; Teichroeb et al. 2012; Gazagne et al. 2020b; Mekonnen et al. 2021). Thermoregulation is also a key factor influencing sleeping site selection strategies, that is, the thermoregulatory hypothesis. Primates may choose sleeping trees that provide shelter from rain or wind and engage in clustering or huddling behavior to reduce heat loss during the night, especially in regions with seasonal weather variations (Eppley et al. 2017; Savagian and Fernandez-Duque 2017; Fei et al. 2019). Other strategies can impact primate fitness, such as the range and resource defense hypothesis regarding intra- or inter-species competition, the safety and stability hypothesis, the social hypothesis (i.e., promoting group cohesion), and the parasite avoidance hypothesis (Bitetti et al. 2000; Kowalewski and Zunino 2005; Smith et al. 2007; Cheyne et al. 2013; Brividoro et al. 2019; Di Rismayanti et al. 2023). However, it should also be considered that primates randomly select sleeping sites with respect to tree species, tree size, and area of the home range as a null hypothesis (von Hippel 1998; Teichroeb et al. 2012; Gazagne et al. 2020b). The choice of sleeping sites reflects a balance among these strategies and can vary significantly between primate species based on their ecological niche, social structure, and environmental conditions. Consequently, investigating sleeping site selection offers valuable insights into primate adaptation, behavior, and ecology and holds significant implications for their conservation.

Studying sleeping site selection in wild-ranging primates presents significant challenges due to dense forest canopies and the elusive nature of unhabituated species to human presence (Gazagne et al. 2020a). Traditional methods for arboreal species consist of following habituated groups from dawn to dusk to collect precise data on sleeping tree locations and behavior (Albert et al. 2011). However, these methods are time-consuming, can disrupt natural behavior and ecology, and raise ethical concerns, including the potential for disease transmission (Gazagne et al. 2020a; Lappan et al. 2020; Piel et al. 2022), limiting their suitability for comprehensive and noninvasive studies of primate sleeping site selection. Recent advancements in technology, particularly the application of thermal infrared imaging (TIR) in conjunction with uncrewed aerial vehicles (drones, hereafter), have emerged as a promising avenue for monitoring forest-dwelling primates (*Pongo pygmaeus* in Burke et al. 2019; *Rhinopithecus roxellana* in He et al. 2020; *Alouatta paliatta* in Kays et al. 2019; *Ateles geoffroyi* in Spaan et al. 2019; *Trachypithecus delacouri* in Gazagne et al. 2023; *Nomascus nasutus* in Wearn et al. 2023; *Nomascus hainanus* in Zhang et al. 2023). By flying above the canopy, this approach leverages the temperature differentials between primates' warm bodies and the cooler background vegetation. It offers the unique advantage of monitoring animals in low-light conditions, mitigating challenges related to animal camouflage or elusiveness, and providing access to survey locations that are often difficult to reach by foot (Wich and Koh 2018). Furthermore, TIR drone surveys provide advantages over ground surveys, including the ability to cover larger areas, achieve accurate detection and population counts, and minimize disturbance, with primates typically exhibiting no observable reaction to drones flying at altitude exceeding 40 m above the canopy (Kays et al. 2019; Spaan et al. 2019). The utilization of TIR-equipped drones holds significant promise for advancing our understanding of primate spatial ecology, including sleeping site selection (Piel et al. 2022).

In this context, our study focuses on a large-bodied colobine endemic to Vietnam and Cambodia, the Critically Endangered black-shanked douc langur (*Pygathrix nigripes*) (Duc et al. 2021). This species is predominantly arboreal and inhabits evergreen, semi-evergreen, and mixed deciduous forest mosaics, as well as coastal dry forests (Duc et al. 2021). Black-shanked douc langurs are primarily folivorous, consuming plant parts from more than 150 different species (Duc et al. 2009). Their diet consists mainly of young and mature leaves (54.6%), supplemented by fruits (29.3% including the whole fruit, seeds, or pulp), flowers (14.6%), and other unidentified items (1.5%), depending on availability (Duc et al. 2009). The species exhibits a fission-fusion social organization, characterized by a range of social structures, including bachelor groups, single males, one male units (OMUs, averaging 7.5 individuals), and multi-male multi-female units (Rawson 2009; O'Brien 2014). Fusion of OMUs into bands can result in groups comprising more than 40 individuals (O'Brien 2014). The home range of an OMU has been estimated at 20.1 ha in evergreen forest in Cambodia (Rawson, 2009) and 12.4 ha in semi-evergreen forest in Vietnam (Duc et al., 2021). The black-shanked douc langur faces pressing threats, including habitat loss, fragmentation, hunting for traditional medicine and local consumption, and pet trade (Duc et al. 2021). These threats emphasize the urgency of comprehensive ecological studies on this Critically Endangered species. However, despite the conservation importance of the black-shanked douc langur, there is a notable paucity of comprehensive knowledge regarding its sleeping site selection behavior. While a few observations of sleeping sites have been documented (cf., Duc 2007; Rawson 2009), the difficulties in gathering data on non-habituated individuals have hindered a more in-depth understanding of their sleeping site preferences. In a recent study conducted in Cát Tiên National Park, southern Vietnam, we demonstrated that TIR drone surveys can be effectively used to monitor large arboreal primates, including black-shanked douc langurs (Gazagne et al. 2024a). Building on this approach, we apply TIR drone technology to detect black-shanked douc langurs within their sleeping sites.

Our research aims to address the knowledge gap by employing TIR imaging drones to explore the biotic factors influencing sleeping site selection among black-shanked douc langurs inhabiting Cát Tiên National Park. Specifically, we tested hypotheses related to predator avoidance and proximity to food sources during a single dry season. Predation risk for black-shanked douc langurs likely comes from reticulated and Burmese pythons (*Python reticulatus* and *Python molurus*) as well as leopard cats (*Prionailurus bengalensis*) (Rawson et al. 2009). We predicted that black-shanked douc langurs would select large, tall trees with dense, concealing foliage and avoid trees with lianas to reduce predator access and detection. Additionally, we predicted that they would sleep in or near feeding trees to maximize energy intake. This prediction is based on the dietary habits of black-shanked douc langur, which show a preference for fruit consumption in the morning, likely as a strategy to offset energy loss during sleep by choosing readily accessible energy sources (Duc et al. 2009). Since our data collection occurred during preprogrammed flights in the dry season (January to April 2023), we were unable to explore aspects associated with seasonal variation, such as thermoregulation. However, we tested the potential disturbance caused by drones during nighttime on douc langurs and discussed the broader applications of TIR drones, alongside other technologies, for further investigating hypotheses regarding sleeping site selection.

Materials and Methods

Study site

Cát Tiên National Park (11°21′ to 11°48′N; 107°10′ to 107°34′E) is located in southern Vietnam, ~150 km northeast of Ho Chi Minh City. We conducted our study in the lowland Eastern Nam Cat Tien sector, which covers an area of 100 sq km, representing ~13.5% of the total national park area (Supplementary Figure S1). This region is relatively flat with hills not exceeding 150 m elevation and is delimited by the Dong Nai river in the eastern part (**Figure 1**). The site experiences a tropical monsoon climate characterized by 2 distinct seasons: A dry season from November to April and a rainy season from May to October. The average annual temperature is 26.7 °C, the average annual rainfall is 2,227 mm and the average humidity level is 82% (CTNP 2020).

Our study area is dominated by secondary evergreen forest, with a prevalence of the species *Lagerstroemia calyculata* (*Lythraceae*) and the genus *Dipterocarpus* (Blanc et al. 2000). Habitat types also include primary evergreen forest, semi-evergreen forest, mixed forest (including bamboos and other plants), bamboo forest, grassland, wetlands, and lakes (Supplementary Figure S2). This protected area harbors a diverse community of primates. The black-shanked douc langur coexists with the southern yellow-cheeked crested gibbon (*Nomascus gabriellae*), the pygmy loris (*Nyciticebus pygmaeus*), the bear macaque (*Macaca arctoides*), the long-tailed macaque (*Macaca fascicularis*), the northern pig-tailed macaque (Macaca *leonina*), and the silvered langur (*Trachypithecus margarita*).

Data collection

Black-shanked douc langur identification

To identify black-shanked douc langurs using TIR imagery with the drone and optimize the flight parameters during our active survey data collection, we conducted pilot surveys from April 2022 to November 2022 (Supplementary Text S1). We used a DJI Mavic 2 Enterprise Advanced drone equipped with a thermal camera featuring a resolution of 640 × 512-pixel and a 48-megapixel standard (RGB) camera. Identification of black-shanked douc langurs was based on several distinguishing features, including their characteristic body shape, social and spatial organization at sleeping site (**Figure 2**), and specific locomotion pattern (Supplementary Text S1 and **Videos S1**, **S2**). Specifically, among morphologically similar arboreal

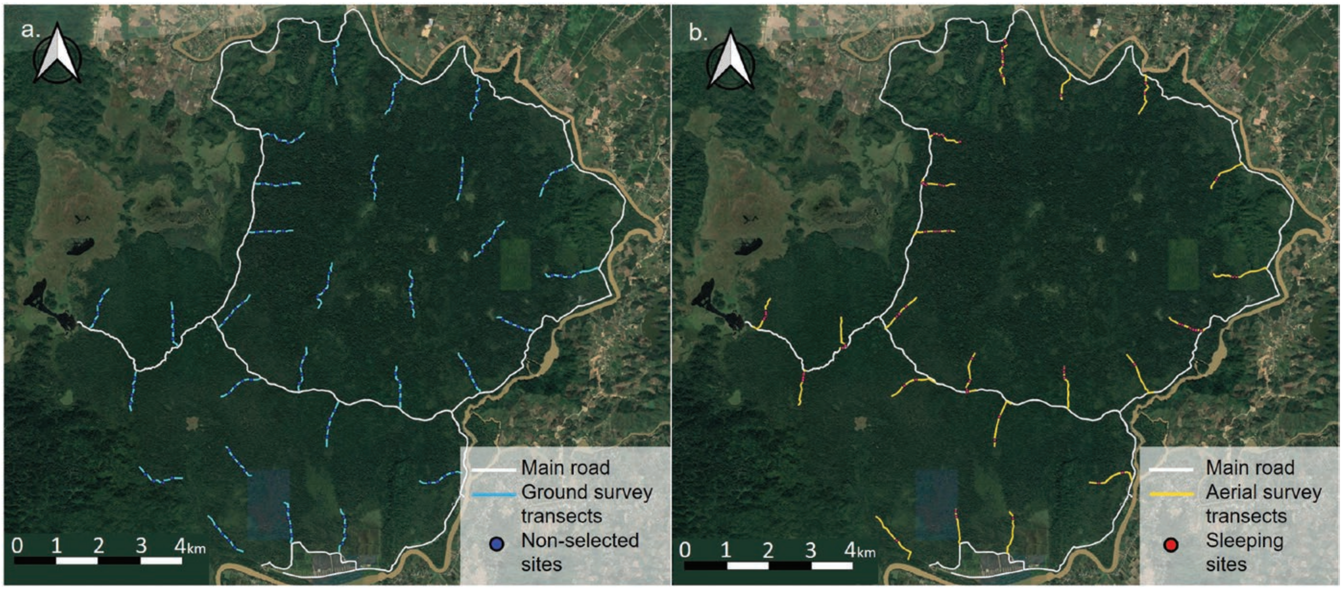

Figure 1. Satellite image of the study area covering approximately 100 km² within the lowland dry-evergreen forests of Eastern Nam Cát Tiên (Cát Tiên National Park, Southern Vietnam): (A) we conducted ground-based surveys and established 116 forest structure plots, semi-systematically positioned along 29 transects, considered as non-selected sites; (B) we conducted aerial surveys along 22 transects adjacent to the main road, overlapping with ground transects, and established 65 forest structure plots at the sleeping sites identified with the TIR drone. All transects are spaced more than 1 km apart. This figure was generated with QGIS (2020, Version 3.16).

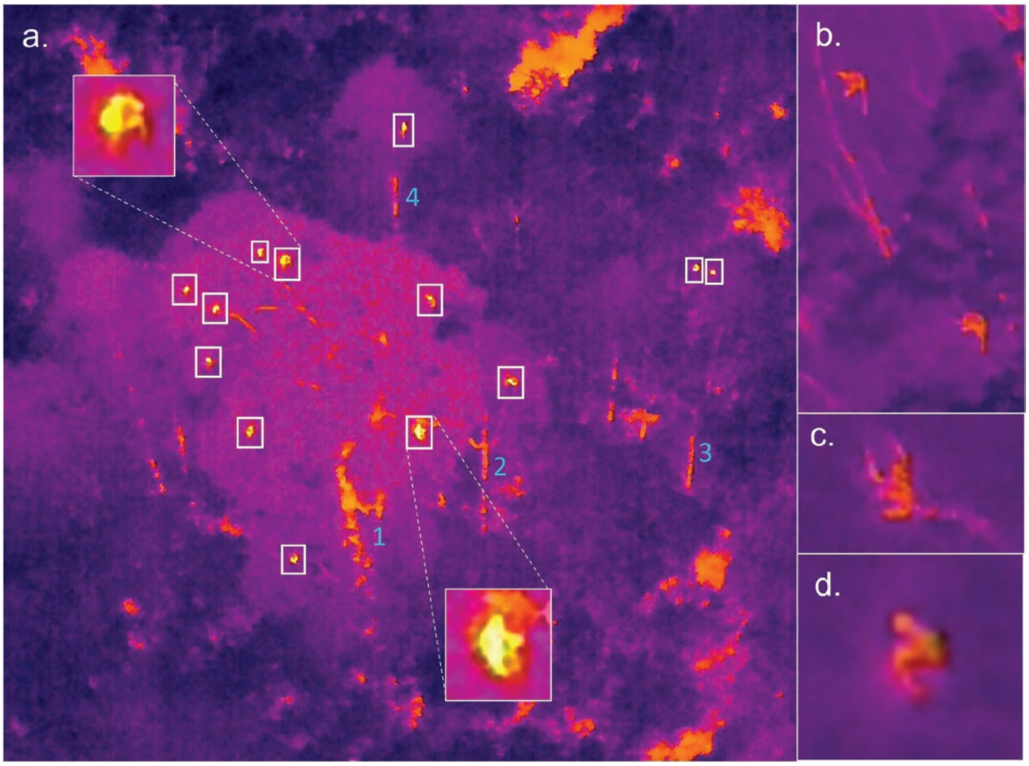

Figure 2. Identification of black-shanked douc langurs via TIR imaging with drones during nocturnal surveys conducted from April 2022 to April 2023. (A) Sleeping site of a group of black-shanked douc langurs comprising 4 sleeping trees (numbering is positioned near the hot tree trunks). We can detect 13 thermal spots of body shapes (highlighted with squares), but the 2 enlargements show cases where 2 individuals are aggregated (confirmed during the subsequent footage showing the movement of individuals within the large emergent sleeping tree), resulting in a count of 15 individuals. Species identification was possible when individuals were inactive (B) or in movement, thanks to their long tail and arms (C an individual is shown jumping, cf. **Video S1 and S2**), or based on their sitting position (D cf. Gazagne et al. 2023).

species, such as silvered langurs and long-tailed macaques, black-shanked douc langurs can be differentiated by their larger body size, prominent belly, longer tail, smaller group sizes, use of fewer sleeping trees, and preference for higher canopy elevations (cf., Gazagne et al. 2024a).

Sleeping site identification and drone disturbance

To detect the sleeping sites of black-shanked douc langurs, we conducted 120 aerial surveys along 22 transects, each surveyed at least once per month (with a minimum of 5 replicates per transect, Figure 1B), spaced more than 1 km apart during the dry season (9 January 2023 to 28 April 2023). We used a DJI Mavic 3 Thermal drone equipped with a 12-µm pixel pitch, Uncooled VOx Microbolometer sensor with a 8–14 µm spectral band, a 640 × 512-pixel resolution at 30-Hz framerate, a 40-mm lens with a 61° diagonal field of view and a 56x hybrid zoom. We programmed 22 flight paths using the DJI RC Pro Enterprise control unit, maintaining a flight speed at 3 m.s^{-1} and a flight altitude of 60 or 70 m above ground level based on the height of the canopy in the surveyed area (maximum canopy height of 35 m) (Burke et al. 2019; Potapov et al. 2021). This altitude ensured minimal disturbance by maintaining a distance of at least 35 m between the drone and the top canopy, while also providing the necessary minimum resolution for animals in the upper canopy to be visible and identified (Burke et al. 2019; Kays et al. 2019; Spaan et al. 2019). Due to the drone's limited reception range (resulting in frequent signal loss in densely forested areas), we could only survey transects adjacent to a main road and had to shorten 18 transects, resulting in average transect length of 940 ± 155 m, ranging from 656 to 1,269 m (Figure 1B). When signal reception with the drone was lost, we activated the return home safety features, but we flew manually the drone back above the transect when the signal was reestablished. On average, each flight lasted 14 min and 33 s ± SD 2 min. We conducted nocturnal flights before sunrise (5:08 AM ± SD 00:21, $N = 99$) or at dusk (7:46 PM ± SD 00:34, $N = 21$), times when the temperature difference between primates and surrounding canopy was optimal (average ambient temperature was 22.4 ± SD 2.7 °C, $N = 120$).

During the outward flight, we set the gimbal angle at 45° to maximize detection and facilitate the identification of black-shanked douc langurs through TIR imaging (Figure 2). Subsequently, we conducted the drone's return flight with a gimbal angle set at 90°, allowing us to pinpoint the location of the sleeping sites detected during the outbound flight. We captured still images of each detection using the Ironbow color palette (Gazagne et al. 2023) and extracted the GPS coordinates (accuracy ± 0.35 m) of the sleeping sites based on still images taken with the gimbal angle set at 90° downward while the drone was flying over the sleeping sites. Each detection could include several black-shanked douc langurs from the same unit or band, but multiple detections could be part of the same social unit. However, we considered detections spaced more than 100 m as belonging to different social units (or groups), based on home range assessments in Vietnam (12.4 ha in Duc et al. 2021). We recorded the number of individuals and social units detected ad libitum. When possible, we noted the number of douc langurs per sleeping tree.

Moreover, we assessed the quality of footage visibility, which could range from poor, fair, or good according to weather conditions (such as temperature, relative humidity, and cloud visibility extracted from flight logs) and reported signal reception (Supplementary Table S1). Nocturnal detections were verified through ground-truthing during diurnal ground surveys conducted along the same 22 transects as each aerial survey (**Figure 1**). These surveys confirmed suspected species detected near the same area during early morning or evening nocturnal surveys (i.e., between 5:30 AM and 5:10 PM, with an average duration of 79 ± SD 17 min, $N = 120$). Ground-truthing was particularly useful for identifying species in nocturnal detections where distinct visible morphological characteristics or imagery resolution were insufficient. However, suspected nocturnal detections of black-shanked douc langurs that could not be confirmed by ground survey ($N = 83$ detections out of $N_{\text{total}} = 183$; 29.3% of TIR drone detections) were excluded from the analyses to prevent potential misidentification. In total, ground surveys covered 29 transects, including the set-up of forest structure plots. These comprised 18 existing permanent ranger trails and 11 newly created transects, all spaced more than 1 km apart to ensure adequate coverage. The average length of the ground transects was 1,143 ± 91 m, ranging from 951 to 1,378 m (**Figure 1A**).

To evaluate the potential disturbance caused by the TIR drone during its nighttime return flight over sleeping sites, we monitored the visible behavior of black-shanked douc langurs through TIR imagery. We categorized their behaviors as follows: *Inactivity*, when there was no visible response from individuals, indicating that they were presumably sleeping; *Movement*, when at least 1 individual within the detection exhibited movement but remained within the sleeping site; and *Flight* behavior, when at least 1 individual within the detection exhibited movement and left the sleeping site.

Forest structure plots at selected sleeping sites and non-selected sites

To select sleeping sites for conducting forest structure plots, we only considered detections of black-shanked douc langurs confirmed by ground surveys. Additionally, we included footage with fair or good visibility, enabling the identification of characteristic tree structures visible in TIR imaging, which could be further verified in the field. To investigate the factors influencing sleeping site selection, we characterized the forest structure by analyzing 181 circular plots with a radius of 11.3 m, resulting in a plot area of 0.04 ha. This plot size is often used in primate habitat studies to ensure adequate representation of tree and vegetation structure by including ~20 trees per plot (Nowak et al. 2008; Gazagne et al. 2020b; Rondeux 2021). Among these plots, 65 were located at the detected sleeping sites (with a combined plot area of 2.6 ha across the 22 transects), while 116 were semi-systematically placed along 29 transects (4 plots per transect, spaced at least 200 m apart) and considered non-selected for sleeping sites (with a total plot area of 4.64 ha) (**Figure 1**).

To characterize the forest structure in each plot, we calculated the mean values of the number of stems and of the diameter at breast height (DBH) for all stems with DBH >10 cm (Gazagne et al. 2020b). We identified the species of each stem when possible, and we assessed trunk coverage and connectivity to the canopy by recording the presence (1) or absence (0) of lianas on stems (Albert et al. 2011). We calculated a liana coverage index for each plot, ranging from 0 (no coverage) to 1 (high coverage). Each plot was subdivided into 4 quadrants using ribbons marking the north, south, east, and west directions. To assess the understorey vegetation density (i.e., horizontal visibility) we used a 4-point scale to indicate the visibility at different distances: 1) (<5 m, low visibility); 2) (5–15 m, moderate visibility); 3) (>15–25 m, high visibility); and 4) (>25 m, very high visibility) (Gazagne et al. 2020b) for each quadrant and calculated a mean score per plot. Similarly, we estimated canopy coverage (i.e., vertical visibility) for each quadrant, using a 4-point scale as follows: 1) (100%–76% leaf coverage, low visibility); 2) (75%–51% leaf coverage, moderate visibility); 3) (50%–26% leaf coverage, high visibility); and 4) (25%–0% leaf coverage, very high visibility) (Albert et al. 2011) and calculated a mean score per plot. We measured the height of the tallest stems in each plot and categorized mean canopy height as follows: 0–5 m; >5–15 m; >15–25 m; and >25 m. Additionally, we assessed the height of each detected sleeping tree, as well as whether they were emergent trees or if the crown was connected to the canopy. Finally, we recorded the presence (1) or absence (0) of rattans and bamboo patches in each plot.

Food abundance index

To assess the availability of nutritional sources at the time of sleeping site identification, we recorded the phenology for at least 10 individual trees of each species identified in the Cat Tien National Park botanical garden (CTNP 2020). In total, we monitored 91 plant species, 53 of which were identified as part of the black-shanked douc langur's diet based on ad libitum behavioral observations from ground surveys and existing literature (Supplementary Table S2). We quantified the presence of young leaves, mature leaves, fruits, and flowers in the crown using a 5-point scale (i.e., phenological score): 0 = no food, 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75 %, and 4 = 76%–100%. We calculated the Food Availability Index (FAI) for each item, each species, and for each month using the following formula: $FAI = D_k B_k P_{km}$, where D represents the density of species k (stems/ha), B is the mean basal area of the trees of each species k (cm²/ha), and P is the mean phenological score of species k during a given month m. We obtained data on the density and basal area of tree species in Nam Cat Tien from the 116 semi-systematic plots placed along 29 transects (**Figure 1A**).

Data analysis

We conducted all statistical analyses using R version 4.3.1 (R Core Team 2023) and considered a critical level of 0.05.

Sleeping site identification

We established a dataframe to store image metadata and subsequently initiated a loop through each still image file. To extract metadata associated with each still image, we used the exif_read() function from the exiftoolr package (O'Brien 2024). This metadata was then structured into a temporary DataFrame, converted to POSIX format for date and time, and subsequently appended to the global DataFrame using rbind() function. This process resulted in a comprehensive DataFrame containing all selected metadata, including the file names, date and time, GPS coordinates, and camera shooting angles.

Sleeping site selection and forest structure characteristics

We used logistic mixed modeling using the *glmmTMB* function from the glmmTMB package (Brooks et al. 2017) to investigate whether the selection of sleeping sites by black-shanked douc langurs was influenced by forest structure characteristics. Specifically, we considered the number of stems, average DBH, understorey vegetation density, canopy coverage, liana coverage index, maximum tree height, the presence or absence of bamboo, and rattan as fixed effects. Prior to analysis, we examined correlations between these variables using the variance inflation factor (VIF) function from the car package (Fox and Weisberg 2018) and found no evidence of multicollinearity (VIF <2). To account for potential spatial dependence or spatial autocorrelation in the selection of sleeping sites by douc langurs, we included transect identity as an intercept random effect. We standardized the continuous variables using the *scale* function to prevent issues of variable dominance. Then, we fitted a full model incorporating all variables and performed automated model selection using the *dredge* function from the MuMin package (Bartoń 2023). Among the best models, we selected the one with the smallest AICc. As a significance test of all the coefficients, validating the selected model, we computed a likelihood ratio test against a null model that included only the random effect. We also calculated McFadden's pseudo-*R*-squared to assess the explanatory capacity of the model.

As a post-hoc analysis, we examined the association between average DBH and tree height, as well as average DBH and liana coverage index, using the Spearman's rank correlation. We conducted a Wilcoxon rank sum test with continuity correction to compare the DBH of trees within the non-selected sites and the sleeping trees within the sleeping sites. Furthermore, we conducted a Pearson's chi-squared test to specifically investigate whether black-shanked douc langurs exhibited preferences for particular canopy heights when selecting sleeping sites. Finally, we employed a chi-squared test to whether sleeping tree selection is influenced by connectivity (i.e., emergent trees vs. trees connected to the rest of the canopy).

Sleeping tree selection and food availability

We conducted a chi-squared goodness-of-fit test to assess the observed frequency of tree species stems within selected sleeping sites in comparison to the expected stem frequencies based on the tree species available in non-selected sites. Additionally, we computed standardized residuals to identify any observed frequencies that exhibited significant deviations from the expected values (Agresti 2007).

Thereafter, we tested whether douc langurs selected preferred tree species for sleeping based on food availability. Initially, we employed logistic mixed modeling to explore the relationship between the probability of a tree species being selected as a sleeping site, considering the month and the availability of mature leaves, young leaves, fruits, or flowers (FAIs as fixed effects). For each tree species, we calculated the proportion of trees used for sleeping, weighted by the number of trees of that species in each plot to reflect their relative abundance in the habitat. We treated the month as a random intercept effect. However, the random effect was negligible, as indicated by small variances and a likelihood ratio test comparing the mixed model to the fixed effect model. Consequently, we used fixed-effect-only models. Since the VIF computed for a model including the 4 items highlighted multicollinearity, we also restricted analysis to univariate models, along with AIC and McFadden's pseudo-*R*-squared, to allow model comparisons.

Results

Sleeping site identification and drone disturbance

During the 120 nocturnal aerial surveys, we recorded black-shanked douc langurs in 94 surveys, totaling 979 individuals from 94 social units. Among these detections, the average number of individuals detected per survey was 10.4 ± SD 8.9 (ranging from 1 to 43), the average number of social units detected per survey was 2.1 ± SD 1.2 (ranging from 1 to 6), and the average number of individuals detected per social unit was 5.0 ± SD 4.4 (ranging from 1 to 34). We identified 114 sleeping sites, detected on both outbound and return flights, during 59 of these 94 surveys using TIR imagery, with 3 sites being reused. We observed an average of 1.9 sleeping site per transect (ranging from 1 to 6) and an average of 2.3 ± SD 1.6 douc langurs per sleeping tree (ranging from 1 to 14, $N = 429$). We determined that 77 of the identified sleeping sites had a fair or good visibility in the footage and analyzed 65 sites for the forest structure plots (**Figure 1B**). Via ground surveys, we observed douc langurs sharing sleeping sites on 6 occasions with pig-tailed macaques, 3 occasions with long-tailed macaques and yellow-cheeked crested gibbons, and one time with silvered langurs.

In total, we recorded 270 detections on the outbound flight (gimbal angle 45°) and 171 detections during the return flight (gimbal angle 90°). This suggests that adjusting the gimbal angle to 45° improves detection, likely enabling us to detect individuals located beneath the canopy trees. As regards potential disturbance of the TIR drone, we never observed flight behavior among the black-shanked douc langurs during nocturnal aerial surveys. During outbound flights, 18.5% of detections showed movement, while 81.5% were inactive. In contrast, on return flights, 28.1% of detections showed movement, and 71.9% were inactive.

Sleeping site selection and forest structure characteristics

The best significant model showed that 5 forest structure factors explained the selection of sleeping sites: Average DBH, number of stems, canopy coverage, liana coverage index, and the presence of bamboo (**Table 1**). However, only canopy coverage reflecting vertical visibility, liana coverage index, and the presence of bamboo had a significant coefficient. Black-shanked douc langurs were less likely to select sleeping sites with low vertical visibility, where bamboo was present, and where lianas covered the trees. Conversely, understorey vegetation density reflecting horizontal visibility, maximum tree height, and the presence of rattan did not affect sleeping site selection.

We tested correlations between average DBH, maximum tree height, and the liana coverage index within the 181 plots. We found a significant negative correlation ($rs = -0.288$, $P < 0.001$) between average DBH and the liana coverage index, indicating that as the average DBH increases, the liana coverage on trees decreases (Supplementary Figure S3). Moreover, the analysis revealed a significant positive correlation between these average DBH and maximum tree heights ($rs = 0.517$, $P < 0.001$), suggesting that plots with larger average DBH are positively associated with taller trees (Table 2). We found that douc langurs selected trees with a larger DBH to sleep in, compared with trees within the non-selected sites ($W = 11196$, $P < 0.001$). Furthermore, the observed distribution across canopy height categories showed a significant difference between sleeping sites and non-selected sites (chi-squared = 10.591, df = 3, $P = 0.014$). Although douc langurs seemingly preferred sleeping sites with a canopy height between >15 and 25 m (constituting 81.5% of the sleeping sites), the practical significance might be modest with non-significant standardized residuals (ranging from −1.92 to 1.45). Finally, we observed a significant preference (chi-squared = 10.714, df = 1, $P = 0.001$) for sleeping trees connected to the canopy ($N = 57$) over emergent sleeping trees ($N = 27$).

Sleeping tree selection and food availability

Among the recorded sleeping trees ($N = 84$), 39 belong to *Lagerstroemia* sp. (*Lythraceae*), 20 are *Afzelia xylocarpa* (*Fabaceae*), 5 are *Tetrameles nudiflora* (*Tetramelaceae*), 4 are *Chukrasia tabularis* (*Meliaceae*), 4 are *Ficus* sp. (*Moraceae*), 2 are *Terminalia* sp. (*Combretaceae*), and one of each represents *Haldina cordifolia* (*Rubiaceae*), *Irvingia malayana* (*Irvingiaceae*), *Mangifera* sp. (*Anacardiaceae*), *Shorea guiso* (*Dipterocarpaceae*), *Sindora siamensis* (*Fabaceae*), *Sterculia thorelii* (*Malvaceae*), *Xerospermum noronhianum* (*Sapindaceae*). Three sleeping trees could not be identified. We found that *Lagerstroemia* sp., *Ficus* sp., *A. xylocarpa*, *T. nudiflora*, and *C. tabularis* were significantly more prevalent in sleeping sites than in non-selected sites (chi-squared = 449.7, df = 31, $P < 0.001$, Figure 3). These findings suggest that black-shanked douc langurs exhibit a preference for selecting these tree species for sleeping.

During ground surveys, we observed black-shanked douc langurs consuming fruits and young leaves from *Lagerstroemia* sp., mature leaves, flowers, and fruits from *Ficus* sp., young and mature leaves, flowers and fruits from *A. xylocarpa*, and mature leaves from *T. nudiflora*, and *C. tabularis*. Finally, upon exploring the relationship between the monthly proportion of sleeping tree use and food availability, univariate models revealed significant relationships of sleeping tree use with fruit FAI (lowest AIC, highest pseudo-R-squared) and a less likely association with mature leaves FAI due to collinearity with fruits FAI (Table 3).

Discussion

By conducting pre-programmed nocturnal thermal imaging drone surveys alongside forest structure plots, our study provides crucial insights into the sleeping site selection of the black-shanked douc langur in Cát Tiên National Park, Vietnam. We found that douc langurs preferentially selected trees and sites which characteristics that reduce the predation risk (e.g., large DBH trees with no lianas) and increase proximity to fruit sources. Our findings also highlight the significant potential of TIR drones in studying primate sleeping behavior and habitat selection, validating therefore an innovative and noninvasive methodological approach to investigate such eco-behavioral questions.

Table 1. Best logistic mixed model of sleeping site selection by black-shanked douc langurs in Cát Tiên National Park (January to April 2023) according to forest structure characteristics, including McFadden's pseudo-*R*-squared and a likelihood ratio test comparing it with the random effect only model

Number of observations = 181 plots		Groups = 29 transects		
Random effect	**Variance**	**Standard deviation**		
Transect (intercept)	**4.777e-09**	**6.911e-05**		
Fixed effects	**Estimates**	**Standard errors**	***Z* values**	***P* values**
Intercept	−1.019	0.239	−4.262	<0.001
Average DBH	0.353	0.227	1.551	0.121
Number of stems	−0.367	0.237	−1.549	0.121
Canopy coverage	−1.024	0.242	−4.224	<0.001
Liana coverage index	−1.163	0.247	−4.711	<0.001
Bamboo presence	−0.906	0.361	−2.511	0.012

Mc Fadden's pseudo R-squared = 0.325
Likelihood ratio test: Chi-squared = 76.764, ddl = 5, $P < 0.001$

Table 2. Physical characteristics of non-selected sites (N = 2,439 stems), sleeping sites (N = 1,287 stems), and sleeping trees (N = 84) of black-shanked douc langurs

		Non-selected sites	Sleeping sites	Sleeping trees
DBH (cm)	Mean ± SD (range)	28.9 ± 33.3 (10–251)	35.6 ± 39.7 (10–271)	127.4 ± 50.4 (22.6–271)
Number of stems	Mean ± SD (range)	21 ± 5.9 (7–46)	19.8 ± 4.6 (9–29)	1.3 (1–3)
Max tree height (m)	Mean ± SD (range)	19.2 ± 5.8 (5–32)	20.0 ± 3.4 (11–26)	20.2 ± 3.1 (11–26)
Canopy height (m)	Dominant canopy height categories (%)	>15–25 (58.6)	>15–25 (81.5)	NA

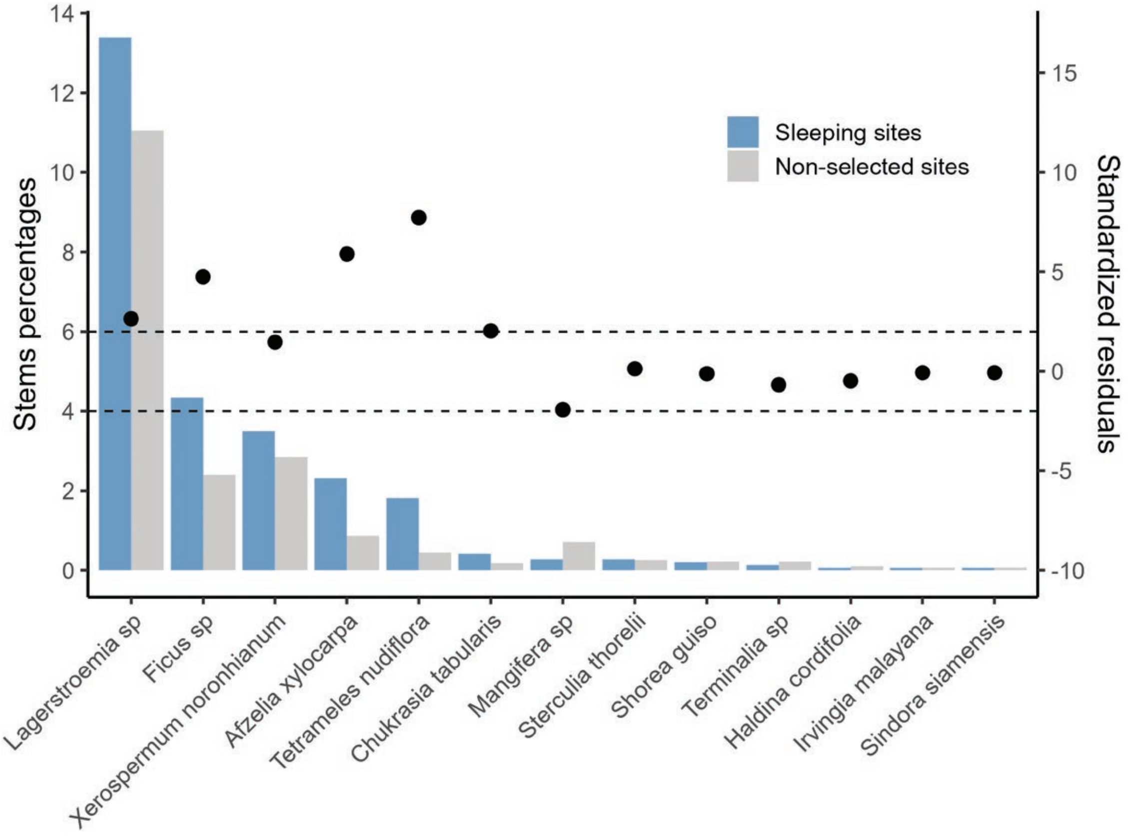

Figure 3. Comparison of species stems percentages between sleeping sites and non-selected sites and the associated standardized residuals for these species (dots). Adjusted residuals are considered significant when they fall outside the 95% confidence interval indicated by the horizontal dashed lines in the scatterplot.

Table 3. Univariate logistic models of the proportion of sleeping tree use for each month (January to April) and species (*Afzelia xylocarpa, Chukrasia tabularis,* Ficus sp., *Lagerstroemia* sp., and *Tetrameles nudiflora*), and the availability of mature leaves, young leaves, fruits and flowers (FAI), along with Mc Fadden's pseudo-*R*-squared and AIC

Fixed effects	Estimates	Standard errors	*Z* values	*P* values
Intercept	−2.535	0.294	−8.618	<0.001
Mature leaves	0.014	0.007	2.163	0.030
Pseudo-*R*-squared = 0.119		AIC = 37.83		
Intercept	−2.130	0.210	−10.1	<0.001
Young leaves	0.0102	0.026	0.386	0.699
Pseudo-*R*-squared = 0.004		AIC = 42.24		
Intercept	−3.315	0.483	−6.865	<0.001
Fruits	0.063	0.020	3.118	0.002
Pseudo-*R*-squared = 0.320		AIC = 30.10		
Intercept	−1.960	0.190	−10.33	<0.001
Flowers	−0.279	0.198	−1.411	0.158
Pseudo-*R*-squared = 0.090		AIC = 38.92		

Sleeping site selection by the black-shanked douc langur

Following the predator avoidance hypothesis, our results showed that black-shanked douc langurs selected larger and taller trees to sleep in, with sites including stems with a larger DBH, and avoided trees covered by lianas (Table 2). These results support our predictions that black-shanked douc langurs would select these features to hinder potential predators' access and detection (Table 4). Additionally, we found that douc langurs preferentially select sleeping trees with crowns that are connected to the adjacent canopy which is consistent with their tendency to select the medium-high canopy strata within a range of 15 to 25 m to sleep. This strategy may serve both to enhance ease escape from predator in case of detection and to facilitate social contact (Di Bitetti et al. 2000; Fan and Jiang 2008; Albert et al. 2011). Contrary to

Table 4. Review of hypotheses and predictions in primate sleeping site selection (excluding species that build nests, sleep in holes, caves, or cliff) We assessed if these predictions can be tested using the TIR imaging drones (Yes vs. No) or in combination with other survey methods besides direct observation at sleeping sites (Y/N). We provided TIR drone survey **Limitations** (**L**), and complementary or alternative **Methods** (**M**) that could be used to test these predictions (cf. methods detailed in Supplementary Text S2). **L1.** Cannot detect individuals sleeping in lower canopy strata or under dense foliage and vine entanglements; **L2.** Difficult to identify and count sympatric species and closely aggregated animals, and to detect individuals near hot tree limbs or trunks; **L3.** Difficult to identify tree species using TIR imagery; **L4.** Limited transmission range between the drone and the controller in densely forested areas; **L5.** Challenging to conduct drone surveys during the rainy season. **M1.** Diurnal aerial surveys with RGB sensors and optical zoom lenses; **M2.** Aerial photogrammetry via RGB and/or LiDAR sensors carried by drones; **M3.** Extending the drone transmission range; **M4.** Wildlife tracking drones to detect GPS, VHF radio or satellite-tagged individuals; **M5.** GPS collars, radio-telemetry ground-tracking, and data-loggers; **M6.** Forest structure plots or line-transects; **M7.** Targeted video recording and camera traps.

Hypothesis	Prediction	Test TIR drones	L 1	L 2	L 3	L 4	L 5	M 1	M 2	M 3	M 4	M 5	M 6	M 7
Predation avoidance	Reuse sleeping sites infrequently and rarely on consecutive nights to avoid predator anticipation[a,c,f,h,l,m]	Y/N			X	X		X		X	X	X		X
	Reuse sleeping sites and trees located in familiar areas to increase chance of successful escape in case of attack[a,e,l]	Y/N			X	X		X		X	X	X		X
	Individuals exhibit a cryptic behavior by entering sleeping sites before sunset and exiting after sunrise, avoiding active nocturnal predators[d,e,g,h,l]	No						X			X	X		X
	Select tree characteristics such as tall height, large DBH, and large crown diameter, to reduce access and detection by predators[d,f,h,l,m]	Y/N*	X						X				X	
	Select sites with concealing dense foliage or enclosed within vine entanglements[d,l]	Y/N*	X						X				X	
	Select trees with an open crown to increase detection of arboreal predators[e]	Y/N*	X						X				X	
	Select trees with high vs. low connectivity to neighboring trees to enhance ease of escape vs. reduce predator access[d,e,h]	Y/N*	X						X				X	
	Select trees without lianas to reduce predator access[e,g,h]	Y/N*	X						X				X	
	Select sites with open understory vegetation to increase predator detection[g]	Y/N*	X						X				X	
	Sleep in sites with steep slope to increase predator detection[d]	Y/N	X						X				X	
	Sleep positioned high in the canopy and/or away from the main trunk to decrease access and detection by predators[f,h]	Yes	X	X										X
	Individuals aggregate at sleeping trees to reduce predation risk through increased vigilance and benefiting from the dilution effect[a,m]	Yes	X	X										X
Access to food	Sleep in or near feeding trees[d,f,l,m]	Y/N*			X			X	X				X	
	Sleep close to the last feeding site of the day or the first feeding site of the next morning[f,j,m]	No						X	X				X	
	Select sleeping sites in habitats with greater food resources compared with habitats with fewer food resources[l]	Y/N			X			X	X				X	
Thermoregulation	Sleep in larger huddles at cooler temperatures[a,i,l,m]	Yes	X	X			X					X		X
	Sleep on larger blanches at cooler temperature to enable huddling[m]	Y/N	X	X			X		X			X	X	X
	Sleep more frequently under dense foliage during hot season[i,l]	Y/N	X	X			X		X			X	X	X
	Sleep more frequently under light foliage and direct sun exposure during dry or cold season[i]	Y/N	X	X			X		X			X	X	X
	Sleep at lower/higher elevations during periods of cooler/warmer temperature[f]	Y/N	X	X			X		X			X	X	X
	Sleep at higher heights, close to the canopy, and under dense foliage with increased rainfall[m]	Y/N	X	X			X		X			X	X	X
	Sleep in sites sheltered from the wind with large trees, large crown diameter, and with vegetation with denser foliage[f,i,l]	Y/N	X	X			X		X			X	X	X
Range and resource defense	Sleep in the periphery of the home range or in the core area to monitor territory boundaries or avoid neighboring groups[c,f,g,j,n]	No						X			X	X		X
	Sleep most often in range of exclusive use[f]	Y/N				X		X		X	X	X		X
Competition	Select different tree species between sympatric species to avoid competition[g]	Y/N		X	X	X		X		X	X	X	X	X
	Reuse of sleeping sites to limit between-group competition[n]	Y/N		X		X		X		X	X	X		X
	Establish sleeping sites at different time to limit competition[c,g]	No						X			X	X		X

Table 4. Continued

Hypothesis	Prediction	Test TIR drones	L 1	L 2	L 3	L 4	L 5	M 1	M 2	M 3	M 4	M 5	M 6	M 7
Social	Select trees with large branches to allow social contact and social bounding[a,b,d]	Y/N		X	X			X	X				X	X
	Select sites with a high number of stems to allow social contact[k]	Y/N		X	X			X	X				X	X
Stability, comfort	Selection of tall and large trees with substantial branches, that provide secure and sheltered platforms for relaxed sleeping positions[b,d,g,j]	Y/N*			X			X	X				X	X
Parasite avoidance	Select different trees every night to avoid recontamination with parasites[a,b,j]	No						X	X				X	
Null	Selection of sleeping tree species is relative to their density within the home range[f]	Y/N				X			X	X	X	X	X	
	Sleep in tree of average height and DBH[f,k]	Y/N*			X				X	X	X	X	X	
	Sleep in all areas of the home range relative to availability[f,k]	No							X		X	X	X	

*Predictions tested or partially tested in this study; Diameter at Breast Height (DBH); Global Positioning System (GPS); Light Detection and Ranging (LiDAR); Thermal InfraRed (TIR); Very High Frequency (VHF); Visible spectrum sensors (RGB).
[a]Di bitetti et al. 2000; [b]Kowalewski and Zunino 2005; [c]Smith et al. 2007; [d]Fan and Jiang 2008; [e]Albert et al. 2011; [f]Teichroeb et al. 2012; [g]Cheyne et al. 2013; [h]Fei et al. 2017; [i]Savagian and Fernandez-Duque 2017; [j]Brividoro et al. 2019; [k]Gazagne et al. 2020b; [l]Mekonnen et al. 2021; [m]Mills et al. 2021; [n]Rismayanti et al. 2023.

our prediction, low canopy coverage significantly increased the probability of sleeping site selection. This selection of trees with open crowns might support an anti-predator strategy by providing better visibility of potential predators, similar to that observed in *Macaca* sp. that share a similar predator community, including nocturnal arboreal cats and pythons (Albert et al. 2011). However, we collected data during dry season, and canopy coverage selection might change seasonally. Furthermore, we cannot exclude that this factor showed significance because TIR cameras are more effective in detecting individuals in the upper canopy or under light foliage coverage (Kays et al. 2019). Extending this study during the rainy season is required to better assess detection bias and to fully understand canopy coverage selection strategies. Finally, douc langurs significantly avoid sleeping sites with bamboo stems, which may serve as an anti-predator strategy by reducing travel routes for predators (Cheyne et al. 2013). Alternatively, bamboo can suppress the growth of other vegetation, adversely affecting habitat quality and consequently reducing the availability of large, tall trees preferred by douc langurs for sleeping (Buziquia et al. 2019).

Another key finding was the positive relationship between monthly fruit or mature leaf availability and the use of sleeping trees, particularly *A. xylocarpa*, *C. tabularis*, *Ficus* species, *Lagerstroemia* species, and *T. nudiflora* in Cát Tiên National Park. Specifically, we observed douc langurs consuming various parts of *A. xylocarpa*, including young and mature leaves, flowers, and immature fruits (green pods with seeds), suggesting it is an essential food resource for douc langurs. This aligns with prior studies showing its predominant use as a feeding tree during the dry season (O'Brien 2014) and its potential role as a fallback resource during periods of low resource abundance (Rawson 2009). *Ficus* species, another important dietary component for the langurs, were noted as a key resource, as their fruits, leaves, and buds provide readily accessible energy (Duc et al. 2009). Seasonal dietary shifts, as described by Duc et al. (2009), provide further context for these findings. While black-shanked douc langurs rely on foliage year-round, dietary diversity decreases during the dry-season, with a greater reliance on leaves, likely influencing sleeping site selection. Complementarily, although we observed douc langurs consuming young leaves and flowers from sleeping trees, they frequently selected sleeping sites near fruit-rich areas, likely to offset energy loss during sleep by accessing readily available energy sources (Duc et al. 2009). This strategic choice minimizes the energy expenditure required for daily travel between sleeping and feeding locations, thus supporting the food proximity hypothesis (**Table 4**). Overall, the observed relationship between food availability and sleeping site use underscores the importance of key species such as *Ficus*, *A. xylocarpa*, and *Lagerstroemia* in meeting the langur's nutritional needs. However, further investigation during the wet season is essential to fully understand how seasonal variations in resource availability affect sleeping site selection. Seasonal data would also help determine whether these species are more frequently used as sleeping trees during different periods of resource abundance.

Using TIR drones to study sleeping site selection in primates

TIR drones offer a novel method for monitoring sleeping sites of non-habituated primate groups with minimal disturbance. Our results indicate that black-shanked douc langurs exhibited a tolerance for drone presence, with fewer than 30% showing movement when the drone flew overhead. This suggests a higher novelty tolerance compared with more cautious species, such as yellow-cheeked crested gibbons and northern pig-tailed macaques (Gazagne et al. 2024a).

Although we aimed to test the predation avoidance and food proximity hypotheses, time and weather constraints limited our exploration of alternative sleeping site selection strategies (**Table 4**). Factors such as thermoregulation and the spatial and social organization of individuals within sleeping sites offer promising avenues for further study with TIR drones. This technology enables investigation into how primates manage body temperature at night, adopt positions for optimal thermoregulation, and explore spatial aggregation and clustering behavior to test both thermoregulation and social hypotheses. Our systematic TIR drone surveys revealed an average of 5 douc langurs per social unit, with more than 2 individuals sharing sleeping trees. In contrast, exploratory manual flights could enhance detection through improved horizontal and vertical scanning of sleeping sites (cf., Supplementary Text S1 and **Table S1**). Despite the limitations of systematic flights, we observed a group with at least 34 individuals, suggesting the fusion of several OMUs in 1 large sleeping site (Rawson 2009). This highlights the potential of TIR drones in studying cryptic behavior and fusion-fission events that are challenging to observe via ground-based surveys. Finally, TIR drones could facilitate the study of range and resource defense among conspecifics and competition between sympatric species, as we observed instances of black-shanked douc langurs sharing sleeping sites with gibbons, silvered langurs, and pig- and long-tailed macaques.

The use of TIR drones has limitations for multispecies studies and testing some primate sleeping site selection hypotheses (**Table 4**). A major limitation is the low-resolution imagery, which makes it difficult to differentiate species with similar morphology or behavior. To improve identification, we recommend combining TIR surveys with RGB sensors and optical zoom lenses during early morning or early evening, when individuals are at their sleeping sites (**Table 4**). This approach can enhance the understanding of primate sleeping behavior and species assemblages, especially in diverse sympatric species (Kays et al. 2019; Pinel-Ramos et al. 2024; Gazagne et al. 2024a). Another significant limitation is weather constraints, as drones have low tolerance for rain, fog, mist, and wind speeds above 10 m/s, which restrict the survey window, particularly during the rainy season when we could not conduct drone surveys. However, newer weather-resistant drones are improving flyability under such conditions (Gao et al. 2021), and other sites with more favorable climates may allow for year-round data collection (Gazagne et al. 2024b). Additionally, detecting closely aggregated animals, individuals near hot tree trunks, or those in multilayer canopies and thick foliage is challenging, often leading to underestimation of group sizes (Kays et al. 2019; Spaan et al. 2019). This inherent limitation introduces detection bias (i.e., "false negative") that needs to be addressed in future studies (Kays et al. 2019; Piel et al. 2022). Adjusting the gimbal angle and using multiple flight heights can enhance detection, especially under the canopy. For studies investigating sleeping site hypotheses in detail (**Table 4**), we recommend systematic flights followed by exploratory manual flights over detected sleeping trees, extracting GPS coordinates of the site's center and scanning surrounding trees. However, hovering flights may cause disturbances (Mulero-Pázmány et al. 2017; Spaan et al. 2019), so researchers should limit hovering time and maintain a safe distance to avoid triggering flight responses (Kays et al. 2019). Prior knowledge of species' ranges and sleeping site locations can help optimize detection (Spaan et al. 2019, Pinel-Ramos et al. 2024) and test factors like sleeping site reuse.

Implications for conservation

Our findings have significant implications for the conservation of the Critically Endangered black-shanked douc langur. Understanding the specific habitat features and preferred tree species of douc langurs can inform habitat management and protection strategies to preserve and restore vital resources. Additionally, this knowledge could be used to select suitable release sites for animal reintroductions by rescue centers. For instance, black-shanked douc langurs exhibited a preference for sleeping in *A. xylocarpa*, a large tree species classified as Endangered, which they also used as a feeding tree. This tree species holds high timber value and is used in traditional medicine (So et al. 2010) and is easily identifiable without botanical knowledge. Protecting the forested area that provides essential feeding and sleeping resource for douc langurs could benefit species conservation and offer socio-economic advantages to local communities. Furthermore, douc langurs frequently utilized secondary evergreen forests as sleeping sites (Supplementary Figure S2). This highlights the importance of protecting the lowland dry-evergreen forests of Eastern Nam Cát Tiên, which remain critical habitats for the douc langur conservation. We demonstrated that the application of TIR drone technology in ecological research provides a noninvasive and efficient method for monitoring wildlife behavior and habitat use. We recommend that conservationists integrate both TIR and RGB drones to assess the habitat requirements for douc langur survival. Additionally, by conducting annual systematic flights, drones can support data collection to estimate the occupancy or abundance of black-shanked douc langurs.

Finally, TIR drone surveys can also be employed to locate sleeping sites at night and facilitate the collection of feces material in the early morning, thus enhancing sample collection efficiency. Collecting fecal samples from sleeping sites for DNA analysis is the least invasive method for health monitoring, individual identification, and providing insights into population genetics and social structure (Arandjelovic and Vigilant, 2018; Piel et al. 2022). This could be an effective method for understanding mating systems, reproductive strategies, dispersal patterns, and the influence of kinship on social behavior and fission-fusion dynamics in douc langurs (Di Fiore 2003). By providing valuable information about primate diet and infectious status, DNA analyses enable the surveillance of population health in wild primates without relying on direct observations of habituated groups (Srivathsan et al. 2016).

Future directions

This study integrates cutting-edge technology with traditional ecological methods to deepen our understanding of primate behavior and habitat selection in the Critically Endangered black-shanked douc langur through the study of sleeping site selection. By using TIR imaging with drones, we expect to open new avenues for studying nocturnal behaviors and habitat use, offering promising opportunities for future research and conservation initiatives. Our nocturnal systematic drone survey methodology has its limitations, particularly in distinguishing black-shanked douc langurs from other sympatric primate species; therefore, it requires diurnal ground surveys for identification. Furthermore, our data collection over 4 months during the dry season cannot provide a full representation of sleeping site selection. Additionally, presumed non-sleeping trees in this study may serve as sleeping trees under varying seasonal conditions or resource availability, emphasizing the importance of year-round, expanded data collection to capture these potential shifts. We recommend further investigations to comprehensively explore primate sleeping site selection using TIR drones, focusing on: 1) targeting large-bodied arboreal species (Gazagne et al. 2024b); 2) assessing drone disturbance during nocturnal operations; 3) conducting year-round manual or systematic flights at varying heights and gimbal angles above sleeping sites to enhance detection and understand species' social behavior and spatial organization at night; and 4) integrating TIR drone surveys with RGB drone surveys during early morning or early evening when individuals are at their sleeping sites for precise species identification. These insights contribute to the broader field of primate ecology and underscore the importance of advanced technologies in wildlife research and management. Incorporating sleeping site selection research into conservation strategies enhances ecological understanding, aids in targeting critical habitats for species survival, supports sustainable development, ecosystem resilience, and biodiversity conservation.

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Authors' Contributions

E.G. conceived and designed the experiment and wrote the manuscript. E.G. and C.G. conducted fieldwork. E.G. and A.H. performed statistical analyses. V.T.N. supported research and fieldwork in Vietnam. F.B. and A.H. supervised E.G. and provided editorial advice.

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Conflict of Interest

The authors declare no conflicts of interest.

Ethics Statement

This study adhered to ethical guidelines for wildlife research. It was purely observational and non-invasive, ensuring no harm or disturbance to the black-shanked douc langurs or their habitat. Data collection complied fully with Vietnamese laws and wildlife regulations.

Data Availability

The data analyzed during the current study as well as the R scripts are available from the corresponding author on reasonable request.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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