BIODIVERSITAS
Volume 24, Number 11, November 2023
Pages: 6200-6208

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d241142

Characteristics of sleeping sites and sleeping trees selected by Celebes crested macaques (*Macaca nigra*) in Tangkoko, North Sulawesi, Indonesia

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Manuscript received: 11 September 2023. Revision accepted: 26 November 2023.

Abstract. *Qomariyah IN, Perwitasari-Farajallah D, Iskandar E, Berthier JM. 2023. Characteristics of sleeping sites and sleeping trees selected by Celebes crested macaques (*Macaca nigra*) in Tangkoko, North Sulawesi, Indonesia. Biodiversitas 24: 6200-6208.* Research on the selection of sleeping sites is imperative in providing information on the fitness and survival of a species. We investigated the characteristics of the sleeping sites and the sleeping trees selected by wild Celebes crested macaques (*Macaca nigra* Desmarest 1822) in Tangkoko Conservation Forest, Bitung City, North Sulawesi Province, Indonesia, as well as their spatial and temporal use. The study was conducted in two groups of macaques for nine months (187 study days) from September 2020 to June 2021. These macaques avoided using the same sleeping site on consecutive nights. Two predator encounters (*Python reticulatus* Schneider 1801) were recorded near the sleeping sites, but pythons caught no monkeys during the study period. The macaques used 58 trees from 13 species as sleeping trees, of which 79% of the sleeping trees were also food trees. *M. nigra* chose sleeping trees with higher diameter, height, and a bigger Important Value Index than the surroundings. The average distance between sleeping trees and feeding trees in the morning and evening were 203 m and 127 m, respectively. These results suggest that optimal foraging strategy and predator avoidance are important factors in selecting sleeping sites, providing a broader understanding of the habitat preferences of the Critically Endangered *M. nigra*.

Keywords: Crested macaque, *Macaca nigra*, optimal foraging, predator avoidance, sleeping site, Tangkoko, yaki

INTRODUCTION

Sleep and sleeping habits are important aspects of animal behavioral ecology. Research on sleeping sites can provide information on how a species can survive and respond to environmental conditions (Anderson 2000). Primates sleep up to half their lives (Smith et al. 2018). Being asleep makes nonhuman primates (hereafter 'primates') vulnerable to many dangers, such as being caught by predators, attacked by other groups, or falling from trees for the species that sleep high up the trees at night (Fruth et al. 2018). These conditions require primates to choose their sleeping sites carefully (Feilen and Marshall 2014). Several hypotheses have been proposed to explain primate strategies in sleeping site selection, i.e., strategies to avoid predators (Savagian and Fernandez-Duque 2017), to increase feeding efficiency (Feilen and Marshall 2017), to avoid pathogen and disease vectors (Samson et al. 2013), to reduce the risk of intergroup competition (Brividoro et al. 2019), thermoregulation (Ellison et al. 2019), and to cope with seasonal changes (Fei et al. 2019). All these different strategies are not mutually excluding and can be relevant simultaneously, depending on the environmental pressures that the animals must deal with in a specific area (e.g., high or low predation pressure, strong food seasonality with periods of food scarcity, high or low inter- and/or intra-species competition for food or space).

Research on sleeping sites and sleeping trees has been carried out previously on various monkey species, including proboscis monkeys (*Nasalis larvatus* van Wurmb 1787) (Feilen and Marshall 2017), spider monkeys (*Ateles geoffroyi* Kuhl 1820) (Velázquez-Vázquez et al. 2015), howler monkeys (*Alouatta caraya* Humboldt 1812) (Brividoro et al. 2019), capuchins (*Sapajus cay* Illiger 1815) (Smith et al. 2017), owl monkeys (*Aotus azarae azarae* Illiger 1815) (Savagian and Fernandez-Duque 2017), baboon (*Papio cynocephalus* Linnaeus 1766) (Markham et al. 2016), titi monkeys (*Callicebus nigrifrons* Spix 1823) (Caselli et al. 2017), silver leaf-monkeys (*Trachypithecus cristatus* Raffles 1821) (Hambali et al. 2016), Northern pig-tailed macaques (*Macaca leonine* Blyth 1863) (Albert et al. 2011; José-Domínguez et al. 2015), and long-tailed macaques (*Macaca fascicularis* Raffles 1821) (Brotcorne et al. 2014). However, the research on sleeping sites and sleeping trees of Celebes crested macaques (*Macaca nigra* Desmarest 1822) has never been done.

The Celebes crested macaque is one of the seven endemic macaques of Sulawesi Island, Indonesia (Fooden 1976). The spatial distribution of this species is limited to the northern Sulawesi Island, Manado Tua, and Talise

Islands. Some individuals were introduced to Bacan Island in the Moluccas Archipelago (Roos et al. 2014). *M. nigra* is a semi-terrestrial primate that consumes more than 145 fruit species from 36 families (O'Brien and Kinnaird 1997). The monkeys spend 60% of their active time on the ground and sleep high up in the trees at night. Home ranges were approximately 2 km^2 per group (Joly et al. 2023). They form large groups of 27 to 97 individuals (O'Brien and Kinnaird 1997). The group size of *M. nigra* is dynamic (Duboscq and Micheletta 2023). Female individuals stay in their natal group (Duboscq 2013). Adult males migrate and switch groups several times throughout their lifetime (Marty et al. 2016). Limited geographical distribution and habitat encroachment put this species at risk of extinction. Some macaques in Tangkoko have an amputated wrist or ankle, probably due to snares, indicating that bush meat hunting is also a potential threat (Kyes et al. 2013). This species is classified as Critically Endangered by the International Union for Conservation of Nature (IUCN) and Appendix II by the Convention on International Trade in Endangered Species (CITES). *M. nigra* is listed as a protected species by the Indonesian government.

This study analyzes the characteristics of sleeping sites and trees and their spatial and temporal use of two groups of Celebes crested macaques in the Tangkoko Nature Reserve, North Sulawesi. This research is useful in investigating habitat preferences and strategies used by this species to improve its fitness and ensure its survival. In the long term, this research can help monitor *M. nigra* populations and, more generally, protect this species efficiently. The information about sleeping site characteristics can be used to build recommendations for determining the preferred location of population surveys and installing camera traps. This study also informs some important areas for forest security patrols so the *M. nigra* population will be protected. Sleeping site selection also indicates the habitat quality and the availability of suitable sleeping sites; this information is important to analyze the carrying capacity of an area and the conservation plan for enrichment. The result of this study may be useful as parameters for habitat viability analysis to decide on release sites for rehabilitated monkeys. The list of sleeping and food tree species can provide recommendations for the best local species to be planted as habitat enrichment in Tangkoko and to reduce human-macaque conflict in the future.

MATERIALS AND METHODS

Time and location

This research was conducted in the Tangkoko Conservation Forest Management Unit (KPHK Tangkoko), Bitung City, North Sulawesi Province, Indonesia (Figure 1). KPHK Tangkoko is located at 1°32'39" N and 125°12'42" E and includes an area of 8,867 ha at an altitude up to 1,350 m above sea level (Whitten et al. 1987). Annual rainfall ranges from 1,550 to 2,400 mm, generally higher between October and May (O'Brien and Kinnaird 1997). The minimum temperature was 24.29°C, and the maximum was 28.51°C (Joly et al. 2023). This study lasted for nine months, from September 2020 to June 2021. The habituation process was conducted at the beginning of the study for 8 consecutive weeks.

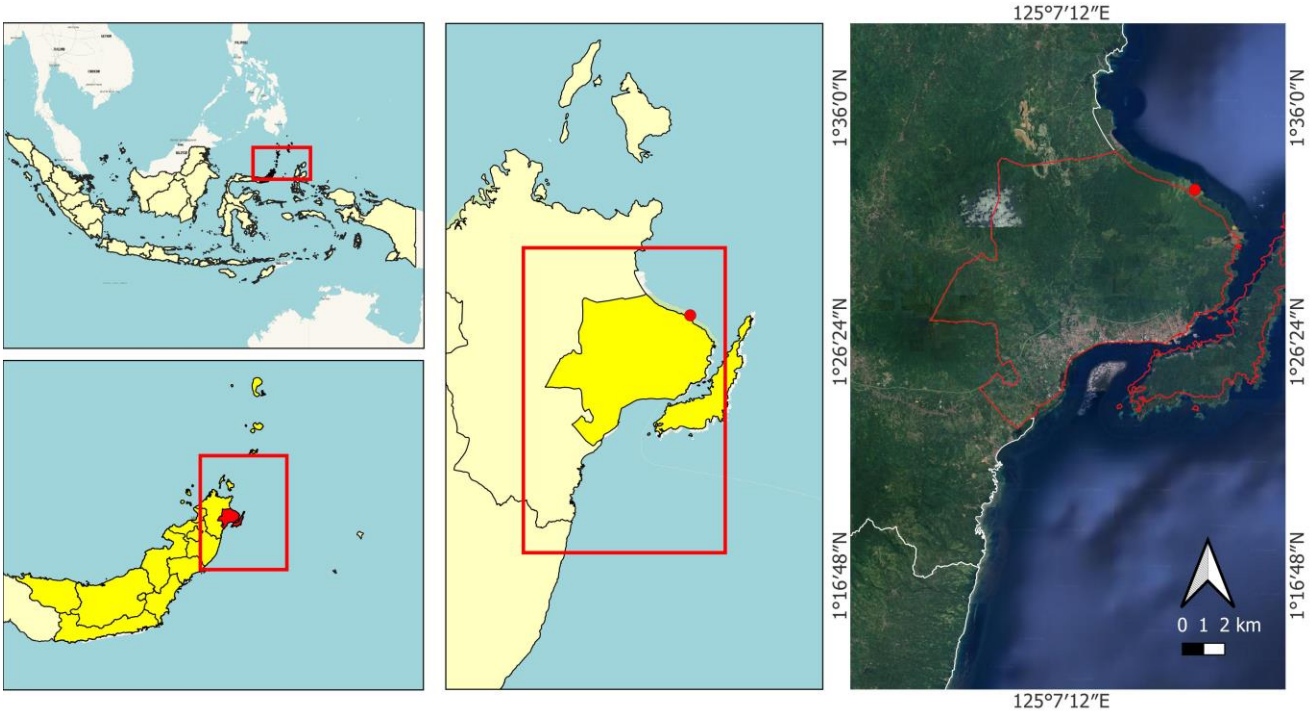

Figure 1. The study area was in the Conservation Forest Management Unit (KPHK) Tangkoko, Bitung City, North Sulawesi Province, Indonesia

Study group

The subjects of this study were two groups of wild *M. nigra*, namely the Pantai Batu 1B (PB1B) and Rambo 1 (R1) groups. At the beginning of our study, the PB1B group had 8 adult males and 19 adult females, while the R1 group had 10 adult males and 42 adult females. At the end of this study, the PB1B group consists of 83 individuals (9 adult males, 21 adult females, and 53 juveniles), while the R1 group consists of 147 individuals (12 adult males, 42 adult females, and 93 juveniles). The monkeys were followed from morning to evening sleeping trees, for 13 hours a day from 5 a.m. to 6 p.m. The total time spent in observation was 2,251 hours (1,084 hours in PB1B and 1,167 hours in R1). The travel tracks of the groups were recorded all day with a GPS Garmin Etrex 10 with one measure every 30 seconds. At the end of the study, we conducted a minimum convex polygon on the QGIS 3.4.5 program to draw a map and measure the home ranges of these two groups.

Sleeping trees coordinates

In this study, we used the following terminology according to Albert et al. (2011) and Thiry et al. (2016): (i) a 'sleeping tree' is one in which the macaques stay overnight; (ii) a 'sleeping site' is an area (100 m x 100 m) within the home range where the macaques spend the night. A sleeping site consists of one or several sleeping trees; (iii) a 'non-sleeping tree' is located on a sleeping site but not used by the macaques to sleep.

We collected the coordinates of the sleeping tree using a GPS Garmin Etrex 10 after the monkeys had climbed the sleeping tree at night. The sleeping trees were marked using marker tape with different colors for each group. All the sleeping tree coordinates were input into the QGIS 3.4.5 program. We added 100 m x 100 m grids in the Tangkoko area with the sleeping trees. Grids represent sleeping sites and are codenamed for further analysis. The horizontal grid is named alphabetically, with the letter A being the code for the westernmost region. The vertical grids are named with numbers, with number 1 being the code for the northernmost region (Figure 2).

Distance between sleeping trees and feeding trees

We recorded the location of the last and first feeding trees in the evening and morning, respectively. According to José-Domínguez et al. (2015) and Brividoro et al. (2019), the feeding site is where most individuals in a monkey group were feeding simultaneously. We performed a scan sampling within a 10-minute interval (Altmann 1974) after all the monkeys climbed down and moved to the feeding site in the morning. Behavior data were divided into 7 categories, i.e., feeding (F), locomotion (L), affiliative behavior (AF), aggressive behavior (AG), monitoring (M), resting (R), and others (O). We only performed scan sampling on adult males and females to identify their appearance and special characteristics; hence, the same individuals would not be sampled twice. We did not include juvenile and adolescent individuals in the scan sampling due to difficulty in identification. A tree was defined as a 'feeding tree' when more than 50% of adult individuals were feeding on it. In the evening, the scan sampling was conducted from 4 p.m. at 10-minute intervals until the monkeys were steady on the sleeping sites. The GPS coordinates of the feeding trees were also recorded. The distances between the sleeping and feeding trees were calculated using the Field Calculator on the QGIS 3.4.5 program.

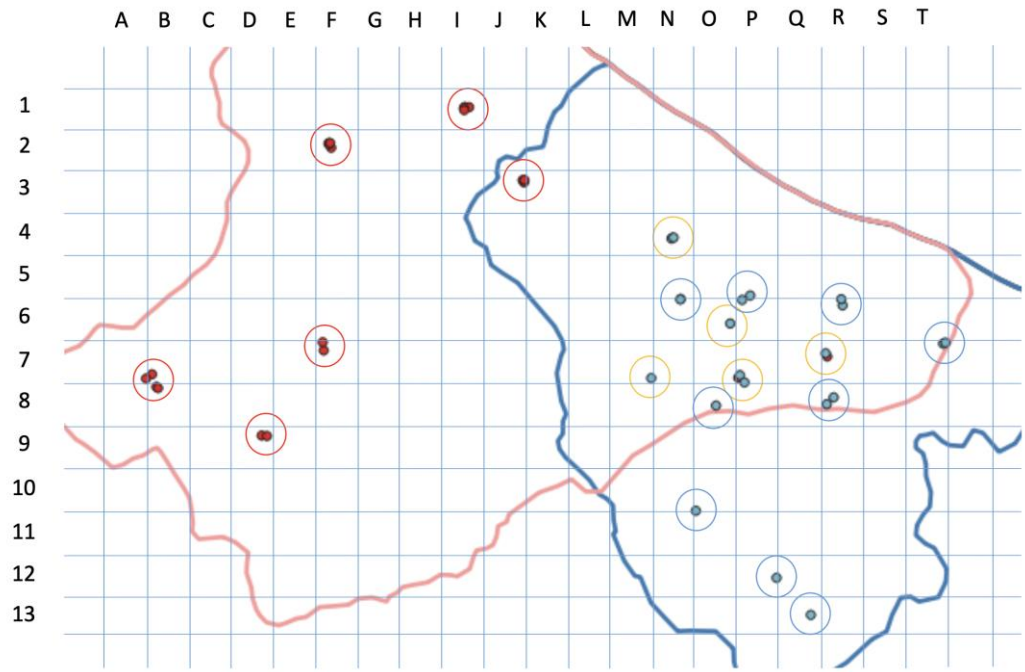

Figure 2. Map of sleeping trees (dots) and sleeping sites (circles) used by two groups of *Macaca nigra*, PB1B in blue and R1 in pink. Yellow circles show the sleeping sites used by both groups. Blue lines are 100 × 100 m grids for sleeping site codenames. Thick lines indicate home ranges of the macaque groups, PB1B in blue and R1 in pink

Predator encounters

Several predator encounters were recorded throughout the study. The main predator of *M. nigra* is the large reticulated pythons (*Python reticulatus* Schneider 1801) that were observed to prey on crested macaques several times (Micheletta et al. 2012; Marty et al. 2017). Other potentially threatening species for the macaques include eagles (*Nisaetus lanceolatus* Temminck & Schlegel 1844), dogs, and humans (Micheletta et al. 2012). The monkeys make alarm calls when they see predators and feel threatened. The data collected included the type of predator, the date and time of the encounter, the group of monkeys observed, and the GPS coordinates of the encounter location.

Sleeping tree identification and measurement

At the end of the study, vegetation plots were made in 22 sleeping areas sized 25 × 25 m each, covering a total area of 13,750 m^2. We identified the tree species and then measured the diameter at breast height (DBH) and height for all trees with diameter ≥10 cm (Albert et al. 2011). The species were classified into food and non-food trees according to the Macaca Nigra Project database and Arismayanti (2022). DBH measurement was done using a tape meter. Tree height data was collected using a Discovery D800 laser range finder. Trees that have marker tapes are categorized as sleeping trees. The other trees were categorized as non-sleeping trees. The importance Value index (IV) was calculated by adding the relative density, relative dominance, and relative frequency of each species as described by Mueller-Dombois and Ellenberg (1974). The statistical comparisons of DBH, height, and IV index between sleeping and non-sleeping trees were performed using the Wilcoxon rank sum test in the R 3.6.3 program with alpha set at 0.05.

RESULTS AND DISCUSSION

Spatial and temporal use and characteristics of sleeping sites

Data from the sleeping site were collected for 187 days, 90 days in the PB1B group, and 97 days in the R1 group. The home range of the PB1B group was 221.91 ha, and the R1 group was 372.85 ha. The PB1B group used 14 sleeping sites, while the R1 group used 11. Five sleeping sites were used by the two groups (Figure 2) in the overlap home range area, i.e., sites with codenames N4, M7, O6, P7, and R7, but both groups never slept in the same location on the same night. The sleeping sites ranged from 1.488 to 175.746 m asl. with an average elevation of 55.43 ± 29.95 m asl.

Generally, the sleeping sites used mainly by the macaques were surrounded by many food trees at the same location or nearby. More precisely, over 90 days of observation of the PB1B group, the sleeping site most frequently used by this group was located in N4 (34%, n=31) (Figure 3). From the tree identification in vegetation plots, many food trees, such as *Leea indica* (Burm.fil.) Merr., *Dracontomelon dao* (Blanco) Merr. & Rolfe, and *Palaquium amboinense* Burck, are found in this location. Furthermore, this sleeping site is only 280 m from the beach, where plenty of *M. nigra* food tree, *Terminalia catappa* L., are present. Regarding the R1 group, over 97 days of observation, the most frequently used sleeping sites of this group were located in F2 (24%, n=23) and I1 (22%, n=21) (Figure 4). The F2 site is near a creek surrounded by many food trees, including *D. dao*, *Ficus variegata*, and *Cananga odorata*. The I1 site also has many food trees, such as *L. indica*.

Over a total of 187 days of observation, in 92% (n=172) of the cases, the macaques changed their sleeping site from the previous night, and in 5.3% of the cases, they used the same sleeping site for two consecutive nights (PB1B group: 6 times; R1 group: 4 times). Very rarely, the macaques used the same sleeping site more than two consecutive nights, i.e., the R1 group used the F2 site for three consecutive nights, and the PB1B group used the N4 site for four consecutive nights. Thus, both F2 and N4 sites are considered the favorite sleeping sites of R1 and PB1B, respectively.

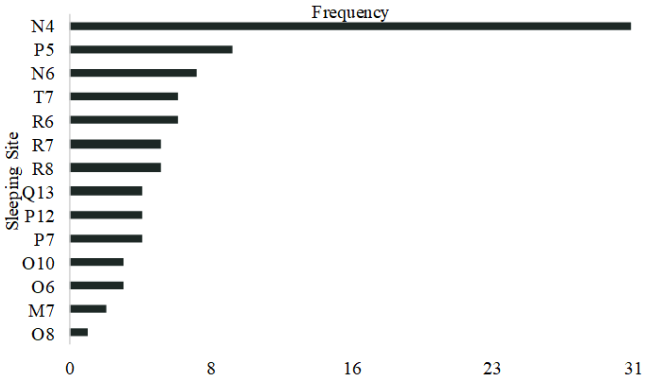

Figure 3. The frequency of sleeping sites used by PB1B group (n = 90 days)

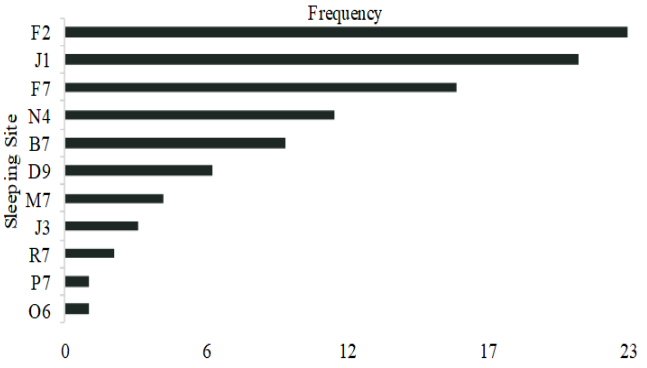

Figure 4. The frequency of sleeping sites used by R1 group (n = 97 days)

Distance between sleeping trees and feeding trees

The PB1B and R1 groups chose sleeping trees near a feeding area in this study. The distance between the sleeping tree and the first feeding tree in the morning ranged from 0 to 488 m with an average distance of 203 ± 107.44 m. (PB1B group (n=53): 178.17 ± 97.97 m; R1 group (n=46): 231.78 ± 111.69 m). The distance between the sleeping tree and the last feeding tree in the evening ranged from 0 to 417 m with an average distance of 127 ± 93.88 m (PB1B group (n=51): 136.15 ± 101.98 m; R1 group (n=45): 116.79 ± 83.71 m).

Predator encounter

Throughout the study, 7 predator encounters (PB1B: 5, R1: 2) were recorded, including 6 encounters with reticulated pythons, the main predator of *M. nigra*, and 1 encounter with a Sulawesi viper snake (*Tropidolaemus laticinctus* Kuch, Gumprecht & Melaun 2007) that is highly venomous. Predator encounters were rare, and no monkeys were caught or bitten during the study. Only 2 of the 7 encounters occurred near a sleeping site, 1 for each group.

Sleeping tree species

We recorded 694 trees from 61 species with diameters larger than 10 cm in 22 vegetation plots; 58 trees from 13 species were used as sleeping trees (Table 1). The species most used as sleeping trees were *F. variegata* (30%, n=17) and *D. dao* (18%, n=11). Both species have an average DBH of over 80 cm and an average height of over 30 meters. Furthermore, 11 of the 13 sleeping tree species were food species consumed by *M. nigra*. Only two species, *Garuga floribunda* Decne. and *Alstonia scholaris* (L.) R.Br., were not food trees, but both species have a high IV index, indicating that they have relatively high density, frequency, and dominance at the sleeping sites selected by these macaques.

Sleeping tree characteristics

The groups selected sleeping trees with dense canopy and many branches, presenting larger diameters (Figure 5), higher heights (Figure 6), and higher IV index (Figure 7) than non-sleeping trees. Indeed, the average DBH of the sleeping trees (91.003 ± 28.66 cm, n=58) was significantly different from the average DBH of non-sleeping trees (24.19 ± 16.98 cm, n=636) (Wilcoxon rank sum test, W=721.5, *p*-value <0.001). The average height of the sleeping trees (32.872 ± 6.001 m, n=58) was significantly different from the average height of the non-sleeping trees (14.46 ± 7.09 m, n=636) (Wilcoxon rank sum test, W=1391.5, *p*-value <0.001). The IV index of non-sleeping trees was also significantly lower than that of the sleeping trees (Wilcoxon rank sum test, W=97.5, *p*-value <0.001).

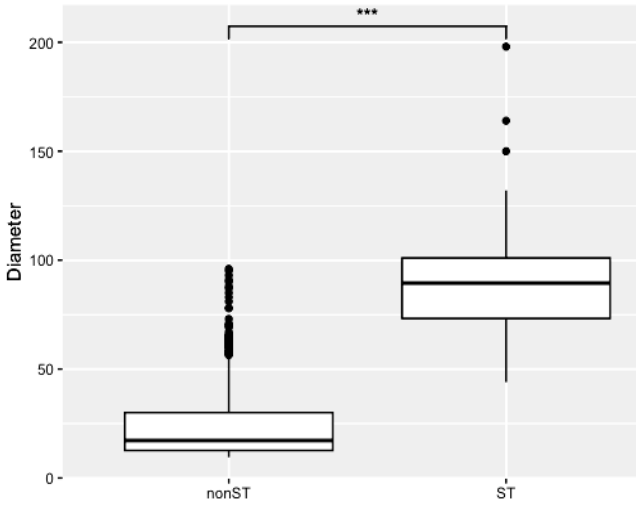

Figure 5. The boxplot of diameter comparison between non-sleeping trees (n=636) and sleeping trees (n=58) was used by two groups of *Macaca nigra*. The diameter of non-sleeping trees was significantly lower than the sleeping trees (Wilcoxon rank sum test, W=721.5, *p*-value < 0.001). The upper end of the box represents 3rd quartile (Q3) and the lower end is the 1st quartile (Q1). The thick line inside the box represents median (Q2). The points outside the box are outlier data

Table 1. The species, DBH, height, and Important Value of the sleeping trees

Sleeping Tree Species	Family	Number of Tree(s)	Average DBH (cm)	Average height (m)	Consumed by *M. nigra*	Important Value (%)
Ficus variegata	Moraceae	17	84.94 ± 24.6	33 ± 4.7	Yes	23
Dracontomelon dao	Anacardiaceae	11	101.4 ± 21.1	38.1 ± 5.3	Yes	20
Garuga floribunda	Burseraceae	10	79.2 ± 15.8	29.1 ± 4.9	No	23
Palaquium amboinense	Sapotaceae	7	80 ± 13.2	30.3 ± 4.4	Yes	24
Vitex quinata	Lamiaceae	3	74.3 ± 4.6	29.3 ± 4.8	Yes	11
Alstonia scholaris	Apocynaceae	2	125.5 ± 34.6	41.6 ± 1.8	No	10
Ficus tinctoria	Moraceae	2	122 ± 59.4	23.9 ± 3.7	Yes	5
Aglaia sp.	Meliaceae	1	46.02.00	30.02.00	Yes	10
Cananga odorata	Annonaceae	1	73	32.02.00	Yes	11
Ficus annulata	Moraceae	1	111	29.01.00	Yes	2
Ficus sp.	Moraceae	1	198	39	Yes	4
Ficus virens	Moraceae	1	94	43.03.00	Yes	1
Syzygium sp.	Myrtaceae	1	126	29.08.00	Yes	7
		58	91.003 ± 28.66	32.872 ± 6		

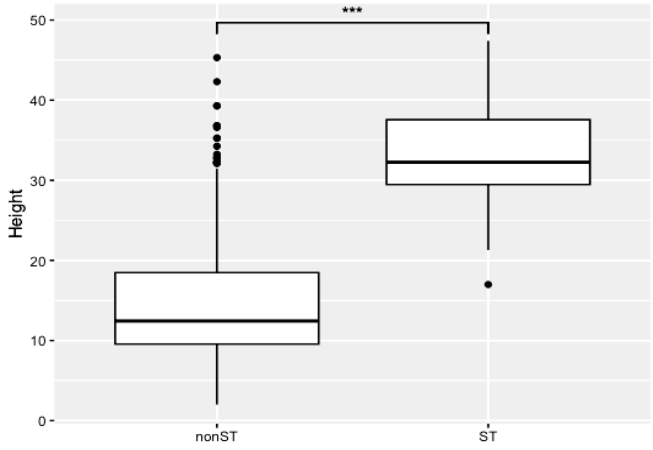

Figure 6. The boxplot of height comparison between non-sleeping trees (n=636) and sleeping trees (n=58) was used by two groups of *Macaca nigra.* The total height of non-sleeping trees and sleeping trees were significantly different (Wilcoxon rank sum test, W=1391.5, *p*-value < 0.001)

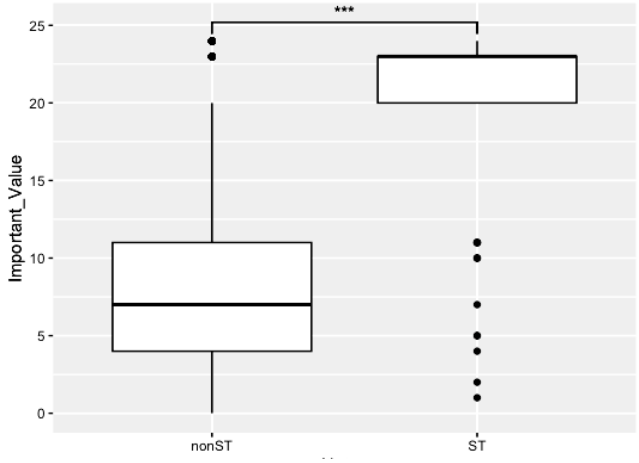

Figure 7. The boxplot of the Important Value index between non-sleeping trees (n=636) and sleeping trees (n=58) was used by two groups of *Macaca nigra.* The IV index of non-sleeping trees was significantly lower than the sleeping trees (Wilcoxon rank sum test, W=97.5, *p*-value < 0.001)

Discussion

These naturalistic observations mainly show that the *M. nigra* groups studied selected sleeping locations close to food sources and avoided sleeping in the same location on consecutive nights. Sleeping trees used by these macaques are generally food tree species, mainly *F. variegata* and *D. dao*, both consumed regularly by *M. nigra.* The monkeys preferably selected sleeping trees with large diameters, high heights, dense canopies, and many branches.

Predator avoidance was a factor that affected the selection of sleeping sites

The results of this study show that *M. nigra* groups rarely sleep at the same site as the previous night and prefer to switch their sleeping sites regularly. This result is similar to several previous studies on other primate species. For example, Northern pig-tailed macaques (*M. leonina*) in Khao Yai National Park, Thailand, did not use any sleeping site consecutively for more than two nights (José-Domínguez et al. 2015). Another study of long-tailed macaques (*M. fascisularis*) in Bali Barat National Park, Indonesia, showed that monkeys avoid using the same site on consecutive nights (Brotcorne et al. 2014).

According to Bidner et al. (2018), frequent switching of sleeping sites could be a strategy to avoid predators, which generally seek prey at night. Sleeping in the same location for several consecutive nights allows predators to easily detect the presence of potential prey (Ellison et al. 2019). During our study period, only two predator encounters occurred near sleeping sites. Following these encounters, the macaques chose to defer for several days before returning to these sleeping sites. Even though the sample size is too small to draw strong conclusions, this finding also supports the anti-predator strategy as a criterion for sleeping site selection in this species.

Choosing trees with greater DBH and height is also assumed to be a strategy to avoid terrestrial predators (Cheyne et al. 2013). Sleeping in tall trees makes it easier for primates to monitor their surroundings, helping them to watch for predators, poachers, and intergroup encounters (Fei et al. 2017). In Tangkoko, the main predators of crested macaques are large reticulated pythons (Micheletta et al. 2012; Marty et al. 2017). Although these big snakes can climb up trees, their progression is quite slow, if not impossible, if the diameter of the tree is too large and conspicuous for the monkeys, giving them plenty of time and good visibility to escape up trees where the smaller branches cannot support the weight of the snake, or in other surrounding trees due to the dense canopy network characterizing these sleeping trees. Finally, although the macaques often changed sleeping sites on consecutive nights, they used a relatively small number of different sleeping sites and regularly returned to the same sleeping sites. A possible explanation is that the monkeys became familiar with these sites, which can facilitate escape routes during night attacks (Albert et al. 2011).

Optimal foraging strategy was a factor affecting sleeping site selection

Previous studies on other species showed that primates sleep close to food and water sources (Anderson 2000). For example, spider monkeys (*Ateles geoffroyi*) in Mexico selected sleeping sites in medium-height semi-evergreen forests with greater fruit availability (Velázquez-Vázquez et al. 2015). Black-and-gold howler monkeys (*A. caraya*) in Northern Argentina used the same site for sleeping and feeding in the morning for 27% of observed nights, and the mean distance from the sleeping site to the first feeding site was 13.8 m (Brividoro et al. 2019). The mean distance from the sleeping site to the feeding area of northern pig-tailed macaques in Thailand was 127 to 227 m (José-Domínguez et al. 2015). This optimal foraging strategy is assumed to increase access to food and reduce energy expenditure (Feilen and Marshall 2017). Sleeping near food

trees will save time and energy to find food (Brotcorne et al. 2014) and allow the monkeys to recover quickly after fasting all night (Anderson 2000; Albert et al. 2011).

The present study's results follow previous studies on other primate species. Indeed, the macaques of Tangkoko chose sleeping sites with many food trees available around them and were sometimes observed using the same tree for both sleeping and feeding. The average distance from the sleeping site and feeding site was relatively short (116-231 m) compared to this species' daily travel path length, which ranged from 448 to 5,881 m with an average of 2,388 m (O'Brien and Kinnaird 1997). These observations suggest that crested macaques also use the optimal foraging strategy as a criterion to select their sleeping sites every night.

Some other studies also showed that, in areas with strong seasonality, food availability affects the selection of sleeping sites for primates (Harrison et al. 2021). The monkeys need to explore further when food is scarce (Hambali et al. 2016), and changing sleeping sites every night and shifting home range to get closer to food sources are parts of the optimal foraging strategy. For instance, Northern pig-tailed macaques in Thailand would sleep near human settlements to access human food during fruit scarcity (Albert et al. 2011). Long-tailed macaques in Bali, Indonesia, also slept more often near visitor zones to eat anthropogenic food when the availability of natural food decreased (Brotcorne et al. 2014). Other primates like *lemurs* also had different sleeping site locations in the wet season and dry season following the food resources (Mandl et al. 2018). Crested macaques eat many fruits, which are the main components of their diet (O'Brien and Kinnaird 1997), whose varieties and availability depend on location and season. At Tangkoko, food is abundant all over the year and food scarcity does not threaten the monkeys. However, during the study period, we could observe temporal shifts in sleeping sites, with some sites frequently used at some points and neglected later. The seasonal shift in food availability might explain this phenomenon. However, as this study was carried out over 9 months only, a systematic analysis of the impact of food seasonality on sleeping site selection over a year was not possible.

Other factors potentially impacting sleeping site selection

Choosing emerging trees with large diameters and many big branches that form dense canopies could also prevent the monkeys from falling from the trees while sleeping. Similar to our study, the long-tailed macaques of Bali preferred sleeping trees with an average DBH of 66.5 cm and a total height of 11.2 m (Brotcorne et al. 2014), while the Northern pig-tailed macaques chose trees with an average height of 20.9 m (Albert et al. 2011). Large trees can withstand extreme weather, such as rain and strong winds, breaking the branches and making the support unstable because they are more stable and sturdier (Brividoro et al. 2019). Dense canopies allow a good connection between the trees, which could help the monkeys to move freely (Albert et al. 2011), for example, to escape quickly when a branch breaks. Indeed, Brividoro et al. (2019) assumed that black-and-gold howler monkeys (*A. caraya*) chose sleeping trees with large diameters to reduce the risk of falling during sleep due to broken branches. Trees with dense canopies and big branches also accommodate large groups with many individuals (Anderson 2000), providing the monkeys with enough space for everyone, safe support, and protection from bad weather. During the observation time of this study, we did not find any dead bodies in the morning, which could indicate that some macaques fell from the trees during the night, suggesting that the characteristics of the sleeping trees chosen by the crested macaques provided good shelters to spend the night safely, even during bad weather.

Switching sleeping sites frequently also reduces the probability of encounters with another group of macaques. This could be detrimental to the monkeys for several reasons. First, the groups are competing for the same food source, which means that their energy intake is reduced (Brividoro et al. 2019). Often, a group will leave the place, causing these monkeys to expend more energy traveling to find another food source. During our observation, the monkeys had intergroup encounters on the way to the first feeding site in the morning, causing the group to run away in another direction, increasing the distance between the sleeping site and the first feeding site. Finally, intergroup encounters are stressful for monkeys and can cause severe or lethal injuries, sometimes severe if not lethal (Martínez-Íñigo et al. 2021). Thus, avoiding intergroup encounters, particularly at feeding sites, is important for the monkeys' fitness; regularly changing sleeping sites could be part of the strategy to reduce this potential threat.

Previous studies also showed that interspecies competition for food resources can affect the sleeping site selection of some primate species. For example, Cheyne et al. (2013) observed that only 19.78% of Bornean gibbons (*Hylobates albibarbis*) sleeping trees were food trees. They suggested it could be a strategy to avoid competition with other frugivores, such as orangutans (*P. pygmaeus*). Interspecific competition does not apply to the crested macaques of Tangkoko since the only frugivorous species that potentially compete for food is the Sulawesi bear cuscus (*Ailurops ursinus*), which does not constitute a real competitor to crested macaques as they stay in small family groups not able to compete with big groups of macaques. This absence of interspecific competition could partially explain the strategy of the crested macaques of sleeping at or close to feeding sites.

Finally, parasite and disease transmission avoidance has also been shown to impact the sleeping site selection of certain primate species (Samson et al. 2013). This factor might also be important in the decision-making regarding sleeping tree selection in crested macaques, but this analysis is beyond the scope of this study.

The results of this naturalistic study inform us about the spatial and temporal use and characteristics of the sleeping sites used by two groups of *M. nigra* in Tangkoko. More precisely, these crested macaques preferably selected sleeping sites located directly at or near food sources and avoided sleeping at the same location on consecutive nights. They also chose sleeping trees with large diameter, tall height, dense canopy, and many branches. These

findings suggest that, similarly to many other primates and particularly other macaque species, the sleeping site selection of crested macaques is mainly driven by the optimal foraging and antipredator strategies. The macaques chose sleeping sites preferentially compared to availability since Tangkoko forest has abundant fruit and emergent trees, and the predator pressure is relatively low. Based on this study, Tangkoko is a very suitable habitat for *M. nigra*. *It* could be a baseline for conservation action and habitat enrichment programs in other *M. nigra* habitats in North Sulawesi.

This new knowledge can be extended to the whole species. It could constitute strong building blocks to implement and improve conservation programs to protect this Critically Endangered species in its entire home range. For example, this study's results could help determine the best locations for camera traps, which are very useful for monitoring populations of non-habituated crested macaques in remote areas. They could also be useful in making decisions regarding the travel paths of patrols, either for protection against poachers for scientific surveys or to prevent human-macaque conflicts around the plantations and villages. Knowing the characteristics of the best sleeping sites for this species is also highly valuable in choosing the best sites for rehabilitation and relocation of new groups of macaques that would increase the genetic diversity of local populations if well managed. Finally, these findings could be informative to the wildlife conservation authorities to define and delimit the areas that should be prioritized for protection in order to preserve the environment of *M. nigra* and many other species living in the same habitat.

ACKNOWLEDGEMENTS

INQ thanks the Ministry of Finance for the LPDP Scholarship that helped fund this study. JMB is funded by the University of Kent, School of Anthropology and Conservation. The authors thank the Natural Resources Conservation Agency (BKSDA) of North Sulawesi for permission to conduct research in the Tangkoko Nature Reserve and all members of the Macaca Nigra Project team for their assistance in data collection. They also thank Institut Pertanian Bogor's colleagues for their valuable discussions in the data analysis. The authors thank the Editor in Chief and reviewers for their constructive, insightful suggestions and valuable comments.

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