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Maternal den preferences, reproductive behavior, and spatial use of a wild *Manis javanica* during maternal and non-maternal stages in Sabah, Borneo

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ABSTRACT: We present a comprehensive long-term (176 d) report on a wild nursing female (6.4 kg, total length: 99 cm) Sunda pangolin *Manis javanica* in a highly fragmented area of Borneo. Using VHF tracking and camera trap monitoring, we aimed to address key research questions related to variations in home range and sleeping site selection during the maternal (nursing) and non-maternal stages. We examined the characteristics of maternal dens and natural behaviors, including activity patterns and interactions with other pangolins, during the nursing period. Camera trap records revealed strictly nocturnal behavior, with peak activity between 00:00 and 03:00 h; the mean (±SD) duration of activity was 64.35 ± 13.64 min. Ten maternal sleeping sites were identified; most sites were well concealed, and 60% were tree hollows. All trees used were mature (≥38 cm diameter at breast height), and all burrows and tree hollows had depths of ≥78 cm. A male pangolin was detected sharing the same site with the pup and/or the female pangolin on 3 separate occasions, with no signs of injury. The female gave birth twice in less than a year, suggesting aseasonal breeding. The 95% MCP home range during the tracked maternal period (63 d) was 1.35 ha, with sleeping sites solely in the forest. However, during the non-maternal period (57 d), the female pangolin used sleeping sites in an oil palm plantation, and the range increased to 8.89 ha. By documenting rare wild data for this elusive species, we provide important insights to inform *in situ* and *ex situ* conservation efforts.

KEY WORDS: *Manis javanica* · Maternal care · Den selection · Home range · Reproduction · Fragmented landscape

1. INTRODUCTION

The Sunda pangolin *Manis javanica* is 1 of the 8 currently recognized pangolin species in the world and 1 of the 4 pangolin species present in Asia. Its range covers Thailand, Laos, Cambodia, Vietnam, Singapore, Brunei, Indonesia, Myanmar, southern China (Yunnan province), and Malaysia (peninsular Malay-

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sia and Malaysian Borneo) (Chong et al. 2020, Cen et al. 2023). A fifth Asian pangolin species was recently described (Gu et al. 2023), highlighting the limited ecological knowledge about wild pangolins despite being considered one of the most trafficked mammals in the world (Challender & Waterman 2017). The Sunda pangolin is listed as Critically Endangered on the IUCN Red List and on CITES as an Appendix I species (Challender & Waterman 2017, Challender et al. 2019). The species population has experienced a dramatic decrease over the past years, mainly due to poaching for the international illegal wildlife trade for use in traditional Chinese medicine and as food in Asian communities (Chong et al. 2020, Xing et al. 2020). This decline is further worsening by the continued destruction of their natural habitat (Chin & Pantel 2009, Hua et al. 2015, Chong et al. 2020). Agricultural expansion has resulted in the fragmentation of extensive forested areas into isolated patches, thereby disrupting ecosystems, isolating wildlife populations, and increasing edge areas that have distinct microclimatic conditions and higher predation and poaching rates compared to core forest areas (Mullu 2016, Challender et al. 2019). These diverse threats have resulted in the implementation of several conservation measures, including the establishment of stricter anti-poaching laws, community engagement programs, and rescue initiatives (Challender et al. 2015). Although these initiatives have demonstrated localized successes, challenges such as limited enforcement capacity and ongoing habitat loss remain prevalent, highlighting the need for systematic evaluations to guide the development of more comprehensive recovery strategies (Hoffmann & Challender 2020). Despite being a protected species in Malaysia, including being listed as a totally protected species under the Wildlife Conservation Enactment 1997 in Sabah, the illegal exploitation of the species across the country continues (Free Malaysia Today 2019, TRAFFIC 2019, The Star 2022, The Straits Times 2020). According to illegal trade records, an estimated 895 000 pangolin individuals were trafficked between 2000 and 2019, with a significant rise in numbers since 2016, and approximately 7 % of all pangolin trade from this period is estimated to be Sunda pangolins (Challender et al. 2020). Additionally, Sabah is an important part of the illegal trade network, with more than 40 t of pangolins (equivalent to ca. 100 000 pangolins) smuggled since August 2017 (TRAFFIC 2019). In Sabah, the Sunda pangolin population is facing an imminent risk of extinction if the current high level of poaching persists (Chin & Pantel 2009, Chong et al. 2020).

Given its ongoing and rapid population decline, Sunda pangolin captive breeding programs and rehabilitation centers have become imperative for the future survival of the species (Hua et al. 2015). While rehabilitation centers sometimes receive pregnant females and/or motherless pangolin pups, the management of these vulnerable individuals poses significant challenges. Although some organizations have managed to successfully breed and hand-rear Sunda pangolins (Zhang et al. 2017, 2020, Cabana et al. 2019, Ngau et al. 2021, Yan et al. 2021, 2022), these efforts remain challenging, partly due to the limited knowledge of reproductive and maternal behavior in the wild (Hua et al. 2015, Wicker et al. 2020). The postnatal care of wild pangolins is poorly documented; however, pups remain in the same resting site with the mother for a few months and clasp to their mother's tail to move from one burrow to the other. Paternal care has not been reported. Although differences in reproductive parameters exist between pangolin species, the general consensus is that most of them exhibit aseasonal breeding and give birth to a single offspring (Gudehus et al. 2020, Hoffmann et al. 2020, Jansen et al. 2020, Mahmood et al. 2020, Pietersen et al. 2020, Wu et al. 2020). Uncertainty about gestation periods, growth rates, weaning age, and time of sexual maturity, as well as limited knowledge on maternal care and normal milk composition remains common among all pangolin species, due to the limited natural observations (Pietersen & Challender 2020). Sun et al. (2024) evidenced a difference in reproductive cycles between captive and wild pangolins, emphasizing the need for wild records to establish accurate reproductive parameters across species. Only 1 study has specifically examined the maternal behavior of wild Sunda pangolins, reporting high site fidelity and maternal care of approximately 4 mo (Lim & Ng 2008). However, uncertainty remains regarding postbirth behaviors and variation across reproductive states. Given the challenges posed by the elusiveness of these animals, their low detection rates, and the lack of distinct individual physical traits in camera trap studies (Khwaja et al. 2019, Willcox et al. 2019, Yan et al. 2022, Shirley et al. 2023), there is a pressing need for ecological research. Such research should aim to improve our understanding of the species' ecology in both natural and human-modified landscapes (Chong et al. 2020).

Although Sunda pangolins are reported to inhabit disturbed areas (Lim & Ng 2008, Wearn et al. 2017, Chong et al. 2020, Panjang et al. 2024), the specific macro- and microhabitat characteristics essential for their reproduction and breeding remain unclear, in-

cluding whether these requirements vary during non-maternal stages. The home ranges of the females reported in the literature (Gray et al. 2023, Panjang 2023) have focused primarily on non-lactating females, resulting in limited information on maternal den usage and site selection. This lack of specific data on the preferences of lactating females may affect the comprehensiveness and effectiveness of future conservation strategies. Lim & Ng (2008) provided valuable insights from 1 wild lactating female, although the observations were limited to 3 dens, all tree hollows. Similarly, we focus on a single pangolin but expand the scope by documenting a wider selection of sleeping sites and including both lactating and non-lactating periods. Long-term reports of wild maternal behavior are fundamental but remain rare due to the scarcity of direct observations and the difficulties of indirect observations outlined above (Willcox et al. 2019, Shirley et al. 2023). Although information about the captive reproduction of Sunda pangolins is available (Yan et al. 2021), reproductive behavior in the wild remains poorly understood, posing challenges for effective conservation and management. A critical gap exists in understanding how home range size and sleeping site (Table 1) selection vary between maternal and non-maternal stages. Additionally, there is limited knowledge of the natural behaviors and interactions that occur during the nursing period among the female, its pup, and other sympatric pangolins.

Very high frequency (VHF) radio tracking combined with the use of non-invasive infrared thermal cameras allows for systematic monitoring of individual animals, offering deeper insights into their movement and ecology (Lim & Ng 2008, Sun et al. 2018). Small VHF transmitters attached to a pangolin scale enable researchers to pinpoint dens accurately, even in deep burrows where GPS signals may not be available, and without disturbing the animal while it rests. However, this method requires a considerable amount of manpower to collect relatively limited data, and following the animals during their active periods without causing distress is challenging.

We seek to address the following key research questions: (1) How do home range size (based on resting locations) and sleeping site selection differ between maternal and non-maternal stages? (2) What natural behaviors and interactions occur during the nursing period between a female pangolin, its pup, and other sympatric pangolins? (3) What are the activity patterns of lactating females and their pups during this period? (4) Do Sunda pangolins exclusively use tree hollows as nursing dens, or do they rely on a broader range of sleeping sites, and what are the characteristics of these maternal resting sites?

By radio-tagging a wild nursing female Sunda pangolin, we were able to monitor, for the first time, the same wild individual from one maternal period to the next, helping us address these key questions. We conducted the study in a severely fragmented area affected by oil palm plantation expansion (Abram & Ancrenaz 2017). This context allows us to offer valuable insights into how pangolins utilize habitats across both natural and human-modified landscapes. With these data, we aim to enhance the understanding of the species' natural maternal behavior and requirements in the wild and to provide valuable reference information for *in situ* and *ex situ* conservation strategies.

2. MATERIALS AND METHODS

2.1. Study site

The Lower Kinabatangan Wildlife Sanctuary is a protected area that extends along the Kinabatangan River in the state of Sabah, Malaysian Borneo. The forest in lower Kinabatangan has been affected by timber extraction in the 1950s and continuous agricultural expansion of oil palm (*Elaeis guineensis*) plantations since the 1990s (Abram & Ancrenaz 2017). The sanctuary was created to protect the remaining forest from further plantation expansion, given the state's extensive land conversion rate over the recent decades, with more than 26% of Sabah's land converted into oil palm plantations (MPOB 2018). The forest lots within the sanctuary are connected by narrow corridors of state-owned and private forests in various stages of degradation (Abram et al. 2014). The study site is located on the southern bank of the Kinabatangan River, between Lots 3 and 6 of the

Table 1. Terms used in the manuscript to refer to the sites utilized by pangolins

Term	Definition
Sleeping/resting site/den	Site used for resting, obtained by very high frequency triangulation in the morning (inactive time) of each day (~08:00 h); pangolins sleep at a site for many hours until they go out to feed and/or explore (Chong et al. 2020, Panjang 2023)
Maternal/nursing site/den	Sleeping site used by the female pangolin and pup during the maternal stage

sanctuary. It consists of a narrow strip of state-owned secondary forest along the river, not exceeding 150 m in width at its broadest part, as shown in Fig. 1. This forest acts as a buffer zone between the oil palm plantation estate and the Kinabatangan River (Abram et al. 2014). The forest and plantations are separated by bamboo ridge barriers and typically deactivated electrical fences.

2.2. VHF tracking, camera trapping, and activity patterns

One female Sunda pangolin (hereafter referred to as MJF01) was captured during the tracking of a sympatric adult male weighing 12 kg (hereafter referred to as MJM02), when both were found sharing the same burrow. MJF01 weighed 6.4 kg, with a total length of 99 cm, and was accompanied by a male pup weighing 1.25 kg and measuring 60 cm. Based on the pup's weight, size, and scale condition, its age was estimated to be between 2 and 2.5 mo, following the criteria outlined in Nguyen et al. (2010). MJF01 was fitted with a VHF tag (TXE-304, 25 g, from Telenax®) attached to a lateral scale near the base of the tail,

using a strap secured with screws, following the method described by Panjang (2023). The pup was kept next to the mother during the tagging procedure. Every 2 d at approximately 08:00 h, we used VHF signal triangulation to locate the sleeping sites used as maternal dens and recorded their GPS point. When a tree hollow or burrow was used as a sleeping site and one or more entrances were identified, a camera trap (Bushnell® No Glow DS 4K IR) was placed in front of the main entrance. The camera was set to record 15 s videos, with no delay between triggers, and it was relocated each time a new sleeping site was identified. Videos were manually analyzed to document behaviors and activity patterns, as they offer visual evidence of maternal conducts, mobility, and physical condition and confirm periods of activity without disturbing the animals. Tracking during active hours was not conducted to minimize stress, and activities were observed by video recordings. Active time event (ATE) was defined as the period from when the pangolin exited the sleeping site until it returned; thus, these time intervals indicate when the animal is active in the forest. If more than 1 exiting— entering event occurred in the same night, each event was recorded as a separate ATE. The sum of all ATEs

MCP %	Maternal*	Non-maternal*
50	**0.6398**	**1.1652**
55	0.6398	1.2830
60	1.1448	1.2830
65	1.2634	3.1327
70	1.2634	3.9453
75	1.2634	5.4086
80	1.2634	5.4086
85	1.2634	6.0864
90	1.3548	8.7266
95	1.3548	8.8957
100	**7.6304**	**9.5856**

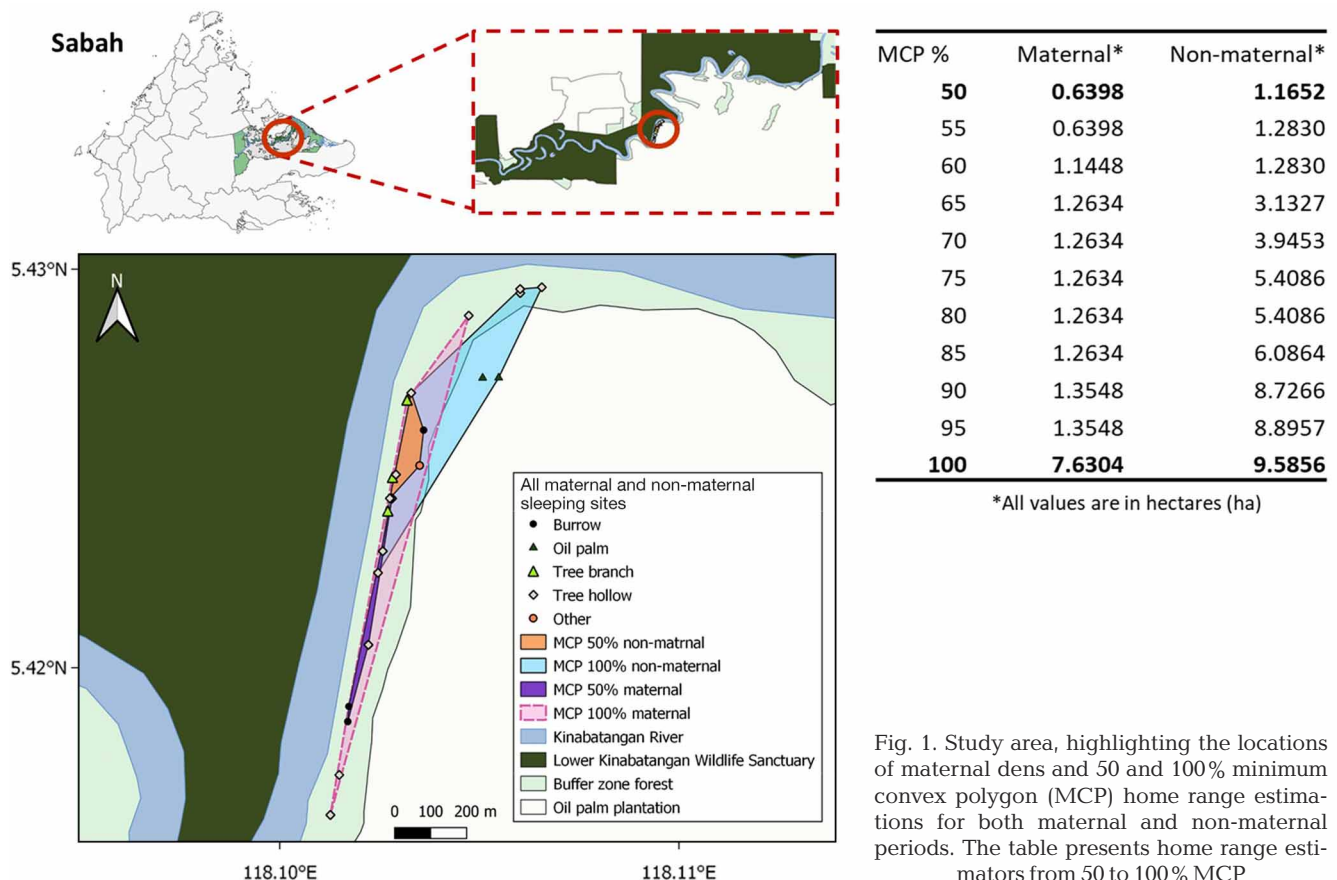*All values are in hectares (ha)

Fig. 1. Study area, highlighting the locations of maternal dens and 50 and 100% minimum convex polygon (MCP) home range estimations for both maternal and non-maternal periods. The table presents home range estimators from 50 to 100% MCP

recorded during a single night was referred to as the total nightly activity (TNA) time, representing the minimum active time for the pangolin during that night. If the sleeping site had multiple entrances, and only videos of the pangolin entering or leaving the sleeping site were recorded, this record was considered only for activity pattern analysis, since the length of activity cannot be calculated. Instances where MJF01 carried the pup or when the pup ventured out by itself were also recorded. The activity pattern was determined based on the time of each entry and exit recorded. The R package 'overlap' (Ridout & Linkie 2009) was used to plot kernel densities from the activity records. MJF01 continued to be tracked after the pup left, but only video records from the maternal phase were analyzed, due to limited footage during the non-maternal period. Occurrences when the tagged sympatric male pangolin (MJM02) shared the same sleeping site were noted.

2.3. Maternal sleeping site assessment and analysis

Maternal sleeping site types were classified as burrow, tree hollow, or tree branch. The assessment for each site was conducted according to Table 3. Not all variables could be measured for each site, as some features were located too high to access. Given the small sample size and the fact that the 3 different types of sleeping sites required different physical measurements, the variables measured could not be statistically compared with one another. Instead, means and SDs were calculated for every variable for each type of sleeping site. A Kruskal-Wallis chi-squared test was performed to determine if the number of nights spent by the pangolin was related to the sleeping site type.

2.4. Home range and sleeping site selection between maternal and non-maternal phases

We compared sleeping site selection and home range during the studied maternal and non-maternal periods of MJF01. The studied maternal period encompassed the time from when MJF01 was captured and tagged until the last video evidence of the pup sharing the sleeping site with MJF01 (63 calendar days). The non-maternal period corresponds to the time from when MJF01 was confirmed to be without the pup until the birth of the next pup (57 calendar days). Distances in a straight line between the sleeping site used the previous night and the next one

(when the animal changes sites) were calculated using the R packages 'sf' (Pebesma 2018) and 'geosphere' (Hijmans 2022). The sum of all distances was divided by the number of relocations to obtain the mean distance between sites (Table 2). A Wilcoxon rank sum test was used to compare the difference in distance between sleeping sites during both periods. Home range estimations using minimum convex polygons (MCPs) and kernel density estimators (KDEs) with a reference bandwidth parameter (h) were calculated using the 'adehabitatHR' package (Calenge 2006, 2011) in R version 4.2.2 (R Core Team 2022). MCP was selected as the primary home range estimator to allow comparison with previous studies (Lim & Ng 2008, Panjang 2023). While MCPs may include areas not used by the animal, they effectively illustrate the area needed to find refuge sites. Our GPS points are highly autocorrelated, as they only represent nursing sites, which are prone to be revisited (Fleming et al. 2015). KDE is sensitive to this type of aggregate data, risking convergence in smoothing parameters (Hemson et al. 2005). Nevertheless, we have added KDE calculations to offer additional information.

For sleeping site comparison during maternal and non-maternal phases, 5 co-variables were evaluated: distance to main river, distance to oil palm plantation, sleeping site type (tree hollow, tree branch, burrow, oil palm tree, and other), location (forest or oil palm plantation), and number of nights per site. Distance to river and distance to plantation were measured using the package 'sf' in R (Pebesma 2018). Days utilizing each site were determined only by tag georeference. Fisher's exact test was selected to analyze correlations between the status (maternal or non-maternal) and the location and type of sleeping site, due to the small sample size. The Wilcoxon rank sum test was used to evaluate the difference between maternal and non-maternal phases for distance to river and distance to oil palm plantation.

For home range differences between maternal and non-maternal periods, a Wilcoxon rank sum test was conducted, accounting for estimations between 50 and 100% MCP during both phases.

Table 2. Distance (m) between consecutive sleeping sites during maternal and non-maternal stages, presenting mean, SD, and minimum and maximum values. Fig. 1 shows the location of sleeping sites

	Mean	SD	Min.	Max.
Maternal	302.71	182.00	62.11	687.97
Non-maternal	250.89	168.00	62.06	612.58

3. RESULTS

3.1. Maternal sleeping sites

Over the span of 63 d, with a total of 38 locations, we identified 10 sleeping sites used by MJF01 and the pup. We confirmed, either by tracking and/or camera trap, that these sites were utilized for 48 nights. Two sleeping sites were categorized as burrows, 6 as tree hollows, and 2 as tree branches. Although tree hollows constituted 60% of all sleeping sites, the Kruskal-Wallis chi-squared test showed that the type of sleeping site did not statistically influence the duration of nights spent at each location (chi-squared = 0.030919, df = 2, p = 0.984)

All maternal sleeping sites were located in the forested areas. The characteristics of each site, along with a summary of key features, are listed in Table 3. In terms of tree hollow and tree branch characteristics, the heights of the trees varied significantly, ranging from 14.44 to 31.8 m (Table 3, Fig. 2). Diameter at breast height (DBH) ranged from 38.85 to 251.59 cm. Two-thirds of the hollows were located above ground level (Table 3, Fig. 2). The directions of the hollow openings varied, facing either up or down, indicating no specific preference by the pangolin. Eighty percent of the sleeping sites had vines around them. Regarding burrow utilization, both SS01 and SS09, located on the riverbank, had multiple entries, with the animal situated 1.2 m from the entry of SS01 and 2.2 m from SS09. Additionally, the width and height of the entries to the sleeping sites varied. SS09, a burrow, had the widest entry at 47 cm, while SS20, a tree hollow, had the tallest entry at 80 cm. In some instances, the same sleeping site was used for multiple consecutive nights, with duration ranging from a single night to a maximum of 10 nights (Table 3).

3.2. Activity pattern and relevant events

A total of 31 camera trap nights were analyzed. In 4 of 10 sleeping sites, we did not capture videos of either pangolin. Two of these sites were trees with many potential paths for climbing, which reduced the likelihood of successful camera placement on the ground. For the other 2 sites, cameras were not set up. From the remaining sites, although videos of the pangolins were not captured every night, 20 ATEs were recorded for MJF01 over 13 nights; this included instances when it went out both with and without the pup (Table 4). Additionally, 1 ATE was recorded exclusively for the pup. A total of 53 independent video records from camera traps were analyzed to determine the pangolin's activity pattern, which revealed a strictly nocturnal behavior by MJF01 during the maternal care period, with a peak of activity between 00:00 and 03:00 h (Fig. 3).

In 3 of the 5 occasions when MJF01 left the sleeping site alone, the pup ventured out by itself, albeit briefly, no longer than 2 min. The pup returned to the sleeping site alone a single time, 34 min before MJF01, marking the only time it was observed not clinging to the mother's tail upon return. Five days later, MJF01 was observed refusing to allow the pup to clasp to its back, and on 1 occasion when the pup did manage to mount it, they returned after only 2 min. The average TNA encompassing all records with and without the pup was 99 min (ranging from 3 to 251 min).

On the morning of 2 August, the pangolin pup was observed leaving and returning to the sleeping site alone (Fig. 4), active for 104 min. Although MJF01 was not recorded on video that day, tracking confirmed its presence at the same location the day before. The following day, MJF01 had moved to a new sleeping site, with video evidence from that night showing only MJF01 climbing the tree. After 4 August, no further videos of the pangolins were obtained, as MJF01 had moved to SS22, a challenging site for camera trap placement due to multiple access routes, as shown in Fig. 2. MJF01 remained at SS22 for 24 nights and shared the site with MJM02 for 6 continuous nights. On 27 August, MJF01 was observed arriving alone at the site. This last period was not considered part of the maternal care phase, as we could not confirm the presence of the pup with the mother during this time. It was categorized as a transition period and not included in the non-maternal analysis either. Thereafter, the mother was observed alone by the camera traps, marking the start of the non-maternal period. Throughout the studied maternal period, MJM02 was detected sharing the same sleeping site with MJF01 and the pup on 2 different occasions. Both adult pangolins were sympatric, as their home ranges overlapped. A comprehensive timeline summarizing the sleeping site usage and key behavioral events during the maternal period is shown in Fig. 5.

On 26 November 2023, MJF01 was recorded with a newly born pup, marking the end of the study period. The estimated birth date was between 1 and 15 November, based on MJF01's use of one of the maternal sleeping sites (SS17) during those 2 wk. From 15 to 26 November, MJF01 was tracked at 2 other previously used maternal dens, never staying for more

Table 3. Characteristics and measurement of sleeping sites used by a female pangolin with a pup. Total number of nights each sleeping site was utilized is based on the combination of very high frequency (VHF) tracking and a camera trap. The number of consecutive nights per occasion that the sleeping site was used is indicated in brackets. For sites with more than 1 entry, measurement was taken from the largest entry. The distance of the animal from the entry point was measured by precise triangulation of the pangolin tag location with a VHF high-gain antenna when it was in a burrow or tree hollow (with an error of around 20 cm) and/or by visual confirmation

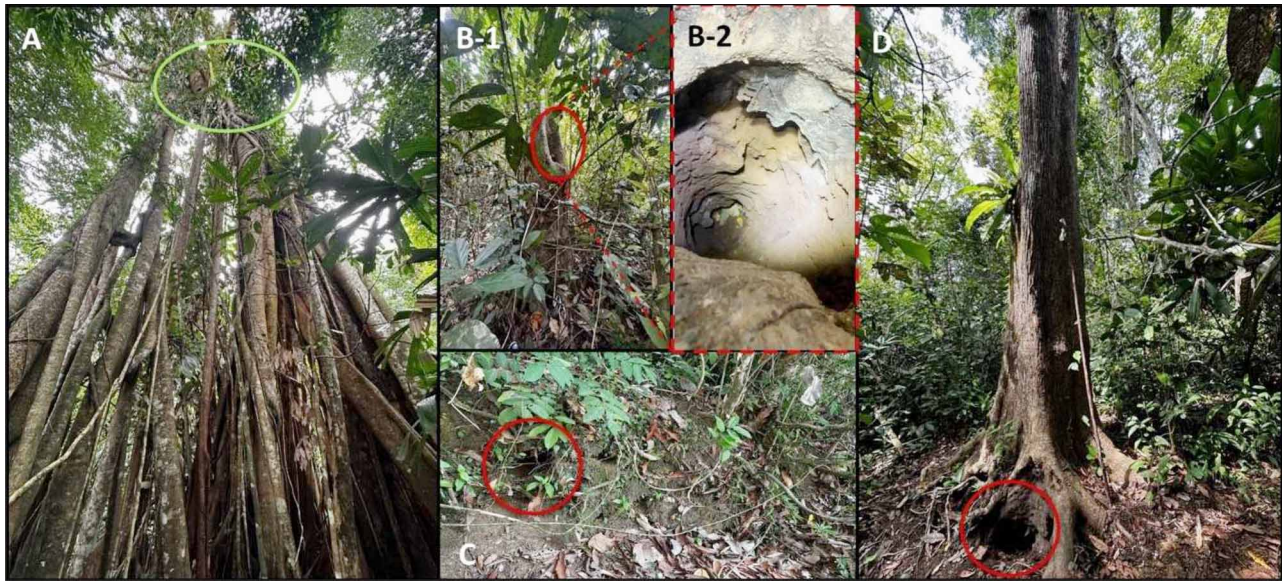| Sleeping site ID	Tree height (m)	Diameter at breast height (cm)	Height of the hollow (cm)	Direction of the hollow	No. of entries	Presence of vines	No. of vines	Distance of animal from entry point (cm)	Entry width (cm)	Entry height (cm)	Perimeter of tree at entry point (cm)	Location	Distance from river (m)	No. of nights
Tree hollow														
SS04	15.2	45.2	412	Down	1	Yes	3	200	15.24	50.8	129.54	Forest	16.2	6 (4 + 2)
SS17	19.2	83.12	0 (ground)	Down	1	No	0	78	22	22	360	Forest	28.15	12 (2 + 8 + 1 + 1)
SS20	19.65	64.65	0 (ground)	Up	1	Yes	1	–	26	80	26	Forest	19.33	1
SS22	31.8	251.59	1449	Up	Multiple	Yes	>10	1449	–	–	–	Forest	22.2	3 (1 + 1 + 1)
SS23	65.5	69.74	156	Down	1	Yes	3	156	20	25	210	Forest	70.57	1
SS15	17.85	38.85	181	Down	1	Yes	4	181	18	38.5	125	Forest	14.51	2
Mean	21.37	92.19	366	–	–	–	–	412.8	20.25	43.26	170.11	–	28.49	4.17
SD	5.94	79.76	552	–	–	–	–	581.11	4.07	23.53	124.6	–	21.17	4.26
Tree branch														
SS03	19.65	50.96	–	Up	–	Yes	6	–	–	–	–	Forest	17.8	12 (10 + 1 + 1)
SS07	14.44	60.83	–	Up	–	Yes	3	–	–	–	–	Forest	13.52	1
Mean	17.05	55.9	–	–	–	–	4.5	–	–	–	–	–	15.66	6.5
SD	3.68	6.98	–	–	–	–	2.12	–	–	–	–	–	3.03	7.78
Burrow														
SS09	–	–	–	–	2	Yes	–	220	47	37	–	Forest	10.65	9 (8 + 1)
SS01	–	–	–	–	>3	No	–	120	19	18	–	Forest	9.06	1
Mean	–	–	–	–	–	–	–	170	33	27.5	–	–	9.86	5
SD	–	–	–	–	–	–	–	70.71	19.8	13.44	–	–	1.12	5.66

Fig. 2. Maternal sleeping sites, with red circles indicating the main entrances. (A) SS22: tree hollows at the top of a *Ficus* tree (green circle), surrounded by many trees and vines connecting to the hollow. (B-1, B-2) SS23: tree hollow oriented downwards (B-1), and view from the entrance looking down (B-2). (C) SS09: burrow showing the main entrance. (D) SS17: one of the most frequently used sites, featuring a tree hollow with an entrance at ground level

Table 4. Summary of the measured camera trap events, including active time event (ATE) and total nightly activity (TNA). Detailed descriptions are provided for each indicator, along with the corresponding number of records and statistical results (mean ± SE; minimum—maximum times in brackets)

	Description	No. of records	Time (min)
ATE	Length of an ATE (measured in min) from the first video appearance of the pangolin as it exits the sleeping site until it re-enters the same sleeping site; more than 1 ATE can occur per night	MJF01 overall (with and without pup): 20 Only MJF01 (without pup): 5 MJF01 with pup: 15 Only pup: 1	64.35 ± 13.64 (2—234) 111.2 ± 33.48 (47—234) 48.73 ± 12.67 (33—170) 104
TNA	Calculated as the sum of all ATEs occurring in a night; at least 1 ATE has to occur per night to obtain the TNA for that night	13 nights	MJF01 overall: 99 ± 17.11 (33—251)

than 3 consecutive days. On 30 October, MJF01 was observed on video moving between sites without a pup. Based on the dates when MJF01 shared the same sleeping site with MJM02 and the estimated birth date, the gestation period was calculated to be between 63 d (minimum) and 165 d (maximum). The time the female was without a pup ranged between 57 and 96 d. Additionally, throughout the study time (176 d), we did not observe any physical harm or movement impediment caused by the tag on MJF01. Similarly, there was no evidence to suggest that the tag impeded the pup's ability to clasp onto its mother's back (Fig. 4).

3.3. Home range and sleeping site differences between maternal and non-maternal period

The high autocorrelation of the location points indicates a high probability that KDE estimates are misrepresentative and thus are provided for reference only (see Table 6). Due to the absence of movement data, our goal was not to provide detailed habitat utilization but rather to estimate the area needed to find suitable sleeping sites. For the maternal period, the 100% MCP (total area) and 50% MCP (core area) yielded areas of 7.63 and 0.63 ha, respectively. During the non-maternal period, the 100% MCP increased to
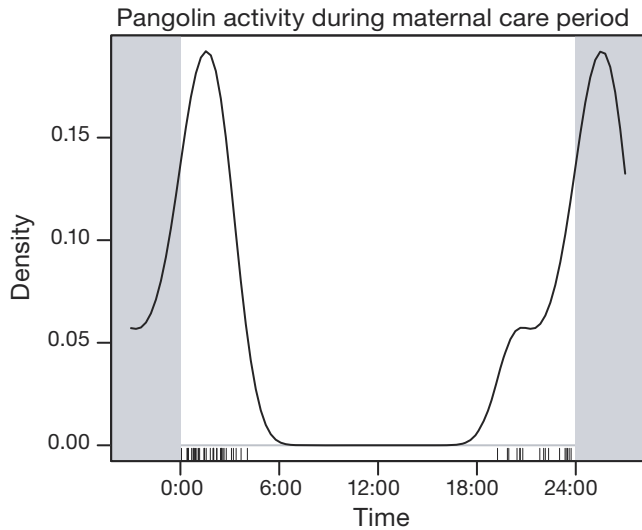
Fig. 3. Activity pattern of a wild female Sunda pangolin during maternal care, based on video records from camera traps placed at sleeping sites. Black lines at the bottom represent each detection event. Density: relative likelihood of an activity event at a given time (probability density of activity events). A total of 53 independent events were recorded over 31 trap nights

9.58 ha and the 50% MCP to 1.16 ha. The Wilcoxon rank sum test indicated that MCP home ranges calculated between 50 and 100% were consistently smaller during the maternal phase (W = 19, p = 0.006, Fig. 1).

The analysis indicated that MJF01 sleeping sites were located exclusively in forested areas during the maternal period, as shown in Fig. 1. During the non-maternal period, MJF01 utilized the oil palm plantation, occupying oil palm trees on 2 different occasions, and another new sleeping site, labelled as other, corresponding to a fallen bamboo area on the plantation border. Fisher's exact test showed a significant effect of location between maternal and non-maternal periods (p = 0.03). Only 1 site (SS20) was utilized in both phases. A comparison of sleeping site types and number of days each type was used in both periods is shown in Fig. 6. The maximum number of consecutives days spent in the same sleeping site during the non-maternal period was 8 d, with a minimum of 1 d. Table 5 shows the mean and SD of the number of consecutive nights each sleeping site was utilized and
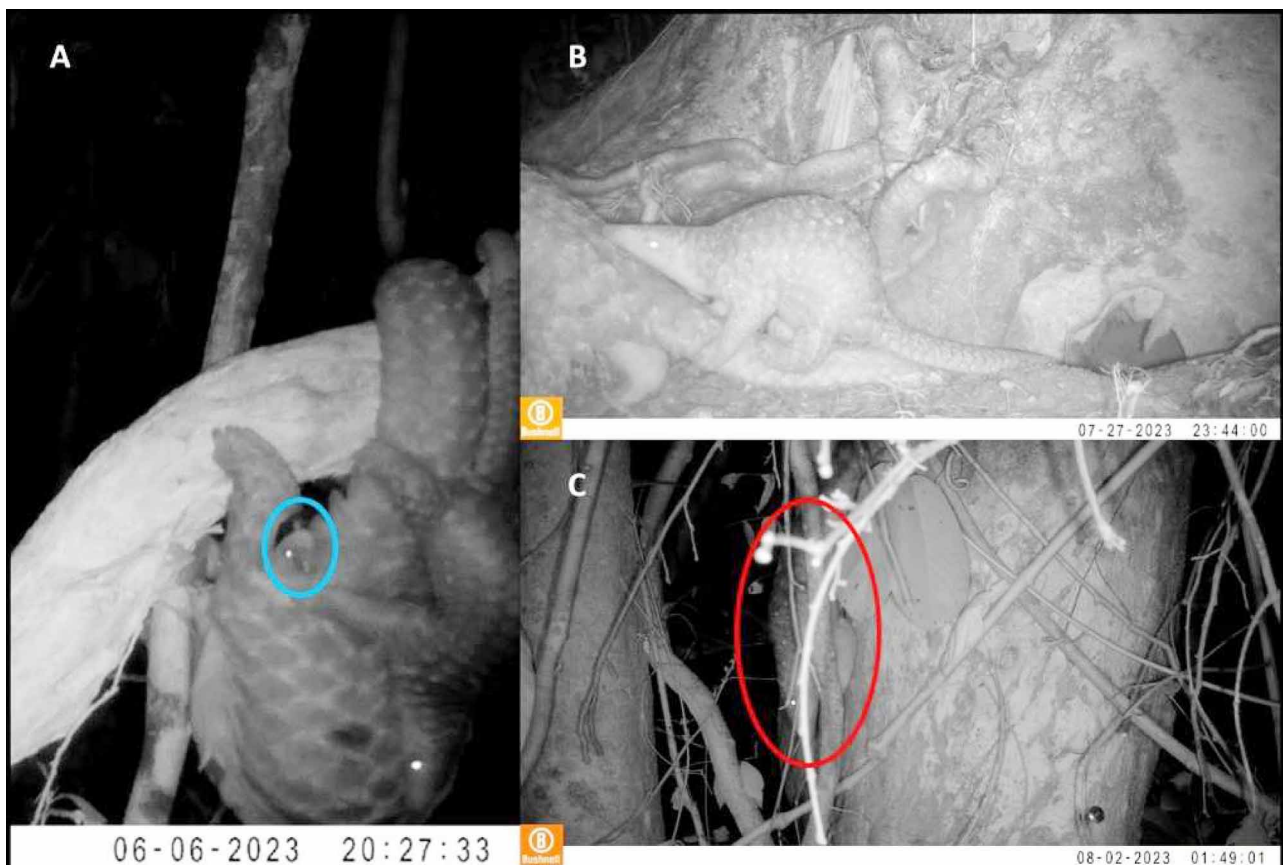

Fig. 4. Photographic evidence of the pup's growth over time, captured from video recordings. (A) Image taken 3 d after capture, showing the VHF tag attachment (blue circle), which does not interfere with the pup's ability to cling to the mother. (B) Image taken almost 2 mo after capture, showing a noticeable size increase of the pup compared to (A). (C) Image of the pup (red circle) climbing down independently
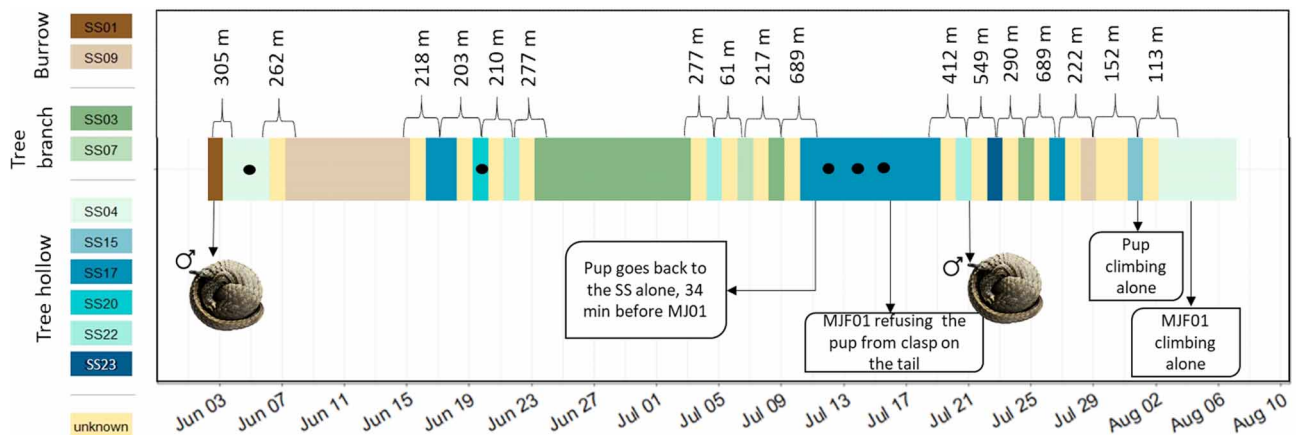
Fig. 5. Summary of the sleeping site utilization timeline between June and August 2023, distances between consecutive sleeping sites (SS), and notable behavioral events. The male pangolin icon indicates occasions when MJM02 shared a sleeping site with MJF01 and its pup. The black point indicates instances when MJF01 left the sleeping site alone. Unknown sleeping site refers to periods when no very high frequency tracking was performed, and sleeping site usage could not be identified by camera traps
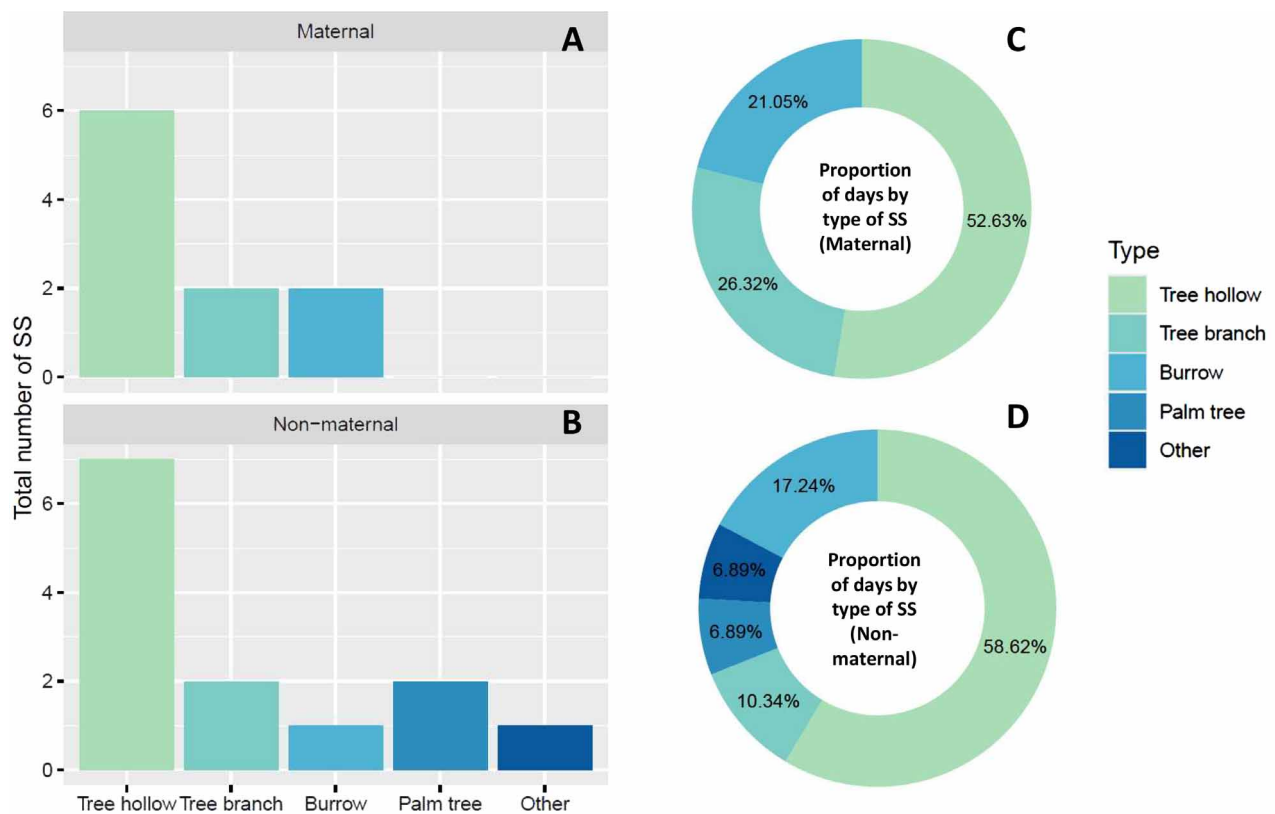

Fig. 6. (A,B) Total number of sleeping sites (SS), categorized by type, during (A) maternal and (B) non-maternal periods. (C,D) Proportion of days each type of sleeping site was used within (C) maternal and (D) non-maternal periods based only on VHF points obtained

the reuse rates. Fisher's exact test indicated no statistical association regarding sleeping site type during maternal and non-maternal periods (p = 0.098).

Statistical differences, by the Wilcoxon rank sum Ftest, were detected in sleeping site selection between maternal and non-maternal periods regarding distance to the oil palm plantation ($W = 710$, p = 0.044) and the river ($W = 301$, p = 0.001). The mean distance to the plantation was greater during the maternal period than during the non-maternal period. Conversely, the

Table 5. Mean and SD of the consecutive numbers of nights spent at each type of sleeping site. Independent times used refers to the number of times each type of site was used, excluding consecutive nights. The reuse rate refers to the same site being used on more than 2 occasions

Sleeping site type	Maternal			Non-maternal		
	Independent times used	Continuous nights Mean	SD	Independent times used	Continuous nights Mean	SD
Tree hollow	12	2.08	2.07	12	1.83	1.34
Tree branch	4	3.25	4.50	2	2	1.41
Burrow	3	3.33	4.04	1	8	—
Palm tree	—	—	—	2	1	0
Other	—	—	—	1	3	—
Total reuse rate (%)	50			46.15		

mean distance to the main river was shorter during the maternal period. Additionally, the mean distance between consecutive sleeping sites was not statistically different between periods according to the Wilcoxon rank sum test ($W = 177$, p = 0.27).

4. DISCUSSION

Sunda pangolins face intense population decline, requiring a deeper understanding of their ecology for effective conservation efforts (Chong et al. 2020). We provided insights on wild maternal behavior and sleeping site selection during the maternal and non-maternal stages in an anthropogenically affected habitat. Although the data correspond to a single individual, this represents the first comprehensive study of this species in Borneo, particularly within a fragmented landscape impacted by oil palm plantations. Despite the adaptability of pangolins to fragmented and degraded habitats (Chin & Pantel 2009), detailed knowledge about their survival strategies, including how they navigate and thrive in plantation environments, remains limited. This single case study serves as a benchmark to enhance our understanding of the species' reproductive ecology within such habitats, even though it is not sufficient to generalize the findings to the whole species, as different contexts and factors can influence individual behaviors. Studying multiple individuals across different landscapes will enhance our understanding of how reproductive ecology varies under different environmental conditions.

Attaching tracking devices to animals can impact their movements and cause injuries, such as the loss of scales or becoming trapped inside a hollow due to the tag preventing the pangolin from fitting through the entrance (Sun et al. 2019, Panjang 2023). We minimize these complications by ensuring that the tag was lightweight (<0.5% of MJF01 body weight) and that the attachment allowed for tag mobility along with the animal (fabric strap between scale and tag). We also observed, via camera trap, that the tag did not impede movements, and the animal was regularly monitored in the field.

Although GPS technology can provide detailed information of movements by attaining several points per day with minimal human effort, it lacks the precision that VHF trackers offer and may not be useful for establishing resting places of fossorial species (Skupien et al. 2016). VHF tags are capable of accurately pinpointing locations, allowing researchers to understand environmental factors influencing den selection and to confirm site fidelity to dens. Some limitations include the significant labor required to gather data points and the risk of disturbing the animal's natural behaviors during active periods by the presence of researchers (Lim & Ng 2008). Combining both tools will be beneficial for a better understanding of pangolin ecology and fine-scale habitat use. In addition, incorporating new technologies, such as VHF drones, could enhance tracking efficiency (Saunders et al. 2022).

We have, for the first time, documented a wild female and wild male Sunda pangolin sharing sleeping sites on more than 1 occasion during the nursing period. Similar observations have been reported in the African Cape pangolin *Smutsia temminckii* and Chinese pangolin *Manis pentadactyla* and were associated with mating behavior (Heath & Coulson 1997, Sun et al. 2021). Successful breeding requires multiple mounting attempts, as repeated copulation may induce ovulation in Sunda pangolins (Zhang et al. 2020, Yan et al. 2021, 2023); thus, cohabitation can increase mating success. Although mating aggression has been observed in captive Sunda pangolins (Zhang

et al. 2020, Ngau et al. 2021, Yan et al. 2023), we found no evident injuries to MJF01, the pup, or MJM02 after sharing sleeping sites, similar to findings by Sun et al. (2021) in Chinese pangolins. It is hypothesized that female pangolins may be receptive to mating during maternal care as a protective strategy for their pups, potentially redirecting male aggression towards reproductive activities and reducing the risk of hostility towards the young. This aligns with the hypothesis that male infanticide may occur to bring the female back into estrus sooner (Agrell et al. 1998). In Chinese, white-bellied *Phataginus tricuspis*, and black-bellied *P. tetradactyla* pangolins, postpartum estrus has been described and conception during nursing corroborated (Gudehus et al. 2020, Jansen et al. 2020, Sun et al. 2021, Arora et al. 2023). Furthermore, the occurrence of births in both April and early November (dry and wet season, respectively, in Sabah) within the same year evidenced that wild Sunda pangolins breed throughout the year and indicates a non-seasonal reproductive pattern, which aligns with previous postulations (Lim & Ng 2008, Zhang et al. 2017, Yan et al. 2023). The brief period without a pup suggests that Sunda pangolins can give birth more than once per year in the wild, likely facilitated by mating while still caring for a pup. Although paternity cannot be confirmed, it is likely that MJF01 became pregnant either while nursing the first pup or shortly after it was weaned, possibly during one of the encounters with MJM02 in the sleeping site. Given that captive records show mating occurs during cohabitation and that the gestation period is around 5 to 6 mo (Zhang et al. 2015, 2017, 2020, Ngau et al. 2021, Yan et al. 2021, 2023), we estimate that conception most likely occurred during the first encounter, providing a gestation period of approximately 151 to 165 d. Delayed implantation in Chinese and white-bellied pangolins may explain variations in gestation periods published for these species (Jansen et al. 2020, Sun et al. 2021, Arora et al. 2023). In this context, it is possible that conception occurred before the monitoring period, although this phenomenon is not yet documented for Sunda pangolins.

At the time of capture, the pup was estimated to be between 2 and 2.5 mo old based on weight and size data from captive pangolins (Nguyen et al. 2010). It became independent from its mother approximately 62 d later, placing weaning age at 4 to 5 mo, consistent with findings from previous studies on captive pangolins (Lim & Ng 2008, Nguyen et al. 2010, Zhang et al. 2015, Cabana et al. 2019). However, incorrect estimation of age is still possible, as the weaning weight of hand-reared Sunda pangolins is reported to be lower than that of those raised by their mothers (Cabana et al. 2019), and the reference data for the species do not always clarify whether the pup was mother reared or not. For Chinese pangolins, wild pups have a higher growth rate than hand-reared pangolins (Sun et al. 2018), yet pups raised by their mothers in captivity had higher growth rates than the wild counterparts, likely related to the higher proportion of carbohydrates in the artificial diets of the captive mothers (Sun et al. 2024). Yan et al. (2022) reported that mother-raised captive Sunda pangolin pups take about 100 d to reach 1 kg; however, no comparisons have been made with wild pups.

Although Gray et al. (2023) and Lim & Ng (2008) documented some daytime pangolin activity in Singapore and Vietnam, these instances were rare. Our own observations, which recorded no daytime activity through camera traps, support the overall consensus of primarily nocturnal behavior (Lim & Ng 2008, Gray et al. 2023, Panjang 2023). The inactive period from 06:00 to 18:00 h is likely associated with resting or remaining within the den during daylight hours. The majority of the ATEs recorded involved the mother and pup, with a mean duration of activity considerably lower (mean ± SE: 48.73 ± 12.67 min) compared to the findings of Lim & Ng (2008), who reported a mean (±SE) duration of activity of 127 ± 13.1 min. Meanwhile, when MJF01 ventured out alone, the mean duration of activity was more than double, and it always involved a tree hollow with only 1 entrance (SS04, SS17). These differences in ATEs may be attributed to protective behavior, suggesting that by reducing time spent outside, the risk of predation is minimized. Alternatively, it could be due to the physical burden of carrying the pup, which may limit the duration the mother can travel. Tree hollows also provided a secure refuge for the pup in the absence of the mother. Further, MJF01 was commonly observed carrying the pup while entering sleeping sites or exiting for foraging, in contrast to the only 5 occasions reported by Lim et al. (2008) and unlike wild Chinese pangolins that only exhibited this behavior while changing burrows (Sun et al. 2018). In some observations at the den's entrance, the pup was seen exploring independently next to MJF01. This suggests that while it may be safer for the pup to cling to the mother during transportation, it can also engage in some autonomous activity as it grows older. Moreover, the pup was observed to return to the sleeping site approximately 30 min before MJF01 on 1 occasion, demonstrating a degree of independent activity. However, it is unknown whether the pup walked independently during foraging or remained clinging to MJF01, as we

were unable to collect data during their active periods without disturbing the animals and potentially interfering with their natural behavior. Sun et al. (2018) described independent behavior outside the burrow in Chinese pangolins from 15 wk of age. Zhang et al. (2015) observed that in captivity, pangolin pups begin to gain independence from their mothers once they start feeding on their own, achieving complete separation after weaning. In the wild, the beginning of independence could involve the pup starting to feed by itself next to the mother and gradually increasing the frequency of these independent feeding events.

Zhang et al. (2017) observed wrestling behavior between a captive infant pangolin and its mother before the age of 4 mo. Although we did not record wrestling behavior, we observed MJF01 refusing to let the pup cling to its back by mid-July, possibly due to the increased size and weight of the pup, as shown in Fig. 4. Zhang et al. (2015) also reported a mother's reluctance to carry its pup during the weaning period. After this event, all mother–pup activities lasted less than 35 min, while MJF01's solo activities exceeded 200 min, and the frequency of sleeping site changes increased, suggesting greater mobility. Additionally, 2 wk later, the pup was observed climbing alone. These observations suggest that by the fourth month, the pup was nearing weaning age, with the mother showing increased reluctance to provide care. In the following transition period, MJF01 remained in the same location for 24 nights, though the pup's presence could not be confirmed. It seems likely that the pup maintained some level of contact with MJF01, experiencing a form of soft release, wherein it could accompany the mother, honing its climbing and foraging skills while gradually becoming more independent. This aligns with findings by Lim & Ng (2008), who documented continuous den usage by the mother and pup for 24 d towards the end of the maternal care period, during which the pup often triggered the camera traps on its own, supporting the notion of a soft release. Unfortunately, the complexity of the sleeping site, comprised of multiple vines and a convergence of several trees forming numerous hollows, made camera trap placement extremely difficult, resulting in no photographic evidence of the pangolins.

The home ranges obtained are based on sleeping site locations only, generating a high rate of autocorrelation, as refuge sites are normally reused (Row & Blouin-Demers 2006). KDE estimations are sensitive to aggregation and to bandwidth selection, which can make comparison between different studies ineffective (Hemson et al. 2005, Row & Blouin-Demers 2006).

Larger dataset size and long-term sampling are needed to better assess autocorrelated data (Fleming et al. 2015). KDE estimations tend to generate higher utilization distributions in sites where dens are clustered, potentially neglecting other used areas. In our study, KDEs also overrepresented regions like the river (not utilized by the tracked animal) when the sleeping sites were near the riverbank. MCP estimations better represent resting home ranges as the total area needed to find refuge and also allow comparison with previous studies.

The maternal home range shows insignificant variation between the 60 and 95% MCP estimates. The discrepancy between the 100 and 95% MCP estimates during the maternal period is attributed to the configuration of the study area (Fig. 1), where one of the sleeping sites was located at the upper range limit, adjacent to a bend in the river. This may have led to an overestimation of the home range by including areas the animal likely does not use. A home range of 1.35 ha (95% MCP) offers a more accurate and stable estimate. However, it is important to note that our data set is limited to sleeping sites and does not account for the pangolin's movements during active periods. Nonetheless, Lim & Ng (2008) found that locations obtained during active periods were situated within the maternal den area, suggesting that the mother tends to stay close to the dens while caring for the pup. Additionally, dens are expected to be near food sources during nursing periods to minimize travel and save energy (Sun et al. 2021); thus, our home range estimates should reflect the overall area used during the maternal stage. The relatively smaller home range that we observed, compared to the limited data available on female Sunda pangolins (Lim & Ng 2008, Gray et al. 2023, Panjang 2023) (Table 6), may be attributed to factors such as food availability (Sun et al. 2021) and forest size. Our direct observations indicate abundant ants and termites in the study area, potentially reducing MJF01's need to travel far in search of food. In addition, the smaller home range may also reflect the limited forest space of the study area, a pattern observed by Gray et al. (2023). Furthermore, the larger home ranges in the studies by Gray et al. (2023) and Panjang (2023) may be partly due to the inclusion of relocated pangolins, where exploratory behavior likely resulted in overestimated home ranges as the animals adjusted to their new environments. During the maternal period, the 100 and 50% MCP home ranges were approximately 20 and 45% smaller, respectively, than during the non-maternal phase, confirming that the area used during maternal periods is reduced. The mean distance be-

Table 6. Summary of available data on female Sunda pangolins home ranges, including data from the current study. The data are separated by reproductive status (maternal or non-maternal) and pangolin category (wild or relocated). MCP: minimum convex polygon; KDE: kernel density estimation; NA: not available; wAKDE: weighted autocorrelated kernel density estimator

Study area	Female status	No. of individuals/ relocation points	Home range estimator (ha)				
			MCP 100%	MCP 95%	MCP 50%	KDE 95%	KDE 50%
Singapore (Lim & Ng 2008)	Wild maternal	1/3 dens over 63 d	6.97	5.63	NA	NA	NA
Vietnam (Gray et al. 2023)	Relocated [a] non-materna	4/min.: 17 max.: 51	NA	NA	NA	168 ± 26 (stable dataset only) wAKDE[b]	76 ± 56 (stable dataset only) wAKDE[b]
Sabah, Malaysian Borneo (Panjang 2023)	Wild non-maternal	1/93	69.1	40.5	18.3	130.2	28.9
Sabah, Malaysian Borneo (Panjang 2023)	Relocated non-maternal[a]	3/min.: 12 max.: 67	1037.9	969.2	393.1	7691	2033
Sabah, Malaysian Borneo (current study)	Wild maternal	1/38	7.63	1.35	0.63	128.25	33.65
Sabah, Malaysian Borneo (current study)	Wild non-maternal	1/29	9.58	8.8	1.16	57.5	13.04

[a]Pangolins that were rescued and later released in new areas
[b]Used instead of KDE

tween sleeping sites during both phases was similar, but the difference in home ranges suggests that females with pups may be restricted to locations offering more suitable refuge. For Chinese pangolins, maternal burrow selection is influenced by familiarity of the environment (Sun et al. 2021). Continued landscape changes, which reduce the availability of adequate nursing dens and food sources, may not only decrease reproduction rates but could also lead to negative outcomes for the mother and pup. Additionally, a statistical comparison of sleeping sites during maternal and non-maternal periods indicates that the factors influencing sleeping site selection are the distances to the plantation and to the river and the location of the site. None of the sleeping sites during the maternal period were in or near the plantation. Instead, all were relatively close to the main river (range: 9.06–70.57 m), with the farthest located in the broadest part of the buffer zone. Given that the study site is a narrow forest strip, this does not necessarily indicate a preference for proximity to the river. Rather, it is likely reflecting that the river represents the farthest point from the plantations. During the non-maternal period, MJF01 utilized the plantation area, sleeping in oil palm trees on 2 occasions and using an area under fallen bamboo at the plantation's border. However, MJF01's decision to avoid seeking refuge in the plantation during the maternal period, despite its proximity, suggests that this area is not

considered suitable for the pup. Potential threats such as humans and domestic dogs, as well as the openness of the area, might deter the mother from using it. Sleeping atop oil palm trees also presents additional risks due to increased exposure. This underscores the critical importance of forested areas during the nursing stage. While oil palm plantations can provide a food source and even shelter for some pangolins, the threats appear to be too significant for female pangolins with pups to seek refuge there.

The only previous record of a maternal home range in Sunda pangolins was reported by Lim & Ng (2008), with a home range of 6.97 ha (100% MCP). They observed a female pangolin and its pup on an island in Singapore for 65 d, using only 3 natal dens. The pangolins typically stayed in each den for less than 10 consecutive days, except for 1 instance where they remained for 24 nights. Lim & Ng (2008) also noted a higher reuse rate of dens by females compared to males in the area. Similarly, we found that females reuse certain sites multiple times, but we also observed instances of single use. However, due to the lack of daily tracking, what appears as single-night use might represent 2 nights. In contrast, our study recorded MJF01 using 10 different sites while nursing, with the longest consecutive stay at a single site being 10 nights; this may be due to differences in den availability between the 2 study sites. Despite this, the similar reuse rate of sleeping sites by MJF01 during

maternal and non-maternal periods (Table 5) suggests that this behavior is not exclusive to the maternal phase, demonstrating site fidelity by the female. However, longer continuous intervals of reuse were observed during the maternal period, contrasting with the lower reuse rate of sleeping sites observed in MJM02 in the same area (~38%). Our observations, those by Lim & Ng (2008), and interviews reported by Newton et al. (2008) all suggest that females and their pups use a limited number of maternal dens regularly rather than constantly moving between locations. Further, our study suggests that MJF01 preferred hollows and burrows that limited visibility from the entrance. This contrasts with MJM02 in the same area, which used sleeping sites regardless of depth and visibility. Additionally, when tree branches were used, the animal could not be seen from the ground due to the dense foliage and vines in the selected tree. Conversely, during the non-maternal phase, the female was visible from the outside on several occasions. Although no statistical differences could be calculated for the variables measured at each maternal sleeping site due to the limited dataset, certain tendencies were observed. Tree hollows were used more frequently (52.63% of the time) than burrows or branches, with certain sites showing higher fidelity. All sleeping sites involving trees had vines around them, likely indicating a preference for more concealed sites or easier climbing. All trees had a DBH greater than 38 cm, emphasizing the importance of mature forests for suitable sleeping sites. While no statistical difference was observed in the type of sleeping sites between maternal and non-maternal phases, tree hollows remained the most frequently used sites in both periods, supporting previous observations by Lim & Ng (2008) and Panjang (2023). Based on our results, we suggest that artificial maternal burrows provided in captivity should be deep to minimize visibility from the outside. If enclosures are too small to accommodate long burrows, dens with upper entrances could be implemented, or natural materials could be used to conceal the entrances of shorter dens.

Panjang (2023) reported that a single female pangolin without a pup had a home range estimated 7 times greater than that of MJF01 during the non-maternal period. The shorter tracking duration in our study may have influenced these estimation differences. Nonetheless, this discrepancy could also be attributed to the fact that our study area consisted of a narrow forest strip bordering an oil palm plantation. Although MJF01 was mostly recorded sleeping in the forest, this does not imply that it did not utilize the

plantation to feed. Therefore, the home range for MJF01 might be underestimated compared to the wild female reported by Panjang (2023) that was tracked in a larger forest patch without direct borders to an oil palm plantation. This distinction suggests that while the female from Panjang (2023) could find both refuge and food throughout its expansive range, our observed pangolin might have foraged in nearby oil palm plantations and then returned to the forest for refuge, emphasizing the importance of forest existing near fragmented landscapes.

By identifying female den selection, we can help to prioritize habitat protection efforts, as den availability can affect species persistence by influencing reproductive parameters. Conservation strategies should focus on maintaining areas with suitable denning conditions, ideally mature forests with large trees, and sufficient food availability so the mothers can avoid excessive movement and elude natural and human predation. Considering the continued habitat fragmentation, we highlight the conservation implication of preserving natural habitats around disturbed landscapes and establishing suitable wildlife corridors that support safe movement of the species while also targeting anti-poaching efforts in these areas. In light of the current threats faced by pangolins, ecological studies are vital for protecting these populations in their natural habitats, especially as efforts to combat the pangolin trade continue.

5. CONCLUSION

We documented the first comprehensive record of a wild female Sunda pangolin from one maternal period to the next. Our findings suggest that Sunda pangolins can breed year-round and that male pangolins can share sleeping sites with females and their pups without necessarily posing a threat to the offspring. Consequently, wild Sunda pangolins may give birth more than once per year. The activity pattern of MJF01 during the maternal period was strictly nocturnal, with less than 2 h spent outside the den with the pup each night, though this duration increased when MJF01 ventured out alone. Maternal dens were mainly tree hollows, although burrows and tree branches were also utilized, and nearly all sleeping sites were concealed and covered with vines. These observations offer insights for enhancing captive breeding efforts by describing natural maternal dens that can be mimicked in captivity, potentially supporting better den design and maternal care management. Additionally, our findings suggest that captive

births could occur twice a year under optimal conditions. Furthermore, they provide wild references for gestation period, weaning age, and maternal behavior. According to our study results, home ranges during the maternal period were consistently smaller than during the non-maternal phase and only included forested areas, highlighting the critical role of mature forests for reproductive success in modified landscapes. Lastly, VHF studies can inform conservation efforts by identifying specific denning habitats that need to be protected. Future research in the reproductive ecology of the species should focus on increasing the wild sample size to standardize parameters as well as examining growth and recruitment rates, age at sexual maturity, dispersal of young, and population demography across different locations.

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