Camera trap data reveal the habitat associations, activity patterns and population density of Indian pangolin (*Manis crassicaudata*) in Maduru Oya National Park, Sri Lanka

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Abstract
*Camera trap data reveal the habitat associations, activity patterns and population density of Indian pangolin (*Manis crassicaudata*) in Maduru Oya National Park, Sri Lanka.* The Indian pangolin (*Manis crassicaudata*) is a solitary, medium–sized mammal native to South Asia. In this study we used camera trap data recorded during a meso–mammal survey conducted from January 2019 to January 2021 to assess the occupancy, habitat associations, population density and activity patterns of Indian pangolins in Maduru Oya National Park (MONP), Sri Lanka. The preferred habitat of the species was dry–mixed forest with an occupancy probability of 0.42 ± 0.19. Occupancy modeling revealed the association of the species with the forested habitats of the park with rich canopy cover, high NDVI scores and abundant termite mounds. Activity of this pangolin was highly nocturnal, reaching a peak after midnight. We observed a considerable spatiotemporal overlap in Indian pangolin activity and human activity, possibly increasing hunting pressure on the species. We estimated occupancy and abundance–based population density (0.73 ± 0.21 indiv./km^2) using the random encounter model for the first time in the study area. These findings could be useful for conservation and management decisions concerning the survival and vital habitats of one of the most trafficked mammals in the world, the Indian pangolin.

Key words: Indian pangolin, Activity patterns, Habitat associations, Population density, Distribution modeling, Occupancy modeling

Resumen
*Los datos obtenidos con cámaras de trampeo revelan la asociación con los hábitats, las pautas de actividad y la densidad de población del pangolín indio (*Manis crassicaudata*) en parque nacional Maduru Oya, en Sri Lanka*. El pangolín indio (*Manis crassicaudata*) es un mamífero solitario de talla media nativo de Asia meridional. En el presente estudio utilizamos datos obtenidos mediante cámaras de trampeo durante un estudio sobre mesomamíferos realizado entre enero de 2019 y enero de 2021, con la finalidad de evaluar la ocupación, la asociación con los hábitats, la densidad de población y las pautas de actividad del pangolín indio en el parque nacional Maduru Oya, en Sri Lanka. El hábitat preferido de la especie fue el bosque mixto–seco con una probabilidad de ocupación de 0,42 ± 0,19. Los modelos de ocupación revelaron la asociación de la especie con los hábitats forestales del parque dotados de una cubierta de dosel abundante, un elevado índice normalizado diferencial de la vegetación y gran cantidad de termiteros. La actividad del pangolín indio fue predominantemente nocturna y alcanzó su máximo después de la medianoche. Observamos una superposición espaciotemporal considerable de la actividad del pangolín indio con la actividad humana, lo que puede crear una cierta presión cinegética sobre la especie. La ocupación de la especie y su densidad de población basada en la abundancia (0,73 ± 0,21 indiv./km^2) se obtuvieron siguiendo el modelo de encuentro aleatorio por primera vez en la zona de estudio. Los resultados de este estudio serán de utilidad para tomar decisiones relativas a la conservación y la gestión de uno de los mamíferos silvestres con los que más se trafica en el mundo (el pangolín indio) y los hábitats vitales para su supervivencia.

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Introduction

Pangolins, also known as scaly anteaters, are elongated amour–plated insectivores with a long tongue and no teeth (Atkins, 2004; Mahmood et al., 2020). Currently, eight extant pangolin species can be found throughout the world (Khwaja et al., 2019; Mahmood et al., 2019). The Indian pangolin, or thick–tailed pangolin (*Manis crassicaudata*) (fig. 1), is the only pangolin species recorded in Sri Lanka (Perera and Karawita, 2020); it is also native to South Asia. These pangolins are medium–sized, solitary, elusive, predominantly nocturnal mammals that belong to the family Manidae and order Pholidota (Mahmood et al., 2020; Perera and Karawita, 2020).

The Indian pangolin lives in a variety of natural environments, ranging from evergreen forests, deciduous forests, open scrublands, and grasslands to human–modified habitats such as urban cultivations and semi–arid areas (Mahmood et al., 2015, 2020, 2021a). Numbers of Indian pangolin, however, are thought to be falling across its range (Mahmood et al., 2021b). Pangolin scales, flesh, and other derivatives are in high demand in East Asian markets, making them one of the most trafficked wild mammals on the planet (Challender et al., 2015; Aditya et al., 2021). As a result, the Convention on International Trade in Endangered Species currently lists all eight pangolin species in Appendix I (CITES, 2021). In recognition of the threats and declining population trends of the species, the International Union for the Conservation of Nature (IUCN) has classified the Indian pangolin as globally Endangered (Mahmood et al., 2021b) and 'Near Threatened' in the National Red List of Sri Lanka (Weerakoon, 2012). The species has been strictly protected under the Flora and Fauna Protection Ordinance (amendment) Act No. 22 of 2009 of Sri Lanka (Perera and Karawita, 2020).

Recent studies on the species in Sri Lanka have investigated the island–wide distribution and threats based on primary (direct field data) and secondary (community science) data (Perera et al., 2017; Karawita and Perera, 2020; Perera and Karawita, 2020; Perera et al., 2022). However, research to generate primary data for this species has only been conducted in a few localities such as Yagirala, Wilpattu and Yala (Karawita et al., 2016, 2018; Perera and Karawita, 2020; Perera et al., 2022). Furthermore, except for Yagirala (wet lowland forest), long–term and continuous field–based data are lacking for the species, which in Sri Lanka is mostly distributed in the lowland forest habitats (Perera and Karawita, 2020). A few studies in the wet zone forests of Sri Lanka have been carried out to investigate the wild population densities, habitat associations and behavior of Indian pangolin in natural habitats (Perera et al., 2017; Karawita et al., 2018, 2020; Perera et al., 2022). The occurrence of this species in dry zone habitats of Sri Lanka has been identified (Karawita and Perera, 2020; Perera and Karawita, 2020). Hence, this study aimed to bridge the gap in knowledge regarding occupancy, habitat associations, population density and activity patterns of Indian pangolin in an important dry zone locality for the species; Maduru Oya National Park (MONP).

Wildlife crimes associated with the species are high in some dry zone areas, including the MONP (Perera and Karawita, 2020). A rising trend in such crimes has been observed in the forms of hunting for subsistence, live capture for sale as meat, and hunting for scales (Perera and Karawita, 2020). MONP is known for the occurrence of Indian pangolin and also for a considerable level of associated wildlife crimes (Karawita and Perera, 2020). Therefore, we also investigated the level of human presence associated with the occupancy of the Indian pangolin within MONP during our study.

Fig. 1. An Indian pangolin captured on a camera trap.

Fig. 1. Un pangolín indio captado con una cámara de trampeo.

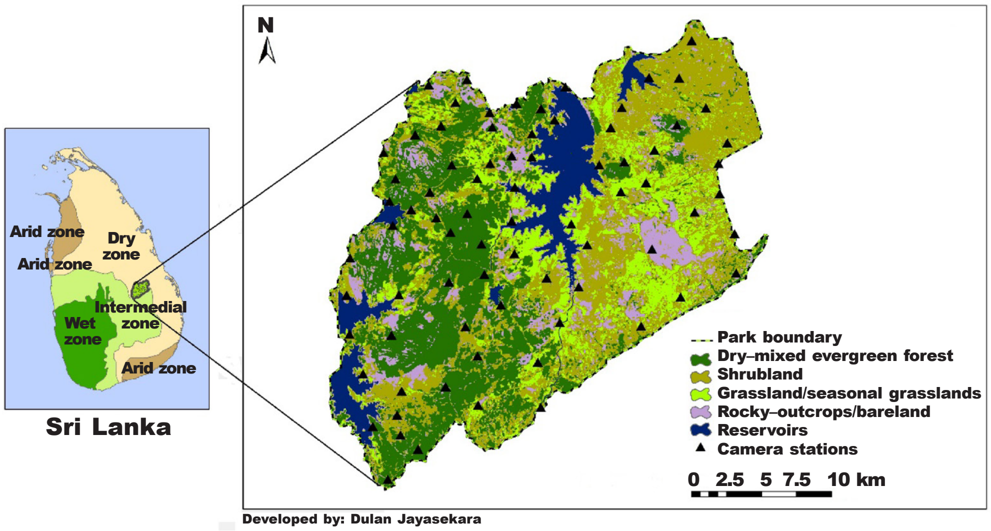

Fig. 2. Map showing the location of Maduru Oya National Park within the climatic zone map of Sri Lanka (left), and habitat categorization of the park adapted from Jayasekara et al. (2021a).

Fig. 2. Mapa del parque nacional Maduru Oya y su localización en el mapa de zonas climáticas de Sri Lanka (a la izquierda) y clasificación de los hábitats del parque adaptada de Jayasekara et al. *(2021a).*

Being the only pangolin species found in Sri Lanka, the Indian pangolin has significant importance for conservation. Its threatened status, coupled with the increasing hunting pressure both locally and internationally, place it at the top of the list as an animal facing significant anthropogenic pressure. The traditional use of pangolins as a delicacy by villagers around forests is well known (Perera et al., 2017; Karawita and Perera, 2020). Furthermore, the accelerating international illegal trade of Indian pangolins (mainly pangolin scales) and the demand from the East–Asian markets (Challender et al., 2015; Perera et al., 2017; Mahmood et al., 2020; Perera and Karawita, 2020) have increased the exploitation rate of the species in its natural habitats in Sri Lanka. Habitat destruction and forest cover loss in the country as a result of numerous anthropogenic activities put this species in further peril. Despite the interest generated as a result of the revelations of trafficking data and CITES listing, little is known about ecology of the Indian pangolin in its natural habitats of Sri Lanka. Except for the work carried out in Yagirala forest reserve (a small forest reserve of in the lowland wet–zone of Sri Lanka) (Karawita et al., 2016; Perera et al., 2017; Karawita et al., 2018, 2020), the present study is one of the first to investigate the ecological aspects of this lesser studied species in the dry lowlands of the island. This is also one of the first efforts to estimate the population density of the species based on camera trap abundance data rather than on burrow counts. This method reduces bias due to heavy reliance on observer skills to locate burrows, issues regarding reproducibility of results, and false presence records by occupancy of other species (Perera et al., 2022). Altogether, determining the spatiotemporal distribution of Indian pangolins, habitat associations, and population density estimation in MONP would facilitate the effective management and conservation planning for the species.

Material and methods

Study area

In this study we used camera trap data, recorded during a meso–mammal survey conducted from January 2019 to January 2021 in MONP (fig. 2). MONP is situated mainly in the dry zone of Sri Lanka bordering the intermediate zone. The climatic conditions are dominated by the north–east monsoon, which persists from October to February. The mean annual rainfall is 1,650 mm and the mean annual temperature is about 27 ºC. Overall evapotranspiration rates usually exceed precipitation levels (Green, 1990). The park lies in the dry zone. However, the southern boundary of the park is near the intermediate zone, which is a narrow geographical area that separates the dry zone from the wet zone. The climax community of the area is tropical, dry mixed evergreen forest. The importance of the park's fauna is its richness, which includes several endemic species (Green, 1990).

Camera trapping

Browning Dark Ops and Browning Strike Force (Browning, USA) wildlife trail cameras were used for camera trapping. All cameras were equipped with IR motion and heat sensor triggered low/no glow

Fig. 3. A camera trap attached to a tree trunk to capture images/videos of Indian pangolins.

Fig. 3. Una cámara de trampeo atada al tronco de un árbol para captar imágenes y vídeos del pangolín indio.

flash, which generates minimal disturbance to the animals. Camera traps were placed representatively in all available habitat types in MONP using a grid of 2 × 2 km plots generated using ArcMap (ESRI, USA). A random camera placement was followed (Jayasekara et al., 2021b). The minimum distance between any two camera stations was greater than 1km. Cameras were placed at 25 cm above the ground and attached to a tree (fig. 3). Logs/metal poles were used to mount the cameras when large trunked trees were not available in the habitat. Camera traps were operating 24h/day with 1 second delay for a minimum of 30 consecutive days at each station. Capture records of Indian pangolins were obtained in the form of photos/videos. Additionally, the presence records of poachers captured in camera traps were used for the analysis. Since unauthorized entry is prohibited in the terrestrial areas of the MONP, we assumed that any humans captured on camera traps were poachers. The absence of uniforms (to differentiate poachers from rangers, fig. 3s in supplementary material) and carrying guns and other equipment were taken as clues of confirmation.

A total of 75 camera trap locations were surveyed. Available habitat types were identified as dry–mixed evergreen forest (DEF) (1197 trap days), shrubland (SHB) (775 trap days), rocky outcrops (ROC) (282 trap days), grasslands (GSL) (423 trap days) and reservoirs (Jayasekara et al., 2021a) (fig. 2). All terrestrial habitats up to the edge of water bodies were considered for sampling.

Habitat/environmental covariates

Habitat type and habitat variables of each camera trap station were recorded. The variables used for the analysis included habitat type, canopy cover (CN), stem density 1 (SD1), stem density 2 (SD2), litter cover (LC), litter depth (LD), ground vegetation (GV), normalized difference vegetation index (NDVI), Euclidean distance to water (EDW), elevation (EL), the abundance of termite mounds (TM) and the relative abundance index of humans (RAIH) (table 1s in supplementary material). Stem density was measured by the modified Point Centered Quarter (PCQ) method by Chen et al. (2009) from the original method of Higgins et al. (1996). Mean distance to the nearest woody plant (< 10 cm from the camera–trap) with a diameter at breast height (DBH) between 1 and 10 cm was measured for SD1, whereas SD2 included plants with a DBH > 10 cm (four distance measurements were taken in four different directions, having the camera as the center point). Stem density was calculated as 1/mean area [distance]^2. Other parameters were measured using quadrates of 2 x 2 m and averaged for each camera location. Litter cover was determined by the photo–point method (Michel et al., 2010) and litter depth was measured using a metal ruler. The abundance of termite mounds was evaluated by visual observation of a 20 × 20 m area around the camera location and a rank of 0–2 was given (0 absent, 1 moderate availability, 2 high availability). At the end of the survey, the camera traps were tested to confirm that they were still operational; if not, the date on the last photograph/video was recorded as the last operational date. We kept the cameras active for an average of ~38 days and cameras were shifted to new locations following the moving survey method to increase the area coverage.

Macroscale parameters were obtained using Arc Map 10.4 (ESRI, Redlands, USA) based GIS techniques. Raster maps were prepared for Euclidean distance to water, normalized difference vegetation index, and elevation. Averaged values for each camera point were obtained using the zonal statistics tool in Arc GIS.

Occupancy modelling

Occupancy of Indian pangolins was estimated using the likelihood–based method (MacKenzie et al., 2002). Species detection history (e.g., 1100100) for each camera location (consisting of binary values with ‘1’ indicating species detection during the sampling occasion and '0'' indicating non–detection) was calculated by visually inspecting camera footage (Otis et al., 1978). It was assumed that each camera site was independent and no animal would move between sites during the survey period (Royle and Nichols, 2003). A survey of 30 days was divided into 10 sampling periods of three days each to increase the detection probability for each sampling period. Detection histories were pooled for two years and entered together as single–season models in PRESENCE v.4 (Proteus Wildlife Research Consultants, New Zealand; http://www.proteus.co.nz). Logistic concerns, such as the low number of cameras and the field situation (high density of Asian elephants) restricted us from conducting seasonal sampling as two consecutive sampling seasons could not be conducted for each camera location. All continuous variables were standardized to *z*–scores prior to analysis (Cooch and White, 2005). To reduce the model over–fitting by having high correlations among covariates, all the covariates were tested using pair–wise analysis for high co–linearity using the Pearson correlation coefficient. Only independent variables were selected for each analysis by removing covariates with > 0.75 r values.

A number of candidate models were defined incorporating possible covariates for the species based on priori hypotheses and available literature regarding factors that could influence site occupancy and detection probability (Kalle, 2013). Models were used to understand how variables could influence species occupancy and habitat use in order to explore the power of covariates. The software program PRESENCE v.4 was used for the model set development.

The psi (ψ) value was interpreted as the overall proportion of a study area used by the Indian pangolins (MacKenzie et al., 2002). A global model that contained all potential covariates for occupancy was produced and detection probability (*p*) was allowed to vary by all covariates. Occupancy probability values obtained for each habitat type were averaged to determine the preferred habitat types.

Activity level and activity patterns

We analysed the time stamp data on camera videos and photo records to generate the activity pattern of Indian pangolins. To determine activity level (a), that is, the proportion of the day that the species is active, we used R version 4.0.3 (R Core Team, 2013) package ‘activity’ (Rowcliffe et al., 2014, 2016; Rowcliffe, 2019). The time stamp data of Indian pangolins captured on camera trap videos was converted to radian time. This was analysed in R with 1,000 iterations. An activity graph was generated based on non–parametric von Mises kernel density (Ridout and Linkie, 2009).

To determine the activity overlap between Indian pangolins and poachers, activity time data were analysed following Ridout and Linkie (2009) using the R package 'overlap' (Meredith and Ridout, 2014) in R bootstrapping with 1000 iterations from the original data. The measure of overlap was calculated using the coefficient of overlapping ($\Delta 1$) (for sample size < 75); 0 (no overlap), 1 (complete overlap) (Ridout and Linkie, 2009; Hearn et al., 2018). Activity overlap graphs were generated based on non–parametric von Mises kernel density (Ridout and Linkie, 2009).

Population density estimation

We used the Random Encounter Model (REM) developed by Rowcliffe et al. (2008) to estimate the density (D, km^{-2}) of Indian pangolin in MONP. The equation,

$$D = (y/t) \times (\pi/v^*r(2 + \theta)$$

was used for the calculation where: y, was the number of capture events; t, the survey effort (camera trapping days); v, the average daily distance travelled (km/day); r, the average distance to the first capture of animals (km); θ, radians, the average angle to the capture animals.

To calculate the day range (v), we estimated the movement speed of Indian pangolins following the method of Rowcliffe et al. (2016). The distance travelled daily (v, day range) was derived using the movement speed (s) and activity level (a) of animals following the equation: v = s x a. We used the activity level calculated in the previous section. The movement speed (s) of each animal was derived from time taken by the animal to move in front of the camera (Pfeffer et al., 2018). We followed the procedure described by Rowcliffe et al. (2016) to calculate the average speed parameter by fitting probability distributions to samples of individual speed observations obtained from video captures. The distance from camera to the animal was measured following the distance grid method described in Jayasekara et al. (2021b). The R package 'fitdistrplus' (Delignette–Muller and Dutang, 2015) was used for model fitting and best fitting models were selected based on Akaike Information Criterion (AIC) values. Density calculations were performed in R bootstrapping with 1000 iterations from the original data. Goodman's (1960) variance of products formula was used to calculate the standard error when required. Coefficient of variation (CV) was obtained using the square root of the variance and the point estimates.

Results

Occupancy and habitat use of the Indian pangolin

Indian pangolins were detected in all four terrestrial habitat types. However, the highest occupancy probability of Indian pangolins was within the dry–mixed

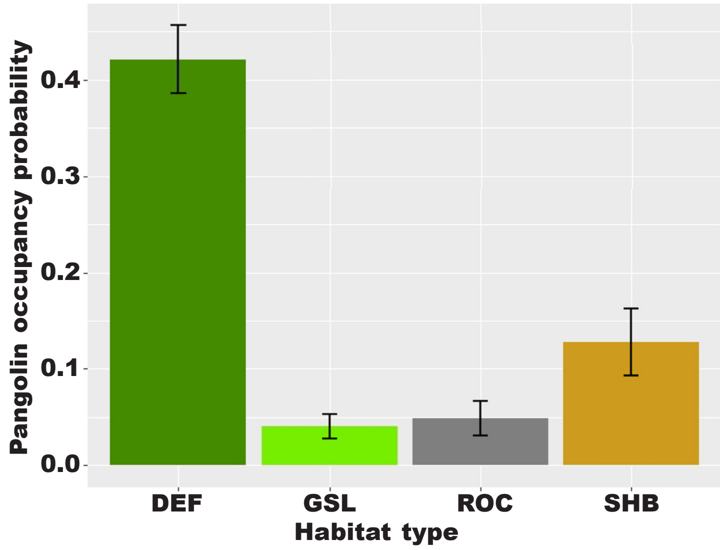

Fig. 4. Habitat occupancy of Indian pangolin in Maduru Oya National Park: DEF, dry–mixed evergreen forest; GSL, grassland; ROC, rocky outcrop; SHB, shrubland.

Fig. 4. Ocupación del hábitat del pangolín indio en el parque nacional Maduru Oya: DEF, bosque seco mixto perennifolio; GSL, pradera; ROC, promontorio rocoso; SHB, matorral.

evergreen forest habitat (0.41 ± 0.19) and it was significantly higher than in the other three habitat types (Kruskal–Wallis, z = 6.04, $p = 0.0001$) (fig. 4). The highest ranked occupancy model included canopy cover and dry–mixed evergreen forest as the most associated covariates which positively influenced the overall occupancy probability of Indian pangolin. Euclidean distance to water, termite mounds and human

Table 1. Highest ranking models for factors influencing the site occupancy of Indian pangolin in Maduru Oya National Park (MONP): ΔAIC, delta AIC; AICw, AIC wiight; MLL, model likelihood; K, number of parameters in the model; Nocc, naïve occupancy; psi(SE), occupancy probability of the species ± standard error; p(SE), detection probability of species ± standard error; "(.)" indicates constant across all camera sites.

Tabla 1. Los mejores modelos para los factores que influyen en la ocupación del pangolín indio en el parque nacional Maduru Oya: ΔAIC, delta AIC; AICw, peso AIC; *MLL, probabilidad de ocupación estimada con el modelo; K, número de parámetros en el modelo; Nocc., ocupación ingenua; psi(SE), probabilidad de ocupación de la especie ± error estándar; p(SE), probabilidad de detección de la especie ± error estándar; "(.)" indica constante en todas las cámaras.*

Model	AIC	ΔAIC	AICw	MLL	K	Nocc.	psi(SE)	p(SE)
psi(CN + DEF), p(Edw)	222.37	0.00	0.215	1.000	5	0.187	0.219 ± 0.027	0.224 ± 0.053
psi(CN + DEF), p(Edw + TM)	222.99	0.62	0.212	0.733	6		0.224 ± 0.027	0.203 ± 0.003
psi(CN + DEF), p(.)	223.14	0.77	0.197	0.681	4		0.197 ±0.024	0.257 ± 0.040
psi(CN + DEF), p(TM)	223.20	0.83	0.191	0.660	5		0.204 ± 0.025	0.230 ± 0.051
psi(CN + DEF), p(Edw + RAIH)	224.31	1.94	0.110	0.379	6		0.222 ± 0.027	0.220 ± 0.004
Model averaged							0.213 ± 0.005	0.226 ± 0.008

Table 2. Untransformed estimates of beta coefficients and standard error (SE) for the covariates contained in the top ranked models of Indian pangolin occupancy.

Tabla 2. Estimaciones sin transformar de los coeficientes beta y el error estándar (SE) de las covariables contenidas en los mejores modelos de ocupación del pangolín indio.

Covariate	Estimate ± SE
Occupancy probability	
Intercept	-2.523 ± 0.681
Canopy cover	1.010 ± 0.434
Dry-mixed evergreen forest	1.639 ± 0.812
Detection probability	
Intercept	-1.349 ± 0.267
Euclidean distance to water	-0.762 ± 0.417

Table 3. Parameters associated with population density estimates of Indian pangolin based on REM: ADD, average detection distance; ADA, average detection angle; PD, population density.

Tabla 3. Parámetros asociados a la estimación de la densidad de población del pangolín indio basada en el modelo de encuentro aleatorio REM): ADD, distancia media de detección; ADA, ángulo medio de detección; PD, densidad de población.

Parameter	Estimate ± SE
Activity level	0.336 ± 0.0340
Speed	1.08 ± 0.09 km/h
Day range	8.70 ± 0.78 km
ADD	3.21 ± 0.26 m
ADA	0.512 ± 0.05 radians
PD	0.73 ± 0.21 indiv./km^2
Coefficient of variation of PD	19.10 %

abundance were also present in the top ranked models that positively influenced the detection probability of pangolins (tables 1, 2).

Spatial distribution of Indian pangolin in MONP

The species was primarily distributed within the western flank of MONP where dry–mixed evergreen forest was prominent (fig. 5). The highest number of presence points for poachers was also recorded in this same region of the park where Indian pangolin occupancy probability was highest (fig. 5).

Temporal activity and activity patterns

Indian pangolin displayed a highly nocturnal activity pattern (nocturnal activity level, 0.633) with an overall activity level of 0.336 ± 0.039. The activity pattern was unimodal; peak activity density and the highest number of encounters were recorded after midnight. The activity level then decreased gradually towards dawn (fig. 6A). The earliest capture record during night was at 19:21 h. There was a single camera trap observation at 06:57 h, and this was the only recorded encounter after 06:00 h in the morning. Pangolins displayed a considerable overlap of activity with humans (poachers) at a Δ score of 0.442 (0.240–0.588). The activity level of poachers also peaked after midnight (fig. 6B).

Population density

The low movement speed of the species coupled with a moderate level of activity resulted in a modest day range of 8.70 ± 0.78 km/day compared to the day ranges recorded by Jayasekara et al. (2021b) for other mammalian species of the park. The average detection distance of Indian pangolins was also relatively higher, indicating high detectability of the species when compared to other meso–mammals of MONP (Jayasekara et al., 2021b). The estimated population density for the species was 0.73 ± 0.21 indiv./km^2 with a reasonable coefficient of variation value of 19.10 % (table 3).

Discussion

Our occupancy estimates for the species at MONP indicate that these dry zone lowlands provide habitat for the species, as was shown from the distribution studies of the Indian pangolin (Karawita and Perera, 2020; Perera and Karawita, 2020). Even though the species was observed in all available habitat types, there was a higher affinity for the dry–mixed evergreen forest habitats of MONP. The dry–mixed forest habitat can therefore be considered the preferred habitat of Indian pangolin in MONP. The occupancy modeling also revealed an association of Indian pangolin occupancy with canopy cover. Though not visible in the generated results, even in the dry–mixed forest, the availability of rocks was observed to some extent at locations of pangolin sightings. The species was more detectable in areas relatively closer to water bodies and where termite mounds were abundant. The high detection probability in areas closer to the water (low EDW) indicates the importance of water sources. Relatively higher productivity in alluvial habitats (Dittus, 2017) would have influenced this higher occupancy (as a result of increased prey availability). An impor-

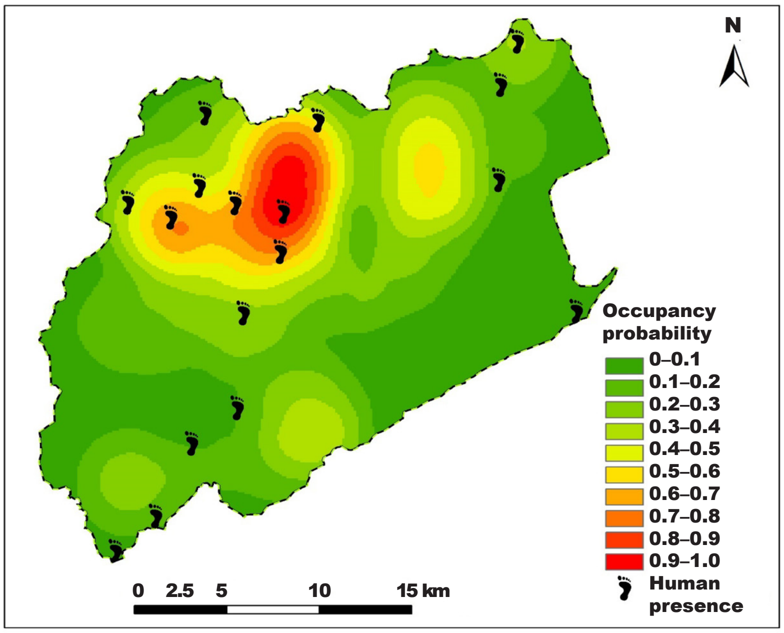

Fig. 5. Modeled distribution map of Indian pangolins in Maduru Oya National Park indicating the occupancy probability based on kernel density. Human presence points (poachers) are also indicated on the map.

Fig. 5. Modelo de la distribución del pangolín indio en el parque nacional Maduru Oya en el que se indica la probabilidad de ocupación basada en la densidad del kernel. En el mapa también se indican los puntos de presencia humana (cazadores furtivos).

tant observation was the higher detection probability recorded for the species in areas where unauthorized human activity was observed. Rather than a behavioral preference of Indian pangolin, this finding would likely have been generated as a consequence of high poaching activity in those areas and targeting hunting of the species. This was further visible in the generated spatial distribution map of the species. Unauthorized human activity should thus be prevented in order to stop hunting of Indian Pangolin and other species in MONP. In the recent past, there have been several raids by park officers that seized pangolins killed by the poachers entering the park. Within the dry–mixed forest habitat of MONP, we observed a number of Indian pangolin burrows dug mostly in association with old termite mounds, rock crevices, and decayed tree cavities near the ground surface (fig. 1s in supplementary material). Outside the protected areas in the dry zone farmlands, we observed man–made traps, called 'Habaka', which the villagers use to trap and kill Indian pangolins.

In a study in Pakistan, Waseem et al. (2020) reported similar habitat preference for the species for forested areas. In our study in MONP, the observations were similar; the Indian pangolins sought cover and protection in the denser forested areas of the park. However, the availability of such suitable habitat is limited. The forested habitats of the western flank of the park were especially identified as good habitats for the species. The conservation and protection of such vital habitats is therefore highly recommended. Despite efforts by the park management, illegal hunting and man–made fires continue to occur in these critical habitats as we observed in our camera trap data and direct observations. We suggest staff numbers in the park should be increased and more ground patrols should be conducted to prevent such illegal activities.

The activity of Indian pangolin was exclusively nocturnal and peak activity after midnight overlapped with the activity of poachers, indicating the higher likelihood of the species being targeted by the local hunters. On several occasions, the camera traps showed the poachers on the same path as the pangolin (fig. 2s in supplementary material).

These data may help park authorities conduct more effective and more efficient raids in targeted areas and in specific time slots in order to apprehend wildlife criminals. This study is possibly the first published record where camera trap–based REM method (Rowcliffe et al., 2008) was applied to determine the population density of this pangolin. In the context of Sri Lanka, the supposed population density of the species (5.69 indiv./km^2) could be overestimated, as recently suggested Mahmood et al. (2020). One very recent study conducted in the same small forest area (< 20 km^2) of Yagirala based on N–mixture models predicted the density of the species as 0.037 ha^{-1} (3.7 indiv./km^2) in the wet

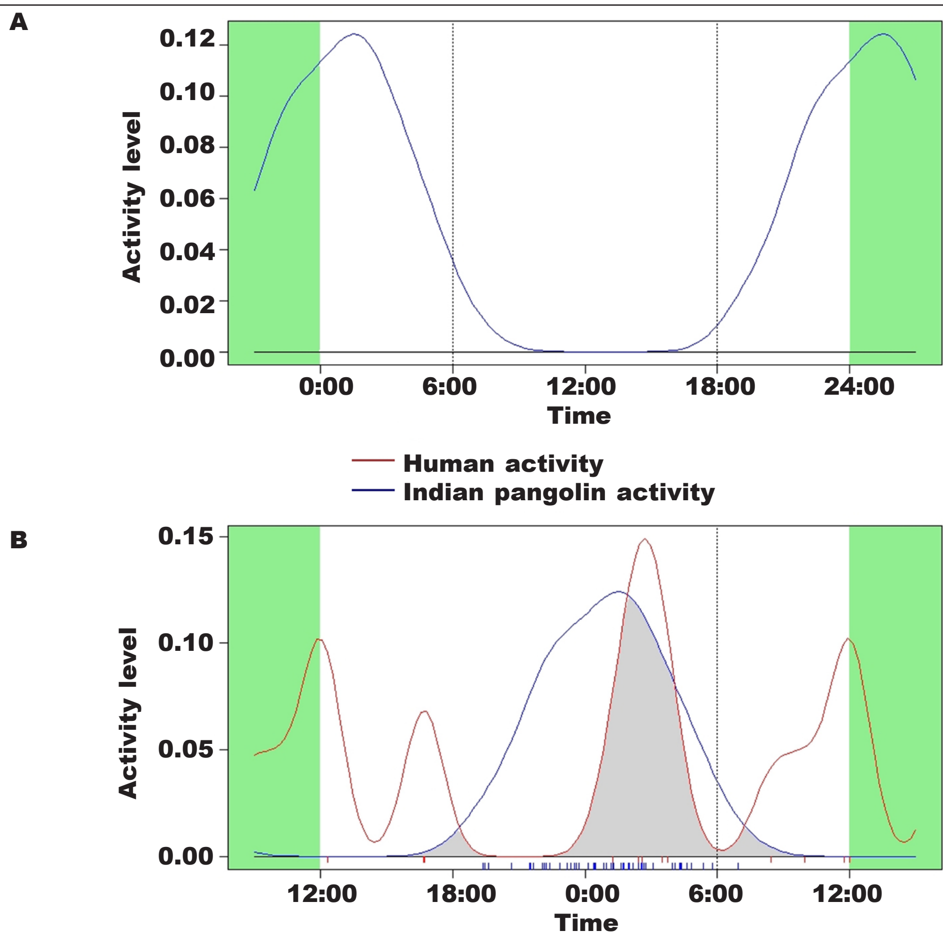

Fig. 6. A, activity pattern of Indian pangolin fitted with circular kernel distributions of radian time; B, activity overlap between Indian pangolin and humans (poachers), grey indicates overlapping activity.

Fig. 6. A, pauta de actividad del pangolín indio ajustada con las distribuciones de kernel circulares del tiempo en radianes; B, superposición de la actividad del pangolín indio y de los humanos (cazadores furtivos); el color gris indica la superposición de la actividad.

zone of Sri Lanka (Perera et al., 2022). However, the accuracy of results could not be compared due to the difference in methodology (N–mixture models) and the lack of CV values in the mentioned paper when compared to the present study which followed the REM method, as used in many other recent studies. The REM–based density estimation in the present study (0.73 indiv./km^2 ~ 0.0073 ha^{-1}) provides more supporting data to calculate the forms of activity level, movement speed, day range, and detection distance. Our density estimate is closer to but higher than most figures recorded elsewhere in the region and that range from 0.00044 to 1.5 indiv./km^2 (Mahmood et al., 2014, 2020), most of which have used burrow counts rather than the actual abundance data. We consider our estimates of a coefficient of variation of 19.1% are accurate and we leave it to the research community to conduct a comparative study applying both the burrow count method and REM to a single community of pangolins so as to investigate the most suitable method to estimate density of the species. Our findings also show the slow–moving nature of the Indian pangolin could be a disadvantage for the species in hostile habitat conditions where it could be hunted and also threatened by the seasonal man–made fires.

As indicated by Khwaja et al. (2019) and Perera et al. (2022) our results suggest that camera traps are an effective tool to monitor an elusive and nocturnal species like the Indian pangolin. The low–glow/no glow invisible flashed camera types used and low height of camera attachment allowed us to monitor the animal's movement and human movements without causing distractions to the behavior. Our observations regarding the ecological and habitat requirements could help the possible ex-situ conservation of this species, which is declining in its natural habitats (Perera et al., 2017; Perera and Karawita, 2020), and the population data generated may be useful to evaluate the status of Indian pangolin. In conclusion, to protect the species in this area there is a need to conserve the species' natural habitat, provide more protection, reduce illegal hunting, and develop awareness programs to educate the local communities.

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Supplementary material

Table 1s. Variables considered for modeling.

Table 1s. Variables consideradas para la elaboración del modelo.

Abbreviation	Variable	Description
CN	Canopy cover	Continuous
Habitat type	Dry–mixed evergreen forest	Categorical
	Shrubland	
	Grassland	
	Rocky outcrops	
	Reservoir/wetlands	
SD1	Stem density 1	Continuous
SD2	Stem density 2	Continuous
LC	Litter cover	Continuous
LD	Litter depth	Continuous
EDW	Euclidean distance to water	Continuous
EL	Elevation	Continuous
NDVI	Normalized difference vegetation index (March)	Continuous
TM	Termite mounds	Categorical
RAIH	Relative abundance index of humans	Continuous

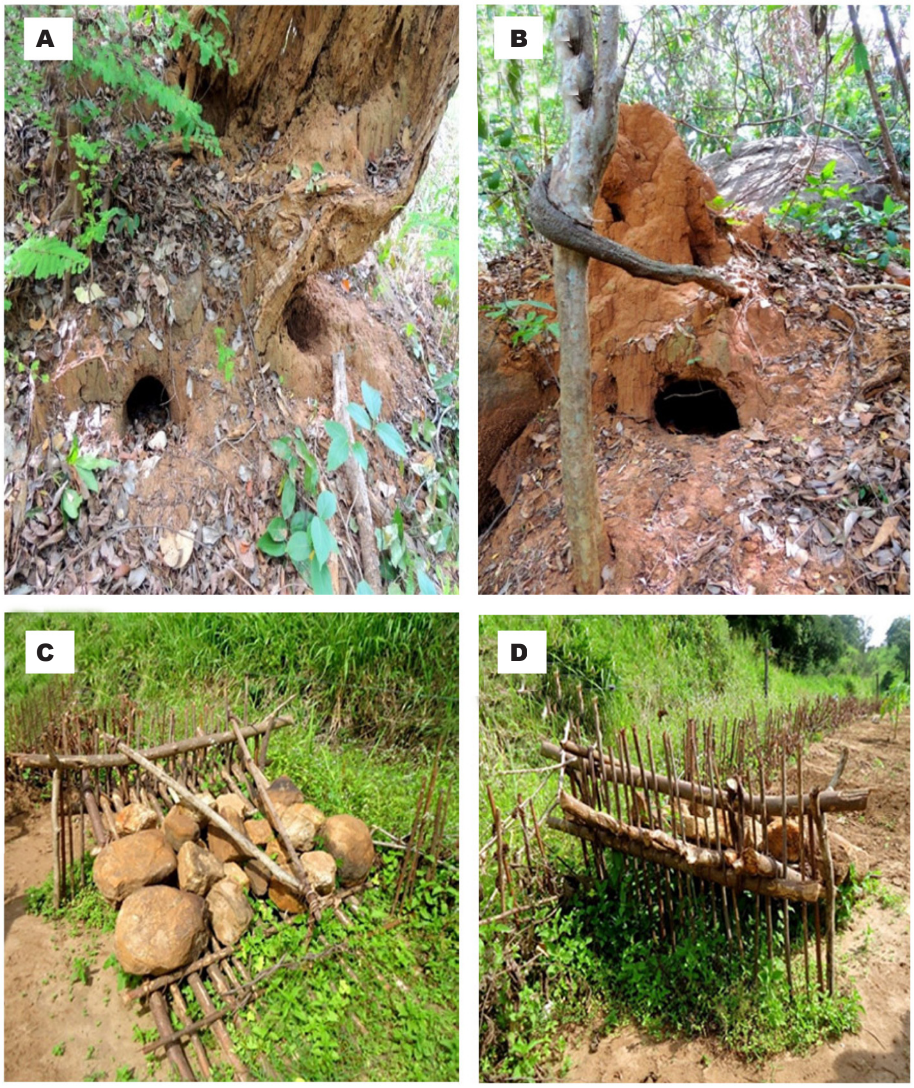

Fig. 1s. A, B, Indian pangolin burrows recorded within the dry-mixed forest habitat; C, D, man–made traps called 'Habaka' which villagers use to kill Indian pangolins in the dry zone farmlands of Sri Lanka.

Fig. 1s. A, B, madrigueras de pangolín indio registradas en el hábitat del bosque mixto-seco; C, D, trampas hechas por el hombre llamadas "Habaka" que los aldeanos utilizan para matar pangolines indios en las tierras agrícolas de las zonas secas de Sri Lanka.

Fig. 2s. A poacher walking in front of the camera at the same location where pangolin activity was observed at a similar time of the night.

Fig. 2s. Un cazador furtivo caminando delante de la cámara en el mismo lugar en que se observó actividad de un pangolín a la misma hora de la noche aproximadamente.

Fig. 3s. A poacher carrying a locally assembled gun, recorded by our camera trap.

Fig. 3s. Un cazador furtivo captado en nuestras cámaras con un fusil ensamblado localmente.