

Using bycatch data to model sun bear *Helarctos malayanus* occupancy in Bukit Barisan Selatan National Park, Sumatra

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Abstract Surveys targeting flagship species frequently record the presence of other species, providing valuable bycatch data to fill knowledge gaps on the ecology of overlooked species. Using bycatch records from camera-trap surveys for the tiger *Panthera tigris*, we model occupancy of the sun bear *Helarctos malayanus*, predict its temporal change in occupancy during 2015–2019 and determine its activity patterns in Bukit Barisan Selatan National Park, part of a UNESCO World Heritage Site in Sumatra, Indonesia. We performed single-season occupancy modelling that considered unequal detection probability from sun bear detection/non-detection records. We found that the sun bear occupancy in the Intensive Protection Zone (i.e. the priority protection area) of the National Park was slightly higher than in the north of the National Park. In the Intensive Protection Zone, sun bear occupancy was estimated to be 0.67 in 2015 and increased to 0.83 in 2019, but this increase was not substantial. The sun bear exhibited a cathemeral activity pattern. Most activity occurred during the day (46.2%), followed by night (21.2%), dusk (20.9%) and dawn (11.7%). We encourage collaboration amongst institutions conducting camera-trap studies in Sumatra to examine the ecology of other threatened yet overlooked species, to assess the broader biodiversity benefits of flagship species conservation and to strengthen science-based conservation efforts.

Keywords Bycatch records, camera trap, charismatic mammal, detection/non-detection, *Helarctos malayanus*, spatial distribution modelling, sun bear

Introduction

Conservation funding tends to be allocated to the research and protection of species with charismatic features that serve as flagship species (Gratwicke et al., 2007; Srivathsa et al., 2022). However, surveys and monitoring of flagship species often also record the occurrence of other species, including threatened yet overlooked species. Camera trapping, a non-invasive method using remote

automated cameras, is often used to monitor wildlife populations (Kucera & Barrett, 2011). There has been an increasing number of studies employing bycatch camera-trap data to fill knowledge gaps on understudied species (e.g. Pusparini et al., 2014; Sunarto et al., 2015; Scotson et al., 2017b; Williams et al., 2021; Sibarani et al., 2022). Non-target species could also benefit from the conservation of flagship species, for example through increased law enforcement in habitats where flagship species co-occur with non-target species. Similarly, patrol teams focusing on halting tiger *Panthera tigris* poaching also handle other forms of wildlife poaching and illegal logging (Risdianto et al., 2016). Here we focus on the ecology of the sun bear *Helarctos malayanus*, using bycatch camera-trap data from surveys for the tiger.

To date, the only studies on sun bear distribution in Sumatra have been in the west-central landscape covering Kerinci Seblat National Park (Linkie et al., 2007; Wong et al., 2012; Wong & Linkie, 2013), despite the species' wide distribution range across Sumatra (Scotson et al., 2017b). Along with Kerinci Seblat and Gunung Leuser, Bukit Barisan Selatan National Park is one of the three national parks forming the UNESCO Tropical Rainforest Heritage of Sumatra, where most species conservation funding is allocated in Sumatra. The south-western Sumatra forest block, within which Bukit Barisan Selatan National Park is located, has been identified as one of the sun bear habitats at risk from isolation because of habitat fragmentation (Scotson, 2019).

The sun bear is categorized as Vulnerable on the IUCN Red List (Scotson et al., 2017a). Across their range in Asia, sun bears are threatened by habitat degradation and habitat loss, potential conflicts with people, illegal hunting for their gall bladder and paws, illegal trading for pets and bycatch from snares set for other species (Crudge et al., 2019). Poaching of sun bears for their gall bladders only occurs occasionally in Sumatra (e.g. Hidayat & Siniwi, 2016), in contrast to the high number of poaching cases in mainland range state countries (Crudge et al., 2019).

Multiple camera-trap surveys have been conducted in Bukit Barisan Selatan National Park to monitor tiger populations (Pusparini et al., 2018; Wildlife Conservation Society–Indonesia Program, unpubl. data 2018–2019). These surveys yielded occurrence records of other species, including the sun bear. Here we model sun bear occupancy in Bukit Barisan Selatan National Park using bycatch camera-trap records for 2015 and 2019 in a core area known as the Intensive Protection Zone. In addition, because

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camera-trap data also provide information on the time of day, we determine the diel activity pattern of sun bears. Because most sun bear photographs did not capture their individually unique chest markings, estimating abundance or population density using a capture–recapture framework was not possible. Instead, we use the detection/non-detection records of sun bears to determine their occupancy across the surveyed areas (MacKenzie et al., 2002).

Study area

The survey was in the 313,572 ha Bukit Barisan Selatan National Park, which is a habitat for the Critically Endangered Sumatran rhinoceros *Dicerorhinus sumatrensis*, Sumatran elephant *Elephas maximus sumatranus* and Sumatran tiger *Panthera tigris sumatrae*. The elevation range of the National Park is 0–1,964 m, comprising lowland rainforest (45%), hill rainforest (34%), lower montane rainforest (17%), upper montane forest (3%) and coastal forest (1%; Bukit Barisan Selatan National Park, 2019). During 2000–2017, the rate of deforestation was 9%, with a remaining forest cover of 249,589 ha in 2017 (Lubis et al., 2018). We surveyed in two areas: (1) the c. 100,000 ha Intensive Protection Zone, which was established in 2015 to protect the last remaining population of Sumatran rhinoceros and is also used to monitor the Sumatran tiger (Pusparini et al., 2018), and (2) the c. 118,000 ha northern part of the

Park, which is separated from the Intensive Protection Zone by modified habitat (Fig. 1).

Methods

Camera-trap surveys

We obtained bycatch camera-trap data from three surveys to estimate tiger population density (Table 1) in the Intensive Protection Zone in 2015 and 2019 and in the northern Park in 2018 (Fig. 1). Camera traps were set according to survey protocols for tiger monitoring: at locations where there were recent signs of tiger or its principle prey species (wild boar *Sus scrofa*, sambar *Rusa unicolor* and southern red muntjac *Muntiacus muntjak*), c. 45 cm above the ground, perpendicular to the target trail and without bait. Two opposing cameras were placed at each location to capture tiger stripe patterns on both flanks.

Occupancy modelling

We used single-season occupancy modelling to estimate sun bear occupancy (MacKenzie et al., 2002, 2017). We performed the modelling separately for each of the three datasets. Following Linkie et al. (2007) and Wong et al. (2012), we considered one sampling occasion as 2 weeks of trap-days. We used data from the whole survey period

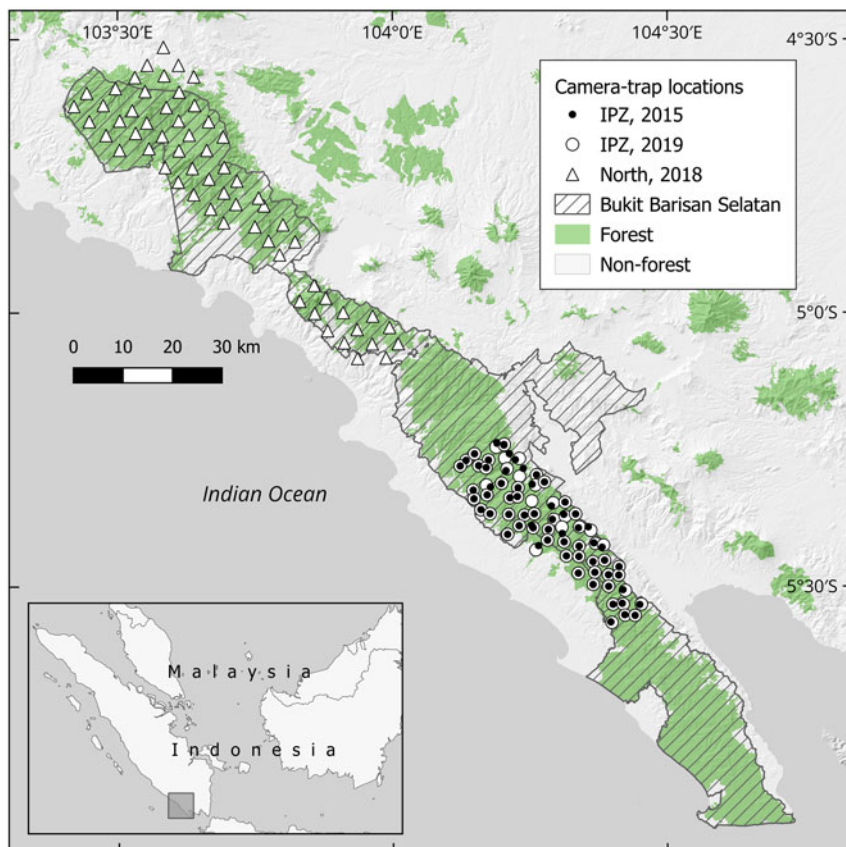


FIG. 1 Camera-trap locations in Bukit Barisan Selatan National Park, Sumatra, Indonesia. The bycatch data of the sun bear *Helarctos malayanus* used for this study came from three camera-trap surveys for the tiger *Panthera tigris*, in the Intensive Protection Zone (IPZ) in 2015 and 2019 and in the north in 2018.

TABLE 1 Details of the three camera-trap surveys in Bukit Barisan Selatan National Park, Sumatra, Indonesia (Fig. 1), from which we obtained bycatch camera-trap records of the sun bear *Helarctos malayanus*.

Variable	Intensive Protection Zone, 2015	North, 2018	Intensive Protection Zone, 2019
Survey period	May–Nov. 2015	Apr.–Oct. 2018	May–Nov. 2019
Total number of trap-days (n)	8,831	6,887	9,195
Mean \pm SD trap-days per location	140 \pm 25.8	113 \pm 12.8	141 \pm 16.2
Elevation range (median), m	164–965 (525)	411–1,657 (949)	164–937 (524)
Camera-trap brand	Panthera	Bushnell, Reconyx	Bushnell, Reconyx
Number of camera-trap locations	63	61	65
Number of locations with sun bear detections	36	28	52
Number of sun bear photographs	261	431	1,882
Number of independent events	115	65	191
Naïve occupancy	0.57	0.46	0.78

(113–140 days per camera trap; Table 1). The periods were longer than used by Linkie et al. (2007) and Wong et al. (2012) but still relatively short compared to the lifespan of the sun bear, so we assumed a demographically closed population. Phumanee et al. (2020) also used focal species lifespan to justify an extended sampling duration for occupancy analysis of ungulate species. Our sampling duration was also shorter than the generation length of the sun bear (10 years; Pacifici et al., 2013), its estimated age at first reproduction (6 years; Pacifici et al., 2013) and first oestrus cycle (2 years; Frederick, 2008), although there remains potential for death or migration within the survey period.

For each dataset we used two predictors, measured at each camera-trap location, to model detection probability: canopy and understory openness. We measured canopy openness using a spherical crown densiometer and understory openness using a 1 \times 1 m tarpaulin gridded into 16 equal-sized squares. At each camera-trap station we measured canopy and understory openness at four points. To measure canopy openness, one observer stood 10 m from the camera-trap position whilst holding the spherical densiometer at elbow height and then counted the number of dots that fell from canopy openings. To measure understory cover, one person stood 10 m from the camera trap whilst holding the tarpaulin vertically; another person stood at the camera-trap position and counted the number of grids that did not overlap understory vegetation. The proportion of grids without overlapping vegetation represented understory openness. We averaged each set of four measurements at each camera-trap station.

We initially considered eight predictors to model the probability of occupancy: elevation, slope, roughness, normalized difference vegetation index (NDVI), and nearest distances to non-forest land, settlements, plantations and roads. We used the NASA Shuttle Radar Topographic Mission digital elevation model at 90-m resolution to represent elevation. We derived slope and roughness layers from the Shuttle Radar Topographic Mission digital elevation model at the same resolution. To calculate NDVI, we

extracted near-infrared and red reflectance values at camera-trap locations from Landsat cloud-free image composites (Hansen et al., 2013) for 2015, 2018 and 2019. We did not use raw Landsat images because our study areas were frequently covered by cloud. We then calculated NDVI using the formula (near-infrared reflectance – red reflectance)/(near-infrared reflectance + red reflectance). To measure nearest distance to non-forest land, settlements and plantations, we used land-use maps of Bukit Barisan Selatan National Park and 5-km buffers in 2015, 2017 (2018 is not available) and 2019 that were created by Bukit Barisan Selatan National Park and the Wildlife Conservation Society–Indonesia Program based on Landsat imaging (unpubl. data). We classified land-use types other than forest as non-forest features, which includes settlements, plantations, grasslands and shrublands. We used road structure maps from the Indonesia Geospatial Portal (2017), which we modified using road data from patrol teams because small roads are often missing from large-scale maps. We measured the nearest distance to non-forest features, settlements, plantations and roads using *dist2Line* in the *geosphere* package (Hijmans, 2022) in *R* 4.3.0 (R Core Team, 2023). Before fitting occupancy models, we tested predictors for multicollinearity, and removed three predictors with correlation coefficients \geq 0.7 (Dormann et al., 2013): roughness ($r = 0.92$), distance to nearest settlement ($r = 0.70$) and distance to nearest plantation ($r = 0.85$), leaving five predictors. We standardized all continuous predictors so that they had a mean of 0 and standard deviation of 1 before including them in the models.

We first fitted four models for detection whilst holding occupancy constant: null model, detection \sim canopy openness, detection \sim understory openness, and detection \sim canopy + understory openness. We used the top-ranked model (i.e. the model with the lowest Akaike information criterion (AIC)) from this first step to fit the full model for occupancy with five predictors whilst retaining the best-supported model for detection from the previous step and then progressively excluded one predictor until further exclusion did not yield a lower AIC (stepwise regression).

We then used the top model from the final step to predict the occupancy of sun bears in each study site. We modelled each of the three datasets separately.

Assessing diel activity patterns

To determine sun bear activity patterns, we used photographic records of sun bears that were separated by at least 30 min (O'Brien et al., 2003; Ridout & Linkie, 2009), and from these we plotted the activity pattern using Kernel density estimation. We also plotted sun bear activity pattern against the nearest distance to non-forest land to determine whether activity pattern was affected by the level of anthropogenic disturbance.

Results

Predicted occupancy of sun bears

From 18,026 trap-nights during two surveys in the Intensive Protection Zone we recorded 2,143 sun bear images comprising 306 independent records. This indicated a naïve occupancy (without correcting for detection probability) that was higher in 2019 than in 2015 (Table 1). The top-ranked model for sun bear occupancy in the Intensive Protection

Zone in 2015 suggested that sun bear occupancy was negatively related to nearest distance to non-forest land, but the relationship was not significant ($\beta = -0.563$, $SE = 0.349$, $P = 0.107$; Table 2). However, in the top-ranked model for 2019 occupancy probability was positively related to NDVI, but this relationship was also not significant ($\beta = 1.130$, $SE = 0.819$, $P = 0.167$). In this model, canopy openness significantly predicted detection probability ($\beta = -0.199$, $SE = 0.111$, $P = 0.072$; Table 3). Based on these models the proportion of the area occupied by sun bears was 0.67 (95% CI = 0.57–1.00) in 2015 and increased to 0.83 (95% CI = 0.77–1.00) in 2019. Because of the considerable overlap between the CIs (Fig. 2), it is reasonable to conclude that sun bear occupancy in the Intensive Protection Zone did not change substantially between the two years.

The top-ranked model for sun bear occupancy in northern Bukit Barisan Selatan National Park was the null model (Table 4). The predicted occupancy for sun bears in this area was 0.59 (95% CI = 0.46–1.00), which is lower than the estimates in the Intensive Protection Zone but not substantially different.

Activity patterns

Most photographs of sun bears were recorded during the day (46.2% during 7.00–17.00), followed by at night (21.2%

TABLE 2 Model selection for occupancy modelling of sun bears in the Intensive Protection Zone of Bukit Barisan Selatan National Park, Sumatra, Indonesia, in 2015.

Model ¹	Number of parameters	AIC ²	Δ AIC ³	R ²
Step 1: Candidate models for detection (p)				
Null model	2	450.75	0.00	0.0000
$\Psi(1) p(\text{can})$	3	451.53	0.78	0.0192
$\Psi(1) p(\text{und})$	3	452.72	1.97	0.0005
$\Psi(1) p(\text{can} + \text{und})$	4	453.50	2.75	0.0196
Step 2: Candidate models for occupancy (Ψ)				
$\Psi(\text{dnf}) p(1)$	3	449.93	0.00	0.044
$\Psi(\text{ndv} + \text{dnf}) p(1)$	4	450.66	0.73	0.063
Null model	2	450.75	0.82	0.000
$\Psi(\text{ndv}) p(1)$	3	451.28	1.35	0.023
$\Psi(\text{ele} + \text{dnf}) p(1)$	4	451.56	1.63	0.049
$\Psi(\text{ele} + \text{ndv} + \text{dnf}) p(1)$	5	451.96	2.03	0.073
$\Psi(\text{ele} + \text{ndv}) p(1)$	4	452.63	2.70	0.033
$\Psi(\text{slo} + \text{ndv} + \text{dnf}) p(1)$	5	452.66	2.73	0.063
$\Psi(\text{ele} + \text{slo} + \text{dnf}) p(1)$	5	453.42	3.49	0.052
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf}) p(1)$	6	453.95	4.02	0.073
$\Psi(\text{ele} + \text{slo} + \text{ndv}) p(1)$	5	454.26	4.33	0.039
$\Psi(\text{ele} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	6	481.87	31.94	-0.444
$\Psi(\text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	6	481.96	32.03	-0.446
$\Psi(\text{ele} + \text{slo} + \text{dnf} + \text{dro}) p(1)$	6	481.96	32.03	-0.446
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dro}) p(1)$	6	482.76	32.83	-0.464
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	7	483.89	33.96	-0.444

¹can, canopy openness; und, understory openness; dnf, nearest distance to non-forest land; ndv, normalized difference vegetation index; ele, elevation; slo, slope; dro, nearest distance to road.

²Akaike information criterion.

³Difference in Akaike information criterion between the corresponding model and the null model.

TABLE 3 Model selection for occupancy modelling of sun bears in the Intensive Protection Zone of Bukit Barisan Selatan National Park, Sumatra, Indonesia, in 2019.

Model ¹	Number of parameters	AIC ²	Δ AIC ³	R ²
Step 1: Candidate models for detection (p)				
$\Psi(1) p(\text{can})$	3	659.45	0.00	0.0471
Null model	2	660.59	1.14	0.0000
$\Psi(1) p(\text{can} + \text{und})$	4	661.11	1.66	0.0521
$\Psi(1) p(\text{und})$	3	662.42	2.97	0.0026
Step 2: Candidate models for occupancy (Ψ)				
$\Psi(\text{dnf} + \text{ndv}) p(1)$	3	449.93	0.00	0.044
$\Psi(\text{ndv} + \text{dnf}) p(1)$	4	450.66	0.73	0.063
Null model	2	450.75	0.82	0.000
$\Psi(\text{ndv}) p(1)$	3	451.28	1.35	0.023
$\Psi(\text{ele} + \text{dnf}) p(1)$	4	451.56	1.63	0.049
$\Psi(\text{ele} + \text{ndv} + \text{dnf}) p(1)$	5	451.96	2.03	0.073
$\Psi(\text{ele} + \text{ndv}) p(1)$	4	452.63	2.70	0.033
$\Psi(\text{slo} + \text{ndv} + \text{dnf}) p(1)$	5	452.66	2.73	0.063
$\Psi(\text{ele} + \text{slo} + \text{dnf}) p(1)$	5	453.42	3.49	0.052
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf}) p(1)$	6	453.95	4.02	0.073
$\Psi(\text{ele} + \text{slo} + \text{ndv}) p(1)$	5	454.26	4.33	0.039
$\Psi(\text{ele} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	6	481.87	31.94	-0.444
$\Psi(\text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	6	481.96	32.03	-0.446
$\Psi(\text{ele} + \text{slo} + \text{dnf} + \text{dro}) p(1)$	6	481.96	32.03	-0.446
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dro}) p(1)$	6	482.76	32.83	-0.464
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(1)$	7	483.89	33.96	-0.444

¹can, canopy openness; und, understory openness; dnf, nearest distance to non-forest land; ndv, normalized difference vegetation index; ele, elevation; slo, slope; dro, nearest distance to road.

²Akaike information criterion.

³Difference in Akaike information criterion between the corresponding model and the null model.

during 19.00–05.00), dusk (20.9% during 17.00–19.00) and dawn (11.7% during 05.00–07.00), indicating a cathemeral activity pattern. The diel activity patterns appeared to be bimodal, with the highest peak at c. 18.00 and the second highest at c. 6.00 (Fig. 3a). When plotted against nearest distance to non-forest land, the bimodal pattern was similar in locations close to modified habitat (< 1 km) and in the forest interior, suggesting that sun bear diel activity was not affected by anthropogenic disturbance (Fig. 3b).

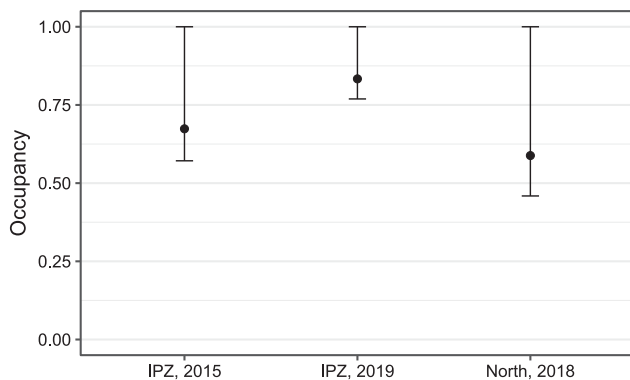


Fig. 2 Estimated proportion of occupied areas in the Intensive Protection Zone (IPZ) and the north of Bukit Barisan Selatan National Park, Sumatra, Indonesia. Bars represent 95% confidence intervals.

Discussion

As far as we are aware, this is the first study to assess the occupancy of sun bears in Bukit Barisan Selatan National Park using camera-trap records, and it adds to the limited body of knowledge regarding this species in insular Southeast Asia. Our results suggest that sun bear occupancy was stable during 2015–2019 in the Intensive Protection Zone, which was established in 2015, and in which ranger patrols are ongoing. The focus of these patrols is to deter hunting of the Sumatran tiger and its prey, and the Sumatran elephant and Sumatran rhinoceros, but this also provides law enforcement benefits to other coexisting species, including the sun bear.

Sun bears are known to prefer low elevation areas away from roads and villages (Wong & Linkie, 2013). This could explain the lower occupancy estimate in the higher-elevation northern Bukit Barisan Selatan National Park (median 949 m elevation, range 411–1,657 m) than in the Intensive Protection Zone (median 525 m, range 164–937 m, Table 1). In our study, the top-ranked models based on data from the Intensive Protection Zone included nearest distance to non-forest land (2015 data) and NDVI (2019 data) as the predictors of occupancy probability, but neither was significant. The top-ranked model based on the northern Bukit Barisan Selatan National Park data was the constant model for the occupancy parameter, suggesting there

TABLE 4 Model selection for occupancy modelling of sun bears in northern Bukit Barisan Selatan National Park, Sumatra, Indonesia, in 2018.

Model ¹	Number of parameters	AIC ²	Δ AIC ³	R ²
Step 1: Candidate models for detection (p)				
Null model	2	315.71	0.00	0.00×10^{00}
$\Psi(1) p(\text{can})$	3	317.33	1.62	6.20×10^{-3}
$\Psi(1) p(\text{und})$	3	317.71	2.00	1.80×10^{-5}
$\Psi(1) p(\text{can} + \text{und})$	4	319.33	3.62	6.30×10^{-3}
Step 2: Candidate models for occupancy (Ψ)				
$\Psi(\text{ndv}) p(\text{can})$	4	657.20	0.00	0.107
$\Psi(\text{ele} + \text{ndv}) p(\text{can})$	5	657.46	0.26	0.131
$\Psi(\text{ndv} + \text{dnf}) p(\text{can})$	5	657.92	0.72	0.125
$\Psi(\text{ele} + \text{ndv} + \text{dnf}) p(\text{can})$	6	658.36	1.16	0.146
$\Psi(\text{ele}) p(\text{can})$	4	659.16	1.96	0.080
$\Psi(\text{ele} + \text{slo} + \text{ndv}) p(\text{can})$	6	659.33	2.13	0.133
$\Psi(1)$	3	659.45	2.25	0.047
$\Psi(\text{slo} + \text{ndv} + \text{dnf}) p(\text{can})$	6	659.68	2.48	0.128
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf}) p(\text{can})$	7	660.13	2.93	0.149
Null model $p(\text{can})$	2	660.59	3.39	0.000
$\Psi(\text{ele} + \text{dnf}) p(\text{can})$	5	660.62	3.42	0.088
$\Psi(\text{ele} + \text{slo} + \text{dnf}) p(\text{can})$	6	660.77	3.57	0.113
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dro}) p(\text{can})$	7	669.29	12.09	0.020
$\Psi(\text{ele} + \text{ndv} + \text{dnf} + \text{dro}) p(\text{can})$	7	675.89	18.69	-0.085
$\Psi(\text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(\text{can})$	7	675.94	18.74	-0.086
$\Psi(\text{ele} + \text{slo} + \text{dnf} + \text{dro}) p(\text{can})$	7	676.10	18.90	-0.089
$\Psi(\text{ele} + \text{slo} + \text{ndv} + \text{dnf} + \text{dro}) p(\text{can})$	8	677.91	20.71	-0.085

¹can, canopy openness; und, understory openness; dnf, nearest distance to non-forest land; ndv, normalized difference vegetation index; ele, elevation; slo, slope; dro, nearest distance to road.

²Akaike information criterion.

³Difference in Akaike information criterion between the corresponding model and the null model.

could be other environmental variables not considered in this study that affected the occupancy and detection probabilities. Bukit Barisan Selatan National Park has an elongated shape, which makes it vulnerable to disturbance from surrounding human-driven land uses (O'Brien et al., 2003), and interior parts of the forest are nevertheless relatively close to forest edges (maxima of 5.3 km in the Intensive Protection Zone and 6.0 km in northern Bukit Barisan Selatan National Park). However, we did not find a strong relationship between sun bear occupancy and nearest distance to modified habitat.

The proportion of area occupied by a species could be correlated with changes in population size (MacKenzie et al., 2002), but this may only be true if the sampling unit size is similar to the home range size of the species. When the sampling unit size is smaller than the home range, an animal is likely to be detected in more than one sampling unit, and hence an increase in area of occupancy could also mean the species is roaming over a larger area because of environmental or behavioural changes. Moreover, stable occupancy of species over time could also occur when the population size decreases and the home range increases. The estimated home range size of a sun bear is $14.8 \pm \text{SD } 6.1 \text{ km}^2$ (Wong et al., 2004), which is larger than the sampling grid size in the Intensive Protection Zone (9.0 km^2).

Therefore, the estimated occupancy of sun bears reported for the Intensive Protection Zone should not be interpreted as an index of population size.

The sun bear detections used in our study were obtained from camera-trap surveys that mainly targeted tigers, and this could have potentially introduced bias because the cameras were set up to maximize tiger detections. However, by-catch offers an opportunity for a region-wide occupancy assessment of sun bears using data collected from tiger surveys. Linkie et al. (2007) suggested the compilation of camera-trap data to determine sun bear occupancy regionally, and this would be possible if the camera traps were installed similarly, as implemented for research on the Asian tapir *Tapirus indicus* across Southeast Asia (Linkie et al., 2013). There have been numerous tiger surveys in Sumatra (especially in national parks) because of the species' flagship status, and these surveys are rich sources of sun bear data. Ministerial coordination would be needed to facilitate the collation of data across surveys. Such data could also be compiled for other threatened species, such as the dhole *Cuon alpinus*, to fill ecological knowledge gaps and to strengthen science-based conservation. We also recommend a multi-species approach, to consider potential interactions amongst coexisting species that could affect their occupancy. Finally, although it is difficult to identify

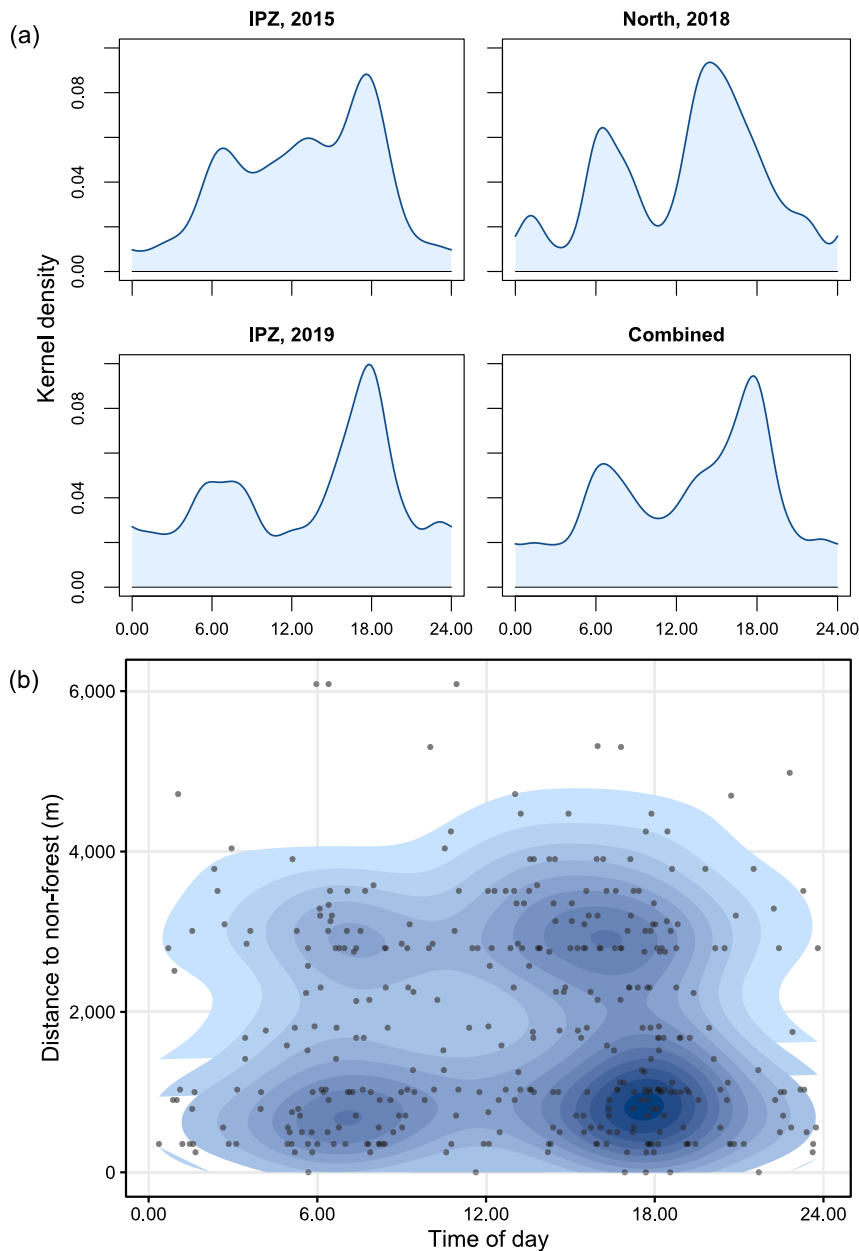


FIG. 3 (a) Kernel density estimation of diel activity patterns of sun bears in the three surveys and combined, and (b) along the gradient of nearest distance to non-forest land.

individuals of species that do not bear characteristic marks such as stripes, comparison of incidental unique features such as scars could be useful to assess the connectivity and movement of species across fragmented habitats.

Author contributions Study conception and design, data preparation and analysis: MCS, IE, RAS; writing: led by MCS, with substantial contributions from all authors.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. Camera-trap surveys were conducted by the Wildlife Conservation Society–Indonesia Program in collaboration with Bukit Barisan Selatan National Park, which granted research permits. An early version of this article was reviewed and approved by the Ministry of Environment and Forestry of the Government of Indonesia. Although our camera traps were set up to capture wildlife, they also unintentionally recorded human activities, including illegal

ones. During the 2018 and 2019 surveys, we placed signs that stated the cameras were deployed for wildlife research. This was done primarily to reduce camera theft, which frequently occurred during the 2015 survey, but also to provide disclosure of the purpose of the research. At the time of the camera-trap surveys, the Wildlife Conservation Society–Indonesia Program and Bukit Barisan Selatan National Park did not yet have formalized procedures to handle photographs of people.

Data availability The data that support the findings of this study are available from the corresponding author with the permission of Bukit Barisan Selatan National Park, which can be requested through the email address btnbbs@gmail.com. Approval from the National Park authority is required to use these data.

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