Terrestrial mammal community richness and temporal overlap between tigers and other carnivores in Bukit Barisan Selatan National Park, Sumatra

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Abstract

Terrestrial mammal community richness and temporal overlap between tigers and other carnivores in Bukit Barisan Selatan National Park, Sumatra. Rapid and widespread biodiversity losses around the world make it important to survey and monitor endangered species, especially in biodiversity hotspots. Bukit Barisan Selatan National Park (BBSNP) is one of the largest conserved areas on the island of Sumatra, and is important for the conservation of many threatened species. Sumatran tigers (*Panthera tigris sumatrae*) are critically endangered and serve as an umbrella species for conservation, but may also affect the activity and distribution of other carnivores. We deployed camera traps for 8 years in an area of Bukit Barisan Selatan National Park (BBSNP) with little human activity to document the local terrestrial mammal community and investigate tiger spatial and temporal overlap with other carnivore species. We detected 39 mammal species including Sumatran tiger and several other threatened mammals. Annual species richness averaged 21.5 (range 19–24) mammals, and remained stable over time. The mammal order significantly affected annual detection of species and the number of cameras where a species was detected, while species conservation status did not. Tigers exhibited a diurnal activity pattern, and had the highest temporal overlap with marbled cats (*Pardofelis marmorata*), dholes (*Cuon alpinus*), and Malayan sun bears (*Helarctos malayanus*), but little overlap with other carnivores. These findings suggest that some smaller carnivores might be adjusting temporal activity to avoid tigers or mesocarnivores. The stable trends in richness of terrestrial mammal species show that BBSNP remains an important hotspot for the conservation of biodiversity.

Key words: Activity patterns, Carnivores, Conservation, Interspecific interactions, *Panthera tigris sumatrae*

Resumen

Riqueza de la comunidad de mamíferos terrestres y solapamiento temporal entre el tigre y otros carnívoros en el Parque Nacional Bukit Barisan Selatan, Sumatra. Debido a la pérdida rápida y generalizada de biodiversidad en todo el mundo, es importante estudiar las especies en peligro de extinción, en especial en zonas de gran biodiversidad, y de hacer un seguimiento de dichas especies. El Parque Nacional Bukit Barisan Selatan (BBSNP en sus siglas en inglés) es una de las mayores zonas de conservación de la isla de Sumatra y es importante para la conservación de muchas especies amenazadas. El tigre de Sumatra (*Panthera tigris sumatrae*) se encuentra en peligro crítico de extinción y sirve de especie paraguas para la conservación, pero también puede afectar a la actividad y la distribución de otros carnívoros. Utilizamos cámaras de trampeo durante 8 años en una zona del Parque Nacional BBSNP con escasa actividad humana, a fin de documentar la comunidad local de mamíferos terrestres y estudiar el solapamiento espacial y temporal del tigre con otras especies de carnívoros. Detectamos 39 especies de mamíferos como el tigre de Sumatra y otros varios mamíferos amenazados. La riqueza anual de especies se situó de media en 21,5 mamíferos (intervalo 19–24) y se mantuvo estable a lo largo del tiempo. A diferencia de la situación de conservación de la especie, el orden de los mamíferos tuvo un efecto significativo en la detección anual de especies y el número de cámaras en las que se detectó una especie. El tigre mostró una pauta de actividad diurna y el mayor solapamiento temporal con el gato jaspeado (*Pardofelis marmorata*), el cuón (*Cuon alpinus*) y el oso malayo (*Helarctos malayanus*), pero poco solapamiento con otros carnívoros. Estos resultados sugieren que algunos carnívoros de menor talla podrían estar ajustando la actividad temporal para

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evitar a los tigres o a mesocarnívoros. La tendencia estable de la riqueza de especies de mamíferos terrestres pone de manifiesto que el BBSNP sigue siendo una zona importante para la conservación de la biodiversidad.

Palabras clave: Pautas de actividad, Carnívoros, Conservación, Interacciones interespecíficas, *Panthera tigris sumatrae*

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Introduction

The effects of humans are widespread and in the past centuries have led to historically high rates of extinction around the world (Pimm et al., 1995; Chapin et al., 1998). In order to guide effective conservation efforts to address biodiversity loss it is important to survey and monitor endangered species and the biodiversity in crucial areas for conservation, such as large protected areas in biodiversity hotspots (Johnson et al., 2009; Gopal et al., 2010). The effects of humans are often strongest on carnivores (Ripple et al., 2014), which occupy high trophic levels and structure ecosystems and community composition through predation and other interspecific interactions (Estes and Palmisano, 1974; McLaren and Peterson, 1994). Carnivores also act as umbrella species as they require large areas for viable populations and through their preservation protect the habitat of many other co–occurring species (Sibarani et al., 2019). Camera trapping is one of the many emerging technologies that is increasingly being used to monitor wildlife (O'Brien, 2008; Karanth and Nichols, 2010), and can be a critical non–invasive tool in documenting cryptic and endangered wildlife (Linkie et al., 2007; Tobler et al., 2008). Surveys of carnivores are important, particularly when they are threatened or endangered, and surveys via camera trap also allow for surveying a diversity of other species.

The Indonesian island of Sumatra is located in one of the global hotspots of biodiversity and represents a conservation priority (Myers et al., 2000). Bukit Barisan Selatan National Park (BBSNP) is one of the largest conserved areas on the island of Sumatra, making it important for the conservation of several critically endangered species (e.g., Sumatran rhinoceros, Dicerorhinus sumatrensis, and Sunda Pangolin, Manis javanica) and subspecies (e.g., Sumatran tigers, Panthera tigris sumatrae; and Sumatran elephant, Elephas maximus sumatranus) (O'Brien and Kinnaird, 1996; Pusparini et al., 2018; Allen et al., 2019). Tigers are an endangered apex carnivore throughout their range (Goodrich et al., 2015), but four subspecies are likely now extinct in the wild (Seidensticker et al., 1973; Goodrich et al., 2015). The Sumatran tiger subspecies is one of the most critically endangered carnivores in the world (Linkie et al., 2008b), and Sumatran tigers serve as an umbrella species for scientific studies and conservation in many areas of their range. As a national park, BBSNP acts as a preserve and stronghold for biodiversity, but there is no buffer between the park and adjacent agriculture, resulting in frequent illegal encroachment into the park (O'Brien and Kinnaird, 1996; Pusparini et al., 2018). Repeated surveys are needed to understand the biodiversity of the park, as well as trends in threatened and endangered populations over time.

The ecology of most carnivore species occurring on Sumatra, including their activity patterns, is poorly studied (Hunter, 2015), but it is important to understand in order to develop effective means for their conservation. The interactions between carnivores are important as the conservation of one species can have detrimental effects on other species, and management plans need to account for interspecific interactions to mitigate these side–effects (Krofel and Jerina, 2016). Camera trapping is frequently used to monitor wildlife, providing a wealth of information on the spatial and temporal activity of species in the local community (Swanson et al., 2015; Rich et al., 2016; Allen et al., 2019). Temporal patterns are important aspects of niche partitioning among sympatric carnivores (Romero–Munoz et al., 2010; Karanth et al. 2017; Herrera et al., 2018), with subordinate carnivores often adjusting their temporal activity to avoid overlap with dominant carnivores (Foster et al., 2013; Lynam et al., 2013; Wang et al., 2015), but not always (Balme et al., 2017; Allen et al., 2018). Determining temporal patterns and overlap among species is a way to inform our understanding of cryptic species and their interactions (e.g., Van Schaik and Griffiths, 1996; Linkie and Ridout, 2011; O'Brien et al., 2003).

We deployed camera traps in BBSNP in Sumatra over eight years to document trends in the local terrestrial mammalian community, as well as temporal overlap between tigers and other carnivores to inform conservation efforts. Our objectives were: (1) Determine the trends in annual mammal species richness, and relative abundance of species in the study area. We hypothesized that trends in richness would be stable due to the relatively short time period of the surveys. We also hypothesized that camera traps would detect higher relative abundances for Artiodactyla than Carnivora which occur at lower densities and primate species due to their arboreal nature. (2) Define factors affecting annual detection for species. We hypothesized that mammals species from lower trophic levels and of lower conservation concern would be detected in more years due to their greater abundance. (3) Compare mammal detections from our camera trapping with previous surveys using track surveys and interviews with local experts from BBNSP by O'Brien and Kinnaird (1996). (4) Determine factors affecting species occupancy. We hypothesized that camera traps would detect higher occupancies for Artiodactyla than Carnivora which occur at lower densities and primate species due to their arboreal nature. We also hypothesized that the conservation status of species would be related to occupancy, with endangered species being detected at fewer cameras then species of less concern. (5) Analyze the temporal overlap of tigers with four other felids and six other carnivores, hypothesizing that subordinate competitor carnivores would have low temporal overlap with the apex predator, the Sumatran tiger (e.g., Lynam et al., 2013; Wang et al., 2015).

Material and methods

Study area

Our study site is located in BBSNP in the South Barisan Range ecosystem on the Indonesian island of Sumatra (fig. 1). BBSNP is the third largest protected area (3,560 km²) on Sumatra (O'Brien and Kinnaird, 1996), spanning two provinces: Lampung and Bengkulu. Topography ranges from coastal plains and lowland rainforest at sea level in the southern peninsula of the park to mountains up to 1,964 m in the middle to northern parts of the park (Pusparini et al., 2018). The park contains montane forest, lowland tropical forest, coastal forest and mangrove forest. Rainfall is most abundant in the monsoon season from November to May, with approximately 3,000–4,000 mm of rainfall (O'Brien et al., 2003); and annual temperatures are between 22 ºC to 35 ºC (O'Brien et al., 2003). BBSNP contains a high diversity of wildlife, with tigers and 76 other species listed in CITES with Endangered to Critical IUCN status.

Field methods

We set camera traps to monitor biodiversity as part of the Tropical Ecology and Assessment Monitoring (TEAM) network for Bukit Barisan (teamnetwork.org). We set two arrays of 30 camera traps placed at a density of 1 camera trap per 2 km^2 (fig. 1) covering a total of 128.43 km^2. We attempted to set each camera trap annually from 2010–2017, and we deployed the camera arrays sequentially rather than simultaneously within the same dry season from April to July (Array 1 from April to May and Array 2 from June to July) to complete at least 30 days of sampling for each point. We placed camera traps in strategic locations on game trails. We set all camera traps in lowland forests, with an elevation range of 16 to 320 m.

Statistical analyses

We defined a detection event as any series of photos triggered by a human or wildlife species. To avoid pseudo–replication, we considered consecutive photo captures of the same species within 30' to be the same event (Rovero and Zimmermann, 2016; Allen et al., 2018). We calculated the number of independent events for each species and relative abundance (RAB) as:

$$RAB = events / trap\ nights \times 1,000$$

and then report the mean annual RAB ($\bar{x}$ RAB) for each species. We calculated annual species richness by totaling the number of unique mammal species detected each year. We also calculated the naïve annual occupancy and mean naïve annual occupancy for each species (Nichols et al., 2007; O'Connell and Bailey, 2011).

We used generalized linear mixed models (GLMMs) to determine if the RAB of species was affected by either their order or conservation status, using the annual RAB of a species as our dependent variable, their order or conservation status as the independent variable, and species as a random effect. We also used GLMs to determine if the number of years a species was detected was affected by either their order or conservation status, using the number of years a species was detected as our dependent variable, their order or conservation status as the independent variable, and species as a random effect. We also compared species richness between our surveys and the previous survey by O'Brien and Kinnaird (1996), using a *t*–test to compare our annual values to the previous value. We then used GLMMS to determine if the occupancy of species varied annually by either their order or conservation status. We used the annual occupancy of a species as our dependent variable, their order or conservation status as the independent variable, and the species as a random effect.

We used kernel density estimation to determine activity patterns and quantify overlap among species (Ridout and Linkie, 2009). We considered interactions with other carnivores for which we obtained > 3 detections. Other felids included Asiatic golden cat (*Catopuma temminckii*), leopard cat (*Prionailurus bengalensis*), marbled cat (*Pardofelis marmorata*), and Sunda clouded leopard (*Neofelis diardi*). Other carnivores included banded linsang (*Prionodon linsang*), banded palm civet (*Hemigalus derbyanus*), binturong (*Arctictis binturong*), dhole (*Cuon alpinus*), masked palm civet (*Paguma larvata*), and sun bear (*Helarctos malayanus*). We changed the time of each event to radians for each species, and then used the overlap package (Meredith and Ridout, 2017) in program R version 3.3.1 (R Core Team, 2016) to fit the data to a circular kernel density and estimated the activity level at each time period from the distribution of the kernel density. We then used the overlapEst function to test for the degree of overlap in activity patterns between tigers and the other species using their Δ_1 scores (where a higher score indicates more overlap). We calculated 95 % confidence intervals by bootstrapping 10,000 estimates of activity for each species, and then using the bootEst and bootCI functions to estimate overlap between each species pair based on the boot0 score.

Results

Sixty camera traps functioned from 2010 to 2017 for a total of 11,896 trap nights, registering 53,120 photos, representing 3,245 independent detection events of 49 species. We detected one critically endangered species, Sunda pangolin ($\bar{x}$ RAB = 1.31), and two critically endangered subspecies, Sumatran tiger ($\bar{x}$ RAB = 2.41) and Sumatran elephant ($\bar{x}$ RAB = 1.42), as well as with seven endangered species and seven vulnerable species (table 1). We found that the mammal order had a significant effect on the relative abundance of species, with Artiodactyla species having higher RAB ($\bar{x}$ = 28.81) than Carnivora species ($\bar{x}$ = 0.78, F = –3.55, p = 0.0004), but not other orders (p > 0.12). The conservation status of species, however, did not have a significant effect on the relative abundance of species (p > 0.51).

Our observed annual species richness averaged 21.5 (range 19–24) mammals, with a relatively stable trend that did not vary significantly across time (df = 7, F = 0.91, p = 0.37). We documented eight species in all eight years, three species in seven years; but nine species were detected in only one year. We found

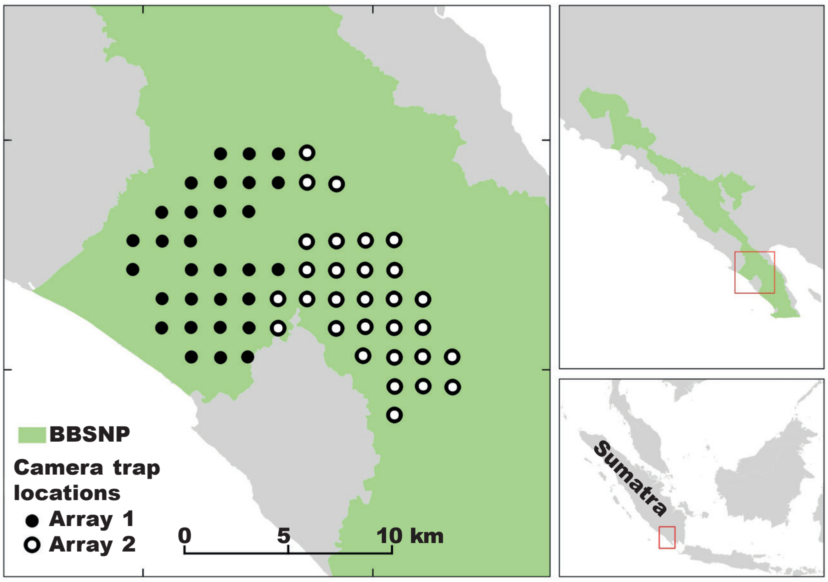

Fig. 1. Study site within Bukit Barisan National Park on the island of Sumatra (BBSNP), and camera trap arrays. We did not display the coordinate reference grids because of conservation concerns and some of the recorded species are hunted for illegal wildlife trading.

Fig. 1. Zona del estudio dentro del Parque Nacional Bukit Barisan en la isla de Sumatra (BBSNP) y disposición de las cámaras de trampeo. No se muestran las cuadrículas de coordenadas de referencia por motivos de conservación y porque algunas de las especies son objeto de caza para el comercio ilegal.

that the mammal order had a significant effect on the number of years detected, with Artiodactyla species found in more years ($\bar{x}$ = 6.50) than Carnivora species ($\bar{x}$ = 3.33, F = –2.81, p = 0.005), but not other orders (p > 0.08) including Eulipotyphla ($\bar{x}$ = 6.00), Perissodactyla ($\bar{x}$ = 8.00), Pholidota ($\bar{x}$ = 7.00), Primates ($\bar{x}$ = 4.00), Proboscidea ($\bar{x}$ = 6.00), Rodentia ($\bar{x}$ = 4.75), or Scandentia ($\bar{x}$ = 4.00). The conservation status of species, however, did not have a significant effect on how many years a species was detected (p > 0.53).

The number of species we observed in any given year did not vary significantly from the previous surveys by O'Brien and Kinnaird (1996) (df = 7, p = 0.77). We detected 39 mammal species, 26 (excluding humans and domestic dogs) of which had not been documented in previous surveys by O'Brien and Kinnaird (1996); but we did not detect eight mammal species which had previously been detected (table 1). We found that the species' order had a significant effect on their occupancy, with Artiodactyla species having significantly higher mean annual occupancy ($\bar{x}$ = 0.28) than Carnivora ($\bar{x}$ = 0.02, T = –3.62, p = 0.0003), but not other orders (p > 0.08). The conservation status of species, however, did not have a significant effect on how many cameras they were documented at annually (p > 0.59).

Tigers exhibited a diurnal activity pattern (fig. 2, 3). We documented four other felid species, all with lower relative abundance than tigers. Marbled cats had a peak of activity in the morning and were active during the day, leading to the highest overlap with tigers (fig. 2). Asian golden cats were crepuscular with their highest activity at dawn, leading to some overlap with tigers, while leopard cats and Sunda clouded leopards were primarily nocturnal and had little overlap with tigers (fig. 2).

We documented six other carnivore species, with banded palm civets and sun bears having higher RAB than tigers. Dholes were diurnal and had the highest temporal overlap with tigers, while Malayan sun bears were cathemeral and had less overlap with tigers. Banded linsangs, banded palm civets, binturongs, and masked palm civets were primarily nocturnal and exhibited little overlap with tigers (fig. 2).

Discussion

BBSNP and other protected areas in Sumatra contain many threatened and endangered species whose populations are imperiled primarily by encroachment and habitat destruction. Effective conservation for species or ecological communities is dependent on international teamwork among government agencies, local communities, and scientific organizations. Using camera trap surveys, we were able to monitor numerous mammal species, including critically endangered Sunda pangolins, Sumatran tigers and Sumatran elephants, along with over a dozen other threatened

Table 1. Mammal species, IUCN status (IUCN: EN, endangered; NT, near threatened; VU, vulnerable;; LC, least concern; CE, critically endangered; NE, not evaluated), number of years documented (N), mean annual relative abundance ($\bar{x}$RAB), mean annual percent area occupied ($\bar{x}$PAO), and whether the species was documented in previous surveys O'Brien and Kinnaird (1996), last column: * subspecies critically endangered

*Tabla 1. Especie de mamífero, situación de la UICN, número de años documentado (N), abundancia media anual relativa ($\bar{x}$RAB), superficie media ocupada anual ($\bar{x}$PAO) y si la especie se había documentado en estudios anteriores O'Brien y Kinnaird (1996), en la última columna: * subespecies en peligro crítico. (Para las abreviaturas de la situación de la IUCN, véase arriba).*

Common name	Scientific name	IUCN	N	$\bar{x}$RAB	$\bar{x}$PAO	
Tiger	*Panthera tigris*	EN*	6	2.41	0.05	Yes
Asian golden cat	*Catopuma temminckii*	NT	6	0.88	0.03	No
Marbled cat	*Pardofelis marmorata*	NT	4	0.6	0.02	No
Sunda clouded leopard	*Neofelis diardi*	VU	3	0.39	0.01	Yes
Leopard cat	*Prionailurus bengalensis*	LC	7	1.07	0.03	No
Oriental small–clawed otter	*Aonyx cinerea*	VU	1	0.10	< 0.01	No
Binturong	*Arctictis binturong*	VU	2	0.34	0.01	No
Small–toothed palm civet	*Arctogalidia trivirgata*	LC	1	0.07	< 0.01	No
Domestic dog	*Canis familiaris*	NE	2	0.15	< 0.01	No
Dhole	*Cuon alpinus*	EN	2	0.33	0.01	No
Otter civet	*Cynogale bennettii*	EN	1	0.07	< 0.01	No
Malayan sun bear	*Helarctos malayanus*	VU	7	2.61	0.07	Yes
Banded palm civet	*Hemigalus derbyanus*	NT	6	2.68	0.07	No
Short–tailed mongoose	*Herpestes brachyurus*	NT	1	0.11	0.00	No
Eurasian otter	*Lutra lutra*	NT	1	0.08	< 0.01	No
Hairy–nosed otter	*Lutra sumatmna*	EN	0	0.00	0.00	Yes
Yellow–throated marten	*Martes flavigula*	LC	1	0.07	0.00	No
Asian palm civet	*Paradoxurus hermaphroditus*	LC	1	0.11	< 0.01	No
Masked palm civet	*Paguma larvata*	LC	6	0.83	0.03	No
Banded linsang	*Prionodon linsang*	LC	4	0.43	0.01	No
Domestic water buffalo	*Bubalus bubalis*	NE	0	0.00	0.00	Yes
Plantain squirrel	*Callosciurus notatus*	LC	0	0.00	0.00	Yes
Sumatran serow	*Capricornis sumatraensis*	VU	3	0.32	0.01	No
Sumatran rhinoceros	*Dicerorhinus sumatrensis*	CE	0	0.00	0.00	Yes
Moonrat	*Echinosorex gymnura*	LC	6	2.34	0.05	No
Sumatran elephant	*Elephas maximus*	EN*	6	1.42	0.03	Yes
Human	*Homo sapiens*	NE	5	1.24	0.03	No
Dark–handed gibbon	*Hylobates agilis*	EN	0	0.00	0.00	Yes
Common porcupine	*Hystrix brachyura*	LC	8	30.34	0.33	No
Three–striped ground squirrel	*Lariscus insignis*	LC	8	9.95	0.10	No
Long–tailed macaque	*Macaca fascicularis*	LC	3	0.24	0.01	Yes
Pigtail Macaque	*Macaca nemestrina*	VU	8	43.76	0.63	No
Sunda pangolin	*Manis javanica*	CE	7	1.31	0.04	No
Red muntjac	*Muntiacus muntjak*	LC	8	71.99	0.71	Yes

Table 1. (Cont.)

Common name	Scientific name	IUCN	N	$\bar{x}$ RAB	$\bar{x}$ PAO	
Sumatran surili	*Presbytis melalophos*	EN	4	0.48	0.02	Yes
Flying fox	*Pteropus vampyrus*	NT	0	0.00	0.00	Yes
Black giant squirrel	*Ratufa bicolor*	NT	0	0.00	0.00	Yes
Sambar deer	*Rusa unicolor*	VU	8	9.69	0.18	Yes
Horse–tailed squirrel	*Sundasciurus hippurus*	NT	1	0.07	< 0.01	No
Wild boar	*Sus scrofa*	LC	8	29.4	0.39	Yes
Siamang	*Symphalangus syndactylus*	EN	1	0.14	< 0.01	Yes
Malayan tapir	*Tapirus indicus*	EN	8	8.07	0.15	Yes
Silvery lutung	*Trachypithecus cristatus*	NT	0	0.00	0.00	Yes
Lesser mouse deer	*Tragulus kanchil*	LC	4	21.99	0.23	No
Greater mouse deer	*Tragulus napu*	LC	8	12.55	0.17	No
Long–tailed porcupine	*Trichys fasciculata*	LC	2	0.63	0.01	No
Large treeshrew	*Tupaia tana*	LC	4	1.37	0.03	No

or endangered mammals. Tigers are threatened and declining worldwide (Seidensticker, 2010; Walston et al., 2010), and protected areas, including BBSNP, are important for their populations (Kawanshi and Sunquist, 2004, Wibisono et al., 2009) our surveys showed the importance of BBSNP to the critically endangered tiger population in Sumatra. High species richness of terrestrial mammal species, which remained similar across the eight years of our survey, also confirms the conservation value of BBSNP and other protected areas for other threatened and endangered mammal species (Linkie et al., 2008a).

Camera trapping is an informative way to gather ecological data, especially for cryptic or rare species, but is best used in conjunction with other surveys. The project documented 26 mammal species with camera trap surveys that had not been detected by O'Brien and Kinnaird (1996) in a previous survey using transects and interviews with local citizens, but our survey missed eight that had been previously documented. The additional species we identified were primarily terrestrial species, while the ones not documented were primarily arboreal species. Both survey methods detected a similar number of species in any given annual survey, though not the same species. Each method has costs and benefits that should be considered in future studies. Camera trapping is effective for documenting terrestrial cryptic mammal species, and can be used 24 hours a day over weeks or months, while transect surveys are more effective for documenting birds and amphibians. There is the possibility of misidentification of photographs or signs with either method, although misidentification should be less frequent for photographs. Using both methods in conjunction is a good approach to document the mammal community, especially in such a critically important area for conservation.

Tigers exhibited diurnal activity patterns and had moderate temporal overlap with marbled cats, dholes, and sun bears, but most other carnivores had little temporal overlap with tigers. Sun bears are known for their arboreal habits and insectivorous–frugivorous diet, and therefore have less overlap in dietary and spatial use with tigers, but are also generally diurnal throughout their range (Fitzgerald and Krausman, 2002). Common leopards (*Panthera pardus*) were extirpated from Sumatra, and now dholes and Sunda clouded leopards are the other carnivores nearest to tigers in size, and may be their closest competitors. Sympatric carnivores that are smaller than their competitors use adaptive strategies, including temporal avoidance, to exploit the same resources and avoid intra–guild predation (Lesmeister et al., 2015; Wang et al., 2015). Contrary to our hypothesis, dholes were also diurnal and exhibited greater temporal overlap with tigers than we expected. This may be due to lack of fear of tigers on the part of dholes (e.g., Burton, 2019). Among felids, Sunda clouded leopards and leopard cats were nocturnal, while Asian golden cats and marbled cats were crepuscular, which is generally in accordance with previous studies (Van Schaik and Griffiths, 2009; Grassman et al., 2005). Temporal patterns and overlap can be complex in ecosystems with many carnivores, as competitive suppression of mesocarnivores by apex carnivores can release subordinate small carnivores from competitive pressure (e.g., Levi and Wilmers, 2012; Wang et al., 2015; Allen et al., 2017), but species are most likely to avoid the species that they perceive as the greatest threat. For example, marbled cats had a high

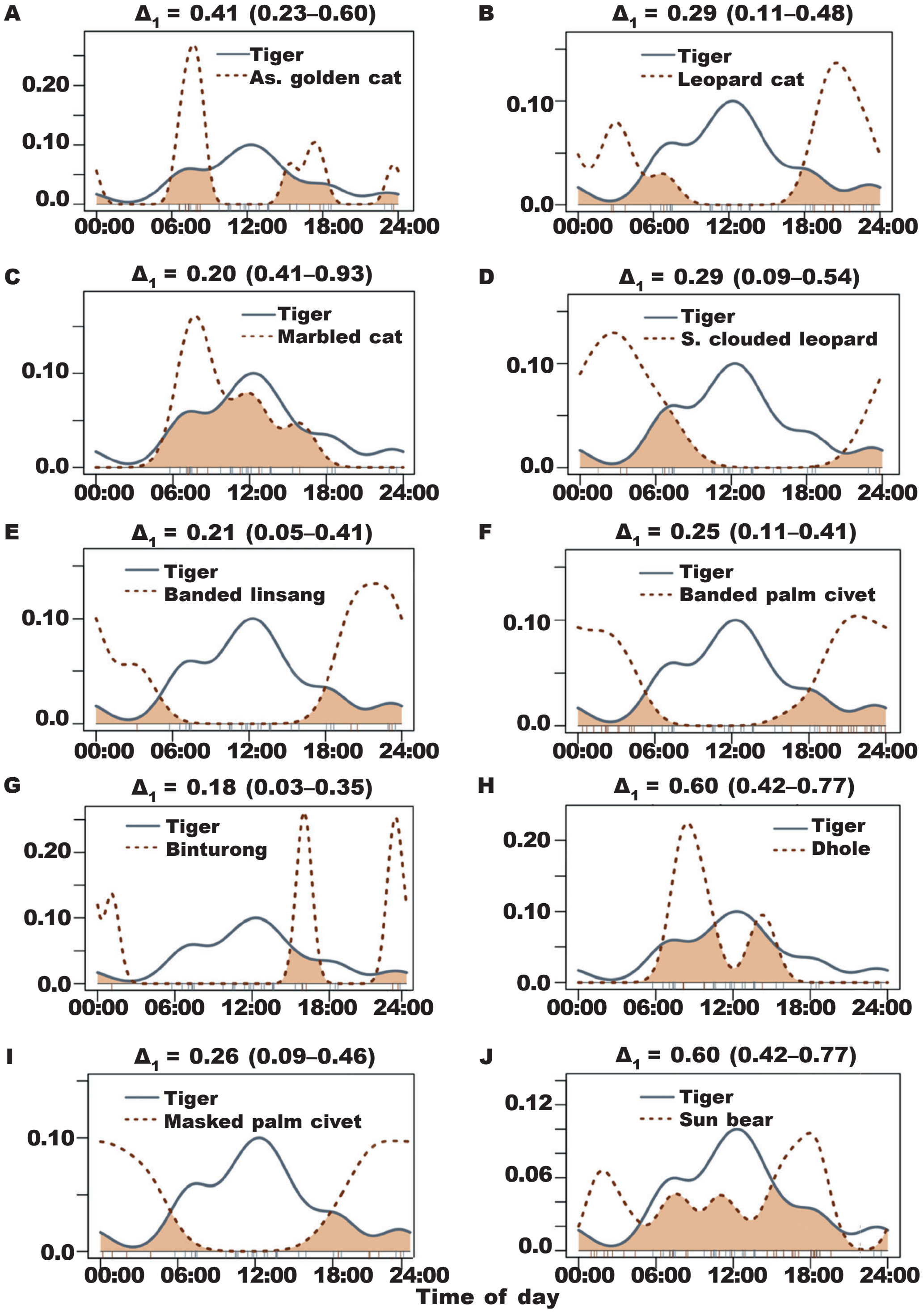

Fig. 2. Temporal activity and overlap (kernel density), of tigers and other carnivores: A, Asian golden cat; B, leopard cat; C, marbled cat; D, Sunda clouded leopard; E, banded linsang; F, banded palm civet; G, binturong; H, dhole; I, masked palm civet; J, sun bear. Tiger activity is represented as a solid line and the other carnivore activity as a dotted line, and temporal overlap as the shaded area.

Fig. 2. Actividad temporal y solapamiento (densidad de kernel) del tigre y otros carnívoros: A, gato dorado asiático; B, gato de Bengala; C, gato jaspeado; D, pantera nebulosa de Borneo; E, linsang rayado; F, civeta de las palmeras rayada; G, binturong; H, cuón; I, civeta de las palmeras enmascarada; J, oso malayo. La actividad del tigre se representa con una línea continua y la de los otros carnívoros con una línea discontinua; el solapamiento temporal es la superficie sombreada.

degree of overlap with tigers, and this may be due to temporally avoiding Sunda clouded leopards. Sunda clouded leopards are also arboreal, which increase the probability of encounters with marbled cats and may thus be perceived as a more direct threat. The temporal patterns and overlap among the carnivore community suggest that tigers may be structuring the carnivore guild, but smaller carnivores may also use different resources (prey and habitat) as a means of limiting competition and overlap with tigers (Karanth et al., 2017).

Camera trapping surveys using TEAM protocols appear effective for monitoring the richness and relative abundance of the terrestrial mammal community, but may best be used in conjunction with other survey methods. Our surveys focused on terrestrial mammals, but camera trapping can also be effective for arboreal species with appropriate adjustments (Gregory et al., 2014). The TEAM protocol is set for short bursts (one month) of camera trapping, and to be effective for monitoring threatened and endangered terrestrial species. Surprisingly, the conservation status of species did not predict the number of years they were detected, relative abundance or occupancy. This may be due to the inherent differences in abundance among species of different trophic levels, or because species can be locally abundant but of conservation concern globally. Our surveys also highlight the importance of BBSNP and other parks for biodiversity and many endangered species, and there is much potential to use BBSNP for future species–specific surveys, including for critically endangered Sunda pangolins, Sumatran tigers or Sumatran elephants. The development of new analyses, such as kernel density overlap (Ridout and Linkie, 2009), help us understand the ecological interactions of species, and development of new techniques in the future should be used for further understanding cryptic species.

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