Predicting preferred prey of Sumatran tigers (*Panthera tigris sumatrae*) via spatiotemporal overlap

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Abstract

The encounter rates carnivores have with prey are dependent on spatial and temporal overlap, and are often highest with their preferred prey. Sumatran tigers *Panthera tigris sumatrae* are critically endangered and dependent on prey populations, but little is known about their prey preferences. We collected 7 years of camera trapping data from Bukit Barisan Selatan National Park to investigate spatial and temporal overlap of tigers with potential prey species. We also developed a novel method to predict predator-prey encounter rates and potential prey preferences from camera trapping data. We documented a minimum of 10 individual tigers with overall relative abundance of 0.24 detections/100 trap nights for the population. Tigers exhibited a diurnal activity pattern and had highest temporal overlap with wild boar *Sus scrofa* (Δ_1 = 0.80) and pigtail macaques *Macaca nemestrina* (Δ_1 = 0.76), but highest spatial overlap with wild boar (AUC = 0.71) and sambar deer *Rusa unicolor* (AUC = 0.66). We created a spatial and temporal composite score and three additional composite scores for adjusted spatial weight and preferred prey mass, and each indicated tigers had the greatest overlap with wild boars followed by sambar deer, their known preferred prey in other areas. Spatial and temporal overlaps are often considered as separate indices, but a composite score may allow better predictions of encounter rates and potential prey preferences. Our findings suggest that prey management efforts in this area should focus on wild boar and sambar deer to ensure a robust prey base for this critically endangered tiger population.

Keywords: activity patterns, composite score, *Panthera tigris*, prey preference, spatial overlap, Sumatra, temporal overlap, tiger

Introduction

Interspecific interactions are important aspects of community ecology, affecting the functional ecology of ecosystems and dictating the ecological niches inhabited by species (Begon et al., 2006). Interactions can be difficult to assess with wildlife, however, especially with cryptic species such as carnivores (Allen et al., 2016; Saggiomo et al., 2017). The encounter rates of carnivores with prey are dependent on their spatial and temporal overlap, and high encounter rates are often a key component of prey preference (Holling, 1959; Fortin et al., 2015). Knowing spatiotemporal overlap of apex carnivores with potential prey may therefore allow inference into prey preferences, as well as patterns in interspecific interactions that can be critical to understanding the ecological functions of an ecosystem and inform effective conservation. Camera trapping is a non-invasive method that is increasingly being used to monitor wildlife and provides a wealth of information on the species richness, behavior, and spatiotemporal activity in given area (Swanson et al., 2015; Rich et al., 2016; Allen et al., 2017).

Tigers *Panthera tigris* are an endangered apex carnivore throughout their range, with four subspecies likely extinct in the wild (Seidensticker et al., 2010; Goodrich et al., 2015). The Sumatran tiger subspecies *P. tigris sumatrae* is critically endangered (Linkie et al., 2008), as are many other species in the Indonesian island of Sumatra (O'Brien & Kinnaird, 1996; Pusparini et al., 2018). Abundance of prey can have strong effects on the abundance and population density of tigers (Karanth et al., 2004; Barber-Meyer et al., 2012), and tiger declines have been linked to declines of prey in Russia and India (Miquelle et al., 1999; Ramakrishnan et al., 1999). The prey preferences of tigers in many areas are unknown, but they are important to inform conservation goals and ensure there is enough prey available in areas critical to tiger conservation. Understanding spatial and temporal patterns and overlap among tigers and prey is a potential method to improve scientific knowledge of the prey preferences of this cryptic and critically endangered subspecies with limited information about its diet (e.g., Linkie & Ridout, 2011; O'Brien et al., 2003).

Bukit Barisan Selatan National Park (BBSNP) is one of the largest conserved areas on the island of Sumatra, making it critical for the conservation of Sumatran tigers, and other species including the endangered Sumatran rhinoceros *Dicerorhinus sumatrensis* and Sumatran elephant *Elephas maximus sumatranus* (O'Brien & Kinnaird, 1996; Pusparini et al., 2018). In a review of tiger conservation objectives, BBSNP was considered an area with relatively abundant tiger habitat that had moderate to high levels of threat for the population because of inadequate conservation measures (Sanderson et al. 2010). Given the importance of BBSNP to tiger conservation, it is important to understand their ecology in this area. Previous studies of activity patterns of Sumatran tigers in the BBSNP gave conflicting results; O'Brien et al. (2003) reported that tigers had a diurnal activity pattern, while Pusparini et al. (2018) reported that tigers had a crepuscular activity pattern with highest activity near dawn. The prey preferences of tigers and abundance of prey is also unknown in the area, but is essential for supporting a robust tiger population. The conflicting reports and lack of information on prey and prey preferences indicate that further research on Sumatran tiger ecology is needed.

We used 7 years of camera trapping data from an area of BBSNP with little human activity to investigate tiger spatiotemporal overlap with potential prey species to inform conservation efforts. Our objectives included: 1) Document the minimum number of individual tigers. 2) Determine the a) temporal overlap and b) spatial overlap of tigers with six potential prey types. 3) Create a composite score from the indices of temporal and spatial overlap as a novel method to predict predator-prey encounter rates and determine potential prey preference. In our analyses of prey species, we included every known tiger prey species in the study area based on a review of tiger dietary studies by Hayward et al. (2012). Based on tiger prey preferences from the studies reviewed from across the range or tigers, we expected sambar deer (*Rusa unicolor*) and wild boar (*Sus scrofa*) to have the highest composite spatiotemporal score.

Materials and Methods

Study Area

Our study site is in BBSNP in the South Barisan Range ecosystem on the Indonesian island of Sumatra (Figure 1). BBSNP is the third largest protected area (3,560 km²) on Sumatra (O'Brien & 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 3000–4000 mm of rainfall (O'Brien et al., 2003); and annual temperatures are between 22°C to 35°C (O'Brien et al., 2003). BBSNP contains a high diversity of wildlife, with tigers and 76 other species listed in CITES with Endangered to Critically Endangered IUCN status.

Field Methods

We set camera traps in BBSNP as part of the Tropical Ecology and Assessment Monitoring (TEAM) Network, which collects long-term biodiversity data in tropical environments globally to guide conservation actions. Our goal with camera traps was to monitor the terrestrial vertebrate community, and we designed our setup to effectively monitor multiple species (Rich et al., 2019). We set two arrays of 30 camera traps using TEAM protocols (TEAM Network, 2011) in sites chosen for accessibility for long-term repeated surveys. We placed camera traps in each array at a density of 1 camera trap per 2 km^2 (Figure 1), and the arrays covered a total of 128.43 km^2. We attempted to set each camera trap annually from 2010-2016, and we deployed the camera trap 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 near animal trails and/or places used regularly by wildlife. We placed camera traps 30-50 cm off the ground with no refractory period between images. We set all camera traps in lowland forests, with an elevation range of 16 to 320 m.

Statistical Analyses

To avoid pseudo-replication, we considered consecutive photo captures of the same species within 30 minutes to be the same detection event (Rovero & Zimmermann, 2016). We calculated the number of independent events for each species for our analyses, but we lumped both mouse deer species (greater mouse deer *Tragulus napu*, and lesser mouse deer *Tragulus kanchil*) into one category based on their similarity as prey and the difficulty in identifying them correctly to the species level from camera trap images (e.g., O'Brien et al., 2003).

We determined a relative abundance index (RAI) as a proxy for abundance for tigers, because RAI has been found to be a more accurate proxy for abundance than occupancy values (Parsons et al., 2017). We calculated the RAI as

$$\textit{relative abundance index} = (\textit{events/trap nights}) \times 100$$

for each camera trap to determine detection events per 100 trap nights (e.g., Allen et al., 2018), and averaged the values from all camera traps to determine an overall mean for the study area. We also used the stripe patterns of individual tigers to identify the minimum number of individuals based on each flank.

We used kernel density estimation to determine activity patterns and quantify overlap among species (Ridout & Linkie, 2009). We reviewed potential prey species for tigers from Hayward et al. (2012) and analyzed those in our study area with >75 events, which included mouse deer spp. (n = 340), Malay tapir *Tapirus indicus* (n = 85), pigtail macaque *Macaca nemestrina* (n = 433), red muntjac *Muntiacus muntjac* (n = 711), sambar deer (n = 102), and wild boar (n = 302). We first changed the time of each event to radians for each species. We then used the *overlap* package (Meredith & 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 using Δ_1 based on our sample sizes. We then used the *overlapEst* function to estimate the degree of overlap in activity patterns between tigers and the potential prey species. We calculated confidence intervals (CI) by bootstrapping 10,000 estimates of activity for each species, and then using the *bootEst* and *bootCI* functions to estimate 95% CI for the overlap between tigers and each potential prey type.

To determine spatial overlap with potential prey species we used the methods of Ngoprasert et al. (2012). We first calculated RAI values for each prey species as done above for tigers, and then scaled the

RAI values for each prey species at each camera trap site to continuous probability values ranging from 0.0 to 1.0 (Ngoprasert et al., 2012), with higher value indicating a higher probability of occurrence. We then created a logistic regression for each prey species using data from each camera trap location. In the logistic regression we used tiger presence as our dependent variable and the probability values of the prey as our independent variable. We then compared spatial overlap of prey species using the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Fielding & Bell, 1997), and quantified the spatial overlap of tigers with given prey species as the AUC values (which range from 0.5 [random] to 1.0 [perfect fit]).

To ease interpretation of how prey species may be grouped we plotted the spatial and temporal overlap of tigers with each potential prey species. The upper right quadrant indicate the most encountered and potentially most preferred prey species (high spatial and high temporal overlap), while the upper left (high temporal but low spatial overlap) and the lower right quadrants (low temporal but high spatial overlap) would indicate potential alternative prey that were encountered opportunistically in space or time and the lower left quadrant (low spatial and low temporal overlap) would indicate species rarely encountered and likely not preferred.

Last, we averaged the spatial and temporal overlap values for each prey species to create a composite (spatial and temporal composite; STC) score (Song et al., 2013) and rank the preference for potential prey species with higher scores indicating higher encounter rate and potentially higher preference.

We hypothesized that this simple composite score could be improved by giving additional weight to variables or including other variables in the score. Because our tiger prey preference in the area is unknown, we included minor 10% adjustments for three other composite scores to determine how they may affect the ranks of potential prey. First, we gave more weight to the spatial value, as spatial overlap with prey is an important aspect of niche selection and resource partitioning for carnivores (Schoener, 1974; du Preez et al., 2017) and may be better predictor of prey species being sought out compared to temporal overlaps. We calculated the spatial adjusted composite (SAC) score as:

(spatial overlap x 0.6) + (temporal overlap x 0.4)

Second, we considered a composite score that also included prey mass, where we considered a benefit (*STC x 1.1*) for prey that have a mass within the preferred size of tigers (60-250 kg; Hayward et al., 2012) and a penalty (*STC x 0.9*) for prey that were outside of the preferred size. We followed the methods of Hayward et al., (2012), by using three-quarters of the mean weight given for adult females to account for young animals being eaten, and used the mass values as reported by Nowak, (1999). We then calculated this mass adjusted composite (MAC) score as:

(spatial overlap x temporal overlap) x mass adjustment

Last, we also calculated a value for a model with the spatial and mass adjusted composite (SMAC) score as:

((spatial overlap x 0.6) + (temporal overlap x 0.4)) x mass adjustment

We then ranked each potential prey species based on each composite scores, with higher scores indicating higher encounter rate and potentially higher preference.

Results

We had 60 camera traps functioning from 2010 to 2016 for a total of 10,018 trap nights and obtained 45,444 photos of 48 species, including 37 mammals. We documented all 6 potential tiger prey species in all 7 years of the study. We detected a total of 10 human events in 4 different years (2012=1, 2013=2, 2015=4, 2016=3), and one domestic dog event in 2016.

We documented a total of 27 tiger events (2010=6, 2011=4, 2012=5, 2013=4, 2014=5, 2015=3, 2016=0), with an overall relative abundance of 0.24 (± 0.08 SE) detections/100 trap nights per camera trap. Based on left flank events we detected a minimum of 10 individual tigers and based on right flank events we detected a minimum of 8 individual tigers (Supplementary Material 1).

We documented 1,987 events of the potential prey species ($RAI_{\text{mouse deer spp.}}$ = 3.39, $RAI_{\text{pigtail macaques}}$ = 4.32, $RAI_{\text{red muntjac}}$ = 7.10, RAI_{sambar} = 1.02, RAI_{tapir} = 0.85, and $RAI_{\text{wild boar}}$ = 3.15). Tigers exhibited a diurnal activity pattern (Figure 2), and had highest temporal overlap with wild boar (Δ_1 = 0.80, 95% CI =

0.72-0.96) and pigtail macaques (Δ_1 = 0.76, 95% CI = 0.57-0.97) (Figure 2, Table 1). Temporal overlap with other potential prey species included sambar deer (Δ_1 = 0.70, 95% CI = 0.54-0.83), red muntjac (Δ_1 = 0.68, 95% CI = 0.54-0.79), mouse deer (Δ_1 = 0.62, 95% CI = 0.48-0.75), and tapirs (Δ_1 = 0.43, 95% CI = 0.27-0.58). Tigers had the highest spatial overlap with wild boar (AUC = 0.71, Table 1) and sambar deer (AUC = 0.66), followed by pigtail macaque (AUC = 0.60), red muntjac (AUC = 0.57), mouse deer (AUC = 0.53) and tapir (AUC = 0.52).

When plotting the potential prey species, wild boar and sambar deer occurred in the upper right quadrant for potential preferred prey, tapirs in the lower left quadrant for potential non-preferred prey, while each of the other prey species occurred in the upper left (high temporal but low spatial overlap) indicating potential alternative prey (Figure 3).

Our STC scores indicated tigers had the greatest spatiotemporal overlap with wild boars (STCS = 0.76; Table 1), which had an 11% greater score than the next highest species (sambar, STCS = 0.68, and pigtail macaques, STCS = 0.68).

Our SAC scores had a similar pattern as our STC score, with wild boars having the highest rank (SAC = 0.77, Table 1), which was 13% greater than the species with the next highest score, and with sambar and pig-tailed macaques having relatively equal values (Table 1). Our MAC scores also indicated that wild boars (MAC = 0.83, Table 1) had the highest rank, with an 11% greater score than the next species. However, the MAC scores showed that sambar (MAC = 0.75) had a 22% greater score than pig-tailed macaques (MAC = 0.61), and was more in line with our predictions for tiger prey preference. Our SMAC scores were similar to our MAC scores, with wild boar (SMAC = 0.84) being 13% greater than sambar (SMAC = 0.74), and sambar being 24% greater than pig-tailed macaques (SMAC = 0.60).

Discussion

Tigers are of special importance as a flagship species for the conservation movement, but are still threatened worldwide (Walston et al., 2010; Seidensticker, 2010; Sibarani et al., 2019), and Sumatran tigers are critically endangered (Linkie et al., 2008). Tiger populations in BBSNP, in Sumatra, and other areas throughout the world are threatened by encroachment and habitat destruction (O'Brien & Kinnaird, 1996; Pusparini et al., 2018), or by poaching of tigers and/or their prey (Linkie et al., 2003, 2008). Effective conservation for any species is dependent on teamwork among countries, government agencies, local communities, and scientific organizations. The TEAM Network is focused on the open sharing of the scientific data it collects and can be used as a model for sharing of data among scientists for conservation.

We found that tigers exhibited diurnal activity patterns, and we created a composite score of spatial and temporal patterns of overlap with potential prey species to inform prey preference and inform tiger conservation (e.g., Karanth et al. 2004; Barber-Meyer et al. 2012). Previous studies of activity patterns of the Sumatran tiger in the same area gave conflicting results as either diurnal (O'Brien et al. 2003) or crepuscular with highest activity near dawn (Pusparini et al. 2018). Our study had lower sample sizes of tiger events than either previous study, but appears to confirm the diurnal activity pattern observed by O'Brien et al. (2003). Potential reason for differences could be due to different sampling techniques, individual variation in behavior, or interactions with humans or other species in different parts of the park. For example, Pusparini et al. (2018) found high rates of illegal human activity (humans with guns), and relative abundances (RAI = 0.99) that were an order of magnitude higher than in our study (RAI = 0.10), which may have caused tigers to change their activity patterns to avoid the threat of humans (e.g., Clinchy et al., 2016). Considering the importance of conserving Sumatran tigers, it is important for future research to understand and attempt to ascertain reasons for these conflicting results from the same park and subpopulation.

A high degree of spatiotemporal overlap does not necessarily indicate prey preference, but it suggests potential for encounter rates between carnivores and their prey, which is a key component of prey preference (Holling, 1959; Fortin et al., 2015). Temporal overlap has been posited as a way of determining prey preferences (Linkie & Ridout, 2011), however, this likely provides an incomplete picture without including spatial overlap (e.g., O'Brien et al., 2003), or other factors including body size and potential avoidance strategies by prey species. We created four composite index scores that simultaneously included both temporal and spatial overlap. Each composite score which appears to accurately rank prey preference of tigers in BBSNP (wild boar and sambar deer as we predicted based on the review by Hayward et al. [2012]) in a simple and effective manner. Our STC score was effective, but including preferred prey mass (as the MAC score) enabled the composite score to better separate sambar and pig-tailed macaques, as we predicted for the preferred prey species of tigers. In our adjusted composite scores we used small (10%) adjustments, but future studies in areas with known prey preferences could conduct sensitivity analyses to determine ideal weighting adjustments to use spatial and temporal composite scores to determine prey preference.

Each of our composite scores mostly indicated the same ranks among potential prey species (with the one exception of tapir having a higher rank than mouse deer in the SMAC score), with wild boar followed by sambar deer. Sambar deer and wild boar are frequently the preferred prey of tigers throughout their range (Basak et al., 2016; Hayward et al., 2012; Seidensticker & McDougal, 1993), and the greater overlap and composite scores for wild boar in this study site may be due to wild boar having a relative abundance approximately three times greater than sambar deer. Species with higher abundance are likely more widely-distributed across the landscape, which could inflate their spatial overlap with predators and potentially overestimate prey preference. Red muntjac, pigtail macaque and mouse deer were indicated as potential alternative prey species with intermediate composite index scores and position in the upper left quadrant on our plot (Figure 3), which indicates high temporal but low spatial overlap with tigers. As expected, tapirs were in our rarely encountered prey category, which also corresponds to the literature data as being infrequent and non-preferred prey of tigers (Hayward et al., 2012). Based on these results we suggest that conservation efforts in the area should be focused on wild boar and sambar deer to ensure a robust prey base for this tiger population. We have found evidence of illegal snares set for sambar deer in the BBSNP, suggesting direct conservation efforts may be necessary.

Prey preference is usually assessed using the ratio of prey killed vs. prey available, and our study shows a possible alternative method to predict prey encounter rates and preference. Determining the amount of prey killed or amount of prey available can be costly and time-intensive compared to using camera traps to passively collect data. Our method of simultaneously plotting spatial and temporal overlap between predator and prey species and designing composite index scores from camera trap data appears useful for inferring the encounter rates of carnivores with prey and appears to have correctly ranked the prey preferences for Sumatran tigers. The inclusion of prey mass appeared to improve upon the STC score, and including mass or other variables such as abundance or habitat preference may allow for more effective inference in future studies, which should also fine-tune the values used in the adjusted composite scores. Further testing of a similar composite score for spatiotemporal overlap should be conducted in other systems with known prey preferences of carnivores (e.g. from dietary analyses) to further evaluate the accuracy of this method, assess general applicability of the method, and further interpret the observed relationships.

Author Contribution Statement

MLA, MCS and MK conceptualized the paper, MCS performed the fieldwork, MLA performed the statistical analyses, MLA, MCS, and MK wrote and revised the manuscript.

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Competing Financial Interest Statement

The authors declare that no competing financial or non-financial interests exist.

Ethical standards

Our research complies with the Code of Conduct set by Oryx, and follows all institutional guidelines. The research is based on passive monitoring, and does not involve human subjects, experimentation with animals and/or collection of specimens.

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Table 1. The indices of each potential prey species used in our study, including relative abundance (detection events per 100 trap nights), temporal overlap, spatial overlap, and the composite scores. STC is a composite of the spatial and temporal indices, SAC is a spatially weighted composite score, MAC is a composite score with added prey body mass in respect to tiger prey preferences, and SMAC is a composite of the SAC and MAC scores. The composite scores offer a method to rank the potential prey species, with higher scores indicating greater encounter rates and potential prey preference. Species are listed according to their STC score.

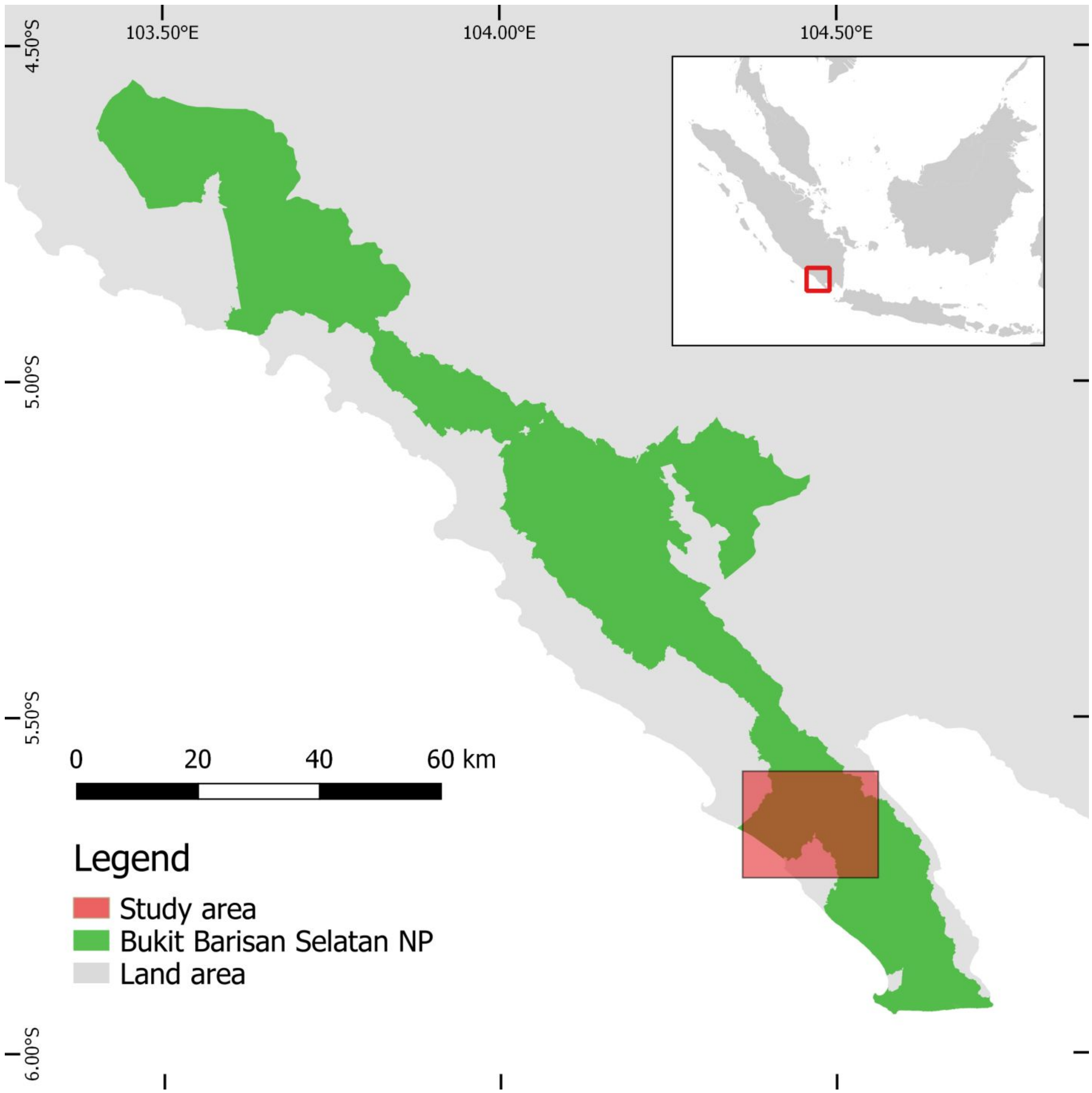
Species	Relative Abundance	Temporal Overlap	Spatial Overlap	STC	SAC	MAC	SMAC
Wild Boar	3.15	0.80	0.71	0.76	0.77	0.83	0.84
Sambar	1.02	0.70	0.66	0.68	0.67	0.75	0.74
Pigtail Macaque	4.32	0.76	0.60	0.68	0.66	0.61	0.60
Red Muntjac	7.10	0.68	0.57	0.63	0.62	0.56	0.56
Mouse Deer	3.39	0.62	0.53	0.58	0.57	0.52	0.51
Tapir	0.85	0.43	0.52	0.48	0.48	0.52	0.53

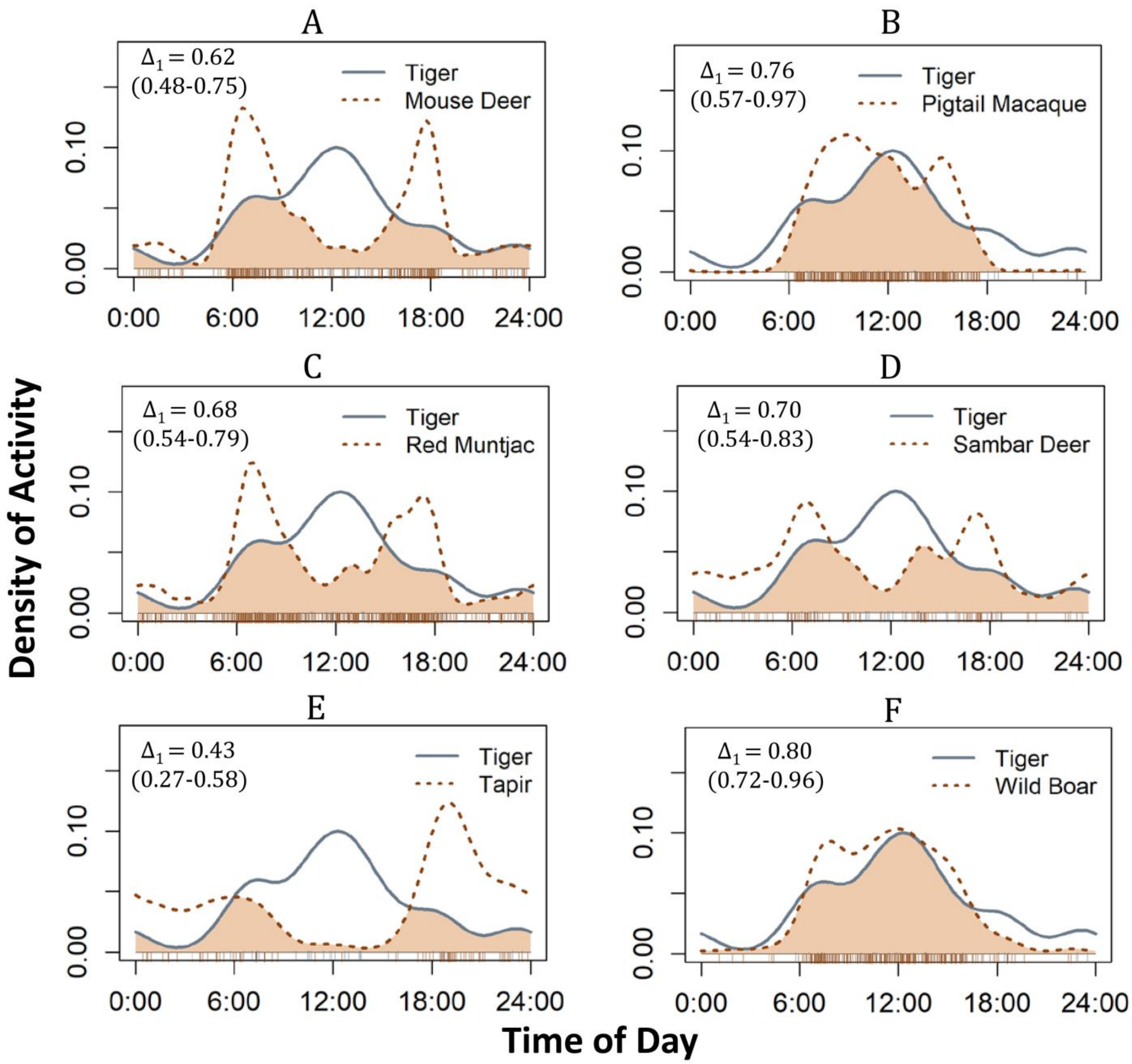
Figure Captions

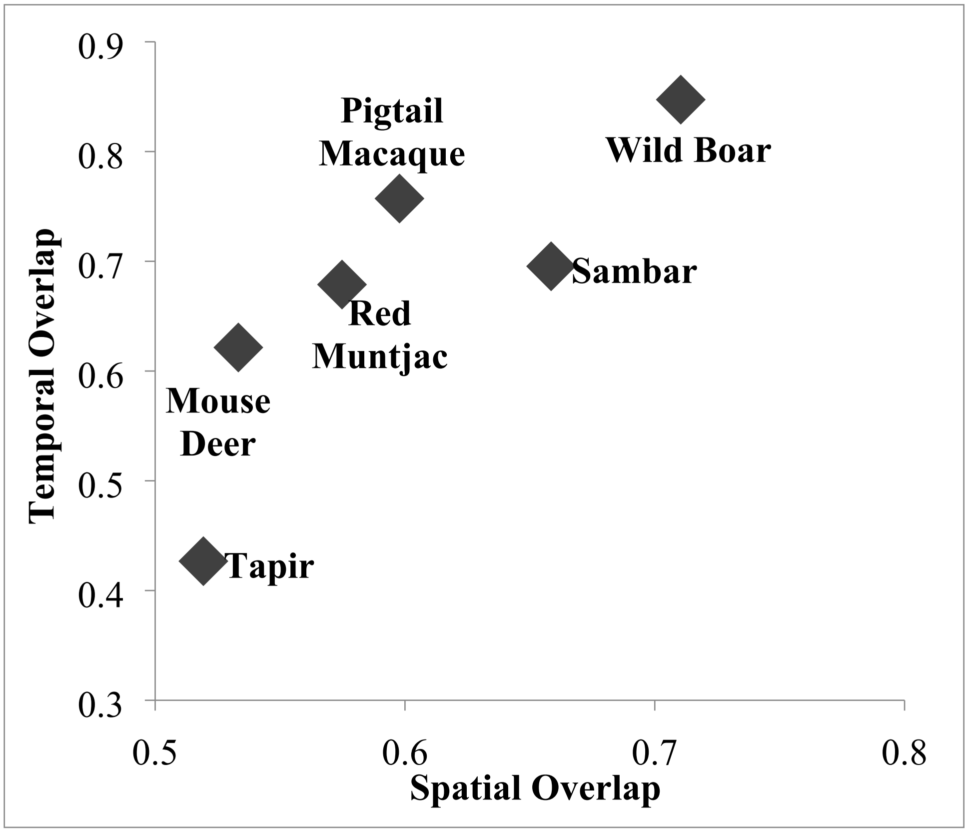
Figure 1. Map of study site within Bukit Barisan Selatan National Park on the island of Sumatra.

Figure 2. The temporal activity and overlap, estimated with kernel densities, of tigers and potential prey species (A = mouse deer species, B = pig-tail macaque, C = red muntjac, D = sambar deer, E = tapir, F = wild boar). Tiger activity is represented as solid lines and the prey activity as a dotted line, with their temporal overlap shown as the shaded area.

Figure 3. The spatial (area under curve; AUC) and temporal (kernel density) overlap of tigers with potential prey species plotted together (with axes scaled to the reported values for ease of comparison).


103.50°E
104.00°E
104.50°E
4.50°S
5.00°S
5.50°S
6.00°S
0
20
40
60 km
Legend
Study area
Bukit Barisan Selatan NP
Land area


A
Δ1 = 0.62
(0.48-0.75)
Tiger
Mouse Deer
B
Δ1 = 0.76
(0.57-0.97)
Tiger
Pigtail Macaque
C
Δ1 = 0.68
(0.54-0.79)
Tiger
Red Muntjac
D
Δ1 = 0.70
(0.54-0.83)
Tiger
Sambar Deer
E
Δ1 = 0.43
(0.27-0.58)
Tiger
Tapir
F
Δ1 = 0.80
(0.72-0.96)
Tiger
Wild Boar
0.00
0.10
0:00
6:00
12:00
18:00
24:00
Density of Activity
Time of Day


0.9
0.8
0.7
0.6
0.5
0.4
0.3
Temporal Overlap
0.5
0.6
0.7
0.8
Spatial Overlap
Pigtail Macaque
Wild Boar
Sambar
Red Muntjac
Mouse Deer
Tapir

List of tiger individuals

Tiger ID	Number of photos*		Number of locations
	Left flank	Right flank	
PTS01	6		1
PTS02	4		1
PTS03	3		1
PTS04	2		1
PTS05	3		1
PTS06	5	11	2
PTS07	7	8	2
PTS08	9		1
PTS09		2	1
PTS10		12	2
PTS11		4	1
PTS12		6	2
PTS13		12	1
PTS16		5	2
PTS18	29		1
PTS19	5		1

*not independent events

Tiger ID	Left flank	Right flank
PTS01		-
PTS02		-
PTS03		-
PTS04		-

PTS05		-
PTS06		
PTS07		
PTS08		-

PTS09	-	
PTS10	-	
PTS11	-	
PTS12	-	

PTS13	-	
PTS16	-	
PTS18		-
PTS19