Spatio-temporal correlations of large predators and their prey in western Thailand

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Abstract. The coexistence of predators with similar morphology can be achieved by avoidance through behavioural, temporal and spatial segregation, which separates niches and reduces competition. Partitioning of space and time can reduce competition by decreasing the frequency of interspecific encounters that exploit a common resource base. We investigated temporal and spatial partitioning of tigers (Panthera tigris), leopards (Panthera pardus), dholes (Cuon alpinus), and their ungulate prey in Thung Yai Naresuan (East) Wildlife Sanctuary in western Thailand from April 2010 to January 2012. We collected camera trap data from 106 locations over 1,817 trap nights. Kernel density estimation and Spearman’s rank correlation were used to quantify temporal and spatial activity patterns. Pianka’s index was used to investigate the temporal and spatial overlap for each species pair. Tigers (crepuscular activity pattern) showed no temporal correlation with leopards (mostly diurnal) or dholes (strongly diurnal), but leopard activity appeared to correlate positively with dhole activity. Tigers exhibited temporal overlap with larger gaur (Bos gaurus) and sambar (Rusa unicolor); leopards did so with barking deer (Muntiacus muntjak) and wild boar (Sus scrofa); and dholes did so with barking deer and wild boar. The spatial correlations of tigers, leopards, and dholes did not significantly overlap, though numerically overlap was higher between felids than with the canid. None of the three predators significantly correlated with prey distribution, except for dholes with sambar. Our findings suggest that tigers, leopards, and dholes co-occur with spatial and temporal partitioning due to differences in prey activity and low overlap in space use correlated to prey preference. The partition in space and time between tigers and leopards can minimise their competition-associated prey activity, while leopards and dholes seem to be more generalist and not spatially correlated with each other.

Keywords. activity, tiger, leopard, dhole, gaur, sambar, Malayan tapir, barking deer, wild boar, camera trap

INTRODUCTION

Interaction between species and the distribution of resources characterise ecological systems and provide essential information needed to understand the roles of species in communities (Schoener, 1974; Thompson, 1982). Spatial and temporal partitioning is a viable strategy for minimising resource competition between species and increasing coexistence (Pianka, 1967; Thompson, 1982; Ramesh et al., 2012). In general, activity patterns and spatial use for each species are influenced by several factors, which include physiological adaptations, food availability, distribution pattern, human disturbance, and life-history strategies (Karanth & Sunquist, 2000).

Interaction between carnivores and herbivores are characterised in terms of predator and prey interactions. Predators affect prey populations and communities by direct and indirect effects on prey behaviours and life histories (Bolnick & Preisser, 2005). Selective predation on prey may result from predators preferring prey of a certain size, behaviour, time, encounter rate, vulnerability, and predation risk (Emlen, 1966; Polisar et al., 2003; Creel et al., 2005; Jenny & Zuberbühler, 2005). This can cause prey to exhibit predator-avoidance behaviour by shifting to other food patches or feeding times, or even aggregating into groups to repel the predators (Abrams, 1984; Overdorff, 1988; Palomares & Caro, 1999; Eccard et al., 2008). Over time, these interactions can result in the evolution of physical and behavioural traits (Dawkins & Krebs, 1979).

However, several predatory species hunting in the same area can increase the pressure on prey populations (Johnsingh, 1992). The coexistence of predators with similar morphology can be achieved by avoidance through behavioural, habitat, temporal, and spatial segregation (Schaller, 1972; Malcolm & van Lawick, 1975; Ramesh, 2010; Ramesh et al., 2012). Such differences in activities separate niches and reduce competition, presumably allowing the coexistence of sympatric living species (Bekoff et al., 1984; Sunquist & Sunquist, 1989).
Fig. 1. Thung Yai Naresuan (East) Wildlife Sanctuary (TYNE), Thailand.
Tigers (*Panthera tigris*), leopards (*Panthera pardus*), and dholes (*Cuon alpinus*) selectively kill prey types of different species, size, and age-sex classes, facilitating their coexistence through ecological separation (Johnsingh, 1992; Karanth & Sunquist, 1995, 2000). Ramesh et al. (2012) found that dholes were temporally segregated from tigers and leopards, while spatial overlap occurred with leopards but not with tigers. Partitioning of space and time can reduce competition by decreasing the frequency of interspecific encounters that exploit a common resource base (Kronfeld-Schor & Dayan, 2003; Ramesh et al., 2012). In Thailand, diet and habitat partitioning between these three main predators and their prey have previously been reported (Rabinowitz, 1989; Rabinowitz & Walker, 1991; Grassman, 1999; Ngoprasert et al., 2007; Simcharoen et al., 2008; Jenks et al., 2012), but less is known about the behavioural mechanisms underlying temporal and spatial partitioning within this group. These large carnivores are also known to occupy Thung Yai Naresuan (East) Wildlife Sanctuary, but the activity patterns of predator and prey within the sanctuary are poorly understood. Thus, this study aims to enhance our understanding of the coexistence of carnivores and their prey in the sanctuary, by using camera traps to: 1) investigate spatial and temporal activity patterns, 2) compare spatial and temporal activity overlap, and 3) evaluate the avoidance among species through the diel cycle.

**MATERIAL AND METHODS**

**Study site.** This study was conducted in Thung Yai Naresuan (East) Wildlife Sanctuary, located in the Western Forest Complex (WEFCOM) along the Thailand-Myanmar border. The sanctuary is adjacent to Huai Kha Khaeng Wildlife Sanctuary, which is located at the core of the WEFCOM and was designated as a Natural World Heritage Site in 1991 (Buergin, 2001; WEFCOM, 2004) (Fig. 1). The Thung Yai Naresuan Wildlife Sanctuary contains a variety of forest types, including mixed deciduous (45%), dry evergreen forest (31%), and hill evergreen forest (15%) (Nakhasathien & Stewart-Cox, 1990). Secondary forest of varying stages of regeneration covers 4% of the sanctuary, and the remaining 5% consists of savanna, deciduous dipterocarp forest, and grassland (Nakhasathien & Stewart-Cox, 1990; Duengkae et al., 2006; Steinmetz et al., 2006). The sanctuary has long been inhabited by the indigenous minority known as “Karen” (Emphandhu, 2003). The vegetation is still largely undisturbed as little logging or shifting cultivation has been practised (Buergin, 2003; Steinmetz et al., 2006). Major rivers in the Thung Yai Naresuan Wildlife Sanctuary are the Mae Klong and the Mae Chan, which feed the Si Nakharin Dam. The sanctuary is characterised by rugged mountainous terrain with elevations rising up to 2,000 m. The lowland zone is found in the western part of the sanctuary (Nakhasathien & Stewart-Cox, 1990; Steinmetz et al., 2006); a moderate altitude zone is located mainly in the centre; and a high, steep zone consisting of mountains ranging from 1,000 to 2,000 m is found in the east (Steinmetz et al., 2006). The climate of this region is monsoonal with a dry season from November to May, and a wet season from May to October (Duengkae et al., 2006; Steinmetz et al., 2006).

**Data collection.** Data were recorded by 106 camera traps (Stealth Cam 1590 with 5.0 megapixels, Grand Prairie, TX; and Bushnell Trophy Cam infrared with 8.0 megapixels, Overland Park, KS) for a total of 1,817 trap days from April 2010 to January 2012. Cameras were set to operate 24 hours per day with three images per trigger, with a one-minute delay for Stealth Cams (minimum setting) and a 30-second delay for Bushnell Trophy Cams to maximise animal detection. All camera trap stations contained a pair of cameras, one of each type to control for detection biases inherent in the different camera models at the location. The units were installed facing each other on both sides of wildlife trails. Each camera trap was placed 0.4–0.5 m from the ground and secured to a tree. All vegetation and debris were cleared from the field of view so that both medium and large animals had the opportunity to be photographed. Cameras were deployed in the field for 15–20 days before batteries and memory cards were replaced. We ensured spatial and temporal independence by minimising trap spacing between camera stations to 2 km (Fig. 2). No baits or lures were used with the camera traps. Each trap location was checked on a weekly basis to reduce their down time from the risks of interference (from humans and large mammals) and to replace batteries and the memory card when necessary. We selected camera sites based on the presence (scats, scrapes, pugmarks, and urination sites) of tigers, leopards, and dholes, and their main prey signs (dung, footprints, calls, and sightings). We placed each camera trap where trails merged or where no alternative trails existed to increase the probability of capturing our target species. Activity patterns were extracted from the camera data for three predators (tigers, leopards, and dholes) and their five major prey species: gaur (*Bos gaurus*), sambar (*Rusa unicolor*), wild boar (*Sus scrofa*), and Malayan tapir (*Tapirus indicus*), based on an earlier food habits study in the adjacent protected area (Phetdee, 2000). Each photograph was stamped with the time and date. To avoid pseudo-replications, we considered the first capture of the animal as an independent record (Yasuda, 2004; Ramesh et al., 2012). Any species captured at both cameras in each camera location at the same time was counted as only one record for analysis. Independence of detections was defined as: 1) consecutive (each continuously following) photographs of different individuals of the same (that is, individually distinguishable because of identifying marks) or different species; 2) consecutive photographs of individuals of the same species (not individually identifiable) when separated by more than 30 min; or 3) non-consecutive photographs of individuals of the same species (e.g., a photograph of one species, then of a different species, then of the first species) (O’Brien et al., 2003; Yasuda, 2004; Gray & Phan, 2011). Only tigers and leopards were individually identified, based on unique patterns on the body (Miththapala et al., 1989; Karanth, 1995). Poor quality photographs in which the species could not be confidently identified were excluded from the analysis. Independent photographs were regarded as a random sample from the underlying distribution that describes the probability of a photograph being taken within any particular interval of the day (Linkie & Ridout, 2011). The probability density function of this distribution was
then referred to as the activity pattern, and we presumed that an animal was equally likely to be photographed at all times when it was active (Ridout & Linkie, 2009; Linkie & Ridout, 2011).

Data analyses. First, we identified prey species most likely utilised by the predators of concern. Previous studies have indicated that tigers are often found to be associated mainly with medium to large mammalian herbivorous prey species, including gaur (*Bos gaurus*), sambar (*Rusa unicolor*), barking deer (*Muntiacus muntjak*), and wild boar (*Sus scrofa*) (Karanth & Sunquist, 1995; Phetdee, 2000; Bhattarai & Kindlmann, 2012). The largest ungulates, gaur and sambar, contribute the greatest biomass consumed by tigers, whereas medium-sized barking deer and wild boar contribute the largest portion of the leopard diet (Karanth & Sunquist, 1995; Hayward et al., 2006). Prey preferred by dholes is generally medium-sized (Karanth & Sunquist, 2000) but can include deer, gaur, banteng (*Bos javanicus*) and other large bovids (Grassman et al., 2005; Andheria et al., 2007; Sillero-Zubiri, 2009; Kamler et al., 2012). For each species, we used a non-parametric kernel density estimation procedure for quantifying the temporal activity patterns between predator and prey (Ridout & Linkie, 2009; Linkie & Ridout, 2011). The kernel density estimation was used to estimate the probability density function of the activity patterns of main predators (tiger, leopard, and dhole) against their main and potential prey (gaur, sambar, tapir, barking deer, and wild boar) (Sillero-Zubiri, 2009; Wang & MacDonald, 2009). Then, we applied a smoothing parameter (bandwidth = 1.2) to generate the temporal predator-prey activity patterns as per Ridout & Linkie (2009). Analyses were performed in the software R and the package Overlap (R Development Core Team, 2017).

To examine the temporal correlation between each pair of predator and prey, we summed all independent photographs for each species by hourly bins over a 24-hour period. We then calculated the percent of photographic captures for each species with the 24-hour cycle (Azlan & Sharma, 2006; Harmsen et al., 2009; Ramesh et al., 2012). We tested the correlation between each predator-prey pair using Spearman’s rank correlation coefficient using the programme SPSS 16.0 (SPSS Inc., Chicago, Illinois, 2007). Then, we evaluated
the probability of temporal overlaps for each pair between predator and prey by using Pianka’s index,

\[ O_{jk} = \sum_{i=1}^{n} \frac{p_{ij} p_{kj}}{\sum p_{ii} \sum p_{jj}} \]

where \( p_i \) is the frequency of occurrence of species 1 and 2 at location \( i \). Pianka’s index \( O \) varies between 0 (total separation) and 1 (total overlap). This index corresponds to the area of intersection of the utilisation histograms of the two species. We assessed Pianka’s indices through Monte Carlo randomisations (5,000 iterations) of relative abundance in each particular hour, to simulate possible overlaps using the programme EcoSim 7.0 (Pianka, 1967; Gotelli & Entsminger, 2004).

We examined spatial overlap among predators and their prey by calculating the photographic rate of each camera trap station as an independent spatial point to reflect the relative abundance of target species, which was based on the assumption that there is an equal probability that all camera traps will capture an animal (Carbone et al., 2001; O’Brien et al., 2003; Azlan & Sharma, 2006). The photographic rate of each species for each camera trap station was defined as the total number of independent photographs divided by the total number of independent records from the total trap nights (Azlan & Sharma, 2006; Ramesh et al., 2012). The photographic rate provided an estimate of abundance of each species, and hence facilitated comparison of spatial use between different species. We observed the relations between predators and prey at each camera trap station by applying Spearman’s rank correlation coefficient as a measure of spatial correlation. We evaluated spatial overlap for each predator-prey pair by using Pianka’s index assessed through Monte Carlo randomisations (5,000 iterations) of relative abundance in each particular location and using the programme EcoSim 7.0 (Pianka, 1967; Gotelli & Entsminger, 2004).

RESULTS

A total of 2,027 photographs was obtained for the eight target species, which equated to 875 independent photographs. The number of independent photographs of each species varied from 22 for gaur to 408 for barking deer (Table 1).

Tigers, leopards, and dholes did not significantly overlap spatially, though numerically overlap was higher between felids than with canid (Table 2). None of the three predators significantly correlated spatially with prey, except for dhole and sambar (0.20, \( P < 0.05 \)). However, tigers and leopards appeared to have the highest spatial overlap with barking deer, while dholes had the highest spatial overlap with sambar and tapir.

Tigers, leopards, and dholes showed activity patterns with minor and major peaks (Fig. 3A, B). Tigers were active throughout the 24-hour period (48% between 0600 and 1800 hours), but had peaks of activity around dawn, dusk, and during the night (Fig. 3A, B). The major peak of tiger activity was in the morning between 0700 and 0900 hours and a minor peak between 2200 and 0000 hours (Fig. 3A). Leopards and dholes had peaks of activity during the day (Fig. 3D). Most leopard activity (63%) was between 0600 and 1800 hours, with a major peak between 0900 and 1100 hours, a minor peak around midnight between 2300 and 0000 hours, and very low activity after midnight (0000 to 0300 hours) (Fig. 3B, C, D). Dholes showed bimodal activity with high diurnal activity (95% between 0600 and 1800 hours and a major peak in activity from 0900 to 1100 hours) and a minor peak in activity between 1600 and 1700 hours (Fig. 3A, D). Tigers showed a crepuscular activity pattern, while leopards tended to be diurnal, and dholes showed a strongly diurnal activity pattern and had more activity during the day than both felids (Fig. 3A). Although temporal activity among the three predators significantly overlapped only between leopard and dhole (Table 2), activity of the tiger, leopard, and dhole overlapped for more than 10 hours of the day (Fig. 3A).

Gaur exhibited several peaks of activity throughout the 24-hour day (i.e., cathemeral; Fig. 4A), with 59% of activity between 0600 and 1800 hours, and a major peak between 1700 and 1800 hours. Sambar were predominantly nocturnal (only 25% of activity between 0600 and 1800 hours), with bimodal peaks between 0000 and 0200 hours and between 0600 and 0800 (Fig. 4B). Tapirs had peaks of activity during the night similar to sambar (peaks between 0600 and 0200 hours and between 0600 and 2200 hours), but tapir activity was more strongly nocturnal (only 4% between 0600 and 0800 hours) (Fig. 4C). In contrast, activity of barking deer and wild boar was strongly diurnal (78% and 93% between 0600 and 1800 hours, respectively). Barking deer had a major activity peak between 0700 and 1100 hours and a minor peak from 1700 to 1900 hours (Fig. 4D), while wild boar had high activity from 0900 to 1100 hours and again from 1400 to 1600 hours (Fig. 4E).

Tigers showed no temporal correlation with leopards or dholes, but exhibited a positive temporal correlation with gaur (0.44, \( P < 0.05 \); Table 2). Leopard activity appeared to correlate positively with that of dholes (0.46, \( P < 0.05 \)) and also showed positive correlations with activity of barking deer (0.47, \( P < 0.05 \)) and wild boar (0.48, \( P < 0.05 \)), but correlated negatively with tapir activity (−0.49, \( P < 0.05 \)). Dhole activity was positively correlated with that of barking deer (0.55, \( P < 0.01 \)) and wild boar (0.47, \( P < 0.05 \)). Tiger activity overlapped with activity of larger gaur (73%) and sambar (64%), but also with activity of barking deer (72%). Leopard activity overlapped with that of barking deer and wild boar, while dhole activity overlapped only with activity of smaller barking deer (80%) and wild boar (77%).

DISCUSSION

Temporal activity correlation. We studied the temporal activity patterns of large predators and prey in Thung Yai Naresuan (East) Wildlife Sanctuary (TYNE). We found leopards and dholes to be strongly active during the day. Tigers were active throughout the day, with major and minor
Table 1. The number of photographs obtained of large predators and their principal prey in Thung Yai Naresuan (East) Wildlife Sanctuary, Thailand.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Number of photographs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Common</td>
</tr>
<tr>
<td>Tiger</td>
<td>Panthera tigris</td>
</tr>
<tr>
<td>Leopard</td>
<td>Panthera pardus</td>
</tr>
<tr>
<td>Dhole</td>
<td>Cuon alpinus</td>
</tr>
<tr>
<td>Gaur</td>
<td>Bos gaurus</td>
</tr>
<tr>
<td>Sambar</td>
<td>Rusa unicolor</td>
</tr>
<tr>
<td>Malayan tapir</td>
<td>Tapirus indicus</td>
</tr>
<tr>
<td>Barking deer</td>
<td>Muntiacus muntjak</td>
</tr>
<tr>
<td>Wild boar</td>
<td>Sus scrofa</td>
</tr>
</tbody>
</table>

Table 2. Spatial and temporal correlations of large predators and their prey in Thung Yai Naresuan (East) Wildlife Sanctuary, Thailand. *P Correlation significant (P < 0.05); †P Correlation significant (P < 0.01).

<table>
<thead>
<tr>
<th>Species pair</th>
<th>Temporal Correlation</th>
<th>Temporal Overlap index</th>
<th>Spatial Correlation</th>
<th>Spatial Overlap index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiger and leopard</td>
<td>0.04</td>
<td>0.58</td>
<td>0.09</td>
<td>0.18</td>
</tr>
<tr>
<td>Tiger and dhole</td>
<td>−0.06</td>
<td>0.37</td>
<td>−0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>Tiger and gaur</td>
<td>0.44*</td>
<td>0.73</td>
<td>0.03</td>
<td>0.17</td>
</tr>
<tr>
<td>Tiger and sambar</td>
<td>0.11</td>
<td>0.64</td>
<td>0.03</td>
<td>0.17</td>
</tr>
<tr>
<td>Tiger and Malayan tapir</td>
<td>−0.12</td>
<td>0.39</td>
<td>0.02</td>
<td>0.11</td>
</tr>
<tr>
<td>Tiger and wild boar</td>
<td>−0.03</td>
<td>0.49</td>
<td>0.13</td>
<td>0.25</td>
</tr>
<tr>
<td>Leopard and dhole</td>
<td>0.46*</td>
<td>0.76</td>
<td>−0.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Leopard and gaur</td>
<td>0.13</td>
<td>0.45</td>
<td>−0.10</td>
<td>0.06</td>
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<tr>
<td>Leopard and sambar</td>
<td>−0.37</td>
<td>0.41</td>
<td>0.01</td>
<td>0.11</td>
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<tr>
<td>Leopard and Malayan tapir</td>
<td>−0.49*</td>
<td>0.17</td>
<td>−0.02</td>
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<tr>
<td>Leopard and barking deer</td>
<td>0.47*</td>
<td>0.80</td>
<td>0.16</td>
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<tr>
<td>Leopard and wild boar</td>
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<td>0.77</td>
<td>0.01</td>
<td>0.21</td>
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<tr>
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<td>0.22</td>
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<td>Dhole and sambar</td>
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<td>0.18</td>
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<tr>
<td>Dhole and barking deer</td>
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<td>0.63</td>
<td>0.03</td>
<td>0.09</td>
</tr>
<tr>
<td>Dhole and wild boar</td>
<td>0.47*</td>
<td>0.57</td>
<td>−0.04</td>
<td>0.05</td>
</tr>
</tbody>
</table>
peaks of activity around dawn and dusk. Previous tiger studies also found similar patterns (Kawanishi & Sunquist, 2004; Azlan & Sharma, 2006; Ridout & Linkie, 2009; Ramesh et al., 2012). Temporal segregation between tiger and leopard was reported by Rabinowitz (1989) and Azlan & Sharma (2006); they found that an adult leopard was largely diurnal (66% and 70% of daily activity, respectively), concluding that leopards were diurnal when tigers occurred in the same area. We found the temporal activity of dholes to be exclusively diurnal (up to 95%), which gave them temporal partitioning from tigers. Camera trap studies in Laos and Malaysia also found strong diurnal dhole activity (Kawanishi & Sunquist, 2004; Kamler et al., 2012; Ramesh et al., 2012), though studies in Thailand by Grassman et al. (2005) and Jenks et al. (2012) found that dholes were primarily diurnal but also active during crepuscular period.

Higher temporal overlap between tiger and leopard than between tiger and dhole was also reported in Mudumalai Tiger Reserve, India (Ramesh et al., 2012). We found that tigers and leopards had a temporal overlap of 58%, while the similar study in India found this temporal overlap to be larger than 80% (Ramesh et al., 2012; Lamichhane et al., 2019), reportedly owing to their similar morphology and hunting strategies (Karanth & Sunquist, 1995; Ramesh et al., 2012). Tigers had significant temporal overlap with gaur but not with small prey such as barking deer and wild boar, perhaps because of a preference for large prey size, as reported elsewhere (Johnsingh, 1983; Karanth & Sunquist, 1995; Bhattacharji & Kindlmann, 2012), and a crepuscular activity pattern (Prayurasiddhi, 1997; Steinmetz, 2004; Steinmetz et al., 2010). The small temporal correlation between tigers and smaller prey could be due to both barking deer and wild boar having had highly diurnal activity, having decreased
Fig. 4. Kernel density estimates of daily activity patterns of tigers and prey species. A, tiger and gaur; B, tiger and sambar; C, tiger and tapir; D, tiger and barking deer; E, tiger and wild boar. The dashed lines are kernel density estimates for tigers and the solid lines are kernel density estimates for the prey species. The shaded areas indicate the overlap coefficient; that is, the area under the minimum of the two density estimates.
Fig. 5. Kernel density estimates of daily activity patterns of leopards and prey species. A, leopard and gaur; B, leopard and sambar; C, leopard and barking deer; D, leopard and tapir; E, leopard and wild boar. The dashed lines are kernel density estimates for leopards and the solid lines are kernel density estimates for the prey species. The shaded areas indicate the overlap coefficient; that is, the area under the minimum of the two density estimates.
Fig. 6. Kernel density estimates of daily activity patterns of dholes and prey species. A, dhole and gaur; B, dhole and sambar; C, dhole and tapir; D, dhole and barking deer; E, dhole and wild boar. The dashed lines are kernel density estimates for dholes and the solid lines are kernel density estimates for the prey species. The shaded areas indicate the overlap coefficient; that is, the area under the minimum of the two density estimates.
their activity when tigers were active. However, a study in Malaysia found that tigers were more diurnal than nocturnal, and that patterns of activity were more similar to those of crepuscular/diurnal species such as barking deer and wild boar (Kawanishi & Sunquist, 2004). Furthermore, a study in Sumatra also found that tigers and barking deer exhibited peaks of activity around dawn and dusk and that temporal overlap between both species was strong (Linkie & Ridout, 2011). Based on camera trap records and abundance estimates, their studies reported that the abundance of large prey such as gaur and sambar was low. The correspondence between the activity patterns of tigers and barking deer was suggested to be due to barking deer being an important tiger prey species in terms of abundance, biomass, and occupancy (Kawanishi & Sunquist, 2004; Linkie & Ridout, 2011).

The diurnal activity of leopards and dholes may be due to the fact that smaller prey such as barking deer and wild boar were more active diurnally. This activity pattern could also have served to enhance temporal separation from tigers. Dholes had no temporal correlation with tigers but correlated temporally with leopards. In contrast, Ramesh et al. (2012) did not observe temporal correlations between dholes and either tigers or leopards. Elsewhere, a correlation in activity between leopards and dholes could have resulted from leopards and dholes consuming similar medium-sized prey that were usually active during the day (Wang & Macdonald, 2009; Ramesh, 2010; Bhattarai & Kindlmann, 2012) and also avoiding tigers, which mainly hunted larger, nocturnal prey (Johnsingh, 1992; Karanth & Sunquist, 1995; Mondal et al., 2012). Prey selection by leopards and dholes may also be associated with a preference for reduced risk of injury during prey capture, which could then be an underlying reason for the lower preference, by leopards and dholes, for large prey (Karanth & Sunquist, 1995).

We found negative temporal correlations between the three predators and tapirs. Tapirs were predominantly nocturnal, while tigers were active primarily during twilight, and leopards and dholes were predominantly diurnal. The camera trap surveys by Lynam (1999), Holden et al. (2003), and Linkie & Ridout (2011) also supported our results. In fact, tapirs do not seem to be a principal prey species of tigers when other prey species are present (Kawanishi & Sunquist, 2004; Andheria et al., 2007; Linkie & Ridout, 2011).

**Spatial activity correlation.** We found no significant spatial correlations among the three predators in the study area. A similar study in India also found no significant spatial correlation between tigers and leopards (Ramesh et al., 2012). Furthermore, Ramesh et al. (2012) reported greater spatial overlap between tigers and leopards than with dholes. Spatial overlap between tigers and leopards was reported in Malaysia, where leopards sometimes used the same areas and trails as tigers (Azlan & Sharma, 2006). However, our tigers and leopards did not appear to overlap much in terms of space use (index = 0.18) as compared to the study by Ramesh et al. (0.71; 2012); other studies indicate that tigers and leopards avoid competition by hunting in different forest types, with different activity patterns as well as different prey species, including some arboreal ones for leopards (Seidensticker, 1976; Odden et al., 2010; Mondal et al., 2012).

Dholes also exhibited spatial segregation from both tigers and leopards, and showed significant spatial overlap with sambar. Besides avoiding the other predators, dholes also have a high proportion of sambar in their diet (Johsingh, 1992; Karanth & Sunquist, 1995; Grassman et al., 2005; Andheria et al., 2007; Thinley et al., 2011; Kamler et al., 2012), therefore prey selection associated with habitat use by the prey may be one of the primary factors influencing their spatial activity pattern.

In summary, the spatial overlap among the three predators was low and insignificant, indicating some characteristic differentiation in the use of spatial resources. A traditional interpretation of low overlap suggests species do so to avoid sharing resources and reduce competition (Gotelli & Graves, 1996).

**Conclusions.** In the period of our study in TYNE, tigers, leopards, and dholes seemed to co-occur with a combination of both spatial and temporal partitioning due to differences in predator and prey activity and low overlap in space use correlated with their prey preferences. Moreover, this survey demonstrated that coexistence between tiger and leopard in TYNE was a result of low density (1.4–1.6 tigers per 100 km², 0.7–0.8 leopards per 100 km², respectively, based on maximum likelihood spatially-explicit capture-recapture; Vinitpornsawan, 2013). The partitioning in space and time between tigers and leopards could minimise competition associated with the activity of their major prey, while leopards and dholes seem to be more generalist predators (Edgaonkar, 2008; Aryal et al., 2015; Gray, 2013; Hayward et al., 2014) and thus may not have been so influenced by spatial correlation with each other. This contrasts with the study in Nagarhole National Park, India (Karanth & Sunquist, 2000), which reported that the three predator species used the same areas and hunted in similar habitats (where prey densities were particularly high), but were similar in partitioning of time and space as their counterparts in the Royal Chitawan National Park and Bardia National Park, Nepal, and Sariska National Park, India (Seidensticker, 1976; Odden et al., 2010; Mondal et al., 2012). Our results did not allow us to conclude whether the spatial and temporal partitioning among tigers, leopards, and dholes were primarily associated with prey size, prey preference, prey density, or even prey distribution. Other studies on prey selection and diet reported that predators selected the most abundant prey species within their preferred size range, which was related to their body size (Johsingh, 1992; Karanth & Sunquist, 1995, 2000; Andheria et al., 2007; Bhattarai & Kindlmann, 2012).

Further temporal and spatial activity studies that include diet, seasonality, and habitat use are needed to better understand inter-specific relationships and coexistence, which will help clarify the use of shared resources through the partitioning of time and space among the large sympatric carnivore communities. Thung Yai Naresuan (East) Wildlife Sanctuary (TYNE) certainly provides a large and contiguous habitat for
the coexistence of tigers, leopards, dholes, and their prey. We suggest that the coexistence of predators in TYNE could be enhanced via the application of habitat management for ungulates, such as the use of controlled burns to maintain grass-base for ungulate recovery, suppressing fires effectively in evergreen forest areas, an ungulate reintroduction programme using ex situ bred species (i.e., Eld’s deer), creating artificial water sources for ungulates, and improving the effectiveness of anti-poaching efforts through ground patrols. In our study area, local people and shifting cultivation occupy the western part of the sanctuary, and these conditions could restrict animal dispersal and movement. In these areas, zoning seems to be a good practice, but management actions including wildlife and habitat monitoring, anti-poaching patrols, increasing awareness of local communities, and working with local governments are essential to achieve a balance between human rights and nature conservation.

ACKNOWLEDGEMENTS

We acknowledge the Wildlife Conservation Society; the U.S. Fish and Wildlife Service: Rhino-Tiger Conservation Fund; and the Thailand Wildlife Research Division, Department of National Parks, Wildlife, and Plant Conservation for supporting this work. Thanks to S. Thongseekhem, head of Thung Yai Naresuan (East) Wildlife Sanctuary; as well as P. Pinyo, P. Kanidthachad, and the TYNE staff; field assistants J. Suwandee and P. Mueangnam; and the graduate student volunteers from the Faculty of Forestry, Kasetsart University. We also thank two anonymous reviewers and the Editor for their insights and helpful comments.

LITERATURE CITED

Vinitpornsawan & Fuller: Predator and prey behaviours in Thailand


