


Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia

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Abstract

Context Understanding how large carnivore guilds survive in human-dominated landscapes is key to inform strategies for their conservation in the face of global carnivore declines. Amur tigers and leopards are recovering across the China-Russia border. However, knowledge is limited about competitive interactions between two large cats in Northeast Asia.

Objectives To assess the spatial, temporal and combined spatiotemporal behavioral mechanisms potentially allow co-occurrence between tigers and leopards in a human-dominated forest landscape.

Methods Based on a large-scale camera-trapping data set in Northeast China, we used three different approaches for quantifying spatiotemporal associations: one spatial method (two-species occupancy

model), one strictly temporal method (activity pattern overlap), and one spatiotemporal method based on multi-response permutation procedures at shared camera trap sites.

Results Spatially, leopards showed no avoidance of the areas highly used by dominant tigers, but their diurnal activity pattern was significantly different from that of tigers. Spatiotemporal overlap analysis showed fine-scale behavioral avoidance when both co-occurred at camera locations, which further facilitates sympatry. Tigers spatially overlapped with humans, but they were less active during the day when human activities were more frequent. In areas with high cattle density, low occurrence of tigers and leopards may reflect the absence of sika deer, an important prey item for both species.

Conclusions This study provides the first empirical evidence that tigers do not limit leopard distributions, at least in our study area in Northeast Asia. Our results highlighted temporal segregation, not large-scaled spatial avoidance, as a key mechanism promoting coexistence of two large carnivores. Understanding these fine- spatial scale (i.e., camera locations) interactions between sympatric carnivores can help devise management strategies for predator guilds in human-dominated landscapes, currently a major global challenge.

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Introduction

Tigers (*Panthera tigris*) and leopards (*Panthera pardus*) co-occur in many locations throughout the tiger's range, and interference competition by tigers toward leopards is widely reported (Odden et al. 2010; Steinmetz et al. 2013; Rayan and Linkie 2016). At some localities, however, a high degree of spatial overlap is reported (Karanth and Sunquist 2000; Karanth et al. 2017). In addition to long term efforts to recover tigers, increasing concern exists for leopards. Along the border between Russia Far East and Northeast China, Amur leopards (*P. p. orientalis*), a subspecies composed of a single isolated population of ~ 90 individuals, overlaps with an even smaller isolated population of ~ 40 individuals of the Amur tiger (*P. t. altaica*) (Feng et al. 2017). Because both species are globally rare and their population sizes are critically small, the governments of Russia and China are seeking to develop a joint conservation strategy for their recovery.

Options for a range expansion in Russia are somewhat limited due to infrastructure development along a transportation and industrial corridor extending northwest from Vladivostok; thus, the opportunity for recovery is to expand existing habitat by creating a landscape westward into the Changbai Mountains in China (Hebblewhite et al. 2012; Wang et al. 2016). The current recovery plan seeks to create a ~ 15,000 km² tiger-leopard landscape that will encompass protected areas and mixed human use sites which in the past have included areas for timber extraction, cattle grazing and some farming. This landscape includes an array of human activities as well as areas dedicated primarily to forest protection.

The task of restoring this landscape and its unique felid guild is a common global conservation problem. Given the extensive space requirements of large carnivores, their conservation not only requires protected areas but also multiple-use zones within working landscapes. For example, Wikramanayake et al. (2011) stressed that tiger recovery in Asia will require maintaining vast landscapes, protecting reserves with breeding tigers and connecting the reserves across the human-dominated matrices to facilitate tiger dispersal. Need for management at these larger scales has motivated a strong research interest in the dynamics of coupled human and natural systems, in which human well-being and biodiversity conservation goals

must be addressed (Liu et al. 2007). Among the various anthropogenic land uses, livestock grazing covers nearly a quarter of the planet's land surface and is deemed the most ubiquitous human activity in land area used (Robinson et al. 2014b). A recent evidence-based review on the effects of grazing on wildlife has indicated that most species responded negatively to livestock, especially species needing denser cover (Schielz and Rubenstein 2016). Worldwide, such threats have increased in recent years, even in many protected areas. For example, giant pandas (*Ailuropoda melanoleuca*) and co-occurring species were displaced as more livestock encroached on the forest habitat in Wanglang Nature Reserve, Southwest China (Li et al. 2017). In the Hyrcanian forest of Iran, livestock grazing had a negative and marked effect on the occupancy of the Persian leopard (*P. p. saxicolor*) and several wild ungulates (Soofi et al. 2018).

Livestock grazing degrades forests in a similar fashion in the temperate mixed forest ecosystem of Northeast Asia, where the Amur tiger and the critically endangered Amur leopard co-occur in eastern Jilin Province, China, and southwest Primorskii Province, Russia (Hebblewhite et al. 2011; Wang et al. 2017). As recently as 20 years ago, tigers and leopards were nearly extirpated from the Chinese side of the border (Tian et al. 2009, 2011; Wikramanayake et al. 2011), but concerted assessment efforts have produced evidence of the recovery of these species in China (Wang et al. 2016; Xiao et al. 2016; Vitkalova et al. 2018). However, these predators are still largely confined to a narrow area along the border with Russia. Our recent studies showed that a combination of cattle grazing and other human land use activities may restrict their expansion further into China, and the authors advocated for strict grazing controls (Wang et al. 2016, 2017, 2018). Past land-use policies in Northeast China encouraged forest extraction and cattle grazing, which negatively influence the abundance and distribution of major ungulate prey and exacerbate human-wildlife conflicts (Soh et al. 2014; Wang et al. 2016).

In seeking to create a tiger-leopard landscape, the Chinese government has ceased timber harvest and is planning to limit livestock grazing to restore habitat that conserves the dwindling populations of tigers and leopards, and their prey, and provides important ecological services to improve human well-being (McLaughlin 2016). These objectives are a high priority for the Chinese government because this is

the only location in the north of the Changbai Mountains, Northeast Asia, where tigers and leopards still co-occur as they once did across this region. It is important that conservation initiatives targeting the recovery of predator guilds carefully examine interspecific interactions (Harihar et al. 2011). Although several detailed studies have been conducted on both tigers and leopards in the region (e.g., population density, habitat use, spatial viability, and prey availability) (Carroll and Miquelle 2006; Hebblewhite et al. 2014; Petrunenko et al. 2016; Sugimoto et al. 2016; Wang et al. 2017, 2018), to date, research is lacking on the competitive interactions between tigers and leopards in Northeast Asia; in particular, how these interactions may be mediated by the environment and human disturbances. Understanding the social and ecological dynamics of these species will inform the management of these felids in landscapes where they share habitats and face conflicts with humans.

Here, we used large-scale camera-trapping data to examine the spatial, temporal and combined spatiotemporal behavioral mechanisms potentially facilitating co-occurrence of these two flagship carnivores at fine spatial scales (i.e., camera locations). We hypothesized that Amur leopards, as the subordinate competitors, would avoid Amur tigers in both space and time to reduce the risk of potentially fatal encounters (Harihar et al. 2011). Human disturbance may influence intraguild competition directly by affecting densities of species or indirectly by reducing habitat quality and prey availability and by constraining the use of space and time (Seidensticker 1976; Terborgh and Estes 2010; Schuette et al. 2013; Karanth et al. 2017). We thus further hypothesized that high levels of human disturbance influence both tiger and leopard distributions and in turn their competitive interactions. Our objectives are to (1) assess if spatial co-occurrence of tigers and leopards is influenced by the occurrence of tigers, (2) determine the degree of temporal overlap among tigers, leopards, prey, cattle and human presence, and (3) estimate the spatiotemporal segregation between tigers and leopards when both co-occur at the camera locations.

Methods

Study area

This research was conducted in the northern section of the Changbai Mountains, China, adjacent to Russia to the east and North Korea to the south (Fig. 1). The approximately 5000-km² study area forms the core of a potential recovery landscape for tigers and leopards in China (Hebblewhite et al. 2012; Wang et al. 2016). Three natural reserves (Hunchun, Wangqing and Laoyeling) are located in the rugged mountainous landscape. The elevations range from 5 to 1477 m. The climate is characterized as a temperate continental monsoon with average annual temperatures ranging from 3.90 to 5.65 °C and a frost-free period of 110–160 days/year. The annual average precipitation is 580–618 mm, with the most precipitation occurring in the summer from June to August. The major vegetation types include Korean pine (*Pinus koraiensis*) forests, oak forests, coniferous forests, natural shrublands, and agricultural areas (Tian et al. 2011). Forest cover is > 92%, and the majority of the forests have been converted into secondary deciduous forests over the past 5 decades (Li et al. 2009a). The main economic activity in the rural areas is free-range cattle grazing; other human activities include the collection of edible ferns, ginseng farming and frog farming (Wang et al. 2016).

Camera trap survey

Camera trapping was conducted continuously from August 2013 to July 2014 (Wang et al. 2018) (Fig. 1). We used 3.6 × 3.6 km grids to guide camera trap placement throughout the study area. On average, there were approximately 20 cameras per female tiger home range (ca. 400 km²) (Hernandez-Blanco et al. 2015). The adjacent camera locations were an average of 2.36 km apart. Within the sampling grids, we maximized detection probability by placing cameras at sites where tigers, leopards, and their prey were likely to travel (e.g., along ridges, valley bottoms, trails, forest roads and near scent-marked trees). The cameras (LTL 6210 M, Shenzhen, China) were fastened to trees approximately 40–80 cm above the ground and were programmed to take videos 24 h/day with a 1-min interval between consecutive videos. We

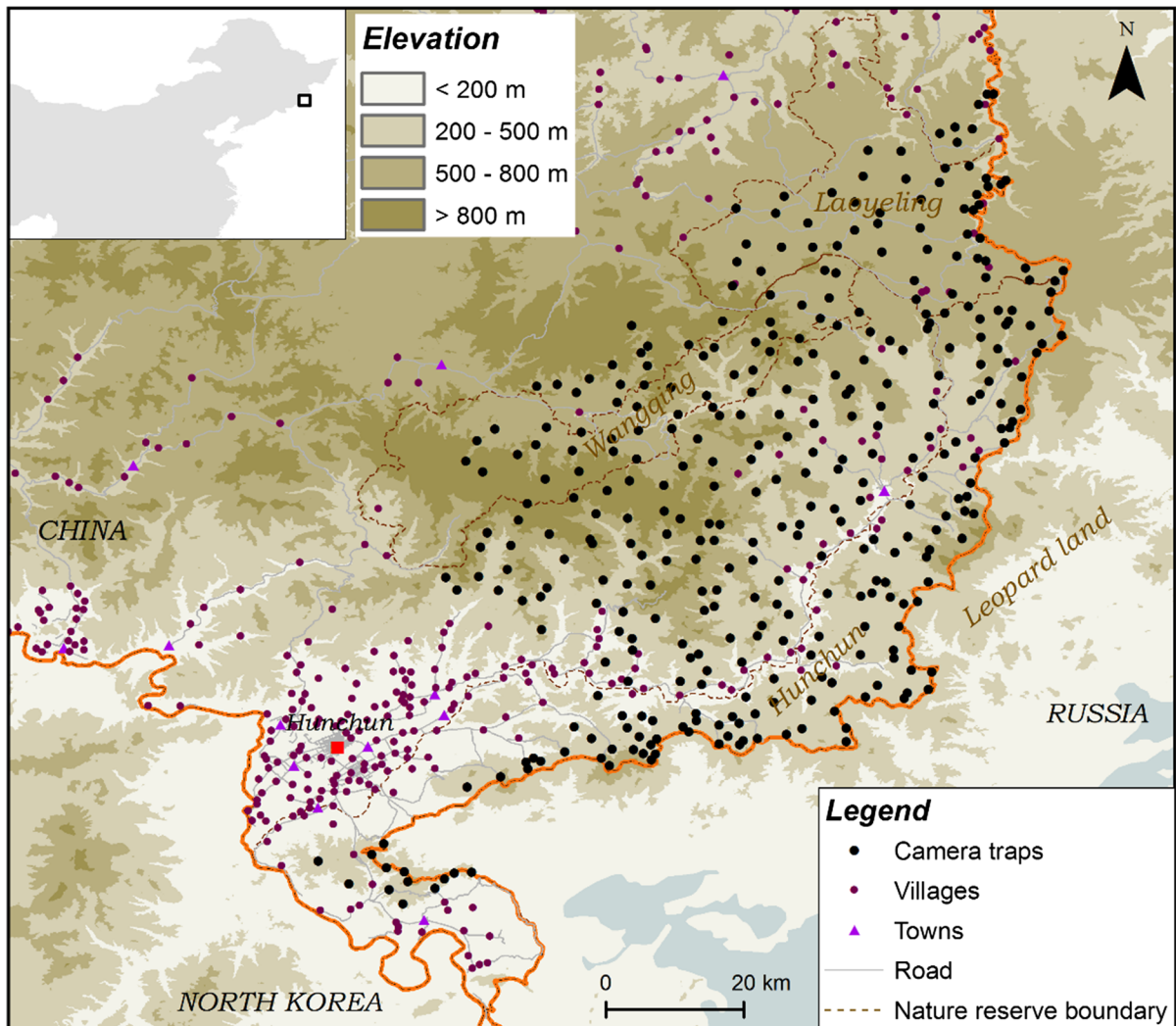


Fig. 1 Maps of the study area showing camera trap sites relative to settlements, roads and nature reserves in the Changbai Mountain Landscape of China. Inset shows the location of the study area in China

visited each camera 5–7 times a year to download the videos and check the batteries.

We analyzed tigers, leopards, three wild ungulates (sika deer *Cervus nippon*, wild boar *Sus scrofa* and roe deer *Capreolus pygargus*), cattle, and human presence (people on foot and vehicles) as camera trap “entities”. We calculated a relative abundance index (RAI) for each entity at each camera trap station from August 2013 to July 2014 as the number of detections per 100 camera trap days. To avoid inflated counts, a single detection was considered as the sighting of an entity within 0.5 h. The number of detections was considered a measure of activity or the encounter rate. Because

snow depth can affect the behavior and distribution of large carnivores (Miquelle et al. 2010), spatiotemporal niche analyses were conducted separately in snow-free periods (from April to October) and snow-cover periods (from November to March).

Spatial co-occurrence

We used an occupancy modeling framework to evaluate the spatial co-occurrence patterns between the two felids while accounting for imperfect detection (MacKenzie 2006). Tigers and leopards in our study had multiple camera-trap sites within their home

range, and thus moved among those sites during sampling. Therefore, we relaxed the assumption of geographical closure typically required for occupancy models and modeled use rather than occupancy.

We defined 2-week periods as temporal replicates and constructed detection histories of the tigers and leopards for each camera site over 26 sampling occasions. Subsequently, we selected a set of biotic and abiotic covariates which we hypothesized would influence the occupancy or detection of the tigers and leopards based on previous studies (e.g., environmental factors, prey availability and disturbance) (Hebblewhite et al. 2014; Wang et al. 2017, 2018). By including these covariates in co-occurrence models, we reduce the likelihood that species interactions is confused with differential habitat selection. Few covariates are typically used in two-species models due to the problems of model convergence (Robinson et al. 2014a; Wang et al. 2015). Initially, we considered 9 variables (elevation, percent tree cover [PTC], the prey richness of three wild ungulates [rich.prey], the RAI of the three major prey species, cattle, people and vehicles) as predictors of tiger and leopard occupancy and the trail type (forest road or ridge at each camera location) and season (snow-off versus snow-on) as predictors of detection. Here we do not interpret the prey's RAI as an index of abundance but rather as the likelihood for a carnivore to encounter an herbivore at each camera trap site (Sollmann et al. 2013). All continuous covariates were standardized prior to analysis. We found no evidence of correlation among the predictors used in the analysis (all correlation coefficients were $< |0.63|$ and had a variance inflation factor < 3 ; Table S1).

Because of the number of the potential combinations of the 8 model parameters (see Table S2), the candidate set of competing models for the conditional two-species parameterization is impractically large. To simplify the a priori size of the candidate model set, we selected models in a two-step process. First, we used single-species, single-season occupancy models to determine the best occupancy covariates for each species (see Appendix S1 for details). Next, we used all the detection and occupancy covariates from the best single-season occupancy models in the conditional two-species co-occurrence models (Richmond et al. 2010). The models where the competitor effect was allowed to vary between two seasons were not a competitive and are thus not considered further. We

conducted two-species occupancy analysis using the program PRESENCE 11.8 (Hines 2017). This final set of models was used to test several hypotheses about the interactions between tiger and leopard occupancy and detection probability. We tested three a priori hypotheses. First, we predicted that leopard (species B) occupancy would be lower at sites also occupied by dominant tigers (species A) due to the risk of intraguild predation (i.e., $\psi_{BA} < \psi_{Ba}$; see Table S2 for parameter definitions). Second, we predicted that the leopard detection probability would also be lower at the co-occupied sites (i.e., $r_B < p_B$), where we expected the leopards to minimize their foraging effort and move more secretively. Finally, we predicted that the detection probability of a leopard within a given sampling interval would depend on the presence of a tiger but would not depend on the detection of a tiger within the same interval (i.e., $r_{BA} = r_{Ba}$). In the present study, we assumed that the tiger detection probability was not affected by leopard presence at the co-occupied sites (i.e., $r_A = p_A$). We thus ran co-occurrence models on p and ψ using the six types of co-occurrence (Table S3). The top model with a $\Delta AIC < 2$ and with high Akaike weights was selected and then was used to calculate the species interaction factor (SIF) between tigers and the leopards. The SIF represents a likelihood ratio of co-occurrence for the two species and calculated as

$$\text{SIF} = \frac{\psi_A \psi_{BA}}{\psi_A (\psi_A \psi_{BA} + (1 - \psi_A) \psi_{Ba})}$$

An SIF = 1 indicates that the two species occur independently. An SIF < 1 indicates that species B is less likely to co-occur with species A than would be expected under independence (i.e., avoidance), whereas an SIF > 1 indicates that species B is more likely to co-occur with species A than would be expected by chance (i.e., aggregation). All parameter estimates are reported \pm unconditional SE and 90% credible intervals (CI) from the best supported two-species occupancy models.

Temporal interactions

All detection events were used to create 24 h activity patterns by ignoring the calendar date for each entity. Circular statistics of each entity within 24 h were calculated in the program Oriana 4.0 (Kovach 2011).

To test whether the mean angles of two independent circular observations differed significantly from each other, we applied Watson's U^2 -test. The coefficient of overlap (Δ , from 0 to 1), implemented in the *overlap* package in R, was also used to assess activity pattern overlap between tigers and leopards as well as the overlap between each felid and each prey species and human disturbances (people, vehicles and cattle) in the different periods (Ridout and Linkie 2009). We obtained 95% confidence intervals for Δ of every pairwise entity from 10,000 bootstrap samples. Lastly, we also used a conditional circular kernel density function to estimate the activity range overlap and the activity range core overlap between the two cats within each season under kernel isopleths of 95% and 50%, respectively (Oliveira-Santos et al. 2013).

Spatiotemporal interactions

Following Karanth et al. (2017), we used multi-response permutation procedures to assess the spatiotemporal segregation between tigers and leopards. This method tests for spatiotemporal segregation and is conditional on the observed space use and the temporal activity patterns of the focal species. At camera sites where both tigers and leopards co-occurred, for each leopard encounter, we calculated the minimum time to encounter tigers, and then we generated the expected statistical distributions of the times-to-encounter by randomly assigning encounter times to the camera trap locations in 1000 simulations. We compared the median observed time-to-encounter with a random simulated distribution of expected times-to-encounter. A longer observed time-to-encounter than would be expected (under an assumption of species independence) reflects species segregation, while a shorter observed time-to-encounter implies species aggregation.

Results

From August 2013 to July 2014, we implemented 65,632 and 49,222 camera trap days in snow-free and snow-cover conditions, respectively. We recorded 356 detections of a tiger and 362 detections of a leopard (Table 1). A total of 21 tigers (9 males, 8 females and 4 cubs) and 33 leopards (13 males, 18 females and 2 cubs) were identified by their unique stripe or spot

patterns. In both seasons, the naïve occupancy of tigers was < 0.20 , and the naïve occupancy of leopards was < 0.30 . The RAI map of tigers and leopards indicates that they were concentrated along the border (Fig. S2a, b). Sika deer sites were also concentrated along the border (Fig. S2c), and roe deer and wild boar were widely distributed (data not shown). Wild boar and roe deer were the most photographed herbivore species, while sika deer was only photographed at 37% of the stations in snow-free conditions and at 20% in snow-cover conditions. In the snow-free areas, human presence (people on foot and vehicle) was recorded on $> 85\%$ of the cameras and accounted for 65% of all detections; cattle triggered approximately 30% of the cameras and accounted for 13% of the detections (Table 1).

Spatial co-occurrence

The top ranked single-species, single-season model for tigers was ψ_A (sika deer + elevation + cattle + roe deer), p_A (trail) (Table S4). It was also the most parsimonious model because all of the remaining models within 2 ΔAIC included “uninformative parameters” that added one or more additional variables (people, vehicle, wild boar) to the top model without reducing the AIC value. Here, because tigers negatively co-occurred with the roe deer and roe deer are a small part of tiger diet (Kerley et al. 2015), we did not include as an ecological correlate. Similarly, the top ranked single-season model for the leopard, ψ_B (rich.prey + cattle + PTC), p_B (trail) was also the most parsimonious. Thus, the single-species, single-season occupancy modes supported elevation, sika deer, and cattle as the best and most informative occupancy covariates for Amur tigers while rich.prey, cattle and PTC were the best covariates for leopards (Table S4). These covariates had respective cumulative AIC weights of > 0.60 and were thus identified as factors influencing habitat use in the conditional two-species occupancy models.

The best two-species model was the first occupancy model ($\psi_A \psi_B p_A p_B r_B$, Akaike weight = 0.70), which is 3.18 times more likely to be the best model than the next model (Akaike weight = 0.22) (Table 2). The top best model indicated that the two large felids occurred independently (SIF = 1). We thus rejected hypothesis 1 and found little support for the leopard occupancy being decreased by the

Table 1 List of each species camera-trapped in Northeast China showing the number of independent detections and naïve occupancy

| | Common name | Detections | | Naïve occupancy | |
|--|------------------|------------|------------|-----------------|------------|
| | | Snow-free | Snow-cover | Snow-free | Snow-cover |
| | Amur tiger | 234 | 122 | 0.180 | 0.133 |
| | Amur leopard | 279 | 83 | 0.289 | 0.142 |
| | Wild boar | 1284 | 347 | 0.815 | 0.376 |
| | Roe deer | 2631 | 928 | 0.879 | 0.639 |
| | Sika deer | 913 | 253 | 0.368 | 0.195 |
| | Human on foot | 8548 | 1403 | 0.848 | 0.435 |
| | Human on vehicle | 7234 | 1901 | 0.329 | 0.234 |
| | Cattle | 3100 | 10 | 0.292 | 0.015 |
| | Total | 24,223 | 5047 | - | - |

Naïve occupancy represents the proportion of sites where the entities were detected at least once

Table 2 The two-species occupancy models examining the interactions between the tigers and leopards

| Occupancy model | Detection model | <i>K</i> | AIC | ΔAIC | <i>w_i</i> |
|-----------------|----------------------|----------|---------|-------|----------------------|
| ψA ψB | <i>pA pB rB</i> | 14 | 3710.67 | 0.00 | 0.70 |
| ψA ψB | <i>pA pB rBA rBa</i> | 16 | 3712.96 | 2.29 | 0.22 |
| ψA ψBA ψBa | <i>pA pB rB</i> | 18 | 3715.76 | 5.09 | 0.06 |
| ψA ψBA ψBa | <i>pA pB rBA rBa</i> | 20 | 3718.07 | 7.40 | 0.02 |
| ψA ψB | <i>pA pB</i> | 12 | 3736.70 | 26.03 | 0.00 |
| ψA ψBA ψBa | <i>pA pB</i> | 16 | 3740.76 | 30.09 | 0.00 |

K is the number of parameters, ΔAIC is the difference in AIC relative to the best model, and *w_i* is the Akaike weight that indicates the relative support for each model. Letters A and B represent Amur tiger and Amur leopard, respectively

The best model indicated that leopard detection, but not occupancy, was affected by the presence of tigers at a camera site. See Table S1 for parameter definitions. A detailed description of each occupancy and detection model is provided in Table S3

presence of tigers ($\psi_{BA} = \psi_{Ba} = 0.40 \pm 0.06$ SE); tigers do not limit the distributions of the leopards. However, we found that the detection probability of leopards was improved at sites in the presence of tigers ($r_B = 0.14 \pm 0.02$ SE vs. $p_B = 0.05 \pm 0.01$ SE), leading us to also reject hypothesis 2. Lastly, based on the top-ranked model, the detection probability of leopards depends on the presence of tigers but does not rely on the detection or nondetection of tigers ($r_{BA} = r_{Ba} = 0.14 \pm 0.02$ SE), which supports hypothesis 3 in that tiger activity at a camera site during a sampling interval did not influence the likelihood of the camera capturing a leopard in the same sampling interval.

The mean probability of tiger occupancy and detection calculated from the best-supported two-species model was 0.27 ± 0.04 SE and 0.09 ± 0.01 SE, respectively. Tigers noticeably preferred sites at a lower elevation (Table 3). Furthermore, tiger

occurrence exhibited a positive significant association with sika deer abundance. Leopard habitat use exhibited a positive association with prey richness and PTC. In addition, both tiger and leopard habitat use was significantly negatively related to heavy cattle grazing (Fig. 2). Finally, tigers were more likely to be detected at locations closer to forest roads, whereas leopards were more likely to be detected on mountain ridge trails (Table 3).

Temporal activity patterns

The temporal activity patterns of tigers and leopards were significantly different in snow-free ($U^2 = 2.41$, $p < 0.001$) and in snow-cover periods ($U^2 = 0.98$, $p < 0.001$), with leopards showing relatively more diurnal activity than tigers (Fig. 3). The mean time activity for tigers and leopards was $21:02 \pm 0:27$ and $10:44 \pm 0:49$ in the snow-free periods and

Table 3 The parameter estimates, standard error (SE) and 90% credible intervals (CI) of the best supported two-species occupancy models for Amur tiger (species A) and Amur leopard (species B) in NE China

| Covariate | Estimate | SE | lowCI | uppCI |
|-----------------------|---------------|------|--------|--------|
| Occupancy model | | | | |
| ψ A: (Intercept) | − 1.22 | 0.22 | − 1.58 | − 0.86 |
| ψ A: Sika deer | 1.77 | 0.45 | 1.03 | 2.52 |
| ψ A: Elevation | − 1.11 | 0.22 | − 1.48 | − 0.75 |
| ψ A: Cattle | − 0.51 | 0.34 | − 1.07 | − 0.06 |
| ψ B: (Intercept) | − 0.71 | 0.21 | − 1.07 | − 0.36 |
| ψ B: Rich.prey | 0.54 | 0.16 | 0.27 | 0.80 |
| ψ B: Cattle | − 1.99 | 0.89 | − 3.46 | − 0.52 |
| ψ B: PTC | 0.36 | 0.17 | 0.08 | 0.65 |
| Detection model | | | | |
| p A: (Intercept) | − 3.61 | 0.28 | − 4.08 | − 3.15 |
| p A: Trail | 1.75 | 0.29 | 1.27 | 2.23 |
| p B: (Intercept) | − 2.67 | 0.15 | − 2.91 | − 2.42 |
| p B: Trail | − 0.43 | 0.25 | − 0.85 | − 0.01 |
| r B: (Intercept) | − 1.22 | 0.15 | − 1.46 | − 0.98 |
| r B: Trail | − 1.27 | 0.23 | − 1.64 | − 0.89 |

Covariates with their 90% CI not encompassing zero (marked in bold) were considered to have a significant effect on tiger or leopard occupancy and detection

21:17 ± 0:43 versus 11:42 ± 0:59 in the snow-cover periods, respectively (Table 4). There was also very low activity overlap at 95% and 50% conditional isopleths between the two felid populations in the snow-free periods (0.54% and 0.23%, respectively) or in the snow-cover periods (0.55% and 0.18%, respectively).

The crepuscular and nocturnal tiger activity overlapping with the three major prey was higher in the snow-free periods (ranging from 0.71 [sika deer] to 0.84 [wild boar]) than in the snow-cover periods (ranging from 0.59 [sika deer] to 0.73 [roe deer]) (Table 5). The greatest temporal overlap was observed between tigers and wild boars ($\Delta = 0.83$, 95% CI 0.78–0.89). The leopard activity overlapped at a higher rate with all prey species, ranging from 0.74 (wild boar) to 0.87 (sika deer) (Table 5 and Fig. S1). In particular, the leopard activity patterns almost sync with those of the roe and sika deer in the snow-cover periods (Fig. S2), with the mean time of activity for leopards not significantly different from that of the roe

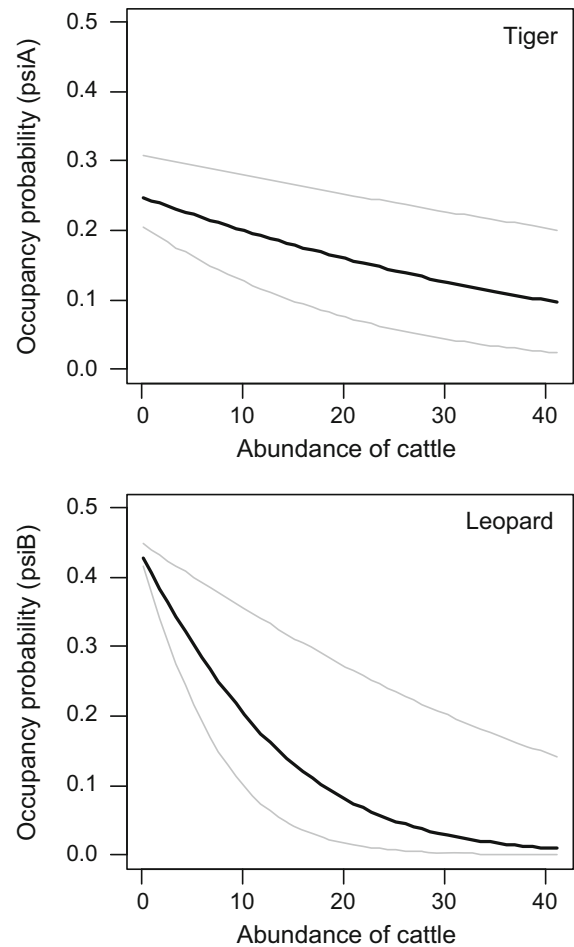


Fig. 2 Occupancy probability estimated from the best-supported two-species models plotted against the relative abundance of cattle (i.e., encounter rates) for the tiger and leopard in Northeast China. Gray lines represent 90% CIs of the effect

(11:25 ± 0:49; $U^2 = 0.18$, $p > 0.05$) and sika deer (13:14 ± 0:28; $U^2 = 0.14$, $p > 0.1$) (Table 4).

Compared with leopards, tigers offset their temporal activities by being less active during the day when the number of people on foot and vehicles peaked ($\Delta < 0.40$) (Table 5 and Fig. S2). Leopards had a relatively much higher temporal overlap with cattle ($\Delta = 0.92$, 95% CI 0.88–0.96) than did tigers ($\Delta = 0.59$, 95% CI 0.53–0.65).

Spatiotemporal interactions

When spatiotemporal overlap occurred, we examined the times-to-encounter between the tigers and leopards to test for behavioral avoidance. The frequency of the

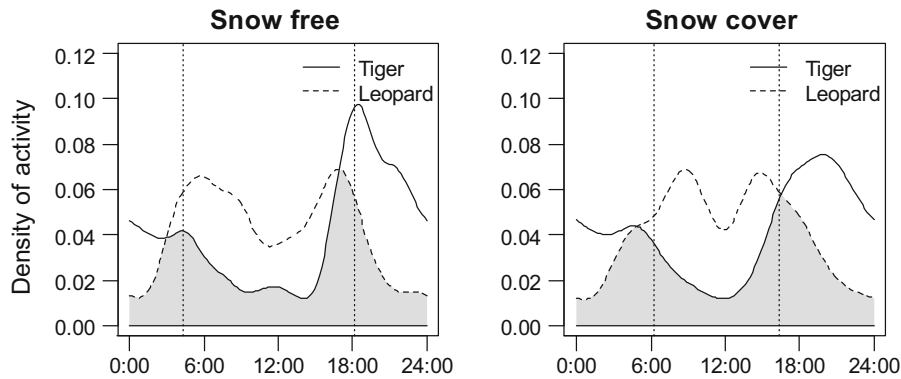


Fig. 3 Temporal overlap of daily activity patterns between tigers and leopards in both snow-free and snow-cover seasons along the China-Russia border. The estimated overlap is represented by the darkened area. Overlap is defined as the

minimum time-to-encounter between the two felids is mostly within 50 days (Fig. 4). The median observed minimum time-to-encounter was 44 days, which was significantly longer than the randomly generated time-to-encounter of 30 days ($p = 0.023$) indicating fine-scale (i.e., exact same point locations) behavioral avoidance.

Discussion

Competitive interactions in space-time

Large, iconic carnivores that occur at low densities are sensitive to a wide array of anthropogenic influences (Ripple et al. 2014; Wolf and Ripple 2017). Where they co-exist and both species are threatened, it is critical to study their competitive interactions. We examined both the overall spatial, temporal and the fine-scale spatiotemporal interactions between Amur tigers and Amur leopards in a heavily disturbed system. Our results highlight that spatially, occupancy of leopards was independent of the presence of tigers, as evidenced by our top two-species occupancy model (Table 2); thus, there is no evidence for interference competition. We hypothesized that leopards would be more cautious in the presence of tigers. However, counter to our expectation, leopards were not more difficult to detect when tigers were present. Interestingly, the opposite condition emerged in our study, with leopards more likely to be detected at sites where tigers were present ($rB > pB$). The apparent co-

area under the curve formed by taking the smaller value of the two activities at each time point. The black dashed vertical lines indicate the approximate times of sunrise and sunset

occurrence of tigers and leopards may be driven by the shared major prey, especially the sika deer (Table 3). We found no large-scaled spatial displacement; tigers and leopards had an SIF of nearly 1. We suspect that the low density of tigers at our site and temporal separation reduces the encounter rate and thus lessens the potential for interference competition. These results are consistent with Steinmetz et al. (2013) and Rayan and Linkie (2016), who suggest that a top-down regulatory effect by tigers on leopards diminishes when tiger density falls below a certain threshold (< 1 adult tigers/100 km²). In contrast, in South Asia where the density of tigers is high, leopards are often forced to range in peripheral habitats where they become focused on livestock (Odden et al. 2010; Harihar et al. 2011). Although at our site, the low tiger density (0.24–0.30 individuals/100 km²) (Xiao et al. 2016; Wang et al. 2018) did not appear to impact leopard density (0.30–0.62 individuals/100 km²) (Qi et al. 2015; Wang et al. 2017), at a finer scale leopards were frequently detected on ridge trails, whereas tigers were most likely to be detected closer to the forest roads in lower-altitude valley bottoms (Table 3), which further facilitates sympatry. Also leopards were more frequently photographed in higher elevation prey-poor habitats in the north part of the area (Fig. S1b); these habitats were avoided by tigers. Use of higher elevation may have lessened potential predation or competitive pressure from tigers. Protecting habitat in high-elevation may also increase landscape connectivity for leopards and tigers aiding their gradual habitat expansion in China.

Table 4 Circular statistics of the temporal activity patterns of tigers, leopards, their major prey and human disturbances in Northeast China

| Variable | Tiger | Leopard | Wild boar | Roe deer | Sika deer | People | Vehicle | Cattle |
|------------------------|------------------------|------------------------|------------------------|-----------------------|------------------------|------------------------|------------------------|------------------------|
| Snow-free | | | | | | | | |
| Number of observations | 235 | 279 | 1284 | 2631 | 913 | 8548 | 7234 | 3100 |
| Mean vector (95% CI) | 21:02 (20:08–21:57) | 10:44 (09:06–12:21) | 18:45 (17:54–19:36) | 4:10 (03:22–04:58) | 6:37 (04:48–08:26) | 10:55 (10:50–10:59) | 11:2 (11:17–11:29) | 11:57 (11:37–12:17) |
| Length of mean vector | 0.368 | 0.193 | 0.173 | 0.128 | 0.096 | 0.66 | 0.589 | 0.275 |
| Concentration | 0.791 | 0.392 | 0.351 | 0.259 | 0.194 | 1.781 | 1.467 | 0.573 |
| Standard error of mean | 0:27 | 0:49 | 0:25 | 0:24 | 0:55 | 0:02 | 0:02 | 0:10 |
| Snow-cover | | | | | | | | |
| Number of observations | 122 | 83 | 347 | 928 | 253 | 1403 | 1901 | 10 |
| Mean vector (95% CI) | 21:17 (19:52–22:43) | 11:42 (9:46–13:38) | 15:01 (14:30–15:33) | 11:25 (9:47–13:03) | 13:14 (12:19–14:09) | 11:02 (10:53–11:11) | 11:57 (11:47–12:08) | – |
| Length of mean vector | 0.327 | 0.294 | 0.505 | 0.106 | 0.351 | 0.755 | 0.6 | – |
| Concentration | 0.693 | 0.614 | 1.167 | 0.214 | 0.75 | 2.408 | 1.509 | – |
| Standard error of mean | 0:43 | 0:59 | 0:16 | 0:49 | 0:28 | 0:04 | 0:05 | – |

The length of the mean vector ranges from 0 to 1 and a larger value indicates that the observations are clustered more closely around the mean. The concentration measures the departure of the distribution from a perfect circle

Table 5 Estimated coefficient of daily activity overlap between species pairs

| Species | Coefficient of temporal overlap with Amur tiger | | Coefficient of temporal overlap with Amur leopard | |
|--------------|---|------------------|---|------------------|
| | Snow-free | Snow-cover | Snow-free | Snow-cover |
| Amur leopard | 0.63 (0.56–0.70) | 0.64 (0.53–0.75) | – | – |
| Wild boar | 0.84 (0.78–0.89) | 0.60 (0.51–0.68) | 0.79 (0.73–0.84) | 0.74 (0.64–0.84) |
| Roe deer | 0.73 (0.67–0.78) | 0.73 (0.65–0.80) | 0.81 (0.76–0.86) | 0.84 (0.77–0.91) |
| Sika deer | 0.71 (0.65–0.77) | 0.59 (0.51–0.68) | 0.87 (0.82–0.92) | 0.83 (0.74–0.91) |
| Cattle | 0.59 (0.53–0.65) | – | 0.92 (0.88–0.96) | – |
| People | 0.30 (0.25–0.35) | 0.26 (0.20–0.33) | 0.62 (0.57–0.67) | 0.62 (0.53–0.71) |
| Vehicle | 0.35 (0.30–0.41) | 0.40 (0.33–0.47) | 0.68 (0.62–0.73) | 0.75 (0.67–0.84) |

The 95% bootstrap confidence interval of the overlap estimates are indicated in parentheses

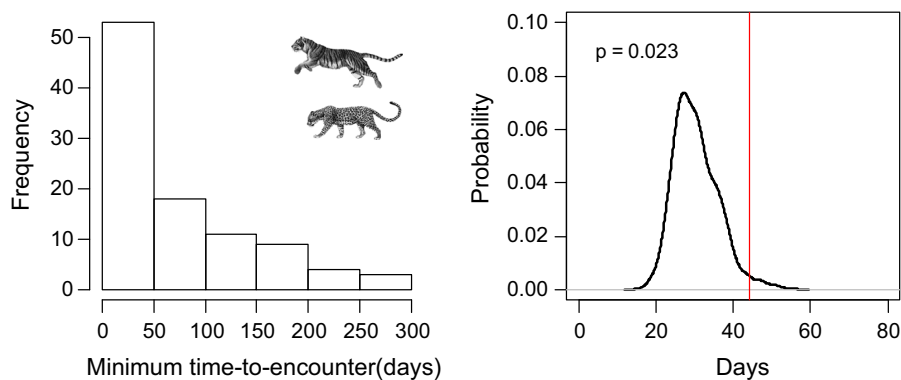


Fig. 4 Spatiotemporal interactions, as shown by the times-to-encounter between the tiger and leopard generated from multi-response permutation procedures. The vertical lines represent the median minimum time-to-encounter between the two species, while the area under the curve shows randomly

Both predators prey primarily on medium to large-sized ungulates (sika deer, wild boar and roe deer), which cumulatively accounted for 92% of tiger diet and 87% of leopard diet (Sugimoto et al. 2016). Thus, there is exploitative competition. For subordinate carnivore species, temporal niche partitioning is an evolutionary strategy for avoiding dominant competitors that respond to interference competition by attempting to kill or drive off the subordinate (Kronfeld-Schor and Dayan 2003; Hayward and Slotow 2009). In this study, temporal overlap analysis indicated that leopards were more active diurnally than tigers in both seasons (Fig. 3). Similarly, in tropical felid communities, temporal separation also allows smaller species to avoid dangerous intraguild aggression (Di Bitetti et al. 2010; Sunarto et al. 2015). In a secondary forest in Peninsular Malaysia, leopards

simulated times-to-encounter. The p-values, representing the proportion of randomly generated times-to-encounter values that are greater than the observed time-to-encounter, are given in each year

were more diurnal when tigers were abundant in the same area (Azlan and Sharma 2006). In this study, diurnal leopards still had a high degree of overlap with their key prey species ($\Delta = 0.74\text{--}0.87$) and a markedly positive spatial relationship with ungulate prey richness (all three prey). Such fine-scale temporal partitioning is also common in Africa where wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) temporally avoid lion (*Panther leo*) and hyena (*Crocuta crocuta*) (Hayward and Slotow 2009).

The influence of human disturbances on interactions

Our findings suggest that tigers and leopards showed different spatiotemporal patterns to avoid human and cattle, which reinforces our earlier results (Wang et al.

2016, 2017, 2018). Local people in our study area frequently used a larger portion of the study area, including the protected lands (Naïve occupancy > 85%). Tigers notably displaced their temporal activity from more diurnal human presence in both seasons; a similar pattern of temporal avoidance was observed in Nepal (Carter et al. 2012). In contrast, temporal partitioning of leopards may increase the likelihood for a leopard to encounter humans at each site. However, our previous findings using the same dataset suggested that ubiquitous human presence on foot and vehicles is responsible for leopard absence in a given space (Wang et al. 2017). Furthermore, Amur leopards select habitat further away from roads and human settlements (Hebblewhite et al. 2011; Wang et al. 2017). This observation contrasts with findings in Nepal and India showing that leopards frequently occur around human settlements to avoid encounters with tigers (Odden and Wegge 2005; Odden et al. 2010; Harihar et al. 2011; Athreya et al. 2013). Thus, it is possible that human presence across our study area decreases spatial encounters between tigers and leopards. In summary, these contrasting patterns imply that the different behavioral decisions by the two carnivores are influenced by the spatial and temporal activities of humans.

Our results also suggest that cattle grazing greatly decreased tiger and leopard habitat use (Fig. 2). Pudyatmoko (2017) reported that leopards were absent in areas with livestock in Baluran National Park, Indonesia, and in India, Sharma et al. (2015) found a threshold density of livestock caused snow leopards (*Panthera uncia*) to decline sharply and become spatially displaced, presumably due to the combination of anthropogenic disturbance and depressed wild ungulate abundance. In our study, tigers and leopards were largely absent in areas where the RAI of livestock was high in the southwest of the study area (only 1 of the 21 tiger individuals and 1 of the 33 leopards were detected) (Fig. S2). Earlier studies speculated that competition between livestock and wild prey is a major constraint to population growth of Amur tigers and leopards in Northeast China (Wang et al. 2016, 2017, 2018).

Areas of high cattle activity appear to be poor habitat for tigers and leopards, primarily because exploitative competition from cattle reduces forage quality and quantity (by 29–70%) in the shrub-herb layer (Fig. S3). Livestock may be particularly

detrimental to sika deer, the dominant prey in the diet of tigers and leopards (composing 25–54% of the total biomass consumed by the tiger and 50% by the leopard, respectively) (Kerley et al. 2015; Sugimoto et al. 2016).

Our occupancy models indicated that the probability of tiger habitat use is primarily a function of sika deer abundance (Fig. S1c). Amur tiger energetics modeling suggests that a highly reproductive tigress requires 2–3 times more food than a solitary tigress to successfully raise young to independence (Miller et al. 2014). It is highly unlikely that a tigress could raise cubs without a large-bodied deer species in her territory (Hayward et al. 2012). Similar loss of large-bodied deer prey also occurred in India, where domestic livestock resulted in a decline in chital (*Axis axis*), sambar (*Cervus unicolor*) and gaur (*Bos gaurus*), thereby decreasing the density of tigers (Madhusudan 2004; Punjabi and Rao 2017).

Currently cattle are left unsupervised to move freely during snow-free periods across the lower elevation areas in our study area. We recorded > 50 cattle killed by tigers every year (Wang et al. 2016). Most attacks were clustered south of Hunchun Nature Reserve where high wild prey density attracted tigers. Despite livestock depredation, tigers do not feed on 25% of the livestock they kill and less than half of the carcass was consumed in 42% of the kills (Li et al. 2009b). This situation appears related to the ubiquitous human presence across the study area as tigers may abandon kills in response to human disturbance. Human disturbance may explain why livestock compose only 4.3% of the biomass consumed by tigers (Kerley et al. 2015).

Conservation implications

At present in Northeast Asia, tigers and leopards only co-occur in the Sino-Russian border landscape. Both populations are small and isolated, and with low prey densities, they are susceptible to stochastic events. Continued expansion of these two predator populations is desperately needed to secure their long-term viability. Lack of interference competition by tigers toward leopards and high dietary overlap indicates that exploitative competition impacts both species. The degree of this impact is unknown, but with roughly twice as many leopards as tigers in this landscape, exploitative competition may have a substantial

impact on both species. Thus intraguild competition argues strongly for the Chinese government to continue its efforts to expand its initiative to create a tiger-leopard landscape. Future research needs to target movement of both tigers and leopards to determine how these species move through areas with higher human density. A better understanding of the fine scale movement patterns of tigers and leopards in the protected components of this newly created landscape as well as their behavior in human wildlife coupled components of the landscape is needed.

In addition to the need to enlarge the landscape to secure larger populations of both species through greater landscape occupancy, this research and previous studies (Wang et al. 2016, 2017, 2018) demonstrate the negative impact of livestock grazing on wild prey, especially sika deer. For tiger and leopard conservation, clear benefits exist for shifting from an economy of timber harvest and livestock herding to an economy that emphasizes tourism and contributions to China's ecological services through integrating biodiversity conservation with carbon sequestration and water conservation.

Recovering wild prey species and reducing or excluding livestock from the forest should be a high management priority. Reducing the abundance of cattle may release sika deer, the dominant prey of tigers and leopards, into areas heavily impacted by cattle grazing. Conservation success stories in Nepal and India reveal valuable lessons to guide these conservation efforts as recovery of wild ungulate, tiger, leopard, and lion populations were recorded in these countries following the exclusion of livestock (Wegge et al. 2009; Singh and Gibson 2011).

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Data availability The dataset analyzed during the current study is available from the long-term Tiger Leopard Observation Network (TLON) in China by request.

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