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Do prey availability, human disturbance and habitat structure drive the daily activity patterns of Amur tigers (*Panthera tigris altaica*)?

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Keywords

Amur tiger; human disturbance; camera traps; activity patterns; spatio-temporal overlap; prey availability; habitat structure; *Panthera tigris altaica*.

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Abstract

The daily activities of animals are influenced by various factors, including their physiological adaptations and preferred habitat distributions, as well as prey availability and human disturbances. For felids, the main drivers of activity patterns appear to be prey availability and anthropogenic disturbances, as suggested by previous studies. In this study, we explore a set of variables that influence the activity patterns of Amur tigers (*Panthera tigris altaica*) in Jilin and Heilongjiang Provinces in north-east China near south-western Primorsky Krai, Russia. This area is currently the only occupied tiger habitat in China. Prey availability (e.g. wild boar, sika deer and roe deer), human disturbances (e.g. human activity, distance to human settlements and intense forest livestock grazing), and habitat structure were analysed. Our results revealed crepuscular and nocturnal activity of Amur tigers. Although the temporal overlaps between the tigers and their prey species were high, the spatial overlap indices were low. Although the presence of tigers decreased near human settlements, tigers showed a preference for walking along roads. Tigers also avoided high-elevation coniferous and mixed hardwood forests. Overall, our results indicated that (1) tigers spatially and temporally avoided human disturbances and tigers respond behaviourally to human disturbances and (2) human disturbances may determine the activity of Amur tigers in north-east China. In the future, to address conflicts between tigers and local humans and to improve tiger conservation, conservation planning should incorporate the spatio-temporal activity patterns of tigers and humans.

Introduction

Animals' daily activity patterns are considered to be affected by environmental and evolutionary factors (Halle, 2000). Animals must adapt their physiology and behaviour to species-specific circadian rhythms that govern their daily activity (Kronfeld-Schor & Dayan, 2003; Dibner, Schibler & Albrecht, 2010; Heurich *et al.*, 2014). In addition, circadian patterns are modulated by external factors, such as habitat selection (Díaz-Ruiz *et al.*, 2016), temporal niche selection (Chavez & Gese, 2006), prey availability (Lucherini *et al.*, 2009) and predation risk (Gliwicz & Dabrowski, 2008). Numerous studies have shown that the daily activity patterns of mammals are altered due to considerable anthropogenic disturbances (Kitchen, Gese & Schauster, 2000; Ohashi *et al.*, 2013; Díaz-Ruiz *et al.*, 2016; Gaynor *et al.*, 2018).

Prey availability, defined as the interaction between prey abundance and accessibility, has been identified as the main driver of the activity patterns of felids (Schmidt, 1999). When prey is abundant, high levels of synchrony between predator and prey, at relevant scales along both spatial and temporal dimensions, can enhance the probability of an encounter, allowing the predator to expend less energy to capture the prey (Weckel, Giuliano & Silver, 2006; Braczkowski *et al.*, 2012; Foster *et al.*, 2013). In addition, the activity patterns of felids are also influenced by anthropogenic disturbances. The activity patterns of bobcat (*Lynx rufus*) in northwest of Los Angeles (Tigas, Van Vuren & Sauvajot, 2002), mountain lions (*Felis concolor*) in northern Arizona (Van Dyke *et al.*, 1986) and leopard (*Panthera pardus*) in Thailand (Ngoprasert, Lynam & Gale, 2007) have shifted their activity patterns under human disturbances.

In this study, we focus on the Amur (or Siberian) tiger (*Panthera tigris altaica*), which is the top predator critical to the sustainability of forest ecosystems in north-eastern China (Feng *et al.*, 2017). Over the past century, the Amur tiger population has consistently declined because of habitat loss, landscape fragmentation, prey depletion and poaching (Miquelle *et al.*, 2010; Feng *et al.*, 2017). At our study site, local-scale human disturbances may influence tiger activity patterns, and tigers may adapt to certain human disturbances with strong behavioural responses. A previous study indicated that Amur tigers are more active at crepuscular and night time and considered the possibility that tiger activity patterns can be explained by either prey availability or human activities (e.g. livestock, human presence on foot/by vehicles) (Wang *et al.*, 2016). Nonetheless, the simultaneous effects of habitat, prey availability and human-related factors (e.g. livestock and human activity) on the activity patterns of Amur tigers are worth examining.

In the current study, we analysed the activity patterns of Amur tiger, prey species of tigers (wild boar, sika deer and roe deer) and the human-related activities in tiger habitat (humans on foot/in vehicles, as well as livestock). We calculated the overlap indices of activity patterns of Amur tigers, prey species and human activities and livestock. Specifically, we estimated the spatial overlap between Amur tigers and prey species and human activities and livestock. Finally, we evaluated the intensity of the drivers of Amur tiger activity patterns, including prey species availability, each human-related activity and ecological correlates (distance to settlement, elevation, distance to the border between China and Russia, type of trail and vegetation), as well as the interactions between these factors. The following two hypotheses were examined: (1) the activity pattern of Amur tigers is adjusted based on the activity patterns of its main prey species to reduce energy expenditures; and (2) the bionomic strategy of Amur tigers is adjusted as the big cat attempts to avoid adverse human disturbances.

Materials and methods

Study location

The study was conducted in the north-eastern section of the Jilin Province and the adjacent south-eastern Heilongjiang Province in north-east China, bordering North Korea and south-western Primorsky Krai, Russia (N 42.54°–43.76°, E 130.56°–131.31°) (Fig. 1). The elevation of the area ranges from 5 to 1477 m a.s.l. (Wang *et al.*, 2017). The major potential regional forest types include spruce-fir (*Picea jezoensis* Maxim) forests at high elevations and mixed coniferous and broad-leaved forests on massive mountains at lower elevations (Xing, 1988). The current forest types are post-logging secondary hardwood forests dominated by Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb.), some coniferous forests on the mountain tops, and mixed hardwood forests on footslopes and along streams. In addition, natural scrublands are observed along forest edges and agricultural lands along roads and streams (Tian *et al.*, 2011). Hebblewhite *et al.* (2012) considered this region to be the highest priority tiger and leopard conservation area in China because it contains large continuous forested habitat patches that connect to the Land of the Leopard National Park, Russia, which is the location of the source populations of Amur tigers and Amur leopards (*Panthera pardus orientalis*) (Feng *et al.*, 2017). The main prey species of the felids include Siberian roe deer (*Capreolus pygargus*), sika deer (*Cervus nippon*), wild boar (*Sus scrofa*), and domestic animals (i.e. cattle and dogs) (Sugimoto *et al.*, 2016; Yang *et al.*, 2018a).

Commercial logging operations in the region ceased completely in 2015. However, ginseng farms, agriculture and mining have recently replaced logging as the main economic activities, and they have led to the deterioration and fragmentation of the habitat. Edible fern harvesting, frog breeding, livestock grazing and firewood collection, which are common in the study area.

Data collection

Our research is a part of the long-term Tiger-Leopard Observation Network (TLON) (Wang *et al.*, 2016; Feng *et al.*, 2017; Yang *et al.*, 2018a,b). The study site was gridded into 334 cells of 3.6 × 3.6 km, and 1 to 4 camera trapping sites (Ltl Acorn 6210M, Zhuhai, China) were installed in each cell along trails, roads and natural ridge routes that wild animals tended to use, although they were not installed in farmland and villages. The cameras were mounted onto trees at approximately 0.4–0.8 m above the ground and set to be continuously active, with a 1-min delay between consecutive videos and the sensitive level of cameras was programmed at low level. The cameras were programmed to record the time and date when a 15-s video was captured. The cameras were visited monthly to download the videos and replace batteries. For the study period, January 2014 to May 2015, the 488 camera traps continuously operated over 204 236 days (mean ± SE: 418.5 ± 4.08 trap days per camera).

To avoid inflated counts caused by repeated detections of the same event, consecutive videos of the same species occurring within 0.5 h were not included in the data analysis (O'Brien, Kinnaird & Wibisono, 2003).

Data analysis

Relationships between the activity patterns of Amur tigers and their prey species and human disturbances

The exact time of sunrise and sunset was determined using Moonrise 3.5 software (The average values used to delineate time of sunrise and sunset during sampling period). Independent detections of tigers and their prey species (determined by pictorial presence) were classified into three categories: diurnal (activity predominantly between 1 h after sunrise and 1 h before sunset); nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise); and crepuscular (peaks of activity through ± 1 h from sunrise and sunset) (Foster *et al.*, 2013). The selection ratios were calculated per species as shown below to determine whether the activity of a

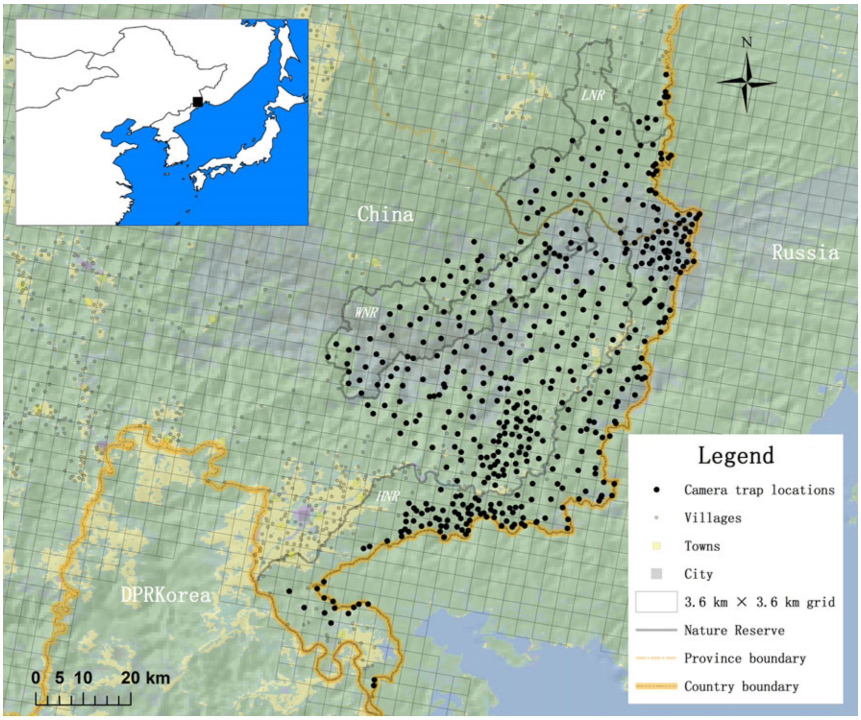

Figure 1 Study area and camera trap locations distributed in Northeast China. The mountainous region includes three nature reserves: the Laoyeling Nature Reserve (LNR), Wangqing National Nature Reserve (WNR) and Hunchun Nature Reserve (HNR), a large tract of unprotected forested and agricultural areas connecting the reserves (HC) and settlements (villages and towns).

species can be classified as predominantly crepuscular, diurnal, or nocturnal (Manly *et al.*, 2007):

$$w_i = o_i/\hat{e}_i$$

where w_i is the tigers' or prey species' selection ratio for the period i; o_i is the proportion of tiger and prey species detected in period i; and $\hat{e}_i$ is the ratio of the length in the period i to the length of all periods. When $w_i > 1$, the time period is highly preferred, whereas when $w_i < 1$, the time period is avoided.

The overlaps between the tigers and their main prey species and human disturbances were measured using the coefficient of overlap, Δ_4, for a large sample size (Ridout & Linkie, 2009; Linkie & Ridout, 2011) and ranged from 0 (no overlap) to 1 (complete overlap). The coefficient is the probability of activities for both species coexisting through kernel density estimates (Ridout & Linkie, 2009; Linkie & Ridout, 2011). Confidence intervals represented the precision of this estimator and were obtained from 10 000 bootstrap samples (Linkie & Ridout, 2011). All analyses were calculated using the *overlap* package (Ridout & Linkie, 2009) of R 3.1.2 (Team, R. C., 2013).

The time synchrony of activities for a pair of species can represent a good indicator of the activity patterns of the two species (Ramesh *et al.*, 2012). The probability density of each time point (dividing 24 h into 512 equal intervals) was estimated via kernel density estimation. Spearman's rank correlation was used to estimate the degree of synchronization of temporal activities between the tigers and their prey species and human disturbances.

Spatial overlap between Amur tigers and their prey species and human disturbances

To investigate spatial overlap, we calculated the Relative Abundance Index (RAI) (in this study, independent events (social species were defined per group as one independent event) per 100 h) (O'Brien *et al.*, 2003) of the Amur tiger, its main prey species and human disturbances for the three time periods (day, night, and crepuscular). The location of each camera trap was considered an independent spatial point, and the RAI of each site in a given time period was correlated between the tiger and its main prey species and human disturbances using Pianka's index (Pianka, 1973), which can reflect the spatial overlaps between tiger and prey and tiger and human disturbances over a given time period (Ramesh *et al.*, 2012). Values of Pianka's index were calculated using R software (Team, R. C., 2013).

Relationships among tiger activity, prey species availability, human disturbances and habitat structure

Records for the Amur tigers, three ungulate species, human activity and livestock were assigned to one of three time periods based on the light level (day, night and crepuscular) at each camera trap site (Table 1).

The habitat structure was considered in the investigation of the drivers of tiger activity patterns. Distances (in m) between the camera trap sites and the nearest human settlement and the nearest border between China and Russia were calculated using ArcGIS 10.1. At each camera trap site, the elevation was recorded by field sampling. We classified the vegetation types as broad-leaved forest, coniferous forest, mixed forest or oak forest and the trail types as animal trail, dirt road, forest trail, logging road or ridge (Table 1). The vegetation types and trail types surrounding each camera trap were identified based on the field sampling.

Generalized linear mixed models (GLMMs) were fitted to model the daily activity of the Amur tiger as a function of the time period (day, night and crepuscular), prey species availability (wild boar, roe deer and sika deer), human-related activities (human activity, livestock and distance to settlement) and habitat structure (elevation, distance to the border between China and Russia, trail type and vegetation) (Table 1). The number of independent Amur tiger events captured at each camera in a given time period was the response variable. An offset of the model was defined as the number of each camera-days × given time period in hours, and it was included in all modelling. The camera trap identity was considered a random effect in our model to distinguish between the effects of non-independent variables, such as environmental alteration and spatial arrangement (van Doormaal *et al.*, 2015). The interactions between the time period and main prey species availability and human disturbances (human activity and grazing) were included in our model as fixed explanatory effects.

To facilitate the interpretation of covariate coefficients and improve convergence, continuous covariates (Table 1) were scaled prior to the analysis (Zero-mean Normalization) (Wang *et al.*, 2017). We also checked for multi-collinearity using the variance inflation factor (VIF), with covariates eliminated from our model at VIF > 3 (Wang *et al.*, 2017). Correlation variables were used to check for the collinearity of variables; a variable was excluded when $|r| > 0.7$ with other covariates. We assessed whether models was affected by overdispersion, and dispersion parameters within a range of 0.5–1.5 were considered acceptable (Zuur *et al.*, 2009). The GLMMs were fitted using the R package *glmmADMB* (Skaug *et al.*, 2011). Next, we used the dredge function from the R package *MuMIn* (Bartoń, 2013) to select the best model. When no single model showed a total model weight >90%, we selected the model at $\Delta AIC_c < 2$ (Burnham & Anderson, 2003). The statistical analyses were performed using R 3.1.2 (Team, R. C., 2013).

Results

Temporal overlap

According to Moonrise 3.5, the average sunrise and sunset times were 05:11 and 17:24, respectively. Amur tigers

Table 1 Variables used for the generalized linear mixed models (GLMMs) to model the drivers of Amur tiger daily activity

Name	Description (range of value)	Category	Source
Wild boar	Numeric, no. of wild boar detected at the specific time period (0–21)	Prey	Camera trap
Roe deer	Numeric, no. of roe deer detected at the specific time period (0–60)	Prey	Camera trap
Sika deer	Numeric, no. of sika deer detected at the specific time period (0–55)	Prey	Camera trap
Human activity	Numeric, no. of human (on foot and by vehicle) detected at the specific time period (0–1948)	Human disturbance	Camera trap
Livestock	Numeric, no. of livestock detected at the specific time period (0–274)	Human disturbance	Camera trap
Distance to settlement	Numeric(m), min. Distance to settlement (328–14 894)	Habitat	China Fundamental Geographic Information Dataset
Elevation	Numeric(m) (58–1349)	Habitat	Field sampling
Distance to boundary	Numeric(m), min. distance between the camera trap sites and the boundary (3–48 212)	Habitat	China Fundamental Geographic Information Dataset
Type of trail	Categorical, animal trail, dirt road, forest trail, logging road and ridge	Habitat	Field sampling
Vegetation	Categorical, broad-leaved forest, coniferous, mixed forest and oak forest	Habitat	Field sampling
Time period	Categorical, crepuscular, day and night		According to the exact time of sunrise and sunset by Moonrise 3.5
Offset	Numeric, No. of camera-days × given time period in hours		Camera trap and exact time of sunrise and sunset by Moonrise 3.5

Note: Dirt road: the main road in our study area used by vehicles; logging road: the abandoned logging road for motorcycles or foot traffic; forest trail: the collection road for local people on foot and linked to the dirt road or logging road; animal road: the road used by animals and local people and not linked to the dirt road or logging road; and ridge: trail on the ridge. Broad-leaved forest: the dominant species of broad-leaved forest is not oak; Coniferous: the dominant species is conifers; Mixed forest: the dominant species is not only broad-leaved tree, but also conifers; Oak forest: the dominant species is oak.

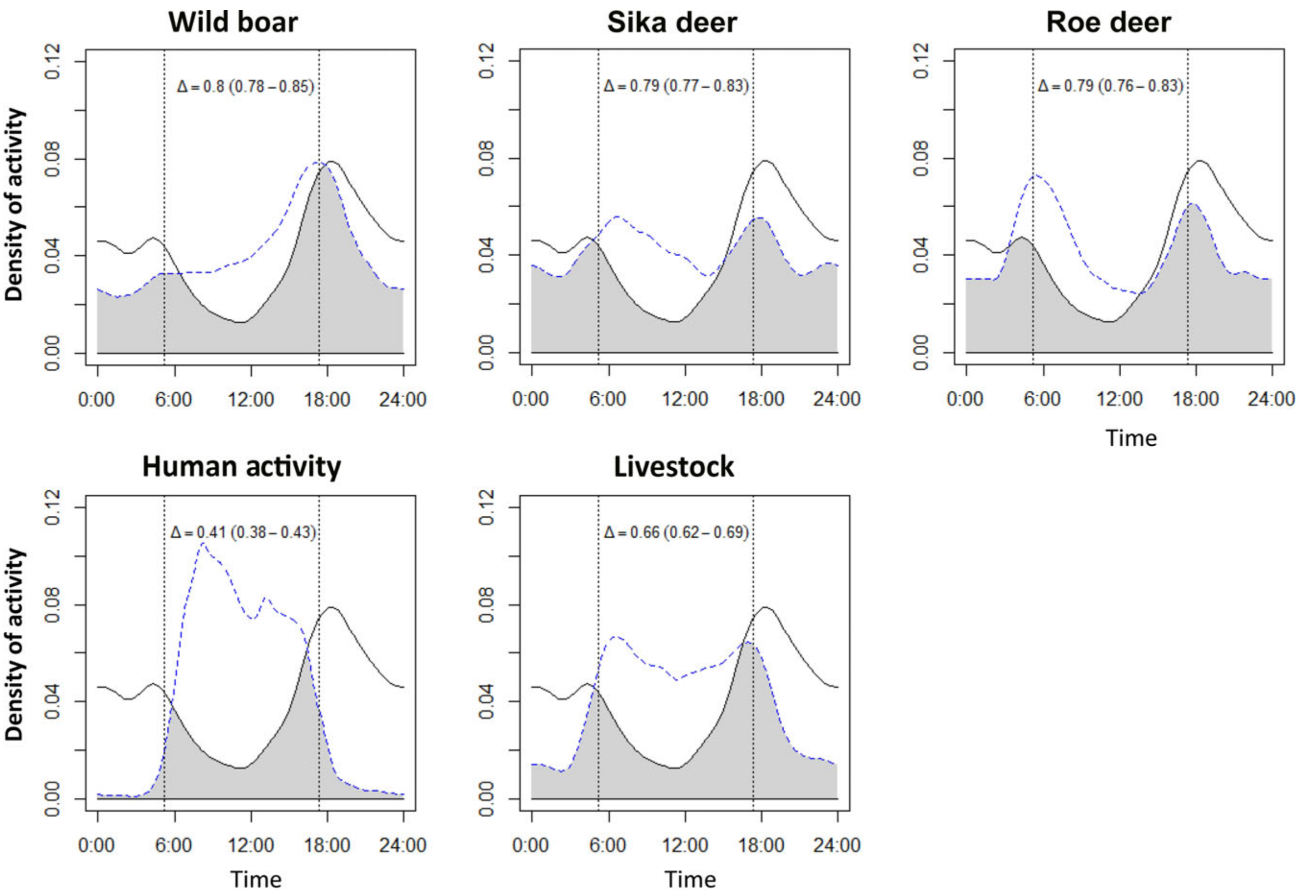

Figure 2 Temporal overlap indices between Amur tigers (solid line) and main prey species (wild boar, sika deer and roe deer) and human disturbances (human activity (human on foot and in vehicles) and livestock)(blue dashed line) based on camera trap data. The vertical dashed line represents the average sunrise and sunset times during the study period in our study area, as determined by Moonrise 3.5.

exhibited two activity peaks, at 04:10 and 18:20 (Fig. 2), and were more active at crepuscular and at night (Table 2). Wild boar and sika deer highly preferred crepuscular and the diurnal period. Wild boar had only one pronounced activity peak, at 17:20, and sika deer were most active at 06:40 and 18:00. We observed that roe deer preferred crepuscular and were most active at 05:10 and 18:00. We detected frequent human activity in the diurnal time period, with activities peaking at 08:30 and 13:00. Livestock grazing was mostly detected during crepuscular and diurnal hours and peaked at 06:30 and 16:40 (Table 2, Fig. 2).

Regarding the main prey species, Amur tigers showed the highest temporal overlap with wild boar, followed by roe deer and sika deer (Fig. 2). The temporal overlap indices between the tigers and human-related activities (livestock grazing and human activities) were lower than those for the prey species (Fig. 2).

The Spearman rank correlation values revealed significantly positive correlations between Amur tigers with wild boar and roe deer ($r = 0.20$ (d.f. = 513), $r = 0.40$ (d.f. = 513)), respectively, but not with sika deer ($r = 0.04$ (d.f. = 513). In contrast, Human activity ($r = -0.61$ (d.f. = 513)) and livestock ($r = -0.20$ (d.f. = 513) showed a significantly negative correlation with Amur tiger ($P < 0.05$).

Table 2 Number of independent detections n (number of events; selection ratio, w_i) in a given time period, and the total number of independent detections of species between 2014 and 2015 in NE China

Species	Total	n (w_i) in given time period Crepuscular	Day	Night
Amur tiger	717	175 (1.46)	164 (0.54)	378 (1.29)
Wild boar	2163	492 (1.36)	967 (1.05)	704 (0.80)
Roe deer	5987	1605 (1.61)	2267 (0.89)	2115 (0.86)
Sika deer	2306	480 (1.25)	1009 (1.03)	817 (0.87)
Human activity	40 312	4759 (0.71)	34 325 (2.01)	1228 (0.07)
Livestock	6387	1508 (1.42)	3679 (1.36)	1200 (0.46)

Spatial overlap

Of the three prey species, sika deer exhibited the highest spatial overlap with Amur tigers. The overlap values for the tiger and human disturbances varied among the different time periods. Tiger and livestock activity did not strongly overlap (Table 3).

Generalized linear mixed models–prey availability, human disturbances and habitat structure as factors explaining Amur tiger activity patterns

The maximum VIF (< 1.89) was less than 3, and $|r| < 0.7$ was found for all the correlated variables, which indicated that all the covariates were retained (Table S1). Eight models showed ΔAIC_c, indicating a total weight of 0.65 (Table 4). The dispersion parameter ranged from 1.189 to 1.242, indicating that none of the models were affected by overdispersion. All habitat covariates and human disturbances were included in the best models (Table 4). The most important variables for explaining Amur tiger activity were elevation, distance to the border, distance to human settlement, habitat type, trail type, time period, wild boar, roe deer and the interaction between time period and human disturbance (human activity and grazing) (Table 5). Sika deer and the interaction between the time period and prey species availability contributed less to explaining the variability in the activity of Amur tigers (relative importance < 0.6; Table 5).

The model-averaged parameter estimates of eight selected models revealed that Amur tiger preferred dirt roads and avoided mixed forest in the study area (Table 5). The nocturnal activity of the Amur tiger increased along with increases in human activity and livestock activity. Surprisingly, the nocturnal tiger activity decreased as sika deer activity increased. Overall, tiger activity increased with increasing distance to human settlements and decreased with increasing distance to the border and elevation.

Discussion

Our results show that Amur tigers exhibit mainly crepuscular and nocturnal behaviours in north-east China (Tables 2 and 5; Fig. 2). This result is consistent with the findings of earlier studies across the area as well as in other tiger distribution regions in Asia (Karanth & Sunquist, 2000; Linkie & Ridout, 2011; Carter *et al.*, 2012; Ramesh *et al.*, 2012; Wang *et al.*, 2016; Yang *et al.*, 2018b).

Compared with predator-prey temporal overlap indices for other mammalian species (0.6) (Foster *et al.*, 2013), the activity overlaps between Amur tigers and prey species were higher than average (Fig. 2). The Spearman rank correlations indicated that the tiger and prey species activities were significantly positively correlated. The activity patterns between the tiger and prey species in this study support the hypothesis that predators adapt their activity to that of the prey species (Foster *et al.*, 2013), which is similar to the suggestion that tiger activity patterns are more strongly correlated with the activity of prey species than avoidance (Karanth & Sunquist, 2000). A high activity overlap between predator and prey species may reduce the foraging energy expenditure for the predator.

Nonetheless, the spatial overlaps between the tiger and prey species were low (Table 3). The low spatial overlap may indicate spatial avoidance by prey species. The GLMMs results revealed that the prey species availability and interactions between the time period and prey species availability were of limited importance for the activity patterns of Amur tigers (Table 5). Brown, Laundré & Gurung (1999) believe that prey can change an activity pattern or spatial distribution as a trade-off between foraging needs and predator avoidance to reduce predation risk, like bighorn sheep (*Ovis canadensis*) spatially avoid pumas (*Puma concolor*) (Altendorf *et al.*, 2001) and tapir (*Tapirus indicus*) temporally avoid tigers (Linkie & Ridout, 2011). The spatial overlap between Amur tigers and prey species observed in this study indicated spatial avoidance by the prey to reduce predation risk, particularly in the case of wild boar (Table 3), which is the main prey species of Amur tigers (Kerley *et al.*, 2015; Sugimoto *et al.*, 2016; Yang *et al.*, 2018a). We speculate that the distributed heterogeneity of tigers in our study area (Xiao *et al.*, 2014; Wang *et al.*, 2016) also explains the low spatial overlap between the tiger and its prey species. Previous studies revealed that the Amur tiger and sika deer were confined to a distribution in the HNR near the Sino-Russian border (Xiao *et al.*, 2014; Wang *et al.*, 2016), and the GLMMs results of the present study indicated that tigers are more active along the border (Table 5); however, certain prey species, particularly wild boar and roe deer, were regularly distributed across the study region. Based on the existing data, we are not sure that the spatial avoidance or the distributed heterogeneity of tigers and prey species cause the low spatial overlap, and further research is needed. Overall, the results suggest that other factors than prey activity reasonably explain the variations in Amur tiger activity patterns (Table 5).

Amur tiger activity decreased where human activities (people on foot/by vehicle and livestock) were intense, although we found that Amur tiger and human activities frequently

Table 3 Spatial overlap between the Amur tigers and main prey species and human disturbance in three time periods in Northeast China

	Pianka's index		
Species pairs	Day	Night	Crepuscular
S01 and S03	0.094 (0.057–0.154)	0.054 (0.031–0.085)	0.080 (0.042–0.136)
S01 and S04	0.063 (0.039–0.108)	0.058 (0.025–0.111)	0.067 (0.039–0.108)
S01 and S05	0.355 (0.233–0.512)	0.342 (0.192–0.539)	0.349 (0.213–0.479)
S01 and S30	0.198 (0.135–0.286)	0.561 (0.323–0.743)	0.217 (0.149–0.310)
S01 and S33	0.019 (0.004–0.049)	0.089 (0.044–0.193)	0.058 (0.017–0.119)

Note: Variables are as follows: S01: Amur tiger; S03: wild boar; S04: roe deer; S05: sika deer; S30: human activity; and S33: livestock.

Table 4 Models explaining the activity patterns of Amur tigers

Model	d.f.	logLik	AIC$_c$	ΔAIC$_c$	*w*	Cum. *w*	Dispersion
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S30 + S33 + TIME × (S30 + S33)	**24**	**−733.76**	**1516.35**	**0.00**	**0.147**	**0.147**	**1.221**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S05 + S30 + S33)	**27**	**−731.01**	**1517.08**	**0.73**	**0.102**	**0.249**	**1.196**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S30 + S33 + TIME × (S30 + S33)	**23**	**−735.33**	**1517.42**	**1.07**	**0.086**	**0.335**	**1.225**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S05 + S30 + S33 + TIME × (S05 + S30 + S33)	**26**	**−732.42**	**1517.82**	**1.47**	**0.070**	**0.405**	**1.199**
ELE + DBO + DST + VEG + TRA + TIME + S04 + S30 + S33 + TIME × (S30 + S33)	**23**	**−735.55**	**1517.86**	**1.51**	**0.069**	**0.474**	**1.242**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S30 + S33)	**25**	**−733.60**	**1518.09**	**1.74**	**0.061**	**0.535**	**1.225**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S04 + S05 + S30 + S33)	**29**	**−729.50**	**1518.21**	**1.86**	**0.058**	**0.593**	**1.189**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S30 + S33 + TIME × (S04 + S30 + S33)	**26**	**−732.67**	**1518.32**	**1.97**	**0.055**	**0.648**	**1.215**
ELE + DBO + DST + VEG + TRA + TIME + S03 + S05 + S30 + S33 + TIME × (S30 + S33)	24	−735.23	1519.29	2.94	0.034	0.682	1.228
ELE + DBO + DST + VEG + TRA + TIME + S30 + S33 + TIME × (S30 + S33)	22	−737.43	1519.55	3.20	0.030	0.712	1.246
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S04 + S30 + S33)	27	−732.37	1519.79	3.44	0.026	0.738	1.221
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S30 + S33 + TIME × (S03 + S30 + S33)	26	−733.43	1519.84	3.49	0.026	0.764	1.217
ELE + DBO + DST + VEG + TRA + TIME + S04 + S05 + S30 + S33 + TIME × (S30 + S33)	24	−735.54	1519.91	3.56	0.025	0.789	1.243
ELE + DBO + DST + VEG + TRA + TIME + S04 + S05 + S30 + S33 + TIME × (S05 + S30 + S33)	26	−733.50	1519.97	3.62	0.024	0.813	1.220
ELE + DBO + DST + VEG + TRA + TIME + S04 + S30 + S33 + TIME × (S04 + S30 + S33)	25	−734.64	1520.18	3.83	0.022	0.835	1.238
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S03 + S05 + S30 + S33)	29	−730.54	1520.29	3.94	0.020	0.855	1.188
ELE + DBO + DST + VEG + TRA + TIME + S03 + S04 + S05 + S30 + S33 + TIME × (S03 + S04 + S05 + S30 + S33)	31	−728.62	1520.62	4.27	0.017	0.872	1.176
ELE + DBO + DST + VEG + TRA + TIME + S03 + S30 + S33 + TIME × (S03 + S30 + S33)	25	−735.02	1520.94	4.59	0.015	0.887	1.221
ELE + DBO + DST + VEG + TRA + TIME + S03 + S05 + S30 + S33 + TIME × (S03 + S05 + S30 + S33)	28	−731.95	1521.02	4.67	0.014	0.901	1.190

Note: We present models with ΔAICc < 2 in bold, as well as models with cumulated weight (Cum. w) = 0.9. The variables are as follows: ELE: elevation; DBO: distance to the boundary; DST: distance to human settlement; VEG: habitat type (broad-leaved forest, coniferous, mixed forest or oak forest); TRA: type of trail (animal trail, dirt road, forest trail, logging road or ridge); TIME: time period (crepuscular, day or night); S03: wild boar; S04: roe deer; S05: sika deer; S30: human activity; and S33: livestock. Interactions between variables are represented by ×.

Table 5 Model-averaged coefficients and standard errors of the variables included in the eight models ($\Delta AIC_c < 2$) that best explained Amur tiger activity

Variable	Estimate	SE	*z*	RI	*P* value
Intercept	−4.153	0.657	6.313	–	**<0.001**
ELE	−1.089	0.180	6.058	1	**<0.001**
DBO	−0.626	0.167	3.740	1	**<0.001**
DST	1.208	0.141	8.543	1	**<0.001**
VEG: Coniferous forest	−0.219	0.928	0.236	1	0.814
VEG: Mixed forest	−1.373	0.386	3.557	1	**<0.001**
VEG: Oak forest	0.321	0.288	1.111	1	0.267
TRA: Dirt road	2.213	0.642	3.446	1	**<0.001**
TRA: Forest trail	0.904	0.665	1.359	1	0.174
TRA: Logging road	0.942	0.658	1.430	1	0.153
TRA: Ridge	0.974	0.648	1.501	1	0.133
TIME: Crepuscular	−0.202	0.190	1.063	1	0.288
TIME: Night	0.800	0.208	3.841	1	**<0.001**
S03	−0.184	0.092	1.994	0.89	**<0.05**
S04	−0.187	0.164	1.143	0.76	0.253
S05	0.070	0.053	1.333	0.45	0.182
S30	−0.177	0.066	2.697	1	**<0.01**
S33	−0.587	0.276	2.120	1	**<0.05**
TIME: Crepuscular × S30	0.087	0.179	0.482	1	0.630
TIME: Night × S30	1.428	0.414	3.445	1	**<0.001**
TIME: Crepuscular × S33	0.482	0.305	1.577	1	0.115
TIME: Night × S33	1.014	0.328	3.090	1	**<0.01**
TIME: Crepuscular × S05	0.037	0.099	0.375	0.36	0.708
TIME: Night × S05	−0.140	0.065	2.136	0.36	**<0.05**
TIME: Crepuscular × S04	−0.397	0.262	1.513	0.17	0.130
TIME: Night × S04	−0.243	0.200	1.217	0.17	0.224

Note: RI is the relative variable importance from the model average. The variables are as follows: ELE: elevation; DBO: distance to the boundary; DST: distance to human settlement; VEG: habitat type (broad-leaved forest, coniferous, mixed forest (Coniferous and broad-leaved mixed forest) or oak forest); TRA: type of trail (animal trail, dirt road, forest trail, logging road or ridge); TIME: time period (crepuscular, day or night); S03: wild boar; S04: roe deer; S05: sika deer; S30: human activity; and S33: livestock.

P values <0.05 are represented in bold. The interactions between variables are represented by ×.

co-occurred during the nocturnal period, which is contrary to general beliefs (Table 5). The temporal overlap between tigers and human disturbances across the study area in north-east China were higher than that in Nepal's Chitwan National Park (Carter *et al.*, 2012) (Fig. 2), although the correlation between the tiger activity peak and human activities was significantly negative. Human activity (on foot/in vehicle) was more common in the diurnal and crepuscular periods (Table 2 and Fig. 2). The lower temporal association and the different activity peaks between tigers and human activities (Fig. 2) appear to indicate that Amur tigers were active at nocturnal and crepuscular period to avoid human activities. The spatial overlap between tiger and human activity was relatively low in the diurnal and crepuscular periods (Table 3). In the nocturnal period, the spatial overlap between human activity and tigers was relatively to daytime high (Table 3). However, according to the GLMMs, tiger activity increased as human activity increased ($P < 0.001$) in the nocturnal period (Table 5). The positive relationship between tigers and humans at night does not appear to be related to an increase in human activity but rather may be caused by the same road type selected by Amur tigers and humans (71.43 and 83.22% of tigers and human activity events occurred on dirt roads at night) (Table 5). Amur tigers showed increased activity on dirt roads, which are energetically efficient pathways for travelling the landscape (Karanth, 1995; Carter *et al.*, 2012).

Human settlements may have caused tigers to alter their space utilization because the animals are warier in areas with higher human disturbance (Carter *et al.*, 2012; Joshi *et al.*, 2013). The GLMMs results indicated that tiger activity decreased near settlements, whereas direct human disturbances increased in these areas (Table 5).

Although, the spatial overlap between tigers and human activity was relatively higher during the nocturnal period, the relationship between tigers and human disturbances indicated that Amur tigers spatially and temporally avoided human disturbances.

Based on the GLMM, Amur tigers preferred lower elevations and avoided coniferous forest and mixed forest (Table 5). In Northeast China, the trails developed for logging and military border patrols are often at valley bottoms, and these trails are energetically efficient for tigers to mark and travel (Carroll & Miquelle, 2006). A strong relationship between Amur tigers and Korean pine (*Pinus koraiensis* Siebold & Zucc.) forests was observed by Carroll & Miquelle (2006). However, the majority of Korean pine forests in Northeast China have been logged, and many low-elevation forests are currently secondary deciduous forests with few conifers (Li *et al.*, 2009). The once predominant mixed Korean pine and hardwood forests in the study area have been gone for decades, and coniferous forests are only found in the high-elevation region, particularly in north HNR near the Sino-Russian border. The avoidance of coniferous forest may be related to the coniferous forest at higher altitude and the Amur tiger's preference for trails to mark and travel.

Overall, our results indicate that Amur tigers and humans can coexist because the tiger behaviourally responds to humans at spatio-temporal scales, and human disturbances may determine the activity of Amur tigers in Northeast China. To avoid human disturbances and increase hunting success, the tigers were more active during crepuscular and nocturnal periods because of the high associated activity of the three main prey species during crepuscular period. In the future, incorporating spatio-temporal activity patterns into conservation plans can help address issues associated with Amur tiger conservation.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Table S1 Correlated variables of all continue covariates.