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Living on the edge: Opportunities for Amur tiger recovery in China

Tianming Wang[a,d,e], J. Andrew Royle[b], James L.D. Smith[c], Liang Zou[a,d,e], Xinyue Lü[a,d,e], Tong Li[a,d,e], Haitao Yang[a,d,e], Zhilin Li[a,d,e], Rongna Feng[a,d,e], Yajing Bian[a,d,e], Limin Feng[a,d,e], Jianping Ge[a,d,e,*]

[a] Ministry of Education Key Laboratory for Biodiversity Science and Engineering, Beijing Normal University, Beijing 100875, China
[b] U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA
[c] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St Paul, MN 55108, USA
[d] State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing 100875, China
[e] College of Life Sciences, Beijing Normal University, Beijing 100875, China

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ABSTRACT

Sporadic sightings of the endangered Amur tiger *Panthera tigris altaica* along the China-Russia border during the late 1990s sparked efforts to expand this subspecies distribution and abundance by restoring potentially suitable habitats in the Changbai Mountains. To guide science-based recovery efforts and provide a baseline for future monitoring of this border population, empirical, quantitative information is needed on what resources and management practices promote or limit the occurrence of tigers in the region. We established a large-scale field camera-trapping network to estimate tiger density, survival and recruitment in the Hunchun Nature Reserve and the surrounding area using an open population spatially explicit capture-recapture model. We then fitted an occupancy model that accounted for detectability and spatial autocorrelation to assess the relative influence of habitat, major prey, disturbance and management on tiger habitat use patterns. Our results show that the ranges of most tigers abut the border with Russia. Tiger densities ranged between 0.20 and 0.27 individuals/100 km^2 over the study area; in the Hunchun Nature Reserve, the tiger density was three times higher than that in the surrounding inland forested area. Tiger occupancy was strongly negatively related to heavy cattle grazing, human settlements and roads and was positively associated with sika deer abundance and vegetation cover. These findings can help to identify the drivers of tiger declines and dispersal limits and refine strategies for tiger conservation in the human-dominated transboundary landscape. Progressively alleviating the impacts of cattle and human disturbances on the forest, and simultaneously addressing the economic needs of local communities, should be key priority actions to increase tiger populations. The long-term goal is to expand tiger distribution by improving habitats for large ungulates.

1. Introduction

Asian forest ecosystems are becoming increasingly fragmented by the extensive intensification of anthropogenic activities (Joshi et al., 2016; Z.W. Li et al., 2009; Wang et al., 2012). As a result, tigers (*Panthera tigris*) have declined steadily since the end of WWII and are on the brink of local extinction in many areas (Gopal et al., 2010; Walston et al., 2010). Tigers, a flagship species and the apex predator in Asia, exemplify the problems faced by most large carnivores worldwide; they have experienced substantial population declines and range contractions during the past century (Dinerstein et al., 2007). Despite decades of conservation actions, human land use has led to a steady loss of habitat and as a result, once large and continuous populations have mostly been subdivided into smaller, less viable populations (Carroll and Miquelle, 2006; Kenney et al., 2014; Rayan and Linkie, 2015; Walston et al., 2010). To better understand the consequences of habitat fragmentation and degradation, recent conservation research has focused on how tigers use and disperse through human-dominated landscapes (Carter et al., 2012; Chanchani et al., 2016).

Attempts at recovering small, threatened populations of Asian carnivores often involve expanding their range beyond extant protected areas and international borders (Carter et al., 2012; Chanchani et al., 2016; Linnell et al., 2016; Smith et al., 1998). In Northeast China recovery of tigers will require expanding conservation efforts beyond the border with Russia into landscapes where human activities and biodiversity conservation must be integrated. This is the case with the

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* Corresponding author at: No. 19, Xinjiekouwai Street, Haidian District, Beijing 100875, China.
E-mail addresses: wangtianming@bnu.edu.cn (T. Wang), aroyle@usgs.gov (J. Andrew Royle), smith017@umn.edu (J.L.D. Smith), fenglimin@bnu.edu.cn (L. Feng), gejp@bnu.edu.cn (J. Ge).

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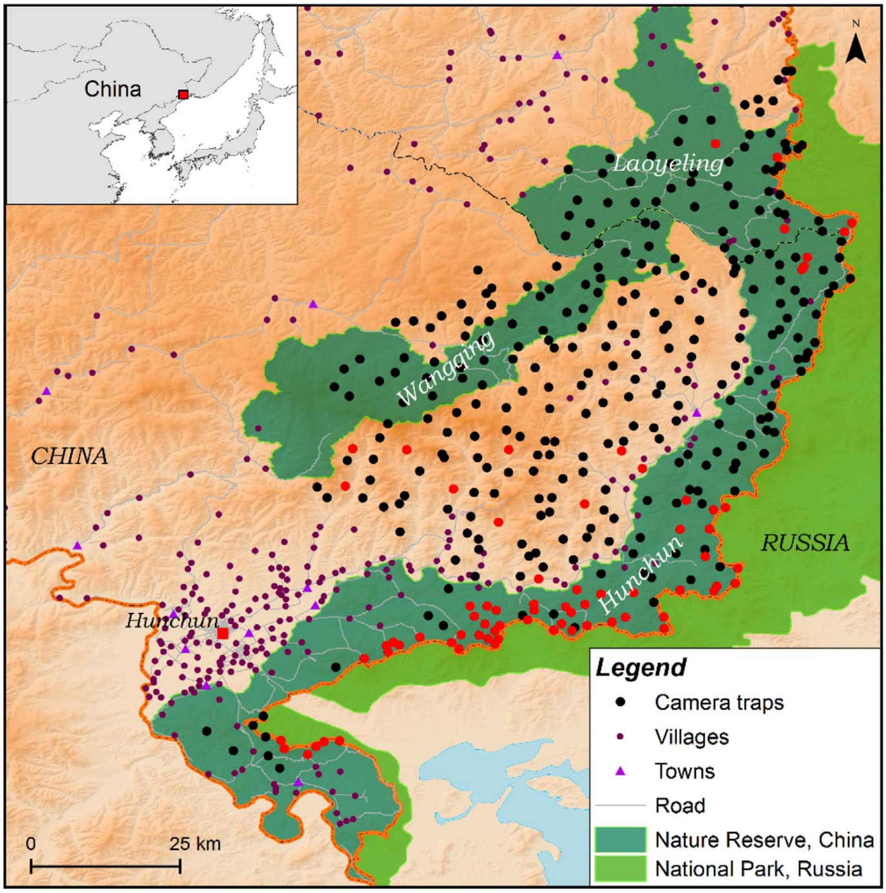

Fig. 1. Monitoring areas of the long-term Tiger-Leopard Observation Network (TLON) in NE China showing camera placement relative to settlements, major roads and nature reserves or national parks. Red dots represent the sample locations (camera traps) where tigers were observed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

endangered Amur (Siberian) tiger (*P. t. altaica*), which occurs on the northern fringe of the tiger's range. This subspecies plays a vital role in structuring the mixed coniferous and broad-leaved forest ecosystems of Northeast Asia (Luo et al., 2004; Miquelle et al., 2010b). Historically, tigers were once distributed widely across much of Northeast China, the Far East of Russia and the Korean Peninsula, but in recent decades they have experienced severe demographic and geographic range contractions due to habitat loss, poaching, prey depletion and disease (Gilbert et al., 2015; Miquelle et al., 2010a; Tian et al., 2011; Wang et al., 2016). Currently < 600 individuals are estimated to remain in two isolated subpopulations confined to the Sikhote-Alin Mountains of Russia (95% of individuals) and the Changbai Mountains along the China-Russia border (5%) (Miquelle et al., 2006; Tian et al., 2009). Movement between the two subpopulations is blocked by an urbanized rail and highway corridor and wetlands (Carroll and Miquelle, 2006; Hebblewhite et al., 2014; Miquelle et al., 2015), resulting in genetic divergence (Henry et al., 2009; Sorokin et al., 2016). This subspecies has the lowest genetic variation of all extant tiger subspecies and the Southwest Primorye/Changbai Mountains population has an estimated effective population size of 11–14 (Alasaad et al., 2011; Dou et al., 2016; Henry et al., 2009). The future of the Amur tiger, especially this smaller, isolated transboundary population is at a crucial threshold. Adequate conservation efforts are needed in Northeast China to restore landscape permeability so that tigers can once again occupy what is now a mixture of natural and human dominated habitat (Pitman et al., 2017; Yumnam et al., 2014).

Since the late 1990s, this border population has gradually increased and is extending its distribution into China (T.M. Wang et al., 2015; Wang et al., 2016; Wang et al., 2014). This transboundary population shares land with the only remaining population of the Amur leopard (*Panthera pardus orientalis*). These carnivores currently compete with local people for limited resources (e.g., food) as agricultural expansion, infrastructure development, and forest logging have seriously jeopardized their viability (Tian et al., 2011; Wang et al., 2016). In particular, changes in land-use policies in the Changbai Mountains have led to an increase in cattle ranching over the past 20 years, which has resulted in habitat degradation and the exacerbation of human-tiger conflicts (Soh et al., 2014; Wang et al., 2016). Thus, a conservation strategy is urgently needed that provides ecological services for human needs and habitat for tigers and leopards.

Despite recent research that has increased the understanding of Amur tiger ecological requirements (e.g., habitat connectivity, prey availability and human disturbance) (Carroll and Miquelle, 2006; Hebblewhite et al., 2014; Miquelle et al., 2010b; Petrunenko et al., 2016), significant knowledge gaps remain. In particular, programs that prioritize the initiation of such recoveries should be evidence-based, requiring assessments of landscape-wide conditions for this population, which are typically unclear in China. To improve the conservation outlook for the tiger, in 2016 the Chinese government initiated a Tiger-Leopard National Park (TLNP) program to expand the Amur tiger and leopard ranges in China (McLaughlin, 2016). The TLNP is connected to the Land of Leopard National Park (LLNP) in southwest Primorye Krai, Russia, but on the Russian side of the border, habitat is limited. In contrast, in China, there is extensive potential habitat, but wildlife face pressure from rapid land-use changes and high levels of anthropogenic activities. In particular, peripheral anthropogenic encroachment and activities have largely confined tigers to the reserve (Wang et al., 2016). Hence, understanding how tiger abundance and habitat use in China vary in response to environmental and anthropogenic factors and existing land management practices (i.e. livestock grazing) is essential for re-establishing tigers in China. There is also a clear need to identify how protection designation (inside and outside protected area) influence tiger occurrence at local and landscape scale, to inform land-use planning and wildlife management.

In this study, we used 12 months of camera trapping data across a ~5000 km^2 landscape to elucidate Amur tiger status and the ecological correlates that predict their distribution and abundance. We estimated the spatially explicit density of tigers across a gradient of habitat protection and anthropogenic disturbances using an open population spatially explicit capture-recapture model. We then used occupancy modeling, accounting for detectability and spatial autocorrelation, to assess the relative influences of habitat, prey, disturbance, and management on tiger distribution and abundance. The results of our research will inform science-based conservation strategies for integrating tiger recovery into a regional landscape-scale plan that includes biodiversity and ecological services.

2. Materials and methods

2.1. Study area

This research was conducted in the northern portion of the Changbai Mountains in Jilin Province, China, adjacent to southwestern Primorsky Krai, Russia, to the east, and North Korea to the southwest (Fig. 1). The approximately 5000-km^2 study area forms the core of a potential recovery landscape for tigers and leopards in China (Hebblewhite et al., 2012; Wang et al., 2016; Wang et al., 2017). Elevations range from 5 to 1477 m. The climate is characterized as temperate continental monsoon with average annual temperatures ranging from 3.90–5.65 °C and a frost-free period of 110–160 days/year (http://www.weather.com.cn). The annual average precipitation is 580–618 mm, with the most precipitation occurring in the summer from June to August. The majority of forests have been logged, and many low-elevation forests have been converted into secondary deciduous forests over the past 5 decades (Z.W. Li et al., 2009).

The prey of tigers in this area includes sika deer (*Cervus nippon*), wild boars (*Sus scrofa*), Siberian roe deer (*Capreolus pygargus*), musk deer (*Moschus moschiferus*), Asiatic black bears (*Ursus thibetanus*), and domestic species (cows and dogs), along with small animals such as Asian badgers (*Meles leucurus*) and raccoon dogs (*Nyctereutes procyonoides*) (Kerley et al., 2015; Tian et al., 2011; Xiao et al., 2014). The average home range of the Amur tiger is 401 and 778 km^2 for females and males, respectively, based on data from the adjacent southwestern Primorsky Krai (Hernandez-Blanco et al., 2015). Together, the tiger and leopard density is < 1 individuals/100 km^2 in this area (Wang et al., 2017; Xiao et al., 2016).

Over the past decade, the study area has been exposed to increasing levels of agricultural and industrial development, particularly mining and new road building, which has led to habitat fragmentation. Since 2015, commercial logging of natural forests has been halted and forest cover has expanded as part of a national plan to promote ecological development. The main economic activity in rural areas is free-range cattle grazing; other human activities include the collection of edible ferns, ginseng farms, and frog farming (Wang et al., 2016).

2.2. Data collection and field methods

This study, conducted from August 2013 to July 2014, was part of a long-term Tiger Leopard Observation Network (TLON) project that employed 356 camera trap stations in the Hunchun Nature Reserve (HNR) and two newly established reserves, Laoyeling and Wangqing, in 2014 (Wang et al., 2016) (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. Within the sampling grids, we maximized the detection probability by placing cameras at sites where tigers, leopards, and their prey are likely to travel (e.g., along ridges, valley bottoms, trails, forest roads and near scent marked trees). We excluded grids on farmland and in villages. The cameras (LTL 6210M, Shenzhen, China) were fastened to trees approximately 40–80 cm above the ground and were programmed to take photographs 24 h/day with a 1-minute interval between consecutive events. Approximately 70% of the stations had two cameras. The cameras were operated continuously throughout the year. We visited each camera 5–7 times a year to download photos and check batteries.

We analyzed tigers, their principal wild prey (sika deer, wild boar and roe deer), domestic livestock, and human presence (e.g., rural people using the forest and border patrols on foot and vehicles) as “entities” in the camera traps. Each tiger was identified both visually and using the pattern-matching software ExtractCompare (Hiby et al., 2009). No single-sided camera trap tiger photo was used unless it matched a photo from a double-sided station. Sex could usually be determined visually. Tiger cubs (< 1 year old) were removed from the density analyses because they usually remain with their mothers and exhibit low capture rates (Barlow et al., 2009; Karanth and Nichols, 1998). We calculated the detection frequency of each entity at each trap station as the number of detections per 100 camera-trap days (Carter et al., 2012; O'Brien et al., 2003). To avoid inflated counts caused by repeated detections of the same event, only one record of a species at a trap site per 0.5 h was included in the data analysis (O'Brien et al., 2003). We use R package “overlap” to estimate the overlapping of the activity patterns of tigers and human presence (Ridout and Linkie, 2009).

2.3. Open population models

We estimated population parameters using a Jolly-Seber model (Gardner et al., 2010; Jolly, 1965; Seber, 1965) and a multi-session model. An spatially explicit capture-recapture (SECR) model is a hierarchical model that explicitly links the spatial locations and movements of individuals (the point process) to the imperfect encounters of individuals in a trapping array (the observation process) (Efford, 2004; Royle et al., 2009). Open SECR models allow the joint modeling of data over periods of time for which closed models may not be appropriate. The accommodate non-closure by incorporating explicit dynamics allowing for individuals entering and leaving the population. The Jolly-Seber SECR model developed by Gardner et al. (2010) is based on a Bayesian Markov chain Monte Carlo (MCMC) framework. This method used data augmentation for the number of individuals alive (N) during each year, per capita recruitment (ρ), and apparent survival rate (φ), where we set augmentation value for N at 150 individuals (Gardner et al., 2010; Royle and Dorazio, 2012; Royle et al., 2009). This study was conducted during 2 consecutive periods made up of 6 months each from August 2013 to July 2014. We calculated ρ as the number of new individuals in the year 2014 divided by the number of animals alive in the year 2013. We note that these parameters should be interpreted as apparent survival and recruitment because the population is susceptible to permanent emigration and immigration which affect estimators of survival and recruitment, respectively.

For the present study, our 6-month sample periods are greater than previously estimated periods of 45 to 90 days necessary for closure for studies of other tiger subspecies (Duangchantrasiri et al., 2016; Karanth and Nichols, 1998). Based on the much lower density (< 0.5 individuals/100 km^2) and lower detection probability of the Amur tigers compared to other subspecies (Xiao et al., 2016), this longer sampling period will be necessary to ensure most individuals are detected two or more times. Moreover, tigers are not known to shift their home range seasonally (Smith et al., 1987). A closure test also was conducted within the *secr* package for each trapping period. Camera trapping data within each period was subdivided into 2-week intervals (13 sampling occasions each). The spatial detection history was constructed according to whether an animal was photographed during an occasion (Table 1). Although monitoring data from neighboring Russia were unavailable, SECR models can account for the detection of “foreign residents” in abundance and density estimates (Bischof et al., 2016). The Jolly-Seber SECR models were fitted using the *jagsUI* package (Kellner, 2016) in the R software environment (version 3.3.1, R Development Core Team,

Table 1
Summary of Amur tigers captured by camera traps in 2013–2014, showing ID number, gender, the number of capture sites, capture frequencies, maximum distance moved (MDM) and capture history over 26 sampling occasions. Fourteen captures were of insufficient quality to allow individual recognition (not shown).

ID	Gender	Sites	Capture frequencies	MDM	Sampling occasion																									
					1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
TIG-02	Male	27	79	51.83	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1
TIG-03	Female	8	30	7.51	0	1	1	1	1	1	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	0	1	1
TIG-04	Female	15	42	26.20	0	0	1	1	1	1	0	1	1	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1
TIG-05	Female	14	14	42.42	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	1	0	0
TIG-08	Male	15	56	31.72	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	1
TIG-09	Female	5	15	21.46	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0
TIG-10	Male	1	1	–	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TIG-11	Male	8	17	23.65	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
TIG-12	Male	5	9	15.38	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TIG-13	Female	6	13	9.49	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
TIG-14	Female	1	1	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TIG-15	Male	3	3	7.56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
TIG-17	Male	3	3	10.72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
TIG-20	Male	11	24	42.19	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0
TIG-22	Female	9	29	15.98	0	0	1	1	1	1	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0	0	1	1	1	1
TIG-23	Male	3	3	14.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
TIG-24	Female	3	3	14.64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

2016). We ran 3 Markov chains with 20,000 iterations each with the first 5000 discarded as burn-in, for a total of 45,000 posterior samples. We checked the convergence of the MCMC simulation by each parameter's trace plot and the Gelman-Rubin statistic (Brooks and Gelman, 1998). We assessed the model goodness-of-fit using the Bayesian P-value, with $0.05 < P < 0.95$ indicating model adequacy (Gelman et al., 1996).

To compare the tiger density inside and outside the HNR (i.e., core population near the border vs. the more dispersed population) in 2013 and 2014, we also ran a maximum likelihood-based multi-session SECR model using the R package *secr* (Efford, 2016). We specified years as different sessions and sex as a group factor. This allowed fitting the model with detection parameters (baseline encounter rate, λ_0, and scale parameter, σ) shared across year and sex to obtain a more precise estimate for the year that had the lowest number of captures. The camera traps were treated as a count detector type that allowed for repeat detections of the same individual at the same camera station per occasion (Efford et al., 2009). Density models were fitted in *secr* using full likelihood with a hazard half-normal function.

We constrained the state-space based on known tiger occupied ranges (Wang et al., 2016). The sea is approximately 20 km to the east and in the west, few tigers were observed from our camera-trap survey area. For both methods, we therefore used a 20-km buffer width around the camera trapping grid and established 2 km × 2 km cells using ArcGIS 10.1 (ESRI, Redlands, CA, USA) as the state-space. We also pre-evaluated a larger buffer (40-km) but found this 20-km buffer should be sufficient to contain all active centers of detectable individuals. Even if this buffer size may not be large enough to account for transients, a recent study shows that density estimates of SECR models are robust even when a fairly large number of transients occur in the population during the sampling period (Royle et al., 2016). We excluded any non-forest habitat within the state-space and assumed that the observed individual- and camera-specific encounter frequencies follow the Poisson encounter model with no temporal or individual behavior variation in detection probability (see Royle et al., 2009 for details). To improve the estimates of detection probability, we accounted for varying effort when cameras were not functioning from errors, damage from cattle, or interference by humans.

2.4. Occupancy models

We assessed the habitat use of tigers across the study area using single-season occupancy models (MacKenzie et al., 2002). These models use detection-nondetection camera-trapping data from repeat surveys to estimate the probability of an animal occurring at least once (Ψ) and being detected at a camera site (p). These models account for imperfect detection and allow both parameters to vary in response to covariates. Given there were multiple camera trap sites within each tiger's home range, it is habitat use, rather than occupancy that we are modeling (Linkie et al., 2006; Mackenzie and Royle, 2005). By sampling year round, we also simplified the interpretation of occupancy probability as the proportion of area used by tigers. We assumed animals move randomly between the fine-scale sampling sites, which relaxed the assumption of geographical closure typically required for occupancy models. In our study, we suspected autocorrelation between adjacent camera locations, which were an average of 2.36 km apart. Thus, to avoid biased estimates of model parameters, we used a hierarchical spatial occupancy model, which explicitly incorporates a spatial random effect and employs a probit link function to increase computational efficiency (Johnson et al., 2013). We first identified supported maximum likelihood-based occupancy models with the *unmarked* package in R (Fiske and Chandler, 2011) and then fit Bayesian versions of the selected models using the *stocc* package in R (Johnson et al., 2013).

We defined 2-week periods as temporal replicates and constructed tiger detection histories for each camera site over 23 sampling occasions. Next, we explored a set of biotic and abiotic covariates that represented hypothesized ecological relationships of habitat for tigers (e.g., habitat structure, prey availability, disturbance and management) (Table 2) (Carter et al., 2012; Chanchani et al., 2016; Harihar et al., 2014; Hebblewhite et al., 2014; Miquelle et al., 2015; Petrunenko et al., 2016). Here, given rapid forest policy changes could greatly reduce cattle abundance in short term, we defined cattle as a management factor. Initially, we considered 10 variables as predictors of tiger occupancy and 5 as predictors of detection. Because tiger occurrence is influenced by topography, we derived 3 topographic covariates from the Shuttle Radar Topography Mission (SRTM) 30 m digital elevation model. These were elevation, vector roughness measure (VRM; e.g., local variation in elevation change) (Sappington et al., 2007) and topographic position index (TPI; e.g., finer scale depressions or ridges) (De Reu et al., 2013). The VRM and TPI were calculated using a circular neighborhood with a 1-km radius. The normalized difference vegetation index (NDVI), derived from the 250 m Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (product MOD13Q1) of the study area, was used as a proxy for vegetation productivity and coverage (Harihar et al., 2014; Pettorelli et al., 2016; Wang et al., 2012).

Table 2
Variables used for occupancy models to model habitat use by Amur tigers.

Name	Description	Categories	Source	Parameter and expected influence
Elevation (Elev)	Numeric (m), elevation of point generated from 30 m DEM	Habitat	Shuttle Radar Topography Mission (SRTM) 1 Arc-Second Global[a]	Ψ (−)
TPI	Numeric, topographic position index	Habitat	Measured from elevation grids[b]	Ψ (−)
VRM	Numeric, vector ruggedness measure	Habitat	Measured from elevation grids	Ψ (+)
NDVI	Numeric, normalized difference vegetation index	Habitat	MODIS Vegetation Indices 250 m 16 day NDVI (MOD13Q1)[c]	Ψ (+)
Distance to border (Dist.border)	Numeric (m), distance to the nearest border from camera	Habitat	China Fundamental Geographic Information Dataset	p (−)
Trail	Categorical, valley forest road or ridge trail	Habitat	Field sampling	p (+)
Wild boar Roe deer Sika deer	Numeric, detection frequencies of each prey species per 100 trap-days	Prey	Camera trap	Ψ (+)
Human presence (Human)	Numeric, detection frequencies of human on foot traffic per 100 trap-days	Disturbance	Camera trap	p (−)
Distance to road (Dist.road)	Numeric (m), distance to the nearest road from camera	Disturbance	Local Forest Resource Distribution Map	Ψ (+), p (+)
Distance to settlement (Dist.settlement)	Numeric (m), distance to the nearest settlement from camera	Disturbance	China Fundamental Geographic Information Dataset	Ψ (+), p (+)
Cattle	Numeric, detection frequencies of cattle per 100 trap-days	Management	Camera trap	Ψ (−)

[a] SRTM dataset (https://lta.cr.usgs.gov/SRTM1Arc).
[b] Topography Tools for ArcGIS 10.1 (http://www.arcgis.com/home/item.html?id=b13b3b40fa3c43d4a23a1a09c5fe96b9).
[c] MODIS vegetation indices (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1).

We calculated the camera site-level average NDVI during 2010–2014 for modeling tiger occupancy. We used the detection frequencies from our camera traps as surrogates for the abundance of each prey species (wild boar, roe deer and sika deer). The detection frequencies for groups of cattle and humans were also taken from the camera detection data as a quantitative measure of human use and grazing intensity. We also used ArcToolbox in ArcGIS 10.1 to calculate the distances to landscape features that may affect the probability of tiger occurrence (e.g., distance from each camera to a settlement, road or international border). During camera deployment, we recorded the trail type (forest dirt road or ridge) at each camera location. All continuous covariates were transformed into standardized z-scores to facilitate the interpretation of the covariate coefficients and to improve model convergence. A variance inflation factor (VIF), which measures multicollinearity among variables, was calculated for all of the covariates, and covariates with a VIF < 3 were retained in the model. Pearson's correlation coefficients were also calculated to further check for evidence of collinearity, and when the correlated variables were $|r| > 0.7$, one variable was excluded from the same model.

We selected models in a 2-step process under a maximum likelihood framework. First, detection probability was modeled as a function of all combinations of the 5 possible detection covariates while maintaining a null reference occupancy model. Subsequently, a candidate set of occupancy models was created based on the statistical significance of individual occupancy covariates (no interactions) and Akaike's information criterion (AIC) using a stepwise covariate selection procedure in the *unmarked* package followed by the model-fitting process described in Schuster and Arcese (2013). In this step, we only included the best-performing detection model as derived from the first step. We then ranked all candidate models by AIC value and considered competitive models as those within 2 ΔAIC of the top performing model (Arnold, 2010; Burnham and Anderson, 2012). We then selected the model with the fewest parameters within 2.0 ΔAIC of the top model (Arnold, 2010). Because the penalty for adding one parameter is +2 AIC, if only one parameter is added but the AIC is within 2 ΔAIC, the model fit was not improved enough to overcome the penalty. We plotted the predicted habitat use probability against each meaningful covariate from our top candidate model ($\Delta \text{AIC} < 2$) across the range of data while holding all the other covariates at their mean value.

Next, we modeled spatial autocorrelation with restricted spatial regression (RSR) using the *stocc* package (Hughes and Haran, 2013; Johnson et al., 2013) and considered all combinations of informative covariates to create a full multivariable model that included the combined effects. Subsequently, we assessed the relative importance of habitat and prey vs. disturbance and management on tiger occurrence. For these models, only covariates that appeared in the highly supported models from the first stage were used. We expected higher support for the model that combined habitat and prey models compared to the model that combined disturbance and management. We set the distance threshold for detecting spatial structure in neighboring sample locations at 12 km based on the average size of female tiger home ranges and the spatial distribution of camera traps (Hernandez-Blanco et al., 2015). We specified flat prior distributions for both the detection and occupancy processes and a gamma (0.5, 0.0005) distribution for the spatial component following Johnson et al. (2013). The Moran cut used in the spatial model was 10% of the number of sites. We allowed the chain to stabilize by running the Gibbs sampler for 400,000 iterations with a burn-in of 100,000 iterations. Every 50th sample was retained for a total of 6000 posterior samples to estimate the parameter mean, SD, and 95% Bayesian credible interval (CI). Covariates are considered to have a significant association with tiger habitat use if their 95% CI do not overlap 0. We used the Geweke diagnostic statistics (Geweke, 1992) and the $|Z| < 1.96$ scores to determine model parameter convergence. We used the posterior predictive loss criterion (PPLC) (Gelfand and Ghosh, 1998) to compare the Bayesian RSR and non-spatial models. We then assessed the robustness of the models using the area under the curve (AUC) of the receiver-operating characteristic. Similar to Broms et al. (2014), we calculated the AUC statistic in the *ROCR* package in R using the median occurrences to compare the predicted vs. observed apparent occupancy among the camera sites.

3. Results

3.1. Abundance and density estimates

From August 2013 to July 2014, a total of 356 detections of tigers were obtained over 114,854 trap-days. A total of 21 individual tigers (9 males, 8 females and 4 cubs) were identified from 342 detections by their unique stripe patterns. Nine of the adult tigers were present in both 2013 and 2014 (Table 1). Each individual was detected an average

Table 3
Posterior estimates of open spatially explicit capture-recapture (SECR) model parameters for the Amur tiger trapping data.

Parameter	Mean	SD	2.50%	50%	97.50%
N_1	22.27	4.60	15.00	22.00	33.00
N_2	29.14	5.00	21.00	29.00	40.00
D_1	0.20	0.04	0.14	0.20	0.30
D_2	0.27	0.05	0.19	0.27	0.37
σ	9.91	0.09	9.67	9.93	10.00
λ_0	0.15	0.02	0.11	0.15	0.20
ρ	0.45	0.77	0.27	0.45	0.55
φ	0.83	0.11	0.57	0.84	0.98

Notes: The number of unique individuals observed over both years was 17. N_1 and N_2 are the number of estimated activity centers in the state-space for 2013 and 2014, respectively. Density (D_1 and D_2) is calculated as animals per 100 km^2. The per capita recruitment is ρ. σ is the scale parameter for the detectability function, which is given in kilometers. λ_0 is the basal encounter rate of a tiger whose activity center is located precisely at a given trap. The apparent survival between the two sampling seasons is φ. The results are based on 3 Markov chains run for 20,000 iterations each and discarding the first 5000 as burn-in, for a total of 45,000 iterations.

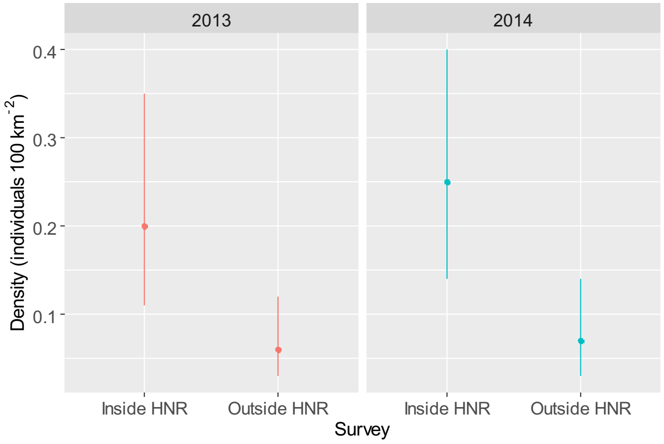

Fig. 2. Tiger density estimates (as the number of individuals per 100 km^2) and 95% confidence intervals calculated from likelihood-based multi-session spatial capture-recapture models. Estimates of tiger density inside and outside of the Hunchun Nature Reserve (HNR) are not independent from one another because tigers are present in both regions.

of 20.12 times and at 8.06 different locations across an area of approximately 5000 km^2. However, the detection frequencies were highly heterogeneous among individuals and sexes: 3 males (TIG-02, TIG-08 and TIG-20) and 3 females (TIG-3, TIG-4 and TIG-22) accounted for 73% of all detections, whereas 2 (TIG-10 and TIG-14) were detected only once in both years (Table 1). The average maximum distance moved (MMDM, ± SE) was 1.25 times larger for males than for females (24.65 ± 5.64 km vs. 19.67 ± 4.51 km).

The Gelman-Rubin convergence diagnostic of $\widehat{R} \leq 1.1$ for each parameter indicated that the Jolly-Seber SECR convergence was adequate, and the Bayesian *P*-value of 0.62 indicated that the model adequately described the data. The posterior mean of the apparent survival rate (φ) was 0.83, and the posterior mean for the apparent per capita recruitment (ρ) was 0.45 (Table 3). The estimated population sizes (i.e., the number of activity centers) for the state-space were 22 (95% CI = 15–33) and 29 (95% CI = 21–40) for 2013 and 2014, respectively (Table 3). Tiger density was 0.20 adult individuals/100 km^2 (95% CI = 0.14–0.30) in 2013 and 0.27 individuals/100 km^2 in 2014 (95% CI = 0.19–0.37) (Table 3). The closure test supported the assumption of population closure during the second 6-month sampling period in 2014 ($z = -0.96$, $P = 0.17$) but did not support the assumption in 2013 ($z = -2.75$, $P = 0.003$). The posterior mean of the baseline encounter rate, λ_0, i.e., the expected capture frequency of an individual whose activity center is located precisely at a trap location, was 0.15. The estimated posterior mean for the movement parameter σ was 9.91 km (Table 3).

The multi-session SECR model showed that the border core population density (0.20 ± 0.06, mean ± SE) inside the HNR was 3.3 times higher than that outside the HNR (0.06 ± 0.02) in 2013 and was 3.6 times higher in 2014 (0.25 ± 0.07 vs. 0.07 ± 0.02) (Fig. 2). The male baseline encounter rate, λ_0, inside the HNR (0.20 ± 0.03) was 6.7 times higher than that outside the HNR (0.03 ± 0.01), and the female baseline encounter rate was 5 times higher (0.10 ± 0.02 vs. 0.02 ± 0.006) (Table S1).

3.2. Determinants of tiger occupancy

All covariates were retained because no significant collinearity was detected (VIF < 3 and r < 0.7) (Fig. S1). Under a maximum likelihood framework, the top-ranked detection model, Ψ (.) p (trail + dist.road + dist.settlement + dist.border + human), was used in the subsequent habitat use analyses (Table S2). Six models of tiger habitat use were competitive (i.e., ΔAIC < 2); following Arnold (2010), we considered models 4 to 6, which differed by one additional parameter but were within two AIC of the top model, to contain 2 uninformative terms (TPI and VRM) (Table S3). Thus, the following covariates: elev, NDVI, dist.road, dist.settlement, wild boar, roe deer, sika deer and cattle were meaningful predictors of tiger occupancy and were used to conduct the Bayesian analysis.

The RSR model provided a better fit than the nonspatial model (PPLC: 403.32 vs. 410.08), indicating that the random spatial effect was warranted. The AUC value for the full RSR model was 0.89, indicating that we correctly predicted tiger's occupancy. Tigers noticeably preferred sites at a lower elevation (with use rapidly declining beyond 800 m) and with a higher NDVI (Table 4 and Fig. 3). Furthermore, tiger occurrence exhibited a positive association with sika deer abundance. Finally, tiger habitat use strongly increased as cameras were set farther away from settlements and roads and was significantly negatively related to heavy cattle grazing (Table 4 and Fig. 3). Contrary to expectation, the model with disturbance and management-related covariates better explained the probabilities of tiger habitat use than the model with habitat and prey covariates (Table 5). A map based on the RSR model shows that sites with a higher probability of habitat use were concentrated along the border and in the southwest parts of the study area, generally fitting well with tiger observations across space

Table 4
The parameter estimates and 95% credible intervals (CI) from a spatial occupancy model for the Amur tiger in NE China. Estimates of beta coefficients are reported for standardized covariates, scaled to mean and standard deviation. Covariates with their 95% CI not encompassing zero (marked in bold) were considered to have a significant association with tiger habitat use and detection. We used the Geweke diagnostic statistics and the $|Z| < 1.96$ score to determine model convergence. See Table 2 for variable definitions and abbreviations.

Model component	Covariate	Mean	SD	95% CI	Z score
Habitat use	(Intercept)	− 0.87	0.56	**(− 2.27, − 0.01)**	0.43
	Elev	− 1.97	0.93	**(− 4.55, − 0.94)**	− 0.45
	NDVI	0.89	0.56	**(0.21, 2.42)**	0.45
	Dist.settlement	1.02	0.65	**(0.25, 2.78)**	0.47
	Dist.road	1.20	0.75	**(0.31, 3.24)**	0.16
	Wild boar	− 0.17	0.29	(− 0.85, 0.34)	0.59
	Roe deer	− 0.56	0.49	(− 1.77, 0.16)	− 1.19
	Sika deer	1.08	0.71	**(0.04, 2.86)**	− 0.48
	Cattle	− 1.09	0.72	**(− 2.95, − 0.18)**	− 0.92
Detection	(Intercept)	− 2.19	0.15	**(− 2.48, − 1.9)**	− 1.49
	Dist.border	− 0.36	0.10	**(− 0.56, − 0.18)**	− 1.27
	Dist.settlement	0.25	0.05	**(0.15, 0.35)**	1.30
	Dist.road	− 0.29	0.06	**(− 0.40, − 0.18)**	0.64
	Trail	0.49	0.14	**(0.20, 0.77)**	0.07
	Human	0.07	0.03	**(0.02, 0.12)**	0.14

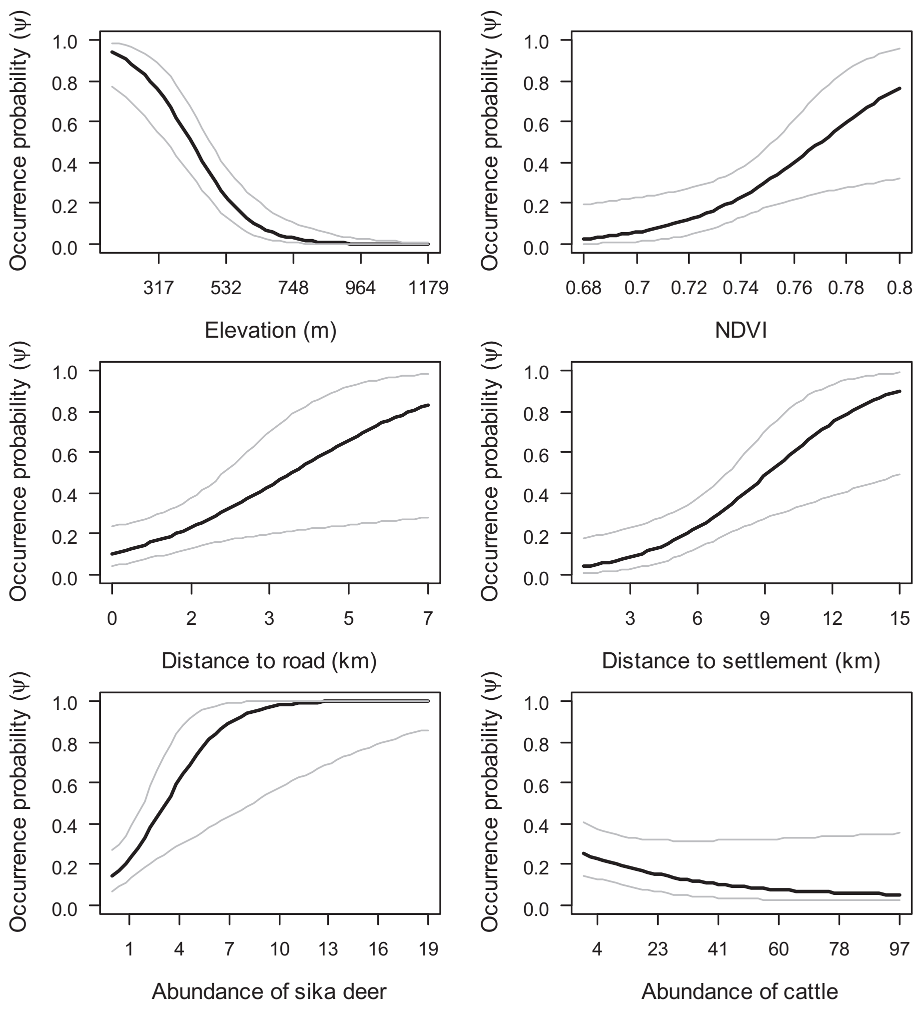

Fig. 3. Tiger occupancy probability with respect to elevation, NDVI, distance to road, distance to settlement, abundance of sika deer, and abundance of cattle (detections per 100 trap-days). The intervals represent 95% credible intervals.

Table 5
A summary of the restricted spatial use model for the Amur tiger, with *p* (trail + dist.road + dist.settlement + dist.border + human), in NE China.

Model	Occupancy covariates	PPLC	AUC
Disturbance and management	dist.road (+), dist.settlement (+), cattle (−)	402.38	0.89
Habitat and prey	elev (−), NDVI (+), sika deer (+)	406.34	0.87

Notes: Symbols: + and −, covariate exerting a positive or negative effect on tiger occurrence, respectively. PPLC is the fitted model's minimum posterior predictive loss (PPLC), and AUC is the area under the curve of the receiver-operating characteristic.

(Fig. 4).

The tiger detection probabilities decreased as cameras were placed farther from the border (Table 4 and Fig. S2). Tigers were more likely to be detected at locations closer to forest roads, away from settlements, and with higher abundances of human presence (i.e., high levels of human presence did not decrease *p*) (Table 4 and Fig. S2). However, tigers were less active during the day when human activity peaked (Fig. S3). The estimated temporal overlap coefficient between tiger and human presence was only 0.31 (95% CI: 0.26–0.35%). With all covariates set to their mean, the tiger detection probability across the study area was 0.12 (SE = 0.01). Tigers were estimated to occur across 35% (95% CI: 28–42%) of the camera trap sites, which is 20% greater than the naïve estimate of habitat use.

4. Discussion

4.1. Tiger population abundance and density

We present the first study of the ecological and anthropogenic correlates that influence the distribution and abundance of a small population of Amur tigers. Twelve months of camera trap data were analyzed using an open population model. Our study differed from other camera trapping studies in that cameras were employed continuously for 12 months. We used this approach for two reasons. First, it allowed us to use an open model to account for fluctuations stemming from demographic changes related to adult survival and subadult dispersal (Duangchantrasiri et al., 2016; Goodrich et al., 2008). And second, continuous sampling is also part of a long-term monitoring strategy to track the response of tigers to management actions seeking to improved tiger habitat. Because tigers demonstrate strong multi-seasonal fidelity to a single home range (Hojnowski et al., 2012; Miquelle et al., 1999; Smith et al., 1987), the open model provides information on apparent population survival and recruitment. Our Jolly-Seber SECR model showed a per capita recruitment of 0.45, which is consistent with the habitat continuity between our study area and the adjacent LLNP in Russia. Given lack of population closure during the first 6-month trapping period, this violation likely, in part, reflects movement of tigers living along the border and thus could lead to the likelihood of biased estimates of density in 2013. Future studies could sample more sites from both countries to reduce the length of sample periods and thereby increase precision and confidence in inferences.

Eight adults were continuously detected for only 1–12 of the

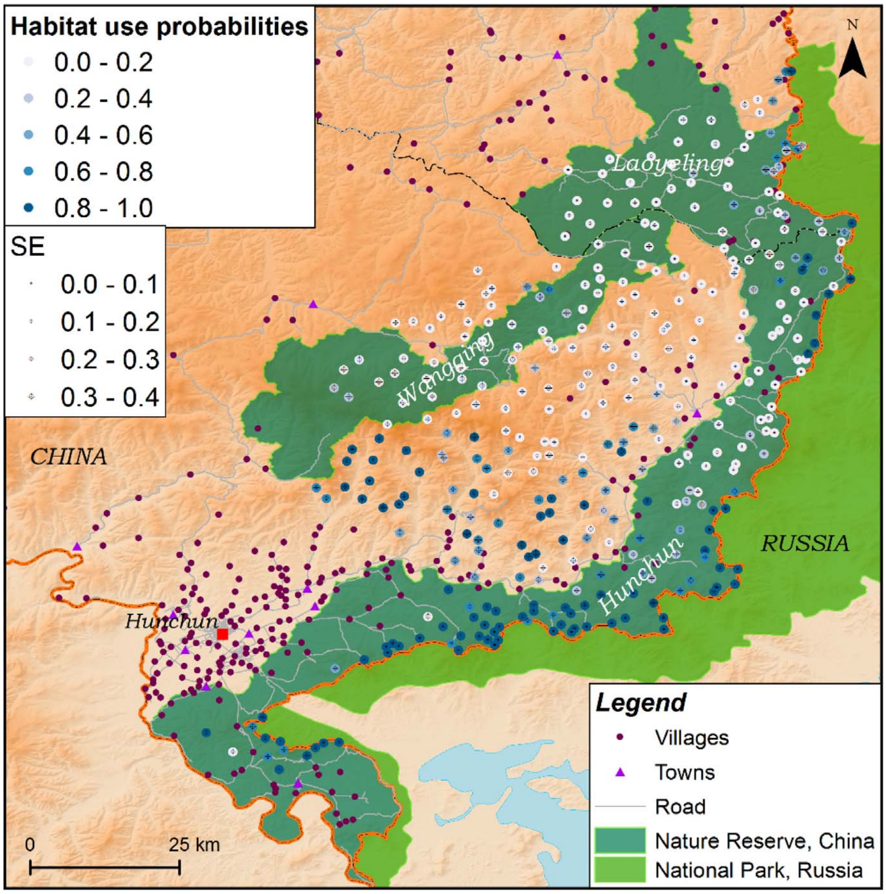

Fig. 4. Predicted habitat use probabilities and standard error (SE) for Amur tigers along the China-Russia border estimated by the restricted spatial regression (RSR) model.

sampling occasions (< half a year) (Table 1). Nine individuals were observed throughout the whole study period; 6 were adult females. If a female remains in the same area for two years, this is strong evidence that she is territorial and therefore a resident breeding animal (Smith et al., 1987). Based on 2-year residency, five of 8 females along the border are resident breeding animals. The sixth resident female (TIG-05) was photographed near the border in 2012 with sub-adult young, and she was subsequently photographed in 2013 with a new litter of 4 cubs approximately 20 km inland from the border. Since then, she has ranged from 10 to 50 km from the border. Her 3-year-old daughter (TIG-22) from her previous litter has taken over her former territory along the border (Wang et al., 2016; Wang et al., 2014). Strong evidence that 6 females reside in our study area also includes photographic evidence of frequent territorial behavior (e.g. scraping, urine spraying, claw marking); this documentation highlights the role of the region as a potential stronghold for the recovery of Amur tigers in China.

Tiger densities ranged between 0.20 and 0.27 individuals/100 km^2 over the study area (Table 3), which is considerably lower than densities reported for tigers in South and southern Asia (1–18 individuals/100 km^2) (Barlow et al., 2009; Carter et al., 2012; Duangchantrasiri et al., 2016; Karanth et al., 2004). Our density estimates are also generally lower than Russian estimates in Ussuriiskii Nature Reserve (0.11–0.59 individuals/100 km^2) (Hernandez-Blanco et al., 2013) or in Sikhote-Alin Biosphere Zapovednik (0.15–0.93 individuals/100 km^2) (Soutyrina et al., 2013).

Most tigers were photographed inside the HNR within 5 km of the southeast border (Fig. 1). We recorded the lowest density estimate (< 0.1 animals/100 km^2) outside the HNR (Fig. 2). In the north and southwest of the study area, heavy cattle grazing and human activities severely degraded the forest understories and posed a threat to tigers, leopards and their principle prey (see discussion below) (Wang et al., 2016; Wang et al., 2017). Wang et al. (2016) documented a high number of livestock killed but identified few tiger locations in areas with high livestock density. These findings suggest that these areas of high livestock density may function as attractive sinks or ecological traps (Kanagaraj et al., 2011). Similar observations were reported in Rajaji National Park, India, where tigers occurred at low densities under anthropogenic influences (intensive forest resource extraction and grazing) (Harihar et al., 2009; Harihar et al., 2011).

4.2. Determinants of tiger habitat use

Not surprisingly, tiger habitat use is influenced by the availability of prey, topography and vegetation characteristics. The importance of elevation on tiger occupancy could be driven by the fact that wild ungulate prey occur mostly in the low elevation forest. Tigers also preferred areas with higher NDVI. These results agree with Hebblewhite et al. (2014) and Rayan and Linkie (2015), who found that tigers preferred lower elevation forest and higher NDVI in Russia and Malaysia, respectively, as such areas are most likely favored by their prey. In Russia, resource selection modeling has revealed that the occurrence of principal prey species increases at lower elevation and that prey select oak and Korean pine mixed forests with high NDVI values, reflecting their dependence on nuts or acorns and higher canopy cover, which occur at lower elevations (Carroll and Miquelle, 2006; Hebblewhite et al., 2014). Thus, it is critical that conservation actions target lower elevation forest (< 800 m).

Our results suggest that human activities and increased occurrence of livestock reduces the probability of tiger occupancy outside of HNR. Tigers select habitats farther away from roads and human settlements, which confirms our expectations based on previous findings (Carroll and Miquelle, 2006). Many studies emphasize the negative effects of human disturbance (e.g., human settlements, roads and livestock) on big cats through prey depletion, direct poaching, habitat encroachment or decreased connectivity at large spatial scales (Barber-Meyer et al., 2013; Bhattarai and Kindlmann, 2013; Joshi et al., 2013; Linkie et al., 2006). Roads in the Russian Far East, which provide access between villages and towns, are reported to reduce Amur tiger survival rates because of collisions with vehicles and increased poaching of both predators and their prey (Goodrich et al., 2008; Kerley et al., 2002). Hebblewhite et al. (2014) observed that wild boar, sika deer and roe deer also avoid areas with high road densities and towns. In our study, tigers spatially overlapped with people on foot and vehicles at a fine spatial scale (i.e., higher detection probability on forest roads), perhaps by using the twilight and night to avoid human disturbance. Increased detection of tigers along forest roads (e.g., abandoned logging roads), however, could also greatly increase access for poachers and, therefore, road closure or access control is needed.

Occupancy modeling indicated that tiger habitat use has a significantly negative correlation with the abundance of domestic cattle (Table 4). Similar results were also observed in the Central Terai Landscape of India, where tiger habitat use declines as human and livestock use increases (Chanchani et al., 2016). Currently > 30% of the study area is grazed by domestic livestock at an average stocking rate of 8–12 cattle/km^2, and if this expanding economy continues to exert unsustainable pressures year-round on the habitat, wild prey density, especially that of sika deer, will be depressed. Wang et al. (2017) reported that the detection frequency for cattle across our study area was 4.0 times greater than that for sika deer. In our study area, cattle, which weigh 400–600 kg, can reduce the plant biomass in the shrub-herb layer by 29–70% (unpublished data). As a consequence, areas intensively grazed by cattle may lower the habitat quality for sika deer, which is the tiger's most common prey in our study area (comprising 25–54% of the total biomass consumed) (Kerley et al., 2015). This matches earlier findings elsewhere that demonstrated wild herbivores are particularly susceptible to competition with livestock by resource limitation and even spatial exclusion (Mishra et al., 2002). F. Wang et al. (2015) reported that habitat overlap with cattle within bamboo forests limited the distribution of giant pandas (*Ailuropoda melanoleuca*) in China; in India, domestic livestock resulted in a decline in chital (*Axis axis*), sambar (*Rusa unicolor*) and gaur (*Bos gaurus*), thereby decreasing the density of tigers (Dave and Jhala, 2011; Madhusudan, 2004).

Cattle are left unattended to roam freely from spring to fall in our study area and thus are also potential prey for tigers. We recorded > 50 livestock killed by tigers every year. However, we suspect that humans disturb tigers feeding on their livestock because tigers do not feed on 25% of the livestock they kill and in 42% of the kills less than half the carcass was consumed (B. Li et al., 2009). The current practice of paying compensation for livestock depredation by tigers exacerbates these conflicts because it reduces the financial risk to herders and encourages grazing of livestock in the forest, which in turn degrades the habitat for wild ungulates (Pettigrew et al., 2012; Soh et al., 2014). Despite the negative impact of cattle grazing, we believe that compensation should continue in the short term because it reduces retaliatory killings of tigers and, if livestock are removed, would not be needed in the long term.

4.3. Conservation implications and recommendations

In conclusion, our study describes the determinants of spatio-temporal variation in abundance and habitat use by Amur tigers along the China-Russia border. Our results demonstrate that this small, isolated tiger population is facing serious hurdles from human activities that are restricting range expansion. To our knowledge, this is the first comprehensive assessment of the status of Amur tigers in China that identifies factors that enhance and limit their distribution. Our findings can help policy makers and managers develop a multi-stage plan to create a landscape that fosters biodiversity connectivity, local sustainable development, and national and global priorities to increase ecosystem integrity.

This research demonstrates that tigers are expanding their range into China. A recent study (Dou et al., 2016; T.M. Wang et al., 2015) and our long-term camera trapping survey revealed that at least three young male tigers have traveled through a series of large forest patches from the border to > 200 km into China. However, reduction in cattle grazing is needed to decrease both human-tiger conflict and competition between livestock and sika deer. To better understand the characteristics of a tiger-permeable landscape, studies on tiger movement are needed. This information will help managers to secure corridors between the current core habitat on the border and forests further inside China.

Finally, we stress that effective protection of tigers and their habitat can only be achieved by state level commitment, legislation, and management. In 2016, the Chinese government developed a plan for expanding the TLNP landscape to 15,000 km^2, which, when combined with the 4000 km^2 Land of Leopard Reserve in Russia, provides a land base for securing a viable tiger population (Hebblewhite et al., 2012). Furthermore, this plan reduces livestock grazing and timber extraction to increase forest cover and habitat connectivity so that tigers can recolonize core forest areas across this landscape. Its scope is similar in spatial scale to the Terai Arc Landscape in India and Nepal (Chanchani et al., 2016; Harihar et al., 2011), and these two landscape approaches have a broad goal of integrating biodiversity objectives and increasing the ecological services that improve human well-being. Our findings were provided to the relevant stakeholders to facilitate this process.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2017.11.008.

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