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A science-based approach to guide Amur leopard recovery in China

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ABSTRACT

The future of the critically endangered Amur leopard (Panthera pardus orientalis) is at a crucial point, and effective conservation strategies implemented within its primary historical range in Northeast China may determine the fate of this species. However, when a conservation plan was first developed for the species, scarce information on the leopards' status existed. To illustrate regional conservation challenges, we focused on the Hunchun Nature Reserve and the surrounding area along the China-Russia border, a potential stronghold for Amur leopard conservation. We conducted large-scale data analysis with a field camera-trapping network to present the first population estimates for this species using a spatially explicit capture-recapture approach. We then used a zero-inflated regression model to analyze the relationship of leopards with major prey species and anthropogenic disturbances. Our results indicate that leopards are returning to China, but most of them are part of a "border population" or are transient; their numbers are far too few to establish a healthy population. The spatial counts of leopards were noticeably high in areas with high prey richness and areas far from settlements and roads. Areas with few prey species and high human and cattle use exhibited a greater probability of "excess absences" of leopards. Mitigating human disturbances by progressively minimizing cattle and human impacts on the forest should be pursued along with habitat expansion for large ungulates, whose presence is essential for leopard occupancy. This study provides crucial information to support Chinese government recovery efforts and for refining conservation practices in human-dominated landscapes to ensure the long-term survival of this species.

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1. Introduction

The increasing pressures resulting from human activities, especially habitat loss, poaching and prey depletion, are likely causing large carnivore declines because of their relatively slow fertility rates, wide ranges and naturally low densities (Chapron et al., 2014; Pimm et al., 2014; Ripple et al., 2014). When population sizes are reduced below certain thresholds, demographic and ecological processes can lead to rapid local extinction, and the loss of a top carnivore often results in an oversimplified ecosystem with unpredictable cascade impacts. Like that of other large carnivores, the habitat of the leopard (Panthera pardus), especially throughout Asia, has been fragmented due to anthropogenic habitat modification and increasing human populations. Once large populations have been subdivided, they become smaller, less viable populations (Dutta et al., 2013; Miquelle et al., 2015). Sometimes and somewhere, the leopard has to share spaces with people in humanuse habitats, employing different strategies to deal with different threats posted by humans (Athreya et al., 2013, 2015).

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Attempts at recovering small, threatened populations of Asian carnivores often involve expanding their range into outside of protected areas in human-dominated landscapes (Carter et al., 2012). This is the case with the endangered Amur leopard (*P.p. orientalis*), which is one of the rarest big cat in the world. This subspecies of leopard once roamed the mixed Korean pine-broadleaved forests of Northeast China, the Sikhote-Alin Mountains of the Russian Far East and northern Korea (Pocock, 1930; Uphyrkina et al., 2002). Since the 1970s, its range has shrunk, and in the late 1990s, the Amur leopard disappeared from most of Northeast China (Feng et al., 2011; Jutzeler et al., 2010; Yang et al., 1998). The subspecies is now confined to approximately 4,000 km² in southwestern Primorsky Krai of Russia and to adjacent habitat in Jilin and Heilongjian Provinces in China (Hebblewhite et al., 2011; Pikunov et al., 2009; Wang et al., 2015b; Xiao et al., 2014). This trans-boundary population of no less than 80 individuals (http:// leopard-land.ru/news/3399), which shares habitat with the Amur tiger (Panthera tigris altaica), is at a viability threshold due to the stresses of habitat isolation, inbreeding, environmental stochasticity, and infectious diseases (Sugimoto et al., 2014; Uphyrkina et al., 2002). Despite the immediacy of the threat, conservation efforts to save leopards in the region have been inadequate to reverse the trend toward extinction.

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To ensure the species' long-term persistence, the effective population size of the Amur leopard must increase, either via reintroduction in southern Sikhote-Alin and/or population expansion into the Changbaishan Mountain ecosystem of China (Hebblewhite et al., 2011; Miquelle et al., 2015; Wang et al., 2015b); the Changbaishan Mountain ecosystem would provide approximately 25,000 km² of potential habitat (Hebblewhite et al., 2012). The last refuge for Amur leopards in southwestern Primorsky Krai holds critical source populations for leopard resettlement in China. To achieve recovery, China and Russia are developing a bilateral conservation strategy for the Amur leopard (Jutzeler et al., 2010; Wang et al., 2015b). The Chinese government has proposed a multi-stage plan for expanding the Amur leopard's range into the Changbaishan Mountain landscape. Restoring this charismatic flagship species in northeast Asian forest ecosystems will catalyze broader conservation efforts in the region.

Currently, this landscape comprises a complex of intact healthy forests and forests with intensive grazing and timber harvests interspersed with rural villages, agricultural lands and medium and large urban centers. There is a lack of information about leopards in China, and in response, the Chinese government is establishing a sciencedriven approach to leopard recovery. Priority research initiatives include population estimations, monitoring the dispersal of leopards and identifying factors that threaten this subspecies so that human activities can be modified to foster leopard recovery.

As elsewhere, the availability and spatial distribution of both domestic and wild prey may play a crucial role in determining the future of large felids (Butler et al., 2013; Karanth et al., 2004; Steinmetz et al., 2013). Other factors include human disturbances (e.g., logging, human settlements, roads, and livestock grazing). Although leopard density is lower closer to human settlements in Africa and Thailand (Henschel et al., 2011; Ngoprasert et al., 2007), leopards also shift to edge habitat to avoid tigers in Nepal, Thailand and India (Carter et al., 2015; Harihar et al., 2011; Steinmetz et al., 2013). Recent results from India further showed that a relatively high density of leopard occurred in human-dominated agricultural landscapes and primarily subsisted on a diet of domestic dogs and livestock (Athreya et al., 2013). The spatial heterogeneity of prey density and competition with tigers determine leopard space use in relation to prey (Carter et al., 2015; Steinmetz et al., 2013). In Northeast China, information on the ecology, habitat use, distribution and abundance of the Amur leopard is needed to guide its recovery.

Camera traps are now widely used to assess wildlife ecology and conservation (Burton et al., 2015; O'Connell et al., 2010), particularly for the study of elusive and rare species such as tigers and leopards (Karanth and Nichols, 1998; Wang and Macdonald, 2009). Population size is a key requirement for informing local decision-making in species-based management and conservation initiatives (Stephens et al., 2015). To facilitate leopard restoration in China, reliable estimates of population size are essential to assessing the effectiveness of conservation interventions. The unique spot patterns on leopards can be used to accurately identify individuals, enabling more precise estimates of population size and dynamics. A recently developed spatially explicit model (Efford et al., 2009; Royle et al., 2009) provides a robust tool with which to directly calculate the densities of this patterned species using photographic capture–recapture data from camera trapping surveys (Athreya et al., 2013; Carter et al., 2015).

In this study, we conducted the first comprehensive assessment of Amur leopard status and habitat requirements and we evaluated the ecological correlates that predict leopard distribution and abundance. We hypothesized that leopards require a threshold density of wild prey and that domestic livestock compete for forage and degrade the habitat of the leopard's natural prey. We also aim to better understand the relationship between the spatial distribution of present-day Amur leopard abundance and spatial patterns of other human disturbance features, represented by human presence, roads and settlements. The results of our research will inform recommendations for integrating leopard recovery into a landscape scale plan that includes leopard and tiger restoration and meets the local and regional ecological service needs.

2. Materials and methods

2.1. Study area

This study was carried out in the northern portion of the Changbai Mountains in Jilin and Heilongjiang Provinces in China, bordering southwestern Primorsky Krai in Russia to the east and North Korea to the southwest (Fig. 1). This region is considered the highest priority Tiger and Leopard Conservation Area in China because it has a large network of habitat patches that are connected to the source populations of tiger and leopard in Russia (Hebblewhite et al., 2012). Three Natural Reserves (Hunchun, Wangqing and Laoyeling) are located in the study area; they form the core of a potential recovery landscape for these felids in China. These reserves are on a rugged, mountainous landscape with elevations ranging from 5 to 1477 m. The major vegetation types include Korean pine (Pinus koraiensis) forests, oak forests, coniferous forests, natural shrublands, and agricultural areas (Hebblewhite et al., 2012; Tian et al., 2011). The majority of forests have been logged, and many low-elevation forests have been converted into secondary deciduous forests over the past 5 decades (Li et al., 2009). The prey of leopards include Siberian roe deer (*Capreolus pygargus*), sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*), along with small animals such as Asian badgers (Meles leucurus), Manchurian hares (Lepus mandshuricus) and raccoon dogs (Nyctereutes procyonoides) (Tian et al., 2011; Xiao et al., 2014). Other predators, including Amur tigers, Asiatic black bears (Ursus thibetanus), Eurasian lynx (Lynx lynx) and sables (Martes zibellina), coexist with the leopard in our study area. 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. Timber harvesting has occurred extensively for decades, and there has recently been a rapid expansion of ginseng farms. Other human activities include the collection of edible ferns, frog farming, cattle grazing and poaching.

2.2. Data collection and field methods

Beginning in 2007, we progressively established a long-term Tiger Leopard Observation Network (TLON) of camera traps along the border with Russia and in the Laoyeling, Hunchun and Wangqing reserves and surrounding areas (Wang et al., 2015a, 2015b) (Fig. 1). The TLON used 3.6×3.6 km grids to guide camera placement. The cameras were placed in grids, except those on farmland and in villages; the cameras were located along trails, roads and ridges, which are common travel for leopards, tigers and their prey. The cameras (currently, LTL6210M, Shenzhen, China) were fastened on trees approximately 40-80 cm above the ground and were programmed to take photographs 24 h/ day with a 1-min interval between consecutive events. Approximately 70% of stations had two cameras and no single sided camera trap leopard photo was used unless it matched a photo from a double sided station. The cameras were operated continuously throughout the year. Each camera was visited monthly to download photos and check batteries. This study (from August 2013 to July 2014) used 356 camera trap stations covering 4858 km².

We analyzed leopards, 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) as "entities" in the camera traps. Each leopard was identified by its unique spot pattern, and the sex could usually be determined due to visible testes. Leopard cubs (<1 year old) were removed from the density analyses because they exhibit high levels of mortality (Athreya et al., 2013). Our identifications of leopard individuals were independently verified by two trained experts in Russia and Thailand, both confirmed the identity of

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Fig. 1. Monitoring areas of the long-term Tiger-Leopard Observation Network (TLON) in NE China showing the camera placement relative to settlements, major roads and nature reserves or national parks.

each leopard individual. We calculated the relative abundance index (RAI) (O'Brien et al., 2003) for each entity at each trap station as the number of detections per 100 camera-trap days.

Given that the heavy snow in the northern study area sometimes resulted in the camera not being triggered, we omitted winter season data (from December to February) in the RAI calculations. To avoid inflated counts caused by repeated detections of the same event, only one record of a species/0.5 h was included in the data analysis (O'Brien et al., 2003). We used the Mann–Whitney *u* statistic to test for significant differences in the RAI of each entity inside and outside of the reserve and in areas with cows and without cows.

2.3. Density models

Leopard density was estimated across the study area from August to November 2013 and from March to June 2014. A 120-day window, made up of 12 occasions of 10 days of consecutive trapping each, was selected from the dataset to meet the population closure assumption and minimize the likelihood of activity centers changing within a trap period (Karanth and Nichols, 1998) while still generating a sufficient number of captures. The spatial detection history was constructed according to whether an animal was photographed during an occasion (Tables S1 and S2). A maximum likelihood-based spatially explicit capture-recapture (SECR) model, which accounts for imperfect detection, was fitted to estimate density using the secr package (Efford, 2015) in the R software environment (version 3.1.2). To improve the estimates of detection probability, we accounted for varying effort from malfunctions, damage from cattle, or interference by humans. The camera traps were treated as proximity detectors that allowed for repeat detections of each individual at a particular trap on any occasion (Efford et al., 2009). The density models were fitted in *secr* using full likelihood with a hazard half-normal function, similar to that used in other big cat studies (Rayan and Linkie, 2015). Given sex-specific differences in the baseline encounter rate (λ_0) and home range size (σ) of elusive carnivores (Efford and Mowat, 2014; Sollmann et al., 2011), we incorporated the sex of leopards as a covariate into the model. The candidate models were then ranked using Akaike's Information Criterion (AIC) and their Akaike weights, with Δ AIC < 2 as competing models (Burnham and Anderson, 2012). A closure test (Otis et al., 1978) was conducted within the *secr* package.

Leopard habitat was gridded as $1 \text{ km} \times 1 \text{ km}$ cells using ArcGIS 10.1(ESRI, Redlands, CA, USA). We used 4 times the root pooled spatial variance to determine the appropriate buffer width (Efford, 2004). We excluded cells with centers more than buffer width from any detector and any non-forest cells within the habitat mask plus the buffer width (Hebblewhite et al., 2011).

2.4. Zero-inflated models

With 69% of the 356 camera trap stations containing zero counts of leopards, the spatial abundance data exhibited zero inflation (Fig. S1). Based on biological knowledge, a leopard may not come to the camera locations because it is in unsuitable habitat (true zero) or a leopard may be only temporarily not present (false zero). Therefore, we used a zero-inflated negative binomial (ZINB) regression model, which treats counts as a binomial-negative binomial distribution mixture (Zuur et al., 2012). The binary component explains "excess zeros" (i.e., the probability that no leopards are detected at a site because it is not suitable) and a negative binomial component that describes the "counts" (referred to as the photographic frequency) at a camera trap

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location. Using zero-inflated models, Ancrenaz et al. (2014) conducted a large-scale species-level analysis of ground-based camera-trapping data to evaluate the influence of anthropogenic forest disturbances on the terrestrial behavior of Bornean orangutans (*Pongo pygmaeus*).

We explored covariates for their ability to predict the habitat preference of leopards on a log and logit scale, respectively. In the count component (log scale), 11 variables were identified as impacting the abundance of leopards, and in the zero component (logit scale), 6 variables were identified as predictors of excess zeros based on previous leopard habitat studies (Carter et al., 2015; Hebblewhite et al., 2011; Miquelle et al., 2015) (Table 1). We used station-specific camera-trap days as offsets to compensate for the variation in the response resulting from the survey effort. Five covariates—including tiger presence; prey richness; and the detection frequencies of major prey species, cattle and humans—were taken from the camera detection data. During camera deployment, we recorded the trail type (road and ridge trail), elevation and forest composition (broad-leafed, mixed or oak forest) at each camera location. The distance from each camera to a settlement or road was calculated using ArcToolbox in ArcGIS 10.1.

We scaled all continuous covariates prior to analysis to facilitate interpretations of the covariate coefficients and to improve convergence in the model. 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. Correlation coefficients were also calculated to further check for collinearity variables, and when the correlated variables were |r| > 0.7, one variable was excluded. Given multiple camera trap locations within the leopard home range, the leopard detection frequencies could be spatially autocorrelated, and we used a residual autocovariate (RAC) in our model (Crase et al., 2012). The spatial structure of residuals was evaluated using a variogram.

The ZINB models were implemented using the R package *pscl*. The models were fit through a backward stepwise selection by dropping the least significant term and refitting the model and continued until only the independent variables with significant coefficients (p < 0.05) were retained. At each step of the stepwise selection, the variables with the highest AIC were dropped. A pseudo-R² measure for the best supported model was used as an indicator of explanatory power. The relative improvement ZINB over negative binomial and zero-inflated Poisson (ZIP) regression models was also assessed using Vuong's test (Vuong, 1989) and a likelihood ratio test (LRT) (Zuur et al., 2009, 2012), respectively. We reported the model coefficient estimates to summarize the behavior of independent variables in relation to leopard abundance.

3. Results

3.1. Abundance

From August 2013 to July 2014, a total of 326 detections of leopards were obtained over 85,454 trap-days. Thirty-three individual leopards (13 males, 18 females and 2 cubs) triggered 31.46% of all camera trap locations (Table 2). For comparison, 19 tigers (15 adults, 2 subadults and 4 cubs) were also detected (N = 268) and photographed in 19.38% of camera trap locations. Inside the reserve, the mean RAI was significantly higher than outside of the reserve for leopards (1.32 times higher) and tigers (9.80) (Mann–Whitney *u* test, *p* < 0.001) (Table 3).

Wild boar and roe deer were photographed at 83% and 90% of the stations, respectively, but only the average RAI of roe deer outside of the reserve was significantly larger than inside (Table 3). The observances of Sika deer with a mean RAI 22.4 times higher in the reserve indicated a strong avoidance of areas outside of the reserve (Mann–Whitney *u* test, *p* < 0.001). The majority (55.25%) of prey detected in the study area were roe deer.

Cattle triggered approximately 31% of all field camera stations and accounted for more than 12% of all detections (Table 2). The mean RAI for cattle across the study area was 13 times greater than for leopards and 1.3–4.0 times greater than for the major prey species. Cattle were recorded at 42% of the camera stations outside of the reserve, with significantly higher RAI than inside of the reserve (Mann–Whitney *u* test, p < 0.001) (Table 3). Cattle sharply reduced the relative abundance of leopards, roe deer and sika deer but not wild boar (Fig. 3).

Human presence was recorded by 85.4% of the cameras and accounted for 64.6% of all detections. The average RAI was approximately three times as pervasive inside the reserve as outside (Table 3).

3.2. Density estimates

Restricting the sampling period to four months yielded 125 and 148 independent leopard detections in 2013 (August–November) and 2014 (March–June), respectively. These detections represented 17 individual adult leopards (9 males and 8 females) in 2013 (Table S1) and 26 individual adult leopards (11 males and 15 females) in 2014 (Table S2). Fifteen of the leopards were present in both 2013 and 2014. There were no data indicating seasonal shifts, but the higher numbers of leopards in 2014 may be immigration from Russia. Each individual was detected an average of 7.4 times and at 5.7 different locations in

Table 1

Variables used for zero-inflated negative binomial (ZINB) regression models to model habitat use by Amur leopards.

Name	Description	Categories	Source	Expected influence part
Tiger presence (Tiger.pres)	Categorical, presence or absence	Sympatric large predators	Camera trap	Count
Richness of prey species (Rich.prey)	Numeric, no. of major prey species detected	Prey	Camera trap	Count, zero
Index of prey abundance (RAI.prey)	Numeric, detection frequencies of major prey species detected	Prey	Camera trap	Count
Vegetation	Categorical, broadleaf, mixed and oak forest	Habitat	Field sampling	Count
Elevation	Numeric (m)	Habitat	Field sampling	Count
Type of trail	Categorical, road or ridge trail	Habitat	Field sampling	Count
Reserve	Categorical, inside or outside	Habitat	China Database on Nature Reserve	Count, zero
Human presence (Human)	Numeric, detection frequencies of human on foot traffic	Human disturbance	Camera trap	Count, zero
Cattle	Numeric, detection frequencies of cattle detected	Human disturbance	Camera trap	Count, zero
Distance to road (Dist.road)	Numeric (m), min. Distance to road	Human disturbance	Local Forest Resource Distribution Map	Count, zero
Distance to settlement (Dist.settlement)	Numeric (m), min. Distance to settlement	Human disturbance	China Fundamental Geographic Information Dataset	Count, zero

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Table 2

List of species and human presence recorded by the camera traps, showing the number of independent detections (N), relative abundance index (RAI, mean \pm SE) and the number of trap sites where the entities were captured in the camera-trapping study area, NE China.

Common name	Ν	% of all detections	RAI	No. of trap stations	% of all trap stations
Amur leopard	326	1.19	0.37 ± 0.05	112	31.46
Amur tiger	268	0.97	0.31 ± 0.06	69	19.38
Wild boar	1482	5.39	1.75 ± 0.11	295	82.87
Roe deer	3108	11.30	3.59 ± 0.19	322	90.45
Sika deer	1035	3.76	1.25 ± 0.18	140	39.33
Human presence	17,750	64.56	22.50 ± 2.63	304	85.39
Cattle grazing	3524	12.82	4.95 ± 1.09	111	31.18
Total	27,493	100	-	356	-

2013, and each was recorded an average of 4.3 times and at 3.0 different locations in 2014 across an area of roughly 5000 km². However, the capture frequencies across the entire study area were heterogeneous among individuals and sexes: two males (LEO-02 and LEO-03) accounted for 42% of all detections, whereas females represented only 29% in both periods (Tables S1 and S2). The average maximum distance moved (MMDM) was 1.76 times and 1.58 times larger for males than for females in 2013 (14.60 \pm 4.97 km vs. 8.29 \pm 1.59 km) and 2014 (16.71 \pm 4.61 km vs. 10.58 \pm 2.16), respectively.

A root pooled spatial variance (RPSV) value of 8190 m was calculated, which resulted in a 33-km buffer width (four times the RPSV). The closure test supported the population closure assumption during a 120-day sampling period in 2014 (z = 0.27, p = 0.61) but did not support the assumption in 2013 (z = -2.96, p = 0.002).

The ΔAIC and AIC weight values indicated that the best model incorporated sex as a covariate (Table 4). The male baseline encounter rate λ_0 (0.10 \pm 0.02) was 2.5 times higher than that of females (0.04 \pm 0.02) in 2013 and was 1.5 times higher in 2014 (0.06 \pm 0.01 vs. 0.04 \pm 0.01) (Table 5). The movement parameter σ was 1.7 times and 1.5 times larger for males than for females in 2013 (5.78 \pm 0.39 km vs. 3.39 \pm 0.50 km) and 2014 (6.97 \pm 0.45 km vs. 4.65 \pm 0.48), respectively. Leopard density was approximately 40% higher in 2014 than in 2013, with 0.30 \pm 0.08 adult individuals/100 km² (95% CI = 0.19–0.50) in 2013 and 0.42 \pm 0.09 individuals/100 km² in 2014 (95% CI = 0.28–0.62), corresponding to an expected leopard abundance of 44 (27–73) and 62 (41–92), respectively (Table 5).

3.3. Determinants of leopard presence and abundance

All 11 covariates were retained because no significant collinearity was detected (VIF < 3 and r < 0.7) (Table S3). There is evidence that the ZINB is significantly superior to the negative binomial (Vuong's test, z = -3.64, p < 0.001) and ZIP (LRT: L = 80.22, df = 1, p < 0.001).

The best supported model and associated significant covariates (p < 0.05) are presented in Table 6. A variogram of the Pearson residuals shows that the spatial correlation pattern is removed by adding the RAC value to the non-spatial ZINB model (Fig. S2), indicating that spatial

autocorrelation significantly contributed to both leopard presence and leopard abundance.

The RAI map indicates that leopards were more abundant along the border, 50 km away from the border in the north, as well as in the reserve (Fig. 2). The ZINB model with RAC had a pseudo- R^2 value of 58% and accounted for this trend, demonstrating strong positive relationships between the probabilities of excess absences (zero model) and heavy cattle grazing and human presence, especially outside the reserve (Table 6). The frequencies of site use (count model) by leopards were noticeably higher on mountain ridge trails, far from settlements and roads, as well as in oak forests, exhibiting a positive association with prey richness. Finally, the leopard spatial counts were not influenced by tiger presence at fine spatial scales (z = 2.63, p = 0.009).

4. Discussion

4.1. Leopard population abundance and density

Benchmark data on changes in the status of small populations of animals are essential for guiding conservation decisions. The SECR model accounted for differences in detection and movement between sexes and across the trapping occasions, providing the first robust density estimates of the Amur leopard in Northeast China on the border of Russia. Our camera traps covered the entire known Amur leopard distribution in China and were distributed at a density of 7 cameras/100 km²; at this density, the chance of "temporary emigrants" was reduced. Leopard densities ranging between 0.30 and 0.42 leopards/100 km² over the study period (Table 5) were lower than leopard densities in Southern Asia (3–9 individuals/100 km²) (Athreya et al., 2013; Borah et al., 2014; Carter et al., 2015; Gray and Prum, 2012). However, our estimates were similar in density to Wangqing Nature Reserve to the north of our study area where density was estimated to be 0.62/100 km² (Qi et al., 2015).

The population closure test indicated lack of closure in 2013. The closure test implicitly assumes equal probability of capture (Otis et al., 1978). Of the 17 capture histories we reported, 4 (24%) were captured only once in 2013 (Table S1). These data are indicative of high heterogeneity in capture probabilities among animals; however, this violation of

Table 3

List of species and human presence recorded by the camera traps, showing the number of independent detections (N), relative abundance index (RAI, mean \pm SE) and the number of trap sites where the entities were captured in portions inside and outside of the reserve in the camera-trapping study area, NE China. Values in bold indicate samples that were significantly different from one another (Mann–Whitney *u* test, *p* < 0.001).

Common name	Inside reserve					Outside reserve				
Amur leopard	Ν	% of all captures	RAI	No. of trap sites	% of all trap sites	N	% of all captures	RAI	No. of trap sites	% of all trap sites
Amur leopard	216	1.12	$\textbf{0.41} \pm \textbf{0.05}$	84	39.44	110	1.35	$\textbf{0.31} \pm \textbf{0.08}$	28	19.58
Amur tiger	253	1.31	$\textbf{0.49} \pm \textbf{0.09}$	57	26.76	15	0.18	$\textbf{0.05} \pm \textbf{0.02}$	12	8.39
Wild boar	921	4.76	1.81 ± 0.14	176	82.63	561	6.88	1.65 ± 0.16	119	83.22
Roe deer	1454	7.52	$\textbf{2.87} \pm \textbf{0.21}$	184	86.38	1654	20.28	$\textbf{4.66} \pm \textbf{0.32}$	138	96.50
Sika deer	1006	5.20	$\textbf{2.02} \pm \textbf{0.29}$	123	57.75	29	0.36	$\textbf{0.09} \pm \textbf{0.03}$	17	11.89
Human presence	14,089	72.85	$\textbf{30.86} \pm \textbf{3.97}$	189	88.73	3661	44.90	$\textbf{10.04} \pm \textbf{2.44}$	115	80.42
Cattle grazing	1400	7.24	$\textbf{4.06} \pm \textbf{1.52}$	51	23.94	2124	26.05	$\textbf{6.27} \pm \textbf{1.50}$	60	41.96
Total	19,339	100.00	-	213	-	8154	100.00	-	143	-

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 Table 4

 Comparison of SECR models fitted to the combined-sex Amur leopard population.

-						-
Model	np	logLik	AIC	ΔAIC	AIC weight	Density (SE)
2013						
$\lambda_0 \sim \text{sex}, \sigma \sim \text{sex}$	6	-542.23	1096.45	0.00	0.79	0.30(0.08)
λ ₀ ~ 1, σ ~ sex	5	-544.58	1099.16	2.71	0.21	0.30(0.07)
λ ₀ ~ 1, σ ~ 1	4	-563.94	1135.89	39.43	0.00	0.25(0.06)
2014						
λ_0 ~ sex, σ ~ sex	6	-736.78	1485.56	0.00	0.71	0.42(0.08)
λ ₀ ~ 1, σ ~ sex	5	-738.69	1487.37	1.81	0.29	0.42(0.08)
$\lambda_0 \sim 1$, $\sigma \sim 1$	4	- 753.33	1514.65	29.09	0.00	0.37(0.07)

Notes: "sex" refers to a two-level categorical individual covariate; np is the number of fitted parameters; logLik is the maximized log likelihood; Δ AIC is the difference in AIC between a particular model and the model with the smallest AIC; SE values are in parentheses; density is calculated as animals per 100 km².

the closure assumption likely, in part, reflects movement of leopards living along the border to areas more inland in Russia. Soisalo and Cavalcanti (2006) also reported violations of the closure assumption when they caught multiple jaguars only once, representing a mimic lack of closure. Given that most individuals (76%) in 2013 were captured two or more times and an average detection frequency of 7.4 times, abundance estimates provide acceptable levels of precision that could be used to guide conservation and management agencies (Gerber et al., 2014). In the future, plans to merge the camera trap data from China and Russia will help resolve the issue of closure.

Despite the current low density of leopards, 31 leopards were recorded within 12 months, three times the number observed 15 years ago (Yang et al., 1998). In 2013, a winter tracking survey counted 50 leopards in Russia (http://www.wildlifeextra.com/go/news/amurleopard-2013.html#cr), which is ~50% more than in 2007 (Pikunov et al., 2009). As a result, dispersal from this increased population in Russia provides good input for leopard recovery in China. Our data indicated that there were at least 14 different increasingly immigrating individuals along the China-Russia border from the Russian leopard population from August 2013 to July 2014 (see Tables S1 and S2), representing a sign of this species' return to China. Despite increasing numbers of leopards in China, camera trapping revealed that only four leopards became localized and in the case of the two females produced and reared young 50 km away from the border (Fig. 2); other individuals were located within 5 km from the border or may have included transients, implying that most areas of the ~5000 km² recovery landscape are not yet suitable habitat for leopards.

4.2. Determinants of leopard presence and abundance

Not surprisingly, prey richness and availability are important for sustaining leopards (Table 6). Similar results have been found in other regions of leopard distribution (Sharma et al., 2015). Contrary to expectations, leopard detections exhibited a significant positive relationship with tiger presence at fine spatial scales (25 locations overlapped with tigers at low altitudes), there is some evidence of temporal niche partitioning. Leopards were 60% diurnal and tigers were 75% nocturnal

Table 5

Amur leopard density estimate (animals per 100 km²), 95% confidence intervals and corresponding magnitude of the detection function (λ_0) and spatial scale parameter (σ) calculated from the final spatially explicit capture–recapture models.

2013 2014 Parameter Mean SE 95% CI Mean SE 95% CI Density 0.30 0.08 0.19–0.50 0.42 0.09 0.28–0.62 N 44 11 27,72 62 12 41.02							
Parameter Mean SE 95% CI Mean SE 95% CI Density 0.30 0.08 0.19-0.50 0.42 0.09 0.28-0.62 N 44 11 27,72 62 12 41.02		2013			2014		
Density 0.30 0.08 0.19–0.50 0.42 0.09 0.28–0.62	Parameter	Mean	SE	95% CI	Mean	SE	95% CI
N 44 11 $27-73$ 62 12 $41-92$ $\lambda 0$ males 0.10 0.02 0.07-0.14 0.06 0.01 0.04-0.08 $\lambda 0$ females 0.04 0.02 0.02-0.09 0.04 0.01 0.02-0.07 σ males 5.78 0.39 5.07-6.60 6.97 0.45 6.14-7.91 σ females 3.39 0.50 2.54-4.51 4.65 0.48 3.80-570	Density N $\lambda 0$ males $\lambda 0$ females σ males σ females	0.30 44 0.10 0.04 5.78 3.39	0.08 11 0.02 0.02 0.39 0.50	0.19-0.50 27-73 0.07-0.14 0.02-0.09 5.07-6.60 2 54-4 51	0.42 62 0.06 0.04 6.97 4.65	0.09 12 0.01 0.01 0.45 0.48	0.28-0.62 41-92 0.04-0.08 0.02-0.07 6.14-7.91 3.80-5.70

Table 6

The best supported zero-inflated negative binomial (ZINB) regression models explaining the relative abundance of Amur leopards, as indicated by the parameter estimates, standard errors (SE), *z* value and *p* value with the autocovariate (RAC). All of the reported estimates of coefficients that marked in bold are significant (p < 0.05). Broad-leafed deciduous forest is the default reference category. See Table 1 for variable definitions and abbreviations.

Covariate	Estimate	SE	z value	p value
Model for 'counts'				
(Intercept)	- 5.30	0.22	-23.63	< 0.001
Tiger.pres	0.54	0.21	2.63	0.009
Rich.prey	0.23	0.09	2.60	0.009
Dist.settlement	0.21	0.10	2.13	0.034
Dist.road	0.26	0.09	2.96	0.003
Ridge trail	0.58	0.20	2.94	0.003
Oak forest	0.44	0.22	2.03	0.043
Mixed forest	0.12	0.23	0.50	0.614
RAC	0.38	0.06	6.40	< 0.001
Model for 'excess zeros'				
(Intercept)	-1.22	1.23	-0.98	0.327
Cattle	8.38	3.39	2.47	0.014
Human	2.80	1.00	2.79	0.005
Inside reserve	- 5.06	1.52	- 3.34	< 0.001
RAC	- 5.48	1.13	- 3.26	0.001

or crepuscular, which was similar to the findings of Azlan and Sharma (2006). We also found support for spatial displacement between the two felids in our study area. Leopards frequently used ridge trails (Table 6), whereas tigers were most likely to occur in lower-altitude valley bottoms (Carroll and Miquelle, 2006). In summary, spatiotemporal avoidance may a driver of sympatric coexistence (Steinmetz et al., 2013; Sunarto et al., 2015).

The zero-inflated models suggested that leopards select habitat farther away from roads and human settlements (Table 6). This is not particularly new information, but it confirms our expectations based on previous findings (Gavashelishvili and Lukarevskiy, 2008; Hebblewhite et al., 2011; Ngoprasert et al., 2007; Qi et al., 2015) despite there is an evidence in Nepal showing that leopards frequently occur around human settlements in order to avoid tiger and hunt easily accessible domestic animals (Odden and Wegge, 2005). Many studies emphasize the negative effects of human disturbance (e.g. human settlement, road and livestock) on big cats through prey depletion, direct poaching 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 are reported to reduce carnivore survival rates because of collisions with vehicles and increased poaching of both carnivores and their prey near roads (Goodrich et al., 2008; Hebblewhite et al., 2014; Kerley et al., 2002). In addition, ubiquitous human presence on foot and traffic is responsible for leopard absence in a given space (zero model, Table 6). Leopards were less active during the highest human activity of the day in an earlier study (Wang et al., 2015b), similar to what was observed in Nepal (Carter et al., 2015) and Thailand (Ngoprasert et al., 2007).

Our data indicated that leopards were largely absent in areas where the RAI of livestock was high (Fig. 2). In Northeast China the cows that are grazing in forests are much larger (400–600 kg) than those grazing in Indian forests and are rarely preyed on by leopards. Furthermore, grazing cattle can subsist on lower protein forage than smaller sika deer and thus degrade potential sika deer habitat. Among 60 locations outside of the reserve that had cattle detections, only 8 detected sika deer. Wang et al. (2015b) speculated that competition between livestock and wild prey is a major constraint to the population growth of Amur leopards in Northeast China and advocated strict grazing controls. Our results confirm a negative correlation between domestic livestock and roe deer and sika deer (Table 4), the leopard's most common prey (Hebblewhite et al., 2011).

Studies elsewhere described a broad spectrum of negative interactions between livestock and wildlife. Wang et al. (2015) reported that habitat overlap with cattle within bamboo forests limited the

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Fig. 2. Spatial patterns of the relative abundance index (RAI) for Amur leopards (left) and cattle (right) in the camera-trapping study area, NE China. Black dots represent sample locations (camera traps) where leopards or cattle were not observed.

distribution of giant pandas (*Ailuropoda melanoleuca*) in China. In India, Sharma et al. (2015) found a threshold density of livestock caused snow leopards to decline sharply. In North America, Africa and South Asia respectively, domestic livestock resulted in a decline in mule deer (*Odocoileus hemionus*), elk (*Cervus elephus*) (Jones, 2000; Stewart et al., 2002), zebra (*Equus burchelli*) (Young et al., 2005), chital (*Axis axis*), sambar (*Cervus unicolor*) and gaur (*Bos gaurus*) (Dave and Jhala, 2011; Madhusudan, 2004).

Our study did not include bottom-up regulatory processes, such as human disturbance influences on vegetation or prey and predator, to determine the nature of the negative relationship between domestic cattle and leopards. One possible consideration in defining the negative associations between leopards and livestock is that adult cattle in this region weight approximately 500 kg well above the preferred weight of leopard prey which is 25 kg (Hayward et al., 2006). Cattle are left unattended, roaming freely from spring to fall in our study area. Livestock remove most herbs, leaf buds and small twigs from trees and shrubs that are preferred by ungulates, thereby degrading the habitat for smaller sized natural prey species that are the preferred weight class of leopards.





More than 30% of the study area is grazed by domestic livestock at an average stocking rate of 8 cattle/km², which is approximately 4 times the density of the wild prey (Qi et al., 2015). The large density difference is responsible for more cattle being lost to tiger depredation (Soh et al., 2014). The current practice of paying compensation for livestock depredation by tiger exacerbates the impact of cattle grazing because it reduces the financial risk to farmers who graze livestock and encourages increased grazing in close proximity to tigers and leopards (Pettigrew et al., 2012; Soh et al., 2014).

4.3. Conservation implications and recommendations

Amur leopards face an immediate risk of extinction because of small population size, heavy human disturbance, and possibly direct competition from tigers. Based on the SECR model estimates in this study, our study area could hold ~60 leopard individuals (Table 5), highlighting the potential importance of the Changbai Mountain forest complex to leopard conservation if inviolate lands are maintained. Due to cattle rearing serving as one important income source for local people, such multi-use forest landscapes are expected to experience continued anthropogenic modifications in the future. Furthermore, ungulate poaching (using snares) pose a significant conservation challenge to further leopard recovery (Soh et al., 2014). Therefore, the currently forested area with intensive cattle and human use is likely to serve as an ecological trap for leopards and their prey (Kanagaraj et al., 2011). However, strategies to expand conservation efforts, including management of leopards, tigers and their prey along with anti-poaching patrolling in human-dominated landscapes, have not been part of comprehensive conservation actions.

The future of wild leopard populations is at a critical point, and conservation strategies implemented over the next decade in Northeast China may well determine the future of the species. The first phase of recovery programs is removal of leopard population from immediate danger of extinction by increasing numbers and habitat as quickly as possible. Thus urgent action is needed to minimize cattle grazing and human activity. A key to this effort is to develop alternative livelihood opportunities for local communities. With provincial and national support, alternative economic and land use strategies can balance biodiversity, local development and long term goals to increase ecological

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services both at the local and national level. Our camera trap data reveal a predominance of females or at least an equal sex ratio exists in the leopard population and that reproduction and dispersal is occurring. These results suggest landscape conservation strategies must be a priority for both China and Russia to provide an opportunity for an increase in numbers of true residents on both sides of the border. Specifically, the hotspot in the North of the area (Fig. 2, left) where serve as an essential connectivity between habitat patches facilitating leopard movement toward inland China from the border. However, most of the potential suitable habitats are outside of the existing protected reserves. We recommend that establishing an ecological corridor or expanding current reserve should be considered by the government for the return of leopards there and elsewhere across Northeast China. Our findings, together with accompanying management recommendations, are guiding knowledge-intensive communications and helping develop a multistage planning process to create a landscape that fosters biodiversity connectivity, local development and national and global priorities to ameliorate climate change and increase ecosystem health.

To enable a leopard population to flourish, special conservation efforts also require an integrated trans-boundary approach. The creation of a trans-boundary reserve and land-use planning that integrates leopard recovery actions with political and economic development agendas should be a conservation priority for the governments of China and Russia. Finally, long-term monitoring of leopards with camera traps across this large forest complex is necessary, as implemented in our study. This monitoring would provide direct insight into leopard conservation status, population sizes and the dispersal process over time on the trans-boundary landscape, thereby informing decisionmakers on the implementation of sound conservation management recommendations.

5. Conclusion

In this study, we provide the first comprehensive evidence documenting the return of Amur leopards to China as well as great detail about their spatial movement limitations. They occur primarily along the border with Russia, but have also begun to occupy areas inland from the border where the density of natural prey is high and domestic cattle is low. Mitigating human disturbance and reducing livestock grazing are important conservation strategies for leopards, but they need to be combined with addressing the needs of local people. Our study provides a science-based approach that will expand Amur leopard distribution and at the same time address the economic needs of local communities.

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Appendixes. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.biocon.2016.03.014.

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