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Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East

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ABSTRACT

The Far Eastern Leopard (*Panthera pardus orientalis*; Schlegel, 1857) is perhaps the world's most endangered large felid subspecies occurring in a single population of ≤ 30 adults, and faces immediate risk of extinction unless additional populations can be established within its historical range in the Russian Far East. We used locations of leopard tracks (and their ungulate prey) collected from snow track surveys from 1997 to 2007 to develop resource selection functions (RSF) to identify potential habitat for reintroduction. We compared models that include prey versus those based on landscape covariates, and also included covariates related to human-induced mortality. To estimate potential population size, we used a habitat-based population estimate based on the ratio of population size and RSF value of occupied range. Far Eastern leopards selected for areas with high ungulate density, lower-elevation Korean pine forests on southwest facing slopes, and in areas far from human activity. Using this RSF model, we identified a total of 10,648 km² in eight patches >500 km² of potential Far Eastern leopard habitat that could harbor a potential population of 105.3 (57.9–147.2) adults. In combination with the existing population, successful reintroductions could result in a total of 139.2 (76.5–194.6) adult leopards, a 3–4-fold increase in population size. Our habitat models assist the reintroduction planning process by identifying factors that predict presence and potential suitable habitat. Identifying the highest quality, most connected patches, in combination with appropriate selection and training of released animals, is recommended for successfully reintroducing Far Eastern leopards, and potentially other endangered carnivores into the wild.

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1. Introduction

Restoration of large carnivores is recognized as an important strategy for biodiversity conservation (Ray et al., 2005), as an indicator of landscape-scale conservation success (Linnell et al., 2000; Carroll et al., 2001), and because of their important trophic role (Berger et al., 2001; Hebblewhite et al., 2005). As a result, policies towards large carnivores in many areas of the world have shifted away from active persecution (Musiani and Paquet, 2004). This paradigm shift has enabled carnivores to recolonize parts of their historic ranges, e.g., wolves (*Canis lupus*) in the European Alps (Breitenmoser, 1998; Marucco and McIntire, 2010), and the north-western USA (Pletscher et al., 1997). However, for many endangered carnivores, favorable policies alone have not been enough, and active reintroductions have been required (Breitenmoser et al., 2001). Reintroductions have established successful populations where

significant dispersal barriers or human persecution still exist, such as Lynx (*Lynx canadensis*) to Colorado (Devineau et al., 2010) and the Swiss Alps (*L. lynx*) (Breitenmoser, 1998), and lions (*Panthera leo*) and other carnivores in Africa (Hayward et al., 2007a; Hunter et al., 2007). Given declining trends for many carnivores, more reintroductions will likely be required in the 21st century (Weber and Rabinowitz, 1996; Dalerum et al., 2009).

The Far Eastern, or Amur leopard (*Panthera pardus orientalis*; Schlegel 1857) is probably the most endangered large felid subspecies in the world, and has been listed as critically endangered on the IUCN red list since 1996 (Jackson and Nowell, 2008). Originally distributed broadly in the southern-most portions of the Russian Far East, Northeast China and much of the Korean peninsula (Pocock, 1930; Nowell and Jackson, 1996), fewer than 10 leopards likely exist in China today (Yang et al., 1998), and the main population occurs in southwestern Primorski Krai (Province) in the Russian Far East (Fig. 1). In 1970 there were no more than 46 individuals in three isolated populations in southern Primorski Krai (Fig. 1) (Abramov and Pikunov, 1974). By 1985, leopards had disappeared from the two northern sites (Pikunov and Korkishko, 1985),

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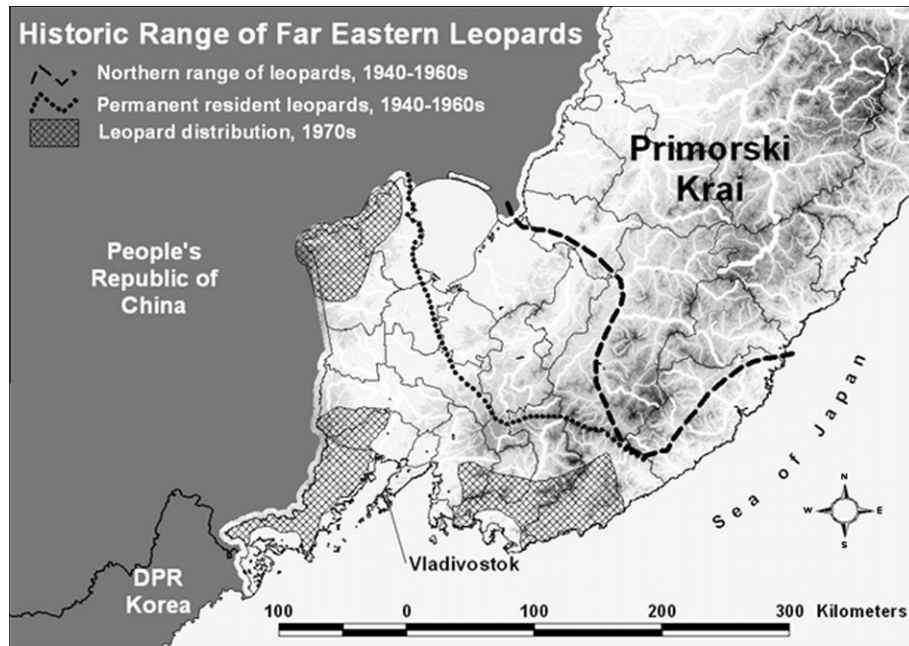


Fig. 1. Historic range of Far Eastern leopards in the southern Russian Far East (based on Heptner and Sludski, 1972, and Abramov and Pikunov, 1974). Currently leopards remain only in the southernmost hatched area in Southwest Primorski Krai (province).

and since then, a small population of 25–35 leopards has persisted in Southwest Primorski Krai (Fig. 1, Pikunov et al., 2009). This isolated population of leopards is faced with imminent extinction from continued poaching, illegal harvest of prey, habitat fragmentation, and inbreeding depression (Miththapala et al., 1996; Uphyrkina et al., 2002). It is critical that numbers of leopards increase to reduce extinction risk. However, given that natural expansion of this population seems unlikely because of high levels of agricultural and infrastructure development surrounding the population in Russia and China, reintroduction of individuals to form additional populations appears to be the best option for increasing numbers in the wild.

Quantitative assessments of reintroduction programs for mammals and birds (Griffith et al., 1989) indicate that one of the primary determinants of success is habitat quality of the release area. Various modeling approaches have been employed to identify potential habitat and colonization patterns of carnivores (Schadt et al., 2002a, b; Cianfrani et al., 2010). For many endangered carnivores, vegetation-based landscape covariates used in many habitat models are insufficient for two reasons. First, human-caused mortality – a parameter not easily tied to landscape covariates – is a primary influence on population persistence for many large carnivore populations (Chapron et al., 2008; Goodrich et al., 2008). Second, in the absence of high human-caused mortality, carnivore densities are correlated with preferred prey density (Karanth et al., 2004; Hayward et al., 2007a,b; Miquelle et al., 2010a). Therefore, to accurately identify potential habitat for reintroductions, it will be necessary to include anthropogenic influences as well as measures of prey abundance (Marucco and McIntire, 2010).

Our goal was to identify and prioritize potential habitat for reintroduction of Far Eastern leopards to their historical range in Russia, as requested by Russian authorities as part of the recovery planning process. We used extensive winter track surveys in the current range of leopards to develop a resource selection function

(RSF, Boyce and McDonald, 1999) that defined the relative probability of leopard occurrence as a function of key resources. We compared models that included estimates of the probability of prey occurrence versus those based on landscape covariates, and also included anthropogenic covariates that relate to human-caused mortality of carnivores in the Russian Far East (Goodrich et al., 2008; Kerley et al., 2002). Next, we extrapolated this RSF to the historic range of Far Eastern leopards to identify best potential reintroduction sites. Using a habitat-based ratio estimator (Boyce and Waller, 2003) and estimates of the current population size, we then predicted leopard population sizes for potential habitat patches. Finally, we used the RSF models to assess connectivity of these patches with a least-cost path analysis (Chetkiewicz and Boyce, 2009). Habitat patch size, potential population size, and connectivity of patches were used as criteria for identifying priority areas for initiating a reintroduction program.

2. Study area

RSF models were first derived for the current range of leopards in Southwest Primorski Krai (current range), and then applied across their historic range in Southern Primorski Krai (historic range, Fig. 1). Their current range encompasses ~7000 km² along the eastern slopes of the East Manchurian Mountains on the border with China. Human activity is concentrated in low elevation agricultural river valleys, along main roads and railways, and near the main cities of Vladivostok (>700,000 people) and Ussurisk (40,000). Coastal areas are dominated by Mongolian oak (*Quercus mongolia*) and birch (*B. costata*, *B. lanata*) forests. Inland areas contain Korean pine (*Pinus koraiensis*), black fir (*Abies holophylla*), and a mixture of deciduous trees such as birch (*Betula* spp.), basswood (*Tilia amurensis*), maples (*Acer* spp.) and others. At higher elevations, conifers such as spruce (*Picea* spp.) fir (*Abies* spp.) and larch (*Larix* spp.) predominate. Two protected areas – Borisovkoe Plateau

wildlife refuge, Barsovy Federal Wildlife Refuge – were merged in 2009 as Leopardovyi Wildlife Refuge, and are now overseen and managed by a third protected area – Kedrovya Pad Zapovednik (strictly protected area) – as a single complex totalling 1218 km².

The historic range of leopards includes approximately 86,000 km² in the southern Sikhote-Alin Mountains (Heptner and Sludski, 1972, Fig. 1). In both Sikhote-Alin and East Manchurian ranges, mountains range from 300 to 1000 m, and while lowlands are dominated by agriculture, the majority of the region (70%) is forested. Current and historic forest cover is similar. Riverine forests are most often comprised of a variety of deciduous species (*Salix schwerinii*, *Ulmus lacinata*, *Chosenia arbutifolia*, *Populus maximoviczii*, *Fraxinus mandshurica*), sometimes mixed with Korean pine. During winter, deep snow cover is considered a limiting factor for leopards (Pikunov and Abramov 1992, Gavashelishvili and Lukarevskiy, 2008), and is shallowest on south-facing slopes and along the coastal areas of the Southern Sikhote-Alin. A number of protected areas occur in the historic range of Far Eastern leopards, increasing the prospects of establishing an additional leopard population.

Leopards prey on a wide variety of species in summer, but during winter they rely almost exclusively on small to medium sized ungulates (Pikunov and Korkishko, 1990; Hayward et al., 2006). The relative abundance of ungulate species has changed over time, and consequently, so has the diet of leopards. In the 1970s and 1980s, Siberian roe deer (*Capreolus pygargus*) were the most common prey of leopards (Pikunov and Korkishko, 1990). Since 1990, sika deer (*C. nippon hortulorum* [Swinhoe, 1864]) have become the dominant ungulate in the diet of leopards (L. Kerley, 1997, unpublished report). Wild boar (*Sus scrofa*) are scattered across both Southwest Primorski and the Sikhote-Alin Mountains, and are also preyed on by leopards, especially young, but less commonly than the smaller deer species (Pikunov and Korkishko, 1990). Recent scat analyses revealed 27% of scats ($n = 62$) contained sika deer, 6% roe deer, 29% unknown deer, and 20% wild boar (L. Kerley, 1997, unpublished report). Therefore, we considered all three prey species as potentially important to leopards. Other sympatric carnivores in both the current and potential range of Far Eastern leopards include Amur tigers (*Panthera tigris altaica*), wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*), Asiatic black bear (*Ursus thibetanus*), and brown bear (*Ursus arctos*).

3. Materials and methods

3.1. Leopard and ungulate track surveys

Six snow track surveys of leopards have been conducted in Southwest Primorski Krai between 1997 and 2005 (Pikunov et al., 1997; Aramilev et al. 1998; Pikunov et al., 2000, 2003, 2009; Aramilev et al., 2000). Snow track surveys were conducted shortly after new snowfall to eliminate double counting (e.g., Jedrzejewska and Jedrzejewski, 1998). A stratification process eliminated areas and vegetation types where the probability of

leopards was very low (e.g. wetlands, grasslands, agricultural areas, settlements) and survey routes were positioned to maximize the probability of encountering leopard tracks both on forest roads, trails and at random through the study area. Either one or two observers walked each route, recording all tracks of leopards on a 1:100,000 map. Track size, age of track, and distance to other tracks were used to develop population estimates (e.g. Miquelle et al., 2007). To develop habitat models, we used $n = 467$ tracks of adult leopards recorded during snow track surveys in 1997, 1998, 2000, 2003 and 2007 (using only one survey in 2000 to maintain balanced yearly data in the RSF) that included 9153 km of survey routes (Table 1). Experts estimated 22–44 individual adult leopards (mean = 33.9, SD = 7.53) from these six surveys, with densities similar to independent remote camera trapping surveys (Kostyria et al., 2003). In addition to standardized leopard surveys, we also collected an additional 239 tracks during additional (e.g. tiger) surveys over 1998–2007 which we used as an out-of-sample validation set for habitat models. Starting in 2000, counts of fresh ungulate tracks (≤ 24 -h old) were also recorded along survey routes in the current range of leopards as an indicator of relative animal abundance (Stephens et al., 2006). We used these 'extra' ungulate tracks to validate ungulate habitat models developed over the entire historic range.

Habitat models across the historic range were developed for sika deer, roe deer, and wild boar based on presence/absence of tracks within 486 survey units (131 km² in size) along 11,473 km of survey routes in 2005 (see Electronic supplementary materials for survey design, Fig. S1). Track count surveys of ungulates were conducted across the historic range of leopards in 2005 as part of a range-wide tiger survey during a 2-week period in February (Miquelle et al., 2006). Survey transects were sampled for ungulate and tiger tracks (as well as leopards in their current distribution) within 24 h of fresh snowfall. We validated ungulate models across the historic range of leopards in southern Sikhote-Alin using a total of 3453 sika deer, 7319 roe deer, and 3658 wild boar tracks collected during the 2005 survey.

3.2. Resource selection function modeling

We used leopard tracks to estimate resource selection by comparing the landscape covariates found at spatial locations of tracks to those at available locations in a used-available design (Manly et al., 2002). We defined the current distribution of leopards as the 99% kernel home range for all Far Eastern leopard tracks recorded during surveys. This resulted in a ~ 6500 km² study area, within which we generated 0.5 random locations/km² of study area ($n = 3500$) to sample availability of landscape covariates. We developed an RSF by estimating coefficients for landscape covariates from fixed-effects logistic regression of used versus available (random) locations (Manly et al., 2002; Boyce and McDonald, 1999). The use-available design yields a relative probability because the sampling fraction is unknown, but can still be used to

Table 1

Summary of Far Eastern leopard snow track surveys and population estimates conducted in Southwest Primorski Krai, 1997–2008.

Year	# Leopard tracks	km surveyed	Citation	Population estimate
1997	48	1136	Pikunov et al. (1997)	25–31
1998	83	1700	Aramilev et al. (1999)	40–44
2000	66	1352	Pikunov et al. (2000) and Aramilev and Fomenko (2000)	22–27
2000	43	1280	Aramilev and Fomenko (2000)	48–52
2003	197	1603	Pikunov et al. (2003)	28–30
2007	96	1741	Pikunov et al. (2009)	25–34
Total	533 ^a	8812	Average	33.9 (SD = 7.53)

^a $n = 467$ were used for development of RSF model.

rank habitat quality and identify drivers of resource selection (Manly et al., 2002; Johnson et al., 2006; Hirzel and Le Lay, 2008).

We adopted a univariate and stepwise model selection process (Hosmer and Lemeshow, 2000). We first screened potential variables for collinearity using a cut-off of $r = 0.5$, and assessed univariate importance of each covariate, testing for linear and non-linear effects. We included individual covariates in a best all-inclusive model for which we then conducted stepwise model selection (Hosmer and Lemeshow, 2000). We evaluated goodness of fit likelihood ratio chi-square test, and residual diagnostics (Hosmer and Lemeshow, 2000). We evaluated predictive capacity using Nagelkerke's pseudo- r^2 , receiver operating curves (ROC), classification success (Hosmer and Lemeshow, 2000), and most importantly, using k-folds cross validation between the top model structure and each year of Far Eastern leopard survey data (Boyce et al., 2002).

3.3. Landscape covariates

We used a combination of environmental, anthropogenic, and biotic spatial covariates to understand Far Eastern leopard and their prey's resource selection (Electronic supplementary materials, Table S1). Environmental covariates included elevation (m), slope, aspect, and hillshade calculated from the Shuttle Radar Topography Mission (SRTM, Reuter et al., 2007) at an approximate 90 m pixel resolution using ARCGIS 9.2 Spatial Analyst. We also used remotely sensed measures of snow cover obtained (MOD10A2) from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite at intermediate (500 m²) resolution (Hall and Riggs, 2007). We used an index of snow cover calculated as the percent (0–100) of winter months (November 1–April 30) during the winter 2004/2005 that each 500 m² MODIS satellite pixel was covered with snow. MODIS snowcover is known to be correlated with snow depth and across years (Hall and Riggs, 2007). We used a spatial vegetation community landcover model that describes 12 vegetation community associations available in the study area. The landcover model was developed for the Russian Far East from Landsat5 images that were visually classified into 53 cover types, and then collapsed into 12 vegetative communities: agricultural fields, grassland meadows, wetlands, regenerating burned/logged forests, shrub communities, oak forests, birch forests, riverine deciduous and mixed conifer-deciduous forests, larch forests, mixed Korean pine-deciduous forests, spruce–fir forests, and alpine (Ermoshin and Aramilev, 2004).

3.4. Ungulate habitat covariates

We included spatial models of the probability of occurrence for the three main ungulate prey species (sika deer, roe deer, and wild boar) as ungulate habitat covariates in the leopard model (sensu Miquelle et al., 1999).

We developed ungulate RSF models from snow track surveys conducted in winter 2005 over the historic range of leopards (Miquelle et al., 2006). Our design followed a used-unused design in which pre-defined units (averaging 131 km²) were surveyed with an average of 0.68 km/km² of surveys; we only used sample units with a minimum of 0.19 km/km² of surveys/unit to ensure probability of detection = 1 (M. Hebblewhite, unpublished data), and treated units without tracks as unused. We then developed RSF models for the three ungulate species using a used-unused design at the scale of the sample units, and compared the same environmental and human covariates as for leopards using logistic regression. Because the sampling fraction is known in this used-unused design, a valid probability can be derived directly from the logistic regression (Manly et al., 2002; Hirzel and Le Lay, 2008). Including this probability of occurrence in leopard habitat models assumes that the probability of occurrence is related to density (e.g., Hirzel and Le Lay, 2008).

We tested this assumption through linear regression of the probability of occurrence against the ln-transformed count of ungulate tracks in a sample unit. Stephens et al. (2006) showed that ungulate snow track count data were related to absolute density through the Formozov algorithm on a theoretical basis (i.e., an independent test of this equation has not been conducted, for example using DISTANCE sampling estimates). Therefore, if occurrence and abundance (counts) are related, inclusion of our ungulate habitat models in the leopard RSF could be interpreted as leopard selection for areas of high ungulate density.

Landscape covariates for ungulate habitat models were averaged using a moving window at the scale of the survey unit to ensure correspondence in scale between the dependent and independent variables in logistic regression. We adopted the same logistic regression modeling approach as for Far Eastern leopards (described above). We validated our ungulate habitat models at the historic and current ranges by evaluating the Spearman's rank correlation between frequency of counts of out-of-sample ungulate tracks and predicted rank-order of habitat ranks (Boyce et al., 2002). Validation of the current range was especially important to test whether our extensive ungulate habitat models predicted observations of ungulates well within the current leopard area (Electronic supplementary materials).

3.5. Delineating potential reintroduction patches

We identified contiguous patches of potential leopard habitat as potential reintroduction sites. First, we extrapolated the top leopard RSF model to their historical range using ARCGIS 9.3.1 (ESRI Ltd., CA). Such extrapolation assumes that the ranges of environmental covariates are the same in the area used to develop the model as the extrapolated area (Hirzel and Le Lay, 2008). We tested this assumption by comparing the mean and standard deviation of the continuous covariates in the current and historic ranges (Hirzel and Le Lay, 2008). We then estimated the cutpoint probability from the RSF model that captured 90% of the observed leopard tracks within their current distribution (Liu et al., 2005). We used this cutpoint to reclassify predictions across the entire historic range into either non-habitat (0 if $w^*(x) < \text{cutpoint}$), or the relative probability if above the cutpoint. We then classified patches into larger patches of 500 km² where >5 breeding female leopards might be able to persist based on the average fixed-kernel home range size of five leopards (home range size ~100 km², A.V. Kostyria, unpublished data). We also retained smaller stepping stone movement patches as potential movement corridors between 100 and 500 km². Patches smaller than 100 km² were dropped.

3.6. Evaluating patch connectivity

We used resource selection functions combined with least cost path analysis to identify potential corridors for movement of leopards. Little is known of large felid behavior during dispersal (Zimmermann et al., 2007), but given the reduced dispersal distance of large felid females (Goodrich et al., 2010), we followed Chetkiewicz and Boyce (2009) in our approach to evaluate connectivity. We calculated relative costs of movements between habitat patches assuming that cost was inversely related to the probability of selection from an RSF (Chetkiewicz and Boyce, 2009). We used the inverse of the RSF as the cost path function in ARCGIS 9.3 to determine the most connected leopard patches >100 km² and identify movement corridors.

3.7. Estimating potential leopard population size

We linked the RSF to estimated population size of Far Eastern leopards (Table 1) to predict the potential number of leopards that

could occupy large (>500 km²) patches of potential leopard habitat. The details of the approach are summarized by Boyce and McDonald (1999) and Johnson and Seip (2008). We summed the total predicted relative probabilities for each leopard patch. Given the estimate for the number of leopards (N , Table S1) in the current range of leopards in Southwest Primorski, we then calculated the total predicted habitat required for each leopard and extrapolated the potential numbers of leopards possible in each potential habitat patch using the following equation:

$$\frac{\sum_{\text{Current}} \hat{W}(x)_i}{N_{\text{Current}}} = \frac{\sum_{\text{Patch}} \hat{W}(x)_i}{N_{\text{Patch}}}$$

where N_{Current} is the Far Eastern leopard population estimate for the existent population in Southwest Primorski (known), $\sum_{\text{Current}} \hat{W}(x)_i$ is the sum of relative probabilities for the RSF for the existent population, and $\sum_j \hat{W}(x)_j$ is the summed predicted habitat probability for leopard patch j . We calculated the 95% confidence interval of potential leopard population sizes using the mean and standard deviation of leopard population counts across years (see results).

4. Results

4.1. Ungulate prey models

In winter all three ungulate species consistently selected oak forests, avoided areas with high road density, and showed weaker selection for areas with low snow cover and lower elevations (Table 2). Sika deer selected birch, Korean pine and regenerating forests, whereas roe deer selected shrub fields, and wild boar selected Korean pine while avoiding agricultural areas (Table 2). Sika deer were more common in Southeast Sikhote-Alin (especially coastal areas) and Southwest Primorski (current range of leopards), whereas roe deer were more common inland, and wild boar were found at intermediate elevations (Table 2, Electronic supplementary materials). Both sika deer and wild boar were more common

closer to protected areas (Table 2). Comparing across species, the sika deer model had the highest classification success (81.7%), ROC score (0.789), Nagelkerke's R^2 ($r_{\text{Nagelkerke}}^2 = 0.38$) and k-folds cross validation both within the current range of leopards ($r_s = 0.96$) and across the historical range ($r_s = 0.91$) (Table 2). The wild boar (current range $r_s = 0.85$, historical range $r_s = 0.84$) and roe deer (current range $r_s = 0.87$, historical range $r_s = 0.93$) models were adequate, with reasonable diagnostics, but did not perform as well as the sika deer model in predicting out-of-sample locations in the current range of leopards (Table 2, Electronic supplementary materials Figs. S2–4). Predicted habitat quality for roe deer, sika deer and wild boar were highly correlated (roe and sika deer, $r = 0.95$; boar and sika deer, $r = 0.83$; boar and roe deer, $r = 0.76$). See Electronic supplementary materials for detailed habitat maps of prey species models.

The assumption that ungulate prey RSF models were related to prey density was borne out for all three individual prey species, and for their combined average. Sika deer occurrence and track counts were the most strongly related (regression of ln-sika count and RSF probability was significant, $F_{1,202} = 140.9$, $P < 0.0005$, $R^2 = 0.41$, Pearson's correlation coefficient $r = 0.64$), followed by roe deer ($F_{1,200} = 45.3$, $P < 0.0005$, $R^2 = 0.21$, Pearson's correlation coefficient $r = 0.45$) and wild boar, which was the weakest ($F_{1,201} = 17.9$, $P < 0.0005$, $R^2 = 0.11$, Pearson's correlation coefficient $r = 0.29$). However, when combined, there was a strong relationship between the counts of all three species and their averaged RSF probability ($F_{1,200} = 95.6$, $P < 0.0005$, $R^2 = 0.37$, Pearson's correlation coefficient $r = 0.61$, Fig. 2), suggesting that the assumption that probability of occurrence was an adequate indicator of abundance was warranted in our study area (see Fig. 3).

4.2. Far Eastern leopard RSF model

Inclusion of any prey covariates dramatically improved model fit and explanatory power, with leopard occurrence increasing

Table 2

Resource selection functions for sika deer, roe deer and wild boar in the Russian Far East in support of Far Eastern leopard habitat modeling during winter 2005. We report the number of used and unused sample units that were used to develop logistic regressions, measures of goodness of fit, and k-folds cross validation Spearman rank correlations between expected and observed frequency of used locations within the historic and current ranges of leopards (see methods). Selectivity coefficients (β) and standard errors for the top model for each species are reported, with bolded coefficients at $P = 0.05$.

	Sika deer		Roe deer		Wild boar	
$N_{\text{used}}/N_{\text{unused}}$ units	147/482, 0.30 prevalence		282/421, 0.67 prevalence		211/421, 0.5 prevalence	
Hosmer Lemeshow LR χ^2 (df = 8)	8.38, $P = 0.40$		4.66, $P = 0.79$		13.91, $P = 0.08$	
Nagelkerke's R^2	0.38		0.16		0.18	
ROC	0.89		0.73		0.70	
%Classification success	83.4%		71.9%		69.8%	
Historic leopard range k-folds r_s	0.91		0.93		0.84	
Current leopard range k-folds r_s	0.96		0.87		0.85	
Covariate	B/SE	SE	B/SE	SE	B/SE	SE
Agriculture	–	–	–	–	-1.82	1.02
Oak	3.68	0.783	1.33	0.60	0.96	0.423
Birch	2.77	1.13	0.74	0.59	–	–
Regen	6.27	3.21	4.65	2.94	–	–
Korean pine	2.11	0.810	–	–	1.27	0.468
Shrubs	–	–	1.17	1.02	–	–
Meadows	–	–	-3.16	1.49	–	–
Distance to Zapovednik	-0.044	0.010	–	–	-0.0177	0.006
Road density/10 km ²	-4.89	1.483	-1.50	0.887	-0.59	0.24
Snow cover (%)	0.16	0.090	-0.023	0.013	-0.007	0.004
Snow quadratic	-0.0023	0.0012	–	–	–	–
Elevation (m)	–	–	-0.0012	0.0008	0.010	0.002
Elevation quadratic	–	–	–	–	-0.000012	2.97e-6
Easting * Northing ^a	-6.75e-13	1.16e-13	2.58e-13	7.63e-14	–	–
Coastal zone	0.11	0.030	-0.15	–	–	–
Intercept ^b	6.29	1.20	0.933	0.480	-0.91	0.773

^a Easting * Northing is a spatial variable created by the multiplication of easting and northing to create a southwest-northeast spatial gradient in sika deer distribution.

^b Intercept includes as the reference category all excluded habitat covariates, for example, for sika deer, the intercept includes agriculture, spruce-fir forests, larch forests deciduous, shrubs, meadows, alpine, wetlands.

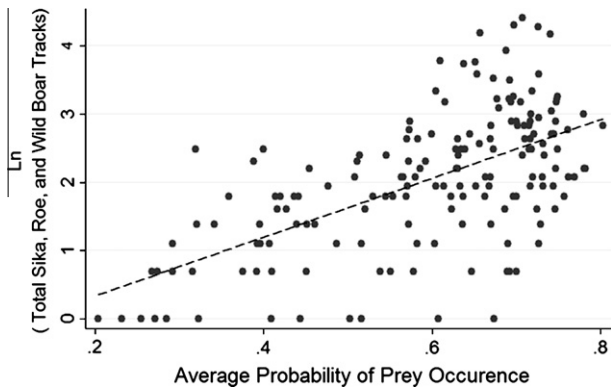


Fig. 2. Relationship between the average probability of occurrence from Resource Selection Function models for each of the three Far Eastern leopard prey species and the natural logarithm of the total number of sika deer, roe deer and wild boar snow tracks in a survey unit in Primorski Krai, Russian Far East, winter 2005. The regression is significant ($F_{1,168} = 95.26$, $P < 0.0005$) and the RSF explains 36% of the variation in the total counts of all three prey species.

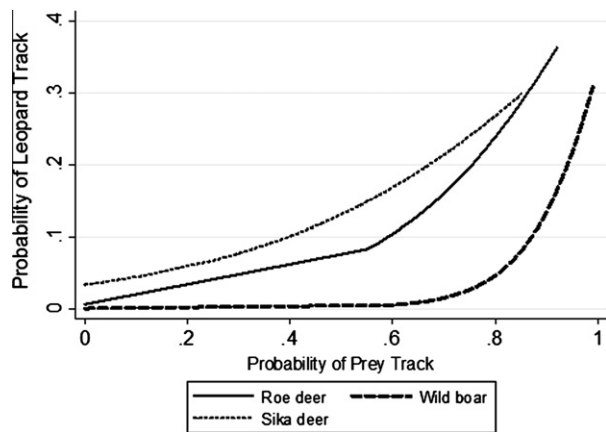


Fig. 3. Relative probability of observing a leopard track as a univariate function of the ungulate habitat models for the three top ungulate species in the diet of Far Eastern leopards, roe deer, sika deer and wild boar, Southwest Primorski Krai, Russian Far East, 1997–2007.

Table 3

Far Eastern leopard resource selection function (RSF) model results and area k-folds predictive cross-validations within the current and historic range of Far Eastern leopards. The top environmental model was compared to different combinations of environmental variables and ungulate prey; sika deer, roe deer, wild boar, all prey species combined (boar + sika + roe), and averaged roe deer and sika deer, Russian Far East, 1997–2007.

Model	Log-likelihood	d.f.	Δ AIC	k-Folds current range	k-Folds historic range
Sika deer	-1535.6	12	0	0.96	0.86
(Boar + sika + roe)	-1538.1	12	2.9	0.95	0.96
Sika + roe	-1548.1	12	24.9	0.92	0.89
Roe deer	-1558.8	12	46.4	0.91	0.92
Wild boar	-1530.2	12	119.2	0.89	0.89
Environment	-1609.1	11	144.9	0.79	0.78

with prey occurrence (Table 3, Fig. 5). For example, the top two prey models (sika Δ AIC = 0, all prey Δ AIC = 2.9) were significantly more likely to be the top model compared to the top model without prey (Δ AIC between models 1 and 2 and the top environment-only model were 142, 144.9, respectively, Table 3). While sika deer was the most important prey species driving leopard resource selection (Table 3, Fig. 5), the present and historic limited distribution of sika deer throughout the former range of leopards

Table 4

Top Far Eastern leopard RSF for the relative probability of selection at the study area scale in the Russian Far East, Southwest Primorski Krai, 1997–2007. Bold values are significant at $p = 0.01$.

Coefficient	B	SE
Deciduous	-0.95	0.460
Meadows	-0.67	0.272
Shrubs	-0.74	0.222
Korean Pine	0.31	0.121
Agriculture	-1.28	0.478
Ungulate Prey	5.27	0.802
Distance to main roads (km)	0.145	0.015
Snow cover (MODIS)	-0.34	0.204
Hillshade	-0.0027	0.0007
Dist (km) to Zapovednik	-0.053	0.007
Elevation (m)	-0.0036	0.0004
Constant, β_0^a	-4.94	0.710

^a The constant (β_0) includes as the reference categories birch, oak, Korean pine, meadow, and agriculture, which were not significantly different from each other.

(Electronic supplementary materials, Fig. S2) and leopard diet selection in our study area cautioned against using a sika deer-only model. The sika deer model also predicted both leopard and sika deer occurrence more poorly in the historical range than the 3-species model (Table 3). Furthermore, because all three prey species models were highly correlated ($r > 0.7$), we could not include them as independent covariates in the same logistic regression model. Therefore, we combined an ‘average’ model as the average RSF score of all three species and used this all-species model as the top predictive model within the historical range of leopards.

The combined 3-prey RSF model showed that leopards avoided deciduous forests, meadows, shrub and agricultural landcover types, but selected for Korean pine (Table 4). Leopards also selected areas farther from main roads, with lower winter snow cover, closer to and inside protected areas, at lower elevations, and lower hillshade values (southerly aspects)(Table 4). Overall model diagnostics revealed good model fit, with a Hosmer and Lemeshow goodness of fit test $\chi^2 = 15.11$ ($P = 0.07$), a ROC score of 0.789, and a 74.3% overall classification success at the optimal cutpoint probability of 0.23. The k-folds cross validation score for the leopard data used to build the RSF model (internal cross validation) was $r_s = 0.95$ (SE = 0.023). When applied to the independent survey data (external cross validation) from 1998 to 2007, the model predicted well, with an $r_s = 0.901$ (SE = 0.049, Fig. 4).

4.3. Delineating potential reintroduction patches and connectivity

Extrapolating the top all-prey leopard RSF model to the historic range of leopards revealed patches of potential leopard habitat adjacent to their current distribution and multiple patches along the coast (Fig. 4). Our comparison of the distributions of spatial covariates between the current and potential habitat revealed wide overlap (Electronic supplementary materials, Tables S2a and b), supporting our extrapolation (Hirzel and Le Lay, 2008) from the current distribution. Applying the $P = 0.23$ cutpoint to the historic range assured 89.2% correct classification of leopard tracks, and ignoring habitat patches $< 500 \text{ km}^2$, identified seven potential habitat patches totaling $10,648 \text{ km}^2$ (Fig. 5). Mean habitat quality, measured by mean area-weighted habitat rank from 1 to 10, of all patches was > 7 , and several patches (e.g. Patch 2) were of higher average habitat quality than the area currently occupied by leopards (Table 4).

Least cost path analysis between potential leopard patches $> 100 \text{ km}^2$ revealed several discontinuous larger areas of potential leopard habitat (Fig. 5). The most connected patches were along the coast. Patches 5, 4, and 8 were the three most connected

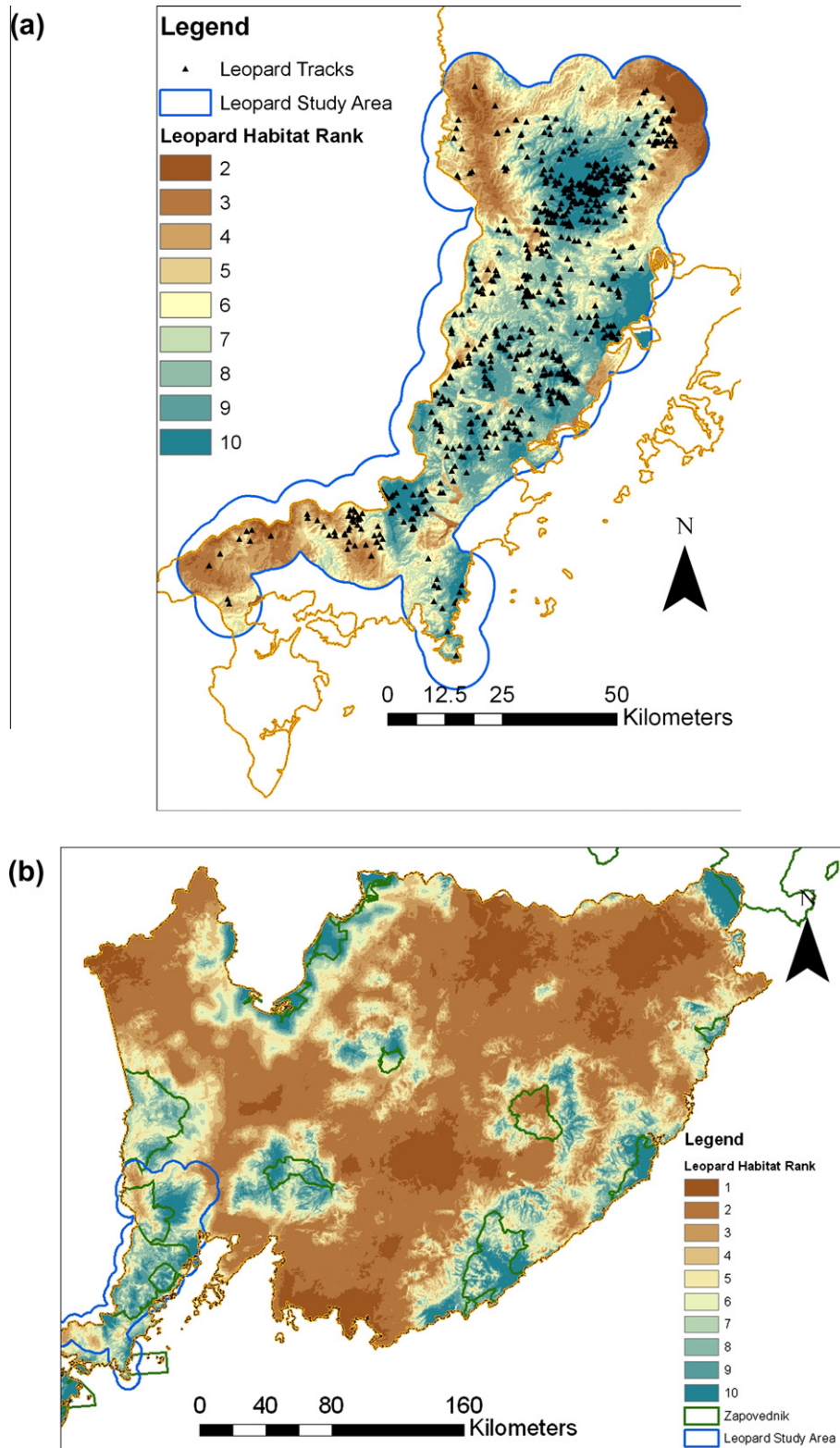


Fig. 4. Predicted Far Eastern leopard habitat quality in the (a) current range of leopards (shown with observed leopard tracks) and (b) across their historic range in southern Primorski Krai (shown with protected areas), predicted from the top “all-prey species” model, Russian Far East. Predicted Far Eastern leopard habitat quality is shown in equal-area decile ranked categories from 1 (low quality) to 10 (high quality).

patches, followed by Patch 2 and then 7 north along the coast via two smaller 100 km² patches. As expected, the existent population in Southwest Primorski population was highly isolated from the next closest potential habitat.

4.4. Estimating potential Far Eastern leopard population size

Using a mean current leopard population size of 33.9 (SD 7.53) individuals, we predicted a total of 139.2 (76.5–194.6) leopards

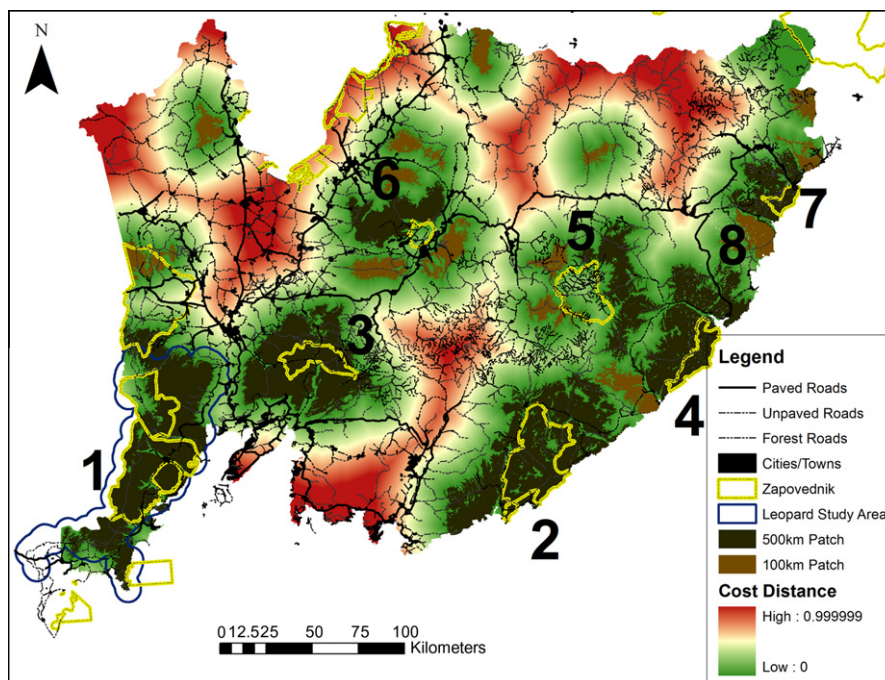


Fig. 5. Least cost path distance between predicted Far Eastern leopard habitat patches (brown > 100 km², green > 500 km²) identified with the top RSF model and 90% classification success cut-point probability, showing cost distance (red indicates high costs) to move between patches. Zapovednik boundaries, cities/towns, and roads (paved, unpaved, forest roads) illustrate high 'cost' movement landscapes. Numbers correspond to patch names in Table 5.

Table 5
Habitat-based population estimates for the eight largest patches of potential Far Eastern leopard habitat within their current and historic range in the southern Russian Far East based on Far Eastern leopard resource selection function models developed in Southwest Primorski Krai with data on leopard distribution collected from 1997 to 2007. Patch name, area, mean habitat quality (measured by mean rank from 1 to 10 of all pixels), and predicted population size (with 95% CI) are shown for each of the eight habitat patches.

#	Patch name	Area (km ²)	Habitat quality	Population size	95% C.I.
1a	SW Primorski – currently occupied ^a	3502	7.69	33.9	(18.6–47.4)
1b	SW Primorski – northern unoccupied area	201	7.81	2.2	(1.2–3.1)
2	Lazo	3379	8.04	34.8	(19.1–48.7)
3	Ussurisk	2451	7.69	23.0	(12.7–32.2)
4	Vasilovski	1210	7.86	16.4	(9.0–22.9)
5	Chuguevski-W. Olga	1019	7.61	8.2	(4.5–11.4)
6	Seniyi Krevet	888	7.48	8.5	(4.7–11.8)
7	Kavelerova-Dalnegorsk	756	7.08	6.9	(3.8–9.6)
8	North Olga	746	9.51	5.4	(3.0–7.5)
	Total potential habitat	10,648	7.95	105.3	(57.9–147.2)
	Total (current + potential)	14,150		139.3	(76.5–194.6)

^a Southwest Primorski Krai is itself split into two areas, inside and outside of the current distribution of Far Eastern leopards to account for potential habitat in this region that is currently not used by leopards.

could potentially occupy all large patches (including the current population) in the southern Russian Far East (Table 5). Excluding the currently occupied patch in Southwest Primorski Krai, an additional 105.3 (57.9–147.2) leopards could be expected to eventually occupy the remaining patches.

5. Discussion

Based on the habitat relationships of the sole remaining population of Far Eastern leopards, we identified >10,000 km² of potential leopard habitat divided into seven large habitat patches within their historic range in the southern Sikhote-Alin in the Russian Far East. These areas could harbor a potential population size of 105.3 (57.9–147.2) additional adult Far Eastern leopards, significantly increasing the population size and geographic distribution of this critically endangered species. Given reproduction and juveniles, and the existing population, this could help achieve

a total population size of ~200 leopards in the wild, dramatically reducing the immediate risk of extinction. Habitat quality in predicted potential habitat patches was similar to currently occupied habitat, and several patches may be of even higher quality. Habitat quality was defined by abundant sika deer, roe deer and secondarily, wild boar populations, in mid-elevation deciduous and mixed conifer forests with greater protection from poaching in areas further from human activity. Because proximity to roads increases the risk of poaching for sympatric Amur tigers (Kerley et al., 2002), greater distance from roads will likely also increase survival for reintroduced leopards. These results, combined with recent carnivore studies (Chapron et al., 2008; Goodrich et al., 2008; Miquelle et al., 2010a,b) emphasize that reintroductions would be most effective if combined with reduced poaching of reintroduced leopards and their ungulate prey. Three coastal potential habitat patches surrounding Lazovski Zapovednik in the south (Patch 2, Fig. 5) and Vasilovski Wildlife Refuge in the north (Patch 4, Fig. 5) were identified as the highest quality and best connected

(Fig. 5, Patches 2, 4, 5, 7, 8) patches that could themselves harbor almost 72 adult leopards (Table 5). Our analyses reinforce current opinion that the existing population is highly isolated and unlikely to colonize patches identified by this study. Our leopard habitat models also emphasize the importance of increasing habitat quality for this existing population by increasing the density of preferred ungulate prey.

Despite optimistic results that indicate suitable habitat exists for Far Eastern leopards in their historic range, identification of a source population for reintroduction is a challenge because of the precariously small size of the only wild population. The remaining wild population is also genetically depauperate and at risk from inbreeding depression (Uphyrkina et al., 2002), and thus too small to risk removal of sufficient individuals to ensure a successful reintroduction. Additional recovery action such as reintroductions into the current population may be needed to overcome potential deleterious effects of inbreeding depression, similar to the Florida panther reintroductions (Johnson et al., 2010). Rearing and training captive leopards for release would also be a challenge, but there are some examples of success with similar sized carnivores such as the Florida panthers and Eurasian Lynx (Belden and Hagedorn, 1993; Linnell et al., 2009). Currently, the captive population of the European Endangered Species Programme (EEP) is being managed to produce surplus pairs that can be moved to release sites, where their offspring can be reared and prepared for release into the wild (Christie, 2009). In lieu of other populations, reintroduction of young from captive Far Eastern leopards reared under careful protocols and close monitoring into the potential habitat we have identified, combined with active efforts to curb poaching of leopards and their prey, provides the best chance for increasing numbers in the wild (Miquelle et al., 2010a,b).

Our modeling approach mirrored recent efforts to identify potential habitat for endangered, recovering, and expanding populations of large carnivores. The expansion of Eurasian lynx has been assisted by modeling potential habitat (Schadt et al., 2002b) based on data from existing populations elsewhere. Similarly, potential habitat for expanding wolves in the Great Lakes of the USA and Italian Alps were predicted using RSF models (Mladenoff et al., 1999) and individually-based models (Marucco and McIntire, 2010). In both cases, model predictions were later borne out by habitat selection patterns by dispersing wolves over a 10-year time span. Our leopard habitat models demonstrate the importance of including prey in defining potential habitat for carnivore reintroduction attempts. Models developed without prey tended to include poorer quality habitat (Li et al., 2010, M. Hebblewhite, unpublished data), and may be overly optimistic. Therefore, we recommend that other studies assessing carnivore reintroduction ensure that habitat is defined using prey resources to improve predictions (Hayward et al., 2007b).

Connectivity will be important to the future viability of Far Eastern leopards once additional populations are established. It is unlikely that dispersal from the existing population will establish additional populations for several reasons. Our connectivity modeling, and concurrent work on tiger habitat modeling in the RFE (Carroll and Miquelle, 2006; Li et al., 2010) confirms that the barrier between leopard Patch 1 and 3 (Fig. 5), formed by the agricultural and transportation corridors north of the city of Vladivostok, likely poses a major barrier to large felids. For example, sympatric populations of Amur tigers in Southwest Primorski are now genetically distinct from tigers occupying the former distribution of leopards in the Sikhote-Alin Mountains (Henry et al., 2009). Moreover, despite the population being potentially saturated with adults, there has been little successful density-dependent dispersal (like other large felids, Robinson et al., 2008), further suggesting that dispersal is unlikely. Therefore, active reintroduction efforts will be needed to recover Far Eastern leopard populations in the

Russian Far East, and re-establishing connectivity between the new population(s) and the existing population will be unlikely without extensive restoration of forestlands.

Our habitat models also reveal some insights into the mechanics of extinction when compared to the historic decline in leopards. In the 1970s, leopards occurred in the northwest corner of southwestern Primorski Krai and just east of Vladivostok (Fig. 1), but these areas are now predicted to be low quality habitat (Figs. 4 and 5). Several factors may explain these apparent contradictions. The habitat patch in the northwest Primorski is very small and presently isolated, but historical connectivity with good habitat and a population of leopards on the Chinese side of the border may have contributed to the persistence of this population (Fig. 1). Also, in southern Sikhote-Alin dramatic changes in prey composition – marked by a large increase in sika deer, especially along the coast, and declines in roe and red deer – have greatly increased the quality of coastal habitat for leopards in comparison to the recent past, making inland areas, where sika deer numbers are lower and snows deeper, less favorable today for leopards. Despite apparent contradictions between current and past distribution, it is also worth acknowledging that historic distribution maps are also likely uncertain as well.

When predicting potential habitat and population sizes of reintroduced carnivores, it is important to acknowledge limitations of both underlying habitat models and population extrapolation methods (Johnson and Seip, 2008; Cianfrani et al., 2010). Our approach assumed: (a) preferred habitats (by leopards and ungulates) retain higher densities (i.e., a positive relationship between occurrence and abundance), (b) the appropriate habitat covariates in the extrapolation region (i.e., historic) were the same as in the model calibration (i.e., current) region, (c) similar selection patterns exist for spatial variables in the calibration and extrapolation areas, and (d) there exists a similar equilibrium relationship between population size and habitat in both the current and historic region (Johnson and Seip, 2008; Cianfrani et al., 2010). For ungulates, we were able to validate the occurrence-abundance assumption, while this remains an untested assumption for the leopard habitat model. Future studies could test this assumption using spatial information about reproductively active female leopards, or leopard mortality sites (e.g., Nielsen et al., 2006). Our comparison of the models with and without prey tested the second assumption that appropriate habitat covariates were measured, and confirmed that prey were key to habitat quality for leopards. But at least two habitat covariates are not adequately addressed by our model. First, infrequent deep snows (especially in inland patches) may greatly decrease probability of persistence of reintroduced leopards and therefore, we recommend focusing reintroduction efforts on coastal habitat patches. Secondly, we did not include tiger habitat quality in assessing potential habitat, despite the concern for potential interspecific competition. Leopards and larger felids coexist elsewhere, however, through niche partitioning of ungulate prey based on body size (Hayward et al., 2008). Furthermore, tiger densities in Southwest Primorski, where tigers and leopards presently co-exist, are similar to those in southern Sikhote-Alin (D. Miquelle, unpublished data), suggesting that levels of competition may be similar. Nonetheless, whether captive-reared leopards will respond appropriately when encountering tigers in the wild is of concern, and special training may be necessary.

Concerning the other main assumptions, we tested whether covariates were similar between the current and historic extrapolation area (Hirzel and Le Lay, 2008), and found wide overlap between all covariates, generally supporting our approach (Electronic supplementary materials, Tables S2a and b). However, across the historic range, sika deer habitat quality was slightly lower, as was the average distance to roads, and areas were further from protected areas. This emphasizes the importance of selecting

a reintroduction site within the entire historic range that is further from human activity with high quality sika deer habitat. The second assumption, the same ungulates occur in both current and historic range, was also supported by a comparison of the historic and current area (Table S2a), and sika deer densities (the most common and important prey) have greatly increased in the historic range of leopards (Aramilev, 2010). Thirdly, it is assumed that the leopard population is at equilibrium such that habitat-population relationships will be the same in potential habitat (Johnson and Seip, 2008). Population stability over the past 30 years, and evidence that leopards inhabit all available habitat in Southwest Primorski, suggest that this population is at equilibrium. However, such equilibrium could easily be lower than potential population size due to persistent poaching, inbreeding depression, or disease. Thus, if the current population is limited by these or other unidentified factors, our extrapolations represent conservative estimates of potential population size. Furthermore, although we validated the relationship between prey occurrence and relative prey density, estimates of true prey density would improve our ability to estimate carrying capacity following recent studies for African carnivores by Hayward et al. (2007a). With true population estimates of ungulates obtained by focused application of the methods of Stephens et al. (2006) in targeted release areas (such as surrounding Lazovski Zapovednik), Hayward et al. (2007a) methods could be applied to derive fine-scale estimates of potential leopard population size. Despite these caveats, however, our approach improves upon simple extrapolations based on home-range (Schadt et al., 2002b), and provides managers and decision-makers a defensible target area and population estimate of the potential for population recovery (Mladenoff et al., 1999; Boyce and Waller, 2003).

6. Conclusion

Our results paint a potentially optimistic future for recovery of Far Eastern leopards, with reintroduction efforts capable of creating a population in the Russian Far East that could be 3–4 times greater than the existent population, with over 10,000 km² of potential habitat in their historic range in the southeastern Sikhote-Alin Mountains. The potential habitat for an additional 105 adult leopards, one in a single population of ~70 individuals centered on Lazovski Zapovednik, dramatically decreases extinction risk and the potential for genetic impoverishment and consequent inbreeding depression, although a population size of ~100 is still at risk of extinction (Brook et al., 2006). Once additional populations are established, augmentation of the existing population with captive reintroduced individuals should be considered to help recover that population, along with ongoing protection of ungulate prey. Similar habitat models could be developed to further recover the current population in adjacent areas of northeastern China and even the DPR of North Korea (e.g., Li et al., 2010), where individuals are occasionally reported.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.03.020.

References

- Abramov, V.K., Pikunov, D.G., 1974. Leopards in the far east of the USSR and their protection. Bull. Moscow Soc. for Nature – Amateur. Sec. Biol. 79 (2), 5–15 (in Russian).
- Aramilev, S.V., 2010. Distribution and Other Aspects of the Ecology of Sika Deer (*Cervus nippon hortulorum* [Swinhoe, 1864]) in the Southern Russian Far East. Abstract Ph.D Dissertation on Biological Science, Institute of Biology and Soils, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 22pp (in Russian).
- Aramilev, V.V., Fomenko, P.V., 2000. Simultaneous Survey of Far Eastern leopards and Amur tigers in Southwest Primorski Krai, Winter 2000. Final report to WCS and WWF.
- Aramilev, V.V., Fomenko, P., Miquelle, D.G., 1999. A 1998 survey of leopards. Zov Taiga 4, 6–11 (in Russian).
- Belden, R.C., Hagedorn, B.W., 1993. Feasibility of translocating panthers into northern Florida. Journal of Wildlife Management 57, 388–397.
- Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001. A mammalian predator–prey imbalance. Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11, 947–960.
- Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends in ecology and evolution 14, 268–272.
- Boyce, M.S., Waller, J.S., 2003. Grizzly Bears for the Bitterroot: Predicting Potential Abundance and Distribution. Wildlife Society Bulletin 31, 670–683.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecological Modelling 157, 281–300.
- Breitenmoser, U., 1998. Large predators in the alps: the fall and rise of man's competitors. Biological Conservation 83, 279–289.
- Breitenmoser, U., Breitenmoser-Würsten, C., Carbyn, L., Funk, S.M., 2001. Assessment of carnivore reintroduction. In: Gittleman, J.L., Funk, S.M., MacDonald, D., Wayne, R.K. (Eds.), Carnivore Conservation – Conservation Biology, vol. 5. Cambridge University Press, Cambridge, pp. 241–281.
- Brook, B.W., Trail, L.W., Bradshaw, C.J.A., 2006. Minimum viable population sizes and global extinction risk are unrelated. Ecology Letters 9, 375–382.
- Carroll, C., Miquelle, D.G., 2006. Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian far east: the role of protected areas and landscape matrix in population persistence. Journal of Applied Ecology 43, 1056–1068.
- Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11, 961–980.
- Chapron, C., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., Clobert, J., 2008. The impact of poaching versus prey depletion on tigers and other large solitary felids. Journal of Applied Ecology 45, 1667–1674.
- Chetkiewicz, C.L.B., Boyce, M.S., 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46, 1036–1047.
- Christie, S., 2009. Breeding Far Eastern leopards for reintroduction; the zoo programme perspective. In: Vargas, A., Breitenmoser, Ch., Breitenmoser, U., (Eds.), Iberian lynx *Ex situ* Conservation: An Interdisciplinary Approach. Fundacion Biodiversidad, pp. 462–476.
- Cianfrani, C., Le Lay, G., Hirzel, A.H., Loy, A., 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? Journal of Applied Ecology 47, 421–430.
- Dalerum, F., Cameron, E.Z., Kunkel, K., Somers, M.J., 2009. Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biology Letters 5, 35–38.
- Devineau, O., Shenk, T.M., White, G.C., Doherty, P.F., Lukacs, P.M., Kahn, R.H., 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. Journal of Applied Ecology 47, 524–531.
- Ermoshin, V.V., Aramilev, V.V., 2004. Main principles of mapping of ungulates and carnivores habitats based on satellite topography data. In: Proceedings of XII Workshop of Geographers of Siberia and the Far East. October 5–7, 2004, Vladivostok, Pacific Institute of Geography FEB RAS. Vladivostok: Izd-vo “K and partners”, pp. 157–159 (in Russian).
- Gavashelishvili, A., Lukarevskiy, V., 2008. Modeling the habitat requirements of leopard *Panthera pardus* in west and central Asia. J. Appl. Ecol. 45, 579–588.
- Goodrich, J.M., Kerley, L.L., Smirnov, E.N., Miquelle, D.G., McDonald, L., Quigley, H.B., Hornocker, M.G., McDonald, T., 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. Journal of Zoology 276, 323–329.
- Goodrich, J., Miquelle, D.G., Smirnov, E., Kerley, L.L., Quigley, H., Hornocker, M., Uphyrkina, O., 2010. Social structure of Amur (Siberian) tigers (*Panthera tigris altaica*) in Sikhote-Alin Biosphere Zapovednik, Russia. Journal of Mammalogy 91, 737–748.
- Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: Status and strategy. Science 245, 477–480.
- Hall, D.K., Riggs, G.A., 2007. Accuracy assessment of the MODIS snow products. Hydrological Processes 21, 1534–1547.

- Hayward, G.D., Kerley, G.I.H., 2008. Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research* 38, 93–108.
- Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology (London)* 270, 298–313.
- Hayward, M.W., Adendorff, J., O'Brien, J., Sholto-Douglas, A., Bissett, C., Moolman, L.C., Bean, P., Fogarty, A., Howarth, D., Slater, R., Kerley, G.I.H., 2007a. The reintroduction of large carnivores to the Eastern Cape Province, South Africa: an assessment. *Oryx* 41, 205–214.
- Hayward, M.W., Hofmeyr, M., O'Brien, J., Kerley, G.I.H., 2007b. Testing predictions of the prey of the lion (*Panthera leo*) derived from modelled prey preferences. *Journal of Wildlife Management* 71, 1567–1575.
- Hebblewhite, M., White, C.A., Nietvelt, C., McKenzie, J.M., Hurd, T.E., Fryxell, J.M., Bayley, S., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144.
- Henry, P., Miquelle, D., Sugimoto, T., McCullough, D.R., Caccione, A., Russello, M.A., 2009. In situ population structure and ex situ representation of the endangered Amur tiger. *Molecular Ecology* 18, 3173–3184.
- Heptner, V.G., Sludski, A.A., 1972. Carnivora (hyaenas and cats). In: Heptner, V.G., Naumov, N.P. (Eds.), *Mammals of the Soviet Union, Part 2, vol. II. Vysshaya Shkola Publishers, Moscow* (in Russian).
- Hirzel, A.H., Le Lay, G., 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45, 1372–1381.
- Hosmer, D.W., Lemeshow, S., 2000. *Applied Logistic Regression*. John Wiley and Sons, New York.
- Hunter, L.T.B., Pretorius, K., Carlisle, L.C., Ricketton, M., Walker, C., Slotow, R., Skinner, J.D., 2007. Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: short-term biological and technical success but equivocal long-term conservation. *Oryx* 41, 196–204.
- Jackson, P., Nowell, K., 2008. *Panthera pardus ssp. orientalis*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.1. <www.iucnredlist.org> (downloaded 08.06.10).
- Jedrzejewska, B., Jedrzejewski, W., 1998. Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study. Springer, Berlin, Germany.
- Johnson, C.J., Seip, D.R., 2008. Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. *Population Ecology* 50, 145–157.
- Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: theoretical motivations and evaluations methods. *Journal of Wildlife Management* 70, 347–357.
- Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C., McBride, R., Jansen, D., Lotz, M., Shindle, D., Howard, J., Wildt, D.E., Penfold, L.M., Hostetler, J.A., Oli, M.K., O'Brien, S.J., 2010. Genetic restoration of the Florida Panther. *Science* 329, 1641–1645.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America* 101, 4854–4858.
- Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, N.G., 2002. Effects of roads and human disturbance on amur tigers. *Conservation Biology* 16, 97–108.
- Kostyria, A.V., Skorodelov, A.S., Miquelle, D.G., Aramilev, V.V., McCullough, D., 2003. Results of camera trap survey in Far Eastern leopard population in southwest Primorski Krai, winter 2002–2003. Report of the Wildlife Conservation Society and Institute of Sustainable Use of Nature Resources, Vladivostok, 23 pp.
- Li, Z., Zimmermann, F., Hebblewhite, M., Purekhovskiy, A., Mörschel, F., Zhu, C., Miquelle, D.G., 2010. Study on the Potential Tiger Habitat in the Changbaishan Area, China. China Forestry Publishing House, 88pp.
- Linnell, J.D.C., Swenson, J.E., Andersen, R., 2000. Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiversity and Conservation* 9, 857–868.
- Linnell, J.D.C., Breitenmoser, U., Breitenmoser-Würsten, C., Odden, J., von Arx, M., 2009. Recovery of Eurasian Lynx in Europe: What Part has Reintroduction Played? Reintroduction of Top-Order Predators. Wiley-Blackwell.
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*, second ed. Kluwer, Boston, USA.
- Marucco, F., McIntire, E.J.B., 2010. Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk: wolves in the Italian Alps. *Journal of Applied Ecology* 47, 789–798.
- Miquelle, D.G., Smirnov, E.N., Merrill, T.W., Myslenkov, A.E., Quigley, H.G., Hornocker, M.G., Schleyer, B., 1999. Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. In: Seidensticker, J., Christie, S., Jackson, P. (Eds.), *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge, UK, pp. 71–99.
- Miquelle, D.G., Pikunov, D.G., Dunishenko, Y.M., Aramilev, V.V., Nikolaev, I.G., Abramov, V.K., Smirnov, E.N., Salkina, G.P., Seryodkin, I.V., Gaponov, V.V., Fomenko, P.V., Litvinov, M.N., Kostyria, A.V., Yudin, V.G., Korkishko, V.G., Murzin, A.A., 2006. A Survey of Amur (Siberian) Tigers in the Russian Far East, 2004–2005. *Wildlife Conservation Society, World Wildlife Fund*, 77pp.
- Miquelle, D.G., Pikunov, D.G., Dunishenko, Y.M., Aramilev, V.V., Nikolaev, I.G., Abramov, V.K., Smirnov, E.N., Salkina, G.P., Seryodkin, I.V., Gaponov, V.V., Fomenko, P.V., Litvinov, M.N., Kostyria, A.V., Yudin, V.G., Korkishko, V.G., Murzin, A.A., 2007. 2005 Amur tiger census. *Cat News* 46, 12–14.
- Miquelle, D.G., Goodrich, J.M., Smirnov, E.N., Stephens, P.A., Zaumyslova, O., Yu-Chapron, G., Kerley, L., Murzin, A.A., Hornocker, M.G., Quigley, H.B., 2010a. The Amur Tiger: a case study of living on the edge. In: MacDonald, D.W., Loveridge, A. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, Oxford, UK, pp. 325–339.
- Miquelle, D.G., Darman, Y., Aramilev, V.V., Hotte, M., Bereznyuk, S., Myslenkov, A.L., Solkin, V.A., Pikunov, D.G., Kostyria, A.V., Christie, S., Lewis, M., Hebblewhite, M., 2010b. A program for reintroduction of the Far Eastern leopard into southern Sikhote-Alin, Primorski Krai, Russian Far East. Vladivostok, Russian Federation.
- Miththapala, S., Seidensticker, J., O'Brien, S.J., 1996. Phylogeographic subspecies recognition in leopards (*Panthera pardus*): molecular genetic variation. *Conservation Biology* 10, 1115–1132.
- Mladenoff, D.J., Sickley, T.A., Wydeven, A.P., 1999. Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. *Ecological Applications* 9, 37–44.
- Musiani, M., Paquet, P.C., 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. *Bioscience* 54, 50–61.
- Nielsen, S.E., Stenhouse, G.B., Boyce, M.S., 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130, 217–229.
- Nowell, K., Jackson, P., 1996. *Wild Cats: Status Survey and Conservation Management Plan*. IUCN/SSC Cat Specialist Group, Gland, Switzerland.
- Pikunov, D.G., Korkishko, V.G., 1985. Present distribution and numbers of leopards (*Panthera pardus*) in the Far East USSR. *Zoology Journal* 64, 897–905 (in Russian).
- Pikunov, D.G., Korkishko, V.G., 1990. The Far Eastern leopard. *Dalnauka, Vladivostok*, 192pp (in Russian).
- Pikunov, D.G., Aramilev, V.V., Fomenko, P.V., Miquelle, D.G., Abramov, V.K., Korkishko, V.G., Nikolaev, I.G., 1997. Leopard Numbers and its Habitat Structure in the Russian Far East. 1997. Final Report to Hornocker Wildlife Institute.
- Pikunov, D.G., Abramov, V.K., Korkishko, V.G., Nikolaev, I.G., Belov, A.I., 2000. "Sweep" survey of far eastern leopards and Amur tigers. In: A Survey of Far Eastern Leopards and Amur Tigers in Southwest Primorski Krai, in 2000. Final report to WCS and WWF.
- Pikunov, D.G., Miquelle, D.G., Abramov, V.K., Nikolaev, I.G., Seryodkin, I.V., Murzin, A.A., Korkishko, V.G., 2003. Results of Population Surveys of Leopards (*Panthera pardus orientalis*) and Tigers (*Panthera tigris altaica*) in Southwest Primorski Krai, Russian Far East. Final Report to WCS and WWF.
- Pikunov, D.G., Seryodkin, I.V., Aramilev, V.V., Nikolaev, I.G., Mursin, A.A., 2009. Numbers of Far Eastern Leopards (*Panthera pardus orientalis*) and Amur Tigers (*Panthera tigris altaica*) in Southwest Primorski Krai, Russian Far East, 2007. *Dalnauka, Vladivostok*, 95pp.
- Pletscher, D.H., Ream, R.R., Boyd, D.K., Fairchild, M.W., Kunkel, K.E., 1997. Population dynamics of a recolonizing wolf population. *Journal of Wildlife Management* 61, 459–465.
- Pocock, R.I., 1930. The panthers and ounces of Asia. *Journal of the Bombay Natural History Society* 34, 63–82, 307–336.
- Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J., 2005. *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, DC, USA.
- Reuter, H.I., Nelson, A., Jarvis, A., 2007. An evaluation of void filling interpolation methods for SRTM data. *International Journal of Geographic Information Science* 21, 983–1008.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications* 18, 1028–1037.
- Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T., Trepl, L., 2002a. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian Lynx. *Ecological Applications* 12, 1469–1483.
- Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C., Trepl, L., 2002b. Assessing the suitability of central European landscapes for the reintroduction of Eurasian Lynx. *Journal of Applied Ecology* 39, 189–203.
- Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G., Myslenkov, A.I., Hayward, G.D., 2006. Estimating population density from indirect sign: track counts and the Formozov–Malyshchev–Pereleshin Formula. *Animal Conservation* 9, 339–348.
- Uphyrkina, O., Miquelle, D., Quigley, H., Driscoll, C., O'Brien, S.J., 2002. Conservation genetics of the far eastern leopard (*Panthera pardus orientalis*). *Journal of Heredity* 93, 303–311.
- Weber, W., Rabinowitz, A., 1996. A global perspective on large carnivore conservation. *Conservation Biology* 10, 1046–1054.
- Yang, S., Jiang, J., Wu, Z., Li, T., Yang, X., Han, X., Miquelle, D.G., Pikunov, D.G., Dunishenko, Y.M., Nikolaev, I.G., 1998. Report on the Sino-Russian Joint Survey of Far Eastern Leopards and Siberian Tigers and Their Habitat in the Sino-Russian Boundary Area, Eastern Jilin Province, China, Winter 1998. A Final Report to the UNDP and the Wildlife Conservation Society.
- Zimmermann, F., Breitenmoser-Würsten, C., Breitenmoser, U., 2007. Importance of dispersal for the expansion of a Eurasian lynx *Lynx lynx* population in a fragmented landscape. *Oryx* 45, 358–368.