Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East

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ABSTRACT

Wild tiger numbers continue to decline despite decades of conservation action. Identification, conservation and restoration of tiger habitat will be a key component of recovering tiger numbers across Asia. To identify suitable habitat for tigers in the Russian Far East, we adopted a niche-based tiger habitat modeling approach, including biotic interactions with ungulate prey species, human activities and environmental variables to identify mechanisms driving selection and distribution of tiger habitat. We conducted >28,000 km of winter snow tracking surveys in 2004/2005 over 266,000 km^2 of potential tiger habitat in 970 sampling units (~171 km^2) to record the presence of tracks of tigers and their ungulate prey. We adopted a used-unused design to estimate Resource Selection Probability Functions (RSPF) for tigers, red deer, roe deer, sika deer, wild boar, musk deer and moose. Tiger habitat was best predicted by a niche-based RSPF model based on biotic interactions with red deer, sika deer and wild boar, as well as avoidance of areas of high human activity and road density. We identified 155,000 km^2 of occupied tiger habitat in the RFE in 17 main habitat patches. Degradation of tiger habitat was most extreme in the southern areas of the Russian Far East, where at least 42% of potential historic tiger habitat has been destroyed. To improve and restore tiger habitat, aggressive conservation efforts to reduce human impacts and increase ungulate densities, tiger reproduction and adult survival will be needed across all tiger habitat identified by our tiger habitat model.

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1. Introduction

The precipitous decline in wild tiger (*Panthera tigris*) numbers over the past century has received wide attention (Dinerstein et al., 2007; Walston et al., 2010) and has generated a recent high-profile global conservation response (Global Tiger Initiative, 2010). In 2010, the political leaders of the 13 tiger range nations met in St. Petersburg and boldly committed to "double the number of wild tigers across their range by 2022". Habitat loss is generally recognized as one of the three key threats driving the tiger decline (along with poaching and prey depletion) with an estimated 93% of tiger habitat lost in the last century (Dinerstein et al., 2007). One of the primary means to achieve the Global Tiger Initiatives bold goal is the identification, conservation and restoration of tiger habitat (Dinerstein et al., 2007; Smith et al., 1998; Wikramanayake et al., 2011).

Many large-scale habitat-modeling exercises are often forced to rely on incomplete information about habitat parameters. With few exceptions, it has only been recently that extensive

countrywide surveys have been conducted to fully map tiger distribution (Jhala et al., 2011; Miquelle et al., 2006; Wibisono et al., 2011). Yet, even with these extensive surveys, the next step of identifying high quality habitats for tigers has not always been conducted, making it difficult to prioritize habitat conservation. For instance, the earliest tiger habitat modeling identified 1.5 million square kilometers of suitable habitat across tiger range using coarse landcover-based information (Wikramanayake et al., 1998). Subsequent conservation planning identified 20 Global priority tiger conservation landscapes (TCL's) necessary to secure the fate of tigers (Dinerstein et al., 2007). Yet, Walston et al. (2010) suggested prioritizing within these TCL's to protect putative source sites based solely on their protected status and potential to hold breeding females. This 'source site' strategy was quickly criticized with, again, large-scale analyses that suggest that achieving the GTI objective of doubling wild tiger populations requires conserving much more than just these core areas (Wikramanayake et al., 2011). Despite the advances in the political will to conserve tigers with the Global Tiger Initiative, however, we still do not have rigorous empirical identification of the basic components of tiger habitat in many TCL's, an understanding of habitat quality, nor empirical evidence of what differentiates sites where reproduction is actually occurring from other tiger habitat. Without a stronger foundation for tiger habitat ecology and conservation, the debate about whether core sites or an entire TCL is required will remain unresolved, potentially distracting conservation efforts.

It is widely acknowledged that, aside from anthropogenic factors, prey abundance and distribution (Karanth et al., 2004) are the key factors driving demography of large carnivores (Carbone and Gittleman, 2002; Karanth et al., 2004; Miquelle et al., 1999; Mitchell and Hebblewhite 2012). Large carnivores such as tigers are habitat generalists, and therefore habitat may be more aptly defined from a niche-based perspective (Gaillard et al., 2010; Mitchell and Hebblewhite, 2012), i.e., as the abiotic and biotic resources and conditions that are required for occupancy, reproduction, and, ultimately, demographic persistence (Gaillard et al., 2010; Mitchell and Hebblewhite, 2012). Most previous tiger habitat modeling approaches used instead a functional habitat mapping approach based, necessarily, on broad-scale landcover or vegetation (Linkie et al., 2006; Wikramanayake et al., 2004). Such approaches are limited in their ability to provide a mechanistic understanding of habitat or identify parameters associated with high reproductive rates or adult female survival, e.g., high quality habitat. We hypothesize that a niche-based approach provides a conceptually stronger method to understand the drivers of habitat selection, and are therefore potentially more valuable for conservation planning. Practically, however, detailed information on prey abundance, especially over large landscapes, is rare. Yet there is a growing recognition in large carnivore and tiger habitat modeling of the importance of understanding prey distribution at large landscape scales for conservation (Barber-Meyer et al., 2013; Hebblewhite et al., 2012; Zhang et al., 2013).

Anthropogenic factors are as important as prey abundance and distribution in determining habitat quality, since virtually the entirety of large carnivore habitat today is under the influence of humans (Crooks et al., 2011; Ripple et al., 2014). This is especially true for wild tigers who face the booming economies and burgeoning human populations of Asia, given that human activity is known to decrease adult and cub survival (Kerley et al., 2002). Therefore, the best approach to defining quality tiger habitat for conservation planning would combine large-scale measures of abiotic conditions, prey resources, and human activity. Such an approach would provide a means of not only identifying habitat, but may allow definition of breeding habitat as well as a means for assessing risk for habitat across the landscape, further assisting the conservation process.

This is an ambitious goal for tigers because of the challenges of collecting range-wide information on prey. Fortunately, there is an opportunity to adopt this approach in the Russian Far East, the only country where tigers have recovered from the verge of extinction, providing a valuable opportunity to assess habitat requirements in a recovered population. Rough estimates suggest that a population in 1940 of only 30–40 Amur tigers (*P. tigris altaica*) recovered to an estimated 430–500 in 2005 (Miquelle et al., 2006). This recovery process has been documented via large-scale surveys that have attempted to map distribution and estimate tiger numbers based on the distribution and abundance of tracks in the snow (Miquelle et al., 2006). While there are multiple problems with converting information on track abundance into population estimates (Hayward et al., 2002; Miquelle et al., 2006; Stephens et al., 2006), the information obtained during recent surveys, where track locations of both tigers and prey have been carefully mapped, provide an extensive data set for determining habitat quality for tigers in the Russian Far East.

We used existing data on location of tracks, collected during a 2005 survey over the entire 266,000 km² range of tigers in the Russian Far East to identify biotic and abiotic drivers of tiger habitat. Conducting such an analysis for the entire Amur tiger population in Russia is particularly challenging because preferred prey, forest types, and human densities vary greatly across the range of tigers. For instance, while wild boar (*Sus scrofa*) appear to be a preferred prey throughout tiger range (Hayward et al., 2012), sika deer (*Cervus nippon*) are the primary prey only in the southern part of Amur tiger range, while red deer (*Cervus elaphus*) are the most common prey item for Amur tigers further north (Miquelle et al., 2010). Incorporation of such variability with regionalized modeling may better predict habitat. Thus, our goals were to: (1) estimate non-prey based habitat parameters that best define potential habitat for Amur tigers using resource selection probability function (RSPF) models (Boyce and McDonald, 1999); (2) develop a suite of RSPF models for ungulate species that could be incorporated into the process of modeling tiger distribution; (3) test the biotic interaction hypothesis that including prey distribution and abundance in RSPF models for tigers improves predictive power of such models; (4) test for regional differences in prey-based resource selection by Amur tigers; (5) use data on the occurrence of females with cubs (family groups can be easily distinguished from track characteristics) to test the hypothesis that tiger habitat quality is correlated with habitat for successful reproduction of Amur tigers in Russia; and finally (6) to operationally define tiger habitat and use the outcomes of this process to identify priority areas of high risk for habitat conservation.

2. Methods

2.1. Study area

Our study area was defined by the range of Amur tigers in the Russian Far East, an area of 266,000 km² (Miquelle et al., 1999) in the provinces of Primorye and Khabarovsk, with 95% in the Sikhote-Alin mountains and 5% in the Changbaishan mountains along the Russian–Chinese border (Fig. 1). There are probably less than 400 adult and subadult tigers in Russia (Miquelle et al., 2006), and less than 20 in China (Hebblewhite et al., 2012). This Tiger Conservation Landscape (TCL) (Dinerstein et al., 2007) represents a merger zone of two bioregions: the East Asian coniferous-deciduous complex and the northern boreal (coniferous) forest, resulting in a mosaic of forest, bioclimatic and human land-use types. Mountains in the Sikhote-Alin range from 500 to 800 m (max 1200 m). Over 72% of Primorye and southern Khabarovsk is forest covered. The original dominant forest was a mixture of Korean pine (*Pinus*

koraiensis) and broad-leaved trees including birch (*Betula spp*), basswood (*Tilia spp.*), and other deciduous species while in the north and at higher elevations, spruce (*Picea spp.*) fir (*Abies spp.*) and larch (*Larix spp.*) are still the dominant species. Most forests have been selectively logged at various times in the past, and human activities, in association with fire, have resulted in conversion of many low elevation forests to secondary oak (*Quercus mongolica*) and birch (*B. costata, B. lanata*, and others) forests. Riverine forests are most often comprised of a variety of deciduous species (*Salix schwerinii, Ulmus lacimata, Chosenia arbutifolia, Populus maximoviczii, Fraxinus mandshurica*, and others), or a mixture of these deciduous species with Korean pine. The climate in this region is monsoonal, with 80% precipitation (650–800 mm in Sikhote-Alin) occurring April–November. January monthly average temperature is −22.6 °C on the inland side of the central Sikhote-Alin Mountains, but the Sea of Japan moderates coastal temperatures (and snow depths) to an average January temperature of −12.4 °C. The frost-free period varies between 105 and 120 days/year. Snow depth varies from 22.6 + 2.9 cm in February in the inland central Sikhote-Alin to only 13.7 + 3.5 cm on the central coast.

The ungulate community is represented by 6 species available to tigers, with red deer, Ussuri wild boar and Siberian roe deer (*Capreolus capreolus*) the most common. Musk deer (*Mochus moschiferus*) were also widespread but restricted to higher elevation spruce-fire forests. Red deer have become rare in the southern part of the study area, where sika deer have replaced them in abundance and in the diet of tigers. Manchurian moose (*Alces alces cameloides*) are near the southern limits of their distribution in central Sikhote-Alin Mountains. Data from seven study areas in Russia confirm that red deer and wild boar are the two primary prey species of tigers (63–92% of kills, collectively) and that combined with sika and roe deer, these four ungulates comprise 81–94% of their diet (Miller et al., 2013; Miquelle et al., 1996). Both species of bears, brown bears (*Ursus arctos*) and Asiatic black bear (*U. thibetanus*), are preyed upon by tigers (Miquelle et al., 2010) and wolf (*Canis lupus*) abundance is inversely related to tiger abundance (Miquelle et al., 2005b).

Approximately 4 million people live in this landscape (Miquelle et al., 2005a) but the majority are concentrated around the capital cities of Vladivostok and Khabarovsk, and along the fertile lowlands associated with the Ussuri and Amur Rivers, (Fig. 1). Nonetheless, small communities are dispersed across the entirety of tiger habitat. People in these small forest communities rely on the fish, wildlife, timber, and other natural resources to provide a means of subsistence and income. Logging roads provide an extensive network, providing relatively easy access to a large percentage of the landscape.

2.2. Tiger and ungulate snow track surveys

We developed tiger and ungulate models using snow track data collected during a range-wide survey conducted during an intensive 3-week period in February and March 2005. We refer to this dataset as the simultaneous surveys. Potentially suitable habitat of tigers was divided into 1096 sampling units (averaging 171 km²) whose boundaries followed divides, river basins, and boundaries of hunting leases (Fig. 1). Data were subsequently collected in 1026 of these sampling units. Within each sampled unit, 1–4 routes (averaging 17 km each) were surveyed by foot, skis, snowshoes, snowmobile, or vehicle, for a total of 1537 routes. Routes were located on roads and trails to maximize the probability of encountering tiger sign, based on local knowledge. Snow depth (and hence elevation) was used to stratify effort, with areas >800 m generally not surveyed. The majority of routes (95%) were covered during a three-week period in February, with 94% of all
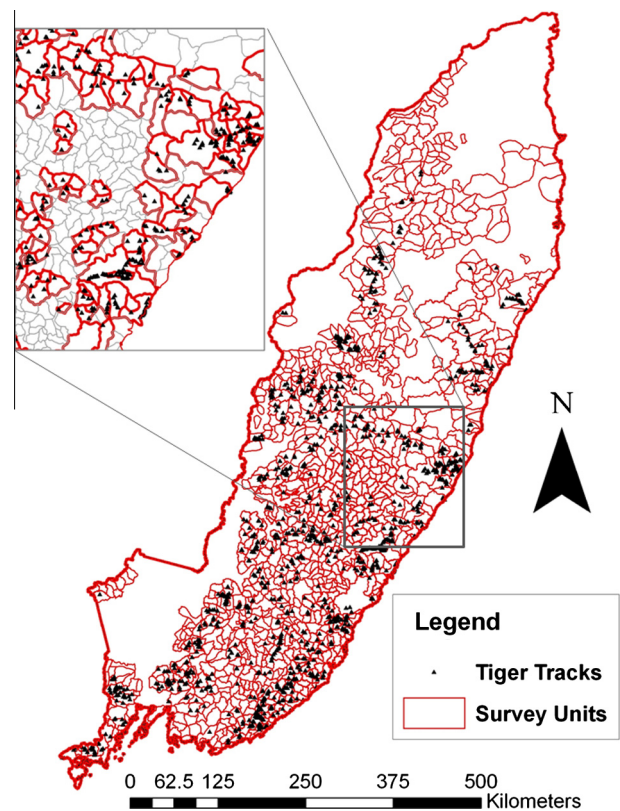

Fig. 1. Sampling design used for surveying presence or absence of tigers and their ungulate prey in the Russian Far East, winter 2004/2005. Inset shows a close up of units with (red survey units) and without (grey survey units) tiger tracks.

tracks reported in a 60-day period. Field personnel (997 people) included scientific staff of institutes and protected areas, wildlife inspectors, and experienced hunters who received training in collecting and reporting data. The number and location of tiger tracks were recorded on a 1:100,000 scale map along with other information including sex and group size (in the case of females with cubs) (Hayward et al., 2002). For ungulate species, location, species and group size was also recorded. A second independent data set of all tiger tracks was collected during the entire winter period (November 2004 through March 2005) within each sampling unit to identify cells where tigers may have been missed during the primary survey period. We call this second validation dataset the extensive tiger survey data.

2.3. Sampling design and scale

Our Resource Selection Probability Function (RSPF) sampling followed a used-unused design at the survey unit (∼171 km²) scale. We used the sampling unit as an appropriate scale of analysis because of its correspondence with the general scale of tiger area requirements (sampling units averaged about half the size of the average annual home range size of adult females – 390 km²; Goodrich et al. (2010). Conceptually, our design corresponds to Johnson's (1980) second-order habitat selection (selection for home ranges in a landscape) across the entire range of tigers in the Russian Far East.

2.4. Detection probability

The used-unused RSPF design assumed detection probabilities of 1.0 within the sample unit. While recent advances in occupancy surveys enable estimation of the detection probability with

multiple sampling instances (MacKenzie et al., 2005), we only had data available from the 2005 survey. The presence of marked tigers in part of our study area allowed us to test this detection assumption. Known radio-collared tigers ($n = 43$ opportunities to detect known tigers within a study area) were detected within a sampling unit 79% of the time using a single survey design. Because occupied units were typically occupied by more than one tiger because of overlapping home ranges (Goodrich et al., 2010), we considered detection probability for survey units to be ~100%.

A second factor affecting detection probability was sampling effort. Survey units were surveyed with variable effort (mean of 26 km/survey unit, 0.1 km to 261.6 km/unit) and thus variable sampling intensity (a mean of 0.195 km/km^2 survey unit area, range 0.0075–2.93 km surveyed/km^2). We used logistic regression to identify the threshold sampling intensity above which there was no statistically significant relationship between sampling intensity (km surveyed/km^2) and detection (presence/absence) of tigers. We repeated this analysis for each ungulate species for development of ungulate habitat models (see below). Using this approach, we found that excluding sampling units with less than 0.023 km/km^2 (i.e., ~4 km in a 171 km sampling unit) resulted in no relationship between sampling intensity and tiger (or ungulate) presence-absence in the remaining sampling units. This threshold (0.023 km/km^2) corresponded to the lower 5th percentile of the sampling intensity, and resulted in excluding 54 sampling units to ensure a 100% detection probability. This left 1026−54 = 972 sample units for analysis.

2.5. Environmental resource covariates

We used a combination of abiotic and biotic spatial covariates to understand Amur tiger and ungulate resource selection (Appendix A). We calculated the average values for each continuous covariate within each survey unit using ARGIS 9.3 (Redlands CA) Zonal Statistics function. For categorical covariates, we calculated the % of the survey unit in each of the landcover categories. To create spatial predictions of the RSPF, we used a moving window analysis to spatially scale covariates appropriately using a circular moving window with a 7.5 km radius, equivalent to 177 km^2 (approximately the mean size of our sampling units). For categorical covariates, the percent was calculated; for example, the percent of a survey unit that was covered by the Korean pine vegetation type.

Abiotic covariates included elevation (m), slope (degrees), and hillshade calculated from the Shuttle Radar Topography Mission (SRTM, http://srtm.usgs.gov) at a 90 m resolution (at this latitude) using ARCGIS 9.2 Spatial Analyst. Hillshade maximized values on southwest facing slopes as an indirect measure of low snow cover during winter. We also used easting and northing to attempt to capture large-scale bioclimatic gradients in species occurrence (e.g., higher moose prevalence at northern latitudes).

Biotic covariates used in the analysis included a spatial vegetation community landcover model (Ermoshin and Aramilev, 2004). Vegetation communities were collapsed into 12 categories; agricultural fields, grassland/meadows, regenerated burns or logged forests, shrub communities, oak, birch, deciduous, larch, Korean pine, spruce-fir, wetland and alpine communities (Appendix A). Spruce-fir was used as the default reference category. We also used remotely sensed measures of primary productivity and snow cover obtained from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite at intermediate (500, 1000 m^2) resolution (Running et al., 2004; Turner et al., 2006). We used net primary productivity (NPP, KG/ha, the MOD17A2 product) as a measure of forage availability for ungulate prey (Heinsch et al., 2003; Running et al., 2004). We used the fractional snow cover calculated as the percent (0–100%) of the winter (November 1 to April 30) during 2004/2005 that each 500 m^2 MODIS satellite pixel was covered with snow based on the MOD10A snow cover product (Klein et al., 1998). During the simultaneous 2004/2005-snow survey, snow cover was 100%, ensuring there was no bias associated with this covariate as our measure of species detection was dependent on snow cover.

For spatial measures of human activity, we calculated the mean distance to human settlements including all cities, towns and villages within each cell. We also calculated the distance to and density of roads (forest, gravel and paved roads) at a range of spatial scales from 500 m to 20 km (500 m, 1 km, 2.5 km, 5 km, 10 km, 20 km). We used different spatial scales for road density because previous studies have shown species-specific responses of carnivores and ungulates to road density (DeCesare et al., 2012; Frair et al., 2008), and we wanted to accommodate differences in road effects as a function of home range size of both ungulates and tigers. Finally, we also calculated distance to protected areas as a measure of the effect of protection from hunting on occurrence. These habitat and human layers were compiled by TIGIS (Pacific Institute of Geography GIS center, Vladivostok, Russia).

2.6. Resource selection probability function modeling

We compared resource selection by tigers and their ungulate prey between used and unused sampling units following a used-unused design (Fig. 1) where individuals were not known and inferences were at the population level (Manly et al., 2002). Used and unused sampling units were then contrasted with logistic regression following:

$$\hat{w} = \exp(\beta_0 + \boldsymbol{\beta X})/(1 + \exp(\beta_0 + \mathbf{X}\boldsymbol{\beta})) \qquad (1)$$

where $\hat{w}(x)$ is the probability of selection as a function of covariates x_n, β_0 is the intercept, and $\mathbf{X}\boldsymbol{\beta}$ is the vector of the coefficients $\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_2$ estimated from fixed-effects logistic regression (Manly et al., 2002). Because of the used-unused design (Fig. 1), $\hat{w}(x)$ is a true probability from 0 to 1 and is referred to as a Resource Selection Probability Function (RSPF) (Manly et al., 2002).

For tiger habitat modeling, we adopted a hierarchical spatial approach. Because of the potential importance of spatial variation, we divided the area into 3 biogeographic zones (north, central, south) to help discriminate different ecological patterns in space. Because of the strong latitudinal gradient in occurrence for some species (e.g., moose, sika deer) we also included northing as a spatial covariate. First, we developed separate prey-based RSPF models within each of the three latitudinal zones to understand the best prey-based tiger habitat model within each zone, and test our objective about spatial variation in tiger selection for prey. We then estimated three regional (entire Russian Far East) RSPF's: an environmental-only model, a prey-based model, and a hybrid model (see below) to test the hypothesis that considering prey enhanced our ability to predict tiger habitat.

2.7. Modeling strategy

We first developed the underlying ungulate RSPF models, followed by the zonal tiger-prey based RSPF models, the regional tiger prey-based RSPF, and then the regional environmental-only tiger RSPF model. Next, we evaluated a hybrid environment + prey-based model. We used AIC (Burnham and Anderson, 1998) to compare between the best regional environmental and prey-based tiger RSPF models to test the hypothesis that biotic interactions improve the definition of tiger habitat. We also used Akaike weights (Burnham and Anderson, 1998) for each of the zone-specific prey-based RSPF models to understand regional differences in prey-based tiger habitat. Finally, we used occurrence of the tracks of females with cubs in model units to develop a logistic

regression model for reproductively active tigers compared to all other units. This reproduction model gave us an opportunity to test the hypothesis that habitat quality (defined using reproduction as a fitness component) was correlated to the probability of tiger selection by regressing predictions from the best tiger RSPF model against the best reproduction model.

We adopted a hybrid model building and model selection approach (Hosmer and Lemeshow, 2000). First, we screened potential covariates for collinearity using a liberal cut-off of $r = 0.6$ combined with variance inflation scores and testing for confounding (Menard, 2002). For example, some of the ungulate prey species models were correlated with each other (Appendix C), but not confounded (Appendix C), so we retained most combinations of ungulate species together. We then assessed univariate importance of each of the covariates first, looking for linear, and non-linear effects using quadratics ($X + X^2$) and Generalized Additive Models (Hastie and Tibshirani, 1990). To identify the road density scale to include in model building, we tested which scale had the best fit (measured using AIC) and greatest explanatory power for each ungulate prey species and for tigers. Once the best functional form of each univariate covariate was determined (Appendices B and C), as well as interaction terms, we included it in a best all-inclusive global model, and then conducted model selection using AIC on all potential subsets (Hosmer and Lemeshow, 2000). We systematically removed and added variables to ensure that the remaining covariates were not unduly confounded, and tested for collinearity amongst retained covariates again using the variance inflation factor test on the final model (Menard, 2002).

We tested goodness of fit of all tiger and prey RSPF models using the Hosmer and Lemeshow (2002) likelihood ratio chi-square test, and by assessing residuals. We evaluated the predictive capacity of the top model using pseudo-r^2, logistic regression diagnostics such as ROC (receiver operating curves), and classification success both at the default cutpoint of $p = 0.5$, and the optimal cutpoint defined by the intersection of sensitivity and specificity curves (Liu et al., 2005). Most importantly, for habitat modeling, we evaluated the predictive capacity of all tiger and prey RSPF models using k-folds cross validation between the top model structure and 5-randomly drawn subsets. K-folds cross-validation follows the logic that if the model was predictive of good tiger (or ungulate) habitat, then there should be a correlation between the frequency of tiger observations in habitat deciles (bins) and the ranked quality of those bins from 1 to 10 (Boyce et al., 2002).

2.8. Mapping tiger habitat

We used the best hybrid tiger model to identify tiger habitat vs. non-habitat using the cutpoint probability from the logistic regression model. However, we chose to minimize the probability of misclassifying occupied tiger habitat (1's, sensitivity) by setting the threshold probability at that level that successfully classified 90% of known tiger locations. We also validated this threshold probability with an out-of-sample dataset of tiger track locations collected during the entire winter November 2004 to April 2005 (see methods).

2.9. Evaluating potential tiger habitat

To assess the potential loss or degradation of habitat, we estimated the potential habitat of tigers using the top environmental-only model's spatial predictions of tiger habitat assuming no human development, i.e. potential habitat setting all human-related covariates to zero (Polfus et al., 2011). This offers a measure of habitat degradation by comparing observed (realized) habitat and potential. We calculated % habitat degradation following:

(Potential Habitat–Realized Habitat)/(Potential Habitat). We report the average % reduction in habitat quality (as measured by reduction of the relative probability of selection) across the RFE by summing the predicted relative probabilities across both the potential and realized habitat model, and summarize habitat degradation by zone.

3. Results

3.1. Tiger and ungulate snow track surveys

During the simultaneous surveys, we surveyed an average of 26 km per average 171-km^2 sample unit, for an average sampling intensity of 0.204 km/km^2. We recorded $n = 1301$ tracks of Amur Tigers over 26,031 km during the simultaneous snow track surveys in February 2005 (Table 1). Tiger tracks occurred in 41% of the sampling units during the simultaneous intensive surveys, and in 59% of units during the extensive winter surveys (Table 1). Females with cubs were reported in only 28% of those units with tigers (12% total). The most abundant ungulate species, by track occurrence, were red deer, followed (in order) by roe deer, wild boar, musk deer, sika deer and moose (Table 1).

3.2. Resource selection probability function modeling

Elevation and slope were too highly correlated ($r = 0.67$) to include together in the same RSPF model. All other pair-wise correlations were <0.3–0.6, so all other environmental variables were included. The strongest response of all ungulates to road density occurred most strongly at the 10 km^2 scale; thus, all road density measures were calculated in a 10 km^2 radius.

3.2.1. Ungulate models
3.2.1.1. *Red Deer.* The red deer RSPF model was significant ($P < 0.0005$), a adequate Hosmer and Lemeshow (H–L) test statistic ($P = 0.0063$), had moderate ROC, classification success and pseudo-r^2 scores, and validated against 5 withheld subsets of red deer tracks very well (Spearman rank correlation $r_s = 0.928$, Table 2). Red deer selected units with a higher proportion of deciduous forests, avoided units with birch forests, oak forests, and shrub areas, and strongly avoided agricultural areas (relative to the intercept, Korean pine and spruce/fir forests) (Table 3). Red deer selected units of intermediate elevations of an average of 451 m elevation (solved by taking the derivative of the elevation quadratic, i.e., $w(x) = 2.657 + 0.006 * \text{elevation} - 0.00000665 * \text{elevation}^2$, Table 2). An increasing percentage of winter snow coverage affected the probability of red deer occurrence in quadratic fashion, with red deer selecting areas of intermediate snow coverage of about 20 cm (Appendix B). Finally, in addition to avoiding agricultural areas, red deer occurrence declined as distance to protected areas increased (Table 3), and varied non-linearly with increasing road

Table 1
Result of snow track surveys during winter 2004/2005 for the simultaneous tiger and ungulate track surveys, and over the entire winter (extensive survey data), in the Russian Far East.

Species/class	# Tracks	# Units	Prevalence
Simultaneous – tigers	1301	430	0.411
Simultaneous – females with cubs	398	124	0.119
Red deer	3244	702	0.674
Roe deer	2608	659	0.633
Wild boar	1687	482	0.463
Sika deer	1392	155	0.149
Moose	330	94	0.090
Musk deer	1337	334	0.321
Extensive surveys – tigers	3908	615	0.591

Table 2
Summary statistics, model diagnostics, and measures of goodness-of-fit for the top RSPF models for ungulate species in the Russian Far East during winter 2004/2005.

Model	Red deer	Roe deer	Sika deer	Wild boar	Musk deer	Moose
N All units	1041	1041	1041	1041	1041	1041
N = 1	702	659	155	482	334	94
LR Chi-square	187.17	192.41	465.60	125.71	311.89	355.96
LR P-value	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005	<0.0005
Pseudo R^2	0.143	0.1406	0.532	0.134	0.2387	0.568
LROC	0.703	0.744	0.947	0.725	0.82	0.966
HL Chi-square test (8 df)	14.82	8.44	237.31	16.4	11.92	2.79
HL p-value	0.063	0.392	0.0001	0.037	0.129	0.949
% Classification (P = 0.5)	74.93	66.67	91.83	64.65	75.41	94.1
Optimal cutpoint	0.67	0.633	0.21	0.46	0.32	0.09
% Classification (P = optimal cutpoint)	68.2	71.18	89.91	68.44	75.7	89.8
Sensitivity (P = optimal cutpoint)	71.08	63.13	88.03	69.29	76.65	87.29%
Spearman rank correlation	0.928	0.931	0.932	0.935	0.948	0.781

Table 3
Logistic regression coefficients for the top random-effects RSPF models for ungulate species in the Russian Far East during winter 2004/2005.

| Coefficients	Red deer	Roe deer	Sika deer	Wild boar	Musk deer	Moose
Parameter	β	β	β	β	β	β
Oak	−1.28***	1.26***	2.77***	0.47	−2.16***	−4.64***
Birch	−0.58	–	2.16**	–	−1.28**	–
Deciduous riverine	4.35**	3.68*	–	–	–	–
Korean Pine	–	0.56*	1.53**	1.27***	.	−5.40***
Larch	2.93**	3.26***	–	–	–	–
Regen	–	–	–	–	–	–
Shrub	−2.28**	–	–	–	−3.51**	−3.57**
Meadow	–	−0.63	–	–	–	−3.38*
Agriculture	−4.60***	−0.86	–	−1.49*	−7.42**	−41.01
Elevation (m)	0.006***	−0.0024***	−0.0012	0.007***	0.007***	−0.0028**
Elevation^2	−6.65E−06***	–	–	−9.78E−06***	−4.63E−06***	–
Percent Snow	−0.096*	−0.026***	−0.0225*	−0.015*	−0.115***	−0.0492**
Snow^2	0.0012**	–	–	–	0.001***	–
Dist. Zapovednik (km)	−0.005**	−0.007***	−0.031***	−0.006***	–	0.02***
Distance to town (km)	–	−0.0083	0.040**	–	0.023***	0.059***
NPP	–	0.00012	–	0.0014*	–	−0.00065**
NPP^2	–	–	–	−9.05E−08*	–	–
Road Density – 10 km	−6.11**	−0.58	−5.28***	−3.18**	−2.89*	−4.41**
Road Density^2	11.46**	–	–	4.50*	8.41**	–
Northing	–	–	−1.47E−05***	–	–	6.84E−07*
Intercept	2.66**	6.06***	71.49***	−4.90*	0.78	2.15

* Statistically significant coefficient for P < 0.10.
** Statistically significant coefficient for P < 0.05.
*** Statistically significant coefficient for P < 0.005.

density (Table 3). Red deer most strongly selected units with lower road densities and avoided units with intermediate road densities, but were found in some units with very high road densities as well (Appendix B). Red deer habitat was primarily located in the lower elevations of the forested valleys of the Sikhote-Alin Mountains, and while red deer habitat occurred throughout the study area, it was especially clumped in the central study area, and constrained by agricultural and anthropogenic development in the south (Fig. 2a).

3.2.1.2. Roe deer. The roe deer RSPF model was also statistically significant (P < 0.0005), had higher ROC scores and H–L test statistics than the red deer model, lower classification success and similar pseudo-r^2 scores (Table 2). K-folds cross validation revealed very similar, and high predictive capacity of the top roe deer model (Spearman rank correlation r_s = 0.931). Roe deer selected units with a higher proportion of oak, deciduous, larch and Korean pine forests, and were less likely to occur in units with more meadows and agriculture (relative to spruce/fir forests) (Table 3). Roe deer avoided higher elevation areas, higher snow cover, and selected areas with higher net primary productivity (Table 3). Roe deer strongly avoided areas with high road densities, but were found closer to towns, and were also slightly more common closer to

protected areas. Roe deer distribution was centered in the southern and central zones, and was concentrated at lower elevations along the edge of human development, along the coastal areas, and at lower elevations (Fig. 2b).

3.2.1.3. Sika deer. Sika deer habitat was strongly influenced by a south-north gradient, reflective of their recent expansion from the south (Fig. 2c). From a model fit perspective, the sika deer model was very significant (P < 0.0005), had amongst the highest pseudo-r^2 values, ROC and % classification success, as well as k-folds cross validation scores, most of which was explained by the strong effect of latitude. Sika deer showed some failure to fit the H–L test which was mostly explained by over-predicting in central areas, which minimized failing to predict sika habitat in the southern areas (as evidenced by the high ROC and sensitivity scores, Table 2). Sika deer occurrence increased in units with high proportions of oak, birch, and Korean pine, declined at higher elevations and areas with increasing snow cover during winter. Sika deer were found farther from towns, closer to protected areas, and far from areas with high road densities. Sika deer were the most common in SW Primorye Krai along the Chinese border, at lower elevations and in the coastal oak and birch forests of southern Primorye Krai (Fig. 2).
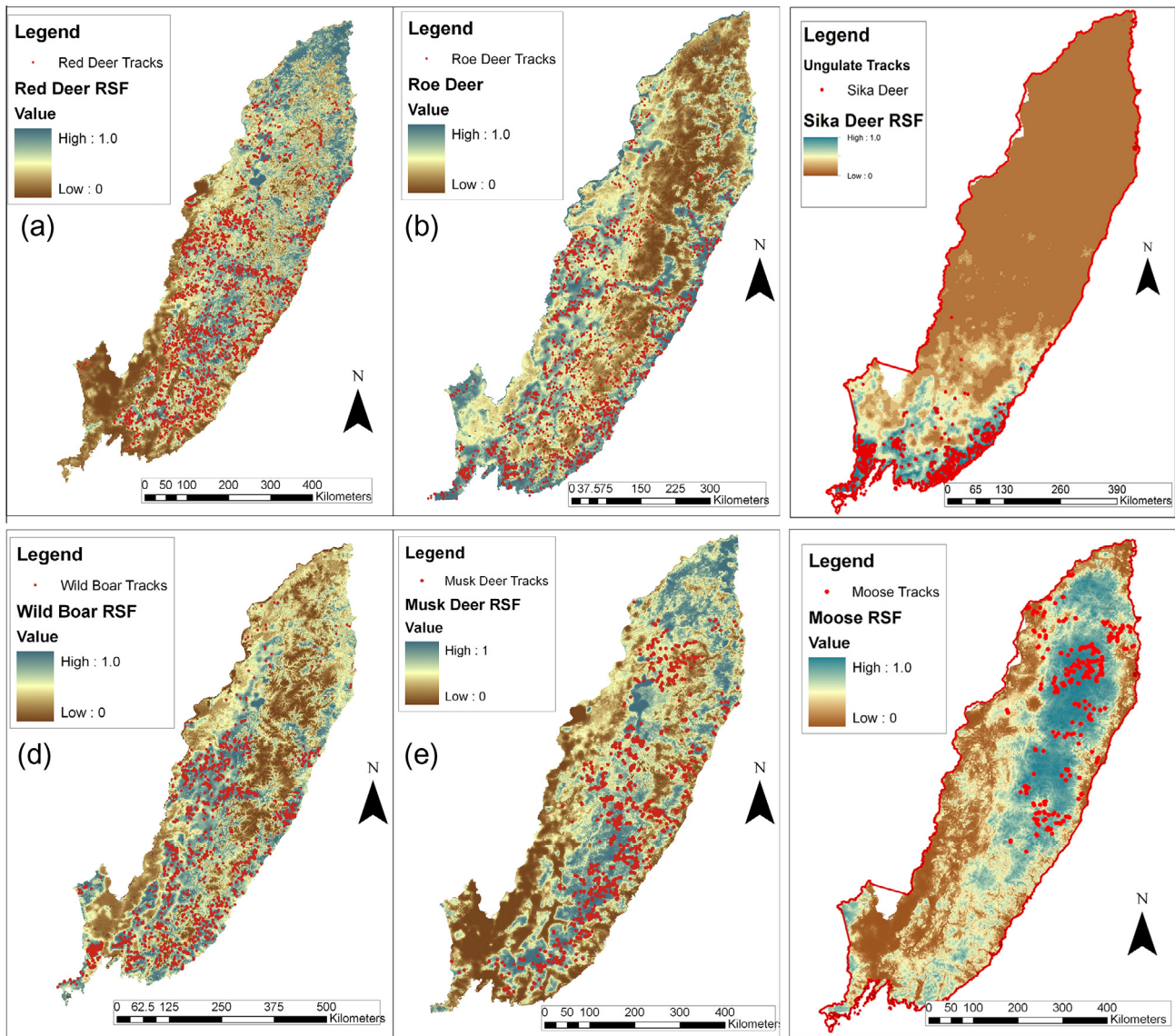
Fig. 2. Ungulate RSPF models projected across the Russian Far East for (a) red deer, (b) roe deer, (c) sika deer, (d) wild boar, (e) musk deer, and (f) moose. Tracks for each species used to develop the model are shown in red, and areas of blue represent areas with a high probability of occurrence.

3.2.1.4. Wild boar. The wild boar RSPF model was statistically significant ($P < 0.0005$), and had similar moderate to good measures of model fit to the red deer model (Table 2). Wild boar also showed some failure of the H–L test ($P = 0.037$) at lower probabilities of wild boar occurrence. K-folds cross validation showed high predictive capacity (Spearman rank correlation $r_s = 0.935$). Wild boar resource selection was driven more by topographic and broader covariates than landcover, as wild boar only seemed to select units with higher proportions of oak and Korean pine forests (reflecting their dependence on mast crops), and strongly avoided agricultural areas (Table 3). Wild boar strongly selected intermediate elevations, with preference peaking at 392 m (Table 3). Increasing snow coverage had a weaker, but still important negative effect on wild boar occurrence. Wild boar also selected areas with intermediate net primary productivity (Table 3). Wild boar occurrence declined weakly with increasing distance to protected areas, but was strongly influenced by road density in a non-linear fashion (Table 3). Wild boar showed selection for intermediate road densities (at a 10 km^2 scale) of about 0.2 km/km^2 (Appendix B) but in general, declined in areas with road densities greater than this

threshold. Wild boar distribution was similar to red deer distribution, centered at intermediate elevations along the forested valleys and ridges of the Sikhote-Alin Mountains (Fig. 2d).

3.2.1.5. Musk deer. The musk deer RSPF model was one of the best all-round habitat models, being strongly statistically significant ($P < 0.0005$), and having higher model diagnostics than the red deer, roe deer and wild boar models (Table 2). Musk deer avoided oak and birch forests, areas with high shrub forests, and strongly avoided agricultural areas. Musk deer preferred units with larch, Korean pine and spruce/fir forests types and showed an intermediate selection for higher elevations around 700 m (Table 3). Within these areas, they showed the strongest avoidance of snow cover of all ungulate species, but again, some non-linear selection for areas with higher snow cover (Appendix B). Musk deer strongly avoided areas close to towns, and had a non-linear pattern of selection for road density, with occurrence strongly associated with low road density (<0.2 km/km^2). Overall, musk deer occurrence was predicted to be highest along the central spine in the southern

Sikhote-Alin Mountains, but extended over a broader area in the northern portion of the study area (Fig. 2e).

3.2.1.6. Moose. Moose occurrence increased at northern latitudes, opposite to sika deer, had high ROC scores, classification success, pseudo-r^2, and passed H–L tests (Table 2). Yet, from a predictive viewpoint, the k-folds cross validation suggested poorer predictive performance than the sika deer and other ungulate species models (Table 2, Spearman rank correlation $r_s = 0.784$). Overall, moose strongly avoided oak, Korean pine and shrubby forests, as well as meadows and almost completely avoided areas with any agriculture (Table 3). They avoided areas at higher elevations with deeper snow, but not as strongly as other species. They seemed to select areas farther from protected areas, but this was probably a spatial artifact of their northern distribution because they strongly selected for areas far from towns and for lower road density (Table 3). Finally, they seemed to be strongly limited by latitude (Table 3, Fig. 2f).

3.2.2. Tiger models
3.2.2.1. Tiger environmental model. At the regional scale, the top environmental covariate-only model was significant (LR χ^2 150.1, $p = 0.0001$) and demonstrated good model fit H–L test, χ^2 4.45, $p = 0.77$). However, the model had mediocre ROC (0.707) and pseudo-R^2 values. In contrast, this model performed very well at predicting habitat ranks using the k-folds cross-validation procedure (Table 4). Tigers selected areas with low densities of roads at a large scale of 20 km radii (roughly equivalent to a tiger home range size), areas close to protected areas, at intermediate elevations (with use peaking around 400 m), and in areas of lower snow cover (Table 4). In terms of landcover, tigers preferred deciduous valleys, Korean Pine forests, and avoided regenerating forests, shrubs and agricultural areas in comparison to their selection of spruce-fir forests, the predominant component of the reference category (Table 4).

3.2.2.2. Prey-based tiger models. Univariate selection functions for tiger occurrence as a function of individual ungulate species RSPF models (Fig. 3a) showed strongest selection for wild boar, red deer, roe deer and sika deer, and avoidance of musk deer and moose habitat. The prey-based tiger RSPF model had the highest AIC, and intermediate model diagnostics compared to the environmental and hybrid models. Compared to the environmental tiger model with a ΔAIC of >20, the regional prey-based model was >200 times
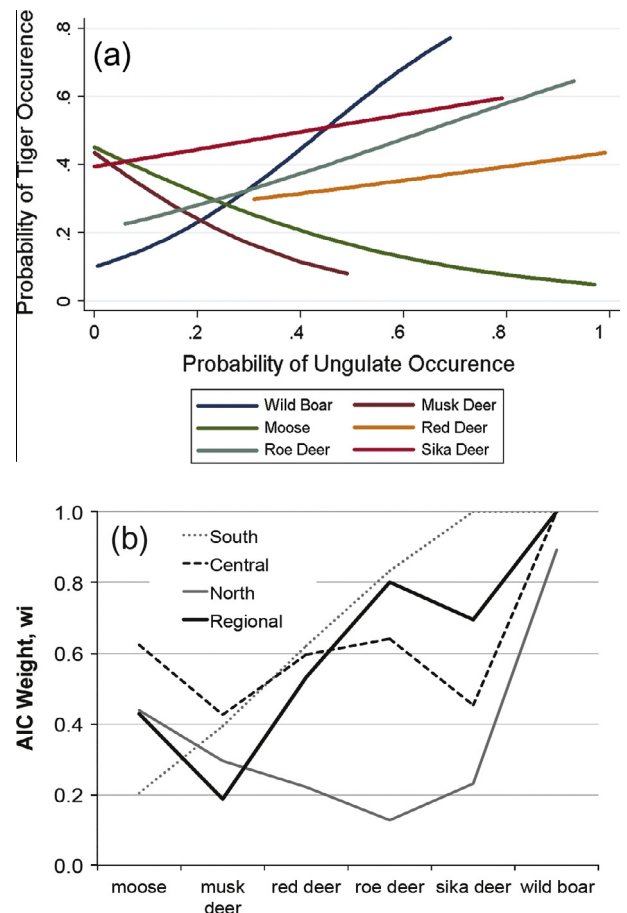
Fig. 3. Relationships between Amur tigers and their multiple prey species in the Russian Far East during winter, 2004/05, showing (a) univariate probability of tiger occurrence with probability of ungulate species occurrence based on in the Russian Far east during winter 2004/2005 based on ungulate and tiger RSPF models, and (b) the relative importance of each ungulate species as a predictor of Amur tiger habitat, based on the AIC weights for ungulate prey RSPF covariates.

more likely to be a better fitting model. The best regional prey-based RSPF model had overall intermediate model performance compared to the environmental and hybrid model, with significant

Table 4
Top environmental-only, prey-only, and hybrid Amur tiger Resource Selection Probability Function (RSPF) models, with model diagnostics and goodness of fit statistics, as well as logistic regression selection coefficients for resource covariates for winter 2004/2005, Russian Far East.

	Prey RSPF		Environ. RSPF		Hybrid RSPF	
AIC	1294.93		1284.63		1259.36	
LR Chi square, P	124.43	<0.0005	144.11	<0.0005	166	
Pseudo R^2	0.188		0.201		0.218	
ROC	0.723		0.707		0.761	
K-folds, SE	0.931	0.023	0.905	0.056	0.951	0.021
Covariates	β	SE	β	SE	β	SE
Red deer RSPF	2.790	0.8876	–	–	2.586	0.9239
Roe deer RSPF	1.015	0.6368	–	–	1.586	0.9339
Sika deer RSPF	0.523	0.3125	–	–	−0.115	0.3443
Wild boar RSPF	4.017	0.7192	–	–	4.640	0.8357
Korean pine	0.645	0.3047	–	–	–	–
Shrub	–	–	−1.943	1.0983	–	–
Agriculture	–	–	−3.052	1.1122	–	–
Elevation	–	–	0.006	0.0016	0.001	0.0006
Elevation^2	–	–	−7.63E−06	1.63E−06	–	–
Snow cover	−0.026	0.0070	–	–	−0.021	0.0077
Dist. to zap (km)	−0.011	0.0024	–	–	−0.010	0.0028
Road density(20 km)	–	–	−1.209	0.6688	–	–
Intercept	−4.899	0.9071	0.506	0.4145	−4.469	1.2047
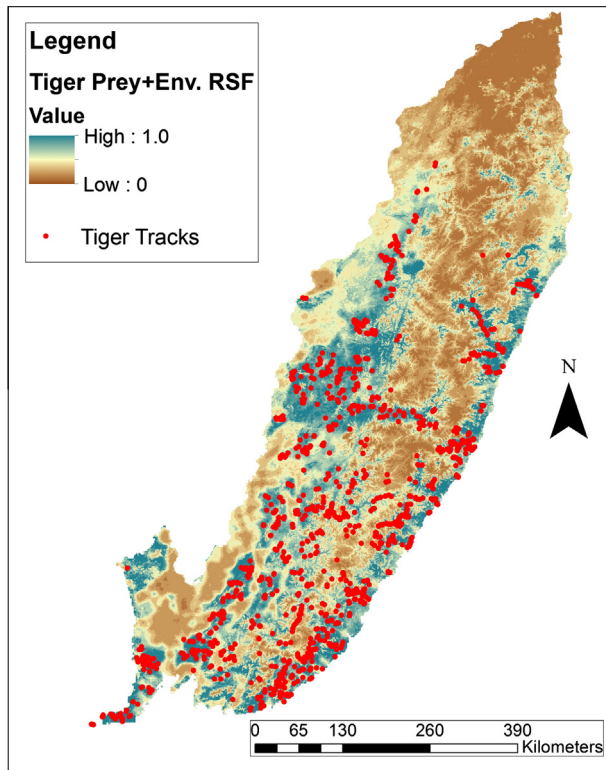
Fig. 4. Top hybrid (Prey RSPF's + Environmental RSPF's) Tiger Resource Selection Probability Function model for winter 2004/2005 in the Russian Far East showing locations of tiger track locations from the simultaneous snow tracking surveys used to develop the RSPF.

Likelihood ratio test p-value < 0.00005, reasonable ROC scores (0.723), and a higher k-folds cross validation Spearman rank correlation coefficient of $r_s = 0.941$ (Table 4). The top regional prey-based tiger RSPF model showed that survey units with tigers were positively correlated with wild boar, followed by red deer, roe deer and then sika deer (Table 4).

3.2.2.3. Hybrid prey and environment tiger model. The best hybrid model had the lowest AIC by a ΔAIC of approximately 25 units, confirming its strong support compared to either the environmental or prey-based RSPF. The hybrid model also had the overall best model diagnostics, with the highest ROC, k-folds, and other model goodness of fit statistics (Table 4). In the hybrid model, tiger occurrence over the entire region was most strongly related to wild boar, followed by red deer, roe deer, and a marginal, statistically weak relationship with sika deer (Table 4). The weak effect of sika deer in the regional model is almost certainly attributable to its restriction to southern zone and hence, model selection uncertainty across zones (Fig. 2c). Over and above the effects of prey, the probability of tiger occurrence in a survey unit declined with increasing snow cover, areas far from protected areas, and increased at higher elevations (Table 4).

3.2.2.4. Zonal prey-based tiger RSPF models. Within zones, the relationship between tiger occurrence and prey RSPF's changed from south to north. In southern zones, tiger habitat was positively predicted by wild boar habitat, then sika deer, and was negatively correlated with roe deer (Table 5), though there was substantial model selection uncertainty that is reflected in the rank ordering of wild boar and sika deer as the most important, followed by roe deer and red deer (Fig. 3b). In the central zone, tiger habitat was positively related to all ungulate species but musk deer, with the top model showing strongest tiger selection for sika deer

Table 5
Zone-specific prey-based Amur tiger RSPF models in the Russian Far East, winter 2004/2005, showing model diagnostics (n, likelihood ratio chi-squared test statistic and p-value, pseudo R^2, ROC, k-folds r_s) and selectivity coefficients for ungulate RSPF models.

|	South		Central		North	
n	416		514		106	
LR χ^2, p-value	73	<0.0005	31.42	<0.0005	15.08	<0.0005
R^2	0.15		0.201		0.291	
ROC	0.701		0.671		0.823	
K-folds r_s	0.844		0.831		0.954	
Covariate	β	SE	β	SE	β	SE
Roe deer RSPF	−3.29	0.923	2.13	0.836	–	–
Sika deer RSPF	1.53	0.469	4.29	2.358	–	–
Wild boar RSPF	4.92	1.113	4.27	1.047	9.19	3.360
Moose RSPF	–	–	2.09	0.971	−3.71	3.573
Red deer RSPF	–	–	3.03	1.663	–	–
Intercept	−0.92	0.353	−5.79	1.704	−4.22	1.137

habitat, followed closely by wild boar, red deer, roe deer and moose. Model selection uncertainty in the AIC weight rankings, however, emphasized that wild boar, then red deer, roe deer and sika deer were the most important prey species (Fig. 3b). In contrast, in the northern zone, tiger habitat was strongly positively related to wild boar habitat, and negatively related to moose habitat (Table 5, Fig. 3b).

3.2.2.5. Reproductive tigress model. Survey units with tigresses and cubs tended to occur more in birch forests, in lower road densities at broad spatial scales (20 km²), closer to protected areas and, most importantly, in areas with high wild boar habitat (Table 6). The overall strength of the reproductive tigress model, however, was relatively modest. For example, the effect of doubling road density from 0.2 km/km to 0.4 km/km in a 20 km² radius (a huge biological effect) decreased the probability of breeding by only 0.1. The strongest effect was shown by changes in wild boar RSPF; doubling wild boar habitat from 0.3 to 0.6 doubled the probability of cubs from 0.1 to 0.2. Although the overall chi-square test was significant ($X^2 = 15.04$, $P = 0.01$), the model had weak explanatory power (pseudo-$R^2 = 0.08$) and a low ROC score (ROC = 0.652) suggesting poor discrimination. Classification success at the optimal cutpoint of $p = 0.12$ was also quite poor with an overall 54.1% classification success, but a sensitivity of 65%. Using the extensive surveys from the whole winter, at this cutpoint, only 55% of the tracks of females with cubs (sensitivity) were correctly classified. Therefore, while these factors were significantly related to the presence of cubs, the biological effects were relatively weak, with the exception of the stronger relationship between wild boar and tiger reproduction. Regardless of these limitations, Fig. 5 shows the strong positive linear relationship of the probability of tiger use and the probability of females with cubs being present. Breeding habitat was correlated with tiger probability with a correlation coefficient of $r = 0.85$ ($R^2 = 0.734$, $n = 1041$ units, $p < 0.00005$). The regression coefficient of 0.27 relating overall tiger habitat to reproductive habitat and near zero intercept suggests only about 30% of tiger habitat supported females with cubs during the survey.

Table 6
Top logistic regression model distinguishing survey units with reproductively active Amur tigers (tigress + cubs) from units with only adult tigers, Russian Far East, winter 2004/05.

Parameter	β	SE	P-value
Birch	1.17	0.631	0.068
Wild Boar	3.36	0.789	<0.0005
Dist. to Zapovednik (km)	−0.008	0.003	0.036
Road density (20 km)	−1.56	0.93	0.078
Intercept	−3.203	<0.005	0.0001
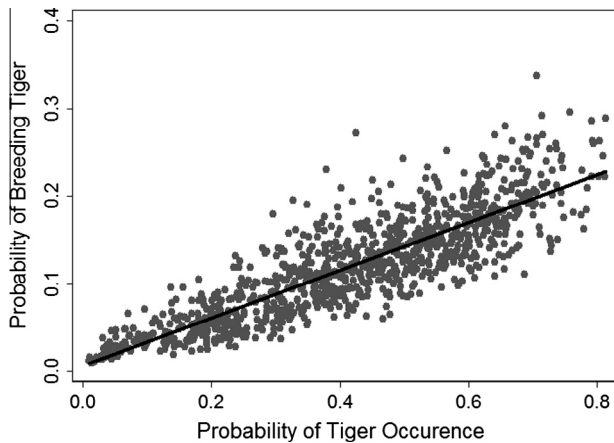
Fig. 5. Validation of the top hybrid (prey + environmental) Amur tiger RSPF model showing a strong relationship to breeding tigress habitat in the Russian Far East, 2004/2005, where the probability of a reproductive tigress = 0.006 + 0.27 * tiger RSPF).

3.3. Identifying tiger habitat

We used the hybrid model to discriminate tiger habitat (1) from non-habitat (0) by examining classification success of tiger tracks used to develop the model (simultaneous survey only) across a range of cutpoint probabilities from 0.21 to 0.42. We found that classification success varied from 96% to 68% from cutpoints of 0.21–0.42, and that the optimal cutpoint, based on the trade-off between sensitivity and specificity, was $p = 0.42$. Classification success for non-habitat (0) locations ranged from 26% to 61% (Table 7). In comparison, classification success of the extensive tiger track data set from the entire winter was lower than for just the simultaneous surveys, and ranged from 40% to 96%. A 93% classification success for simultaneous survey data set resulted in a cutpoint probability of 0.25 to delineate tiger habitat from non-habitat. This cutpoint classified 90.5% of all extensive tiger tracks correctly, but only classified non-habitat correctly about 32% of the time. A cutpoint of 0.25 seemed to be the threshold between achieving ~90% classification of tiger habitat because by 0.31, classification success of especially the extensive survey tiger tracks dropped dramatically. Therefore, we selected $P = 0.25$ as the cutpoint probability to delineate tiger habitat. However, hundreds of small, isolated patches remained that would not effectively contribute to tiger habitat. We used a threshold patch size of 200 km^2 based on the smallest size of a female tiger home range observed in Sikhote-Alin Zapovednik (Goodrich et al., 2010) to remove smaller, isolated patches. Moreover, the two most northerly counties of Khabarovskii Krai did not contain any tigers, despite containing predicted (potential) tiger habitat. Therefore, we removed all tiger habitat patches from these two northerly counties. This resulted in a total of 155,230 km^2 of tiger habitat distributed in 17 patches ranging in size from 249 km^2 to the largest contiguous patch of tiger habitat

along the western slopes of the Sikhote-Alin Mountains of 119,797 km^2.

Using the top environmental-only model's spatial predictions of tiger habitat with and without human development in the study area, we estimated that there has been approximately only a 19% reduction in habitat quality (Fig. 6c). Habitat loss was greatest in the southern interior zone (42% habitat loss in the area north and west of Vladivostok along the Chinese border), followed by the southern coastal region (17%), central interior (16%), northern coastal area (12%), central coast (10%), and northern interior regions (10%).

4. Discussion

4.1. Identifying Amur tiger habitat

Amur tigers currently occupy about 155,000 km^2 of 266,000 km^2 (59%) in our study area in the forests of the Russian Far East. While we were moderately successful in defining potential tiger habitat using non-prey based habitat parameters (our first objective), we found that the hybrid model based on prey distribution was 200 times more likely to be a better fit. Thus, Amur tiger habitat was predicted best by a hybrid model that includes the spatial distributions of both human activities and that of primary ungulate prey of tigers. These results confirm that including both biotic interactions in large-scale habitat models improve their predictive and mechanistic utility, and that habitat for large carnivores should be considered a function of the distributions of their large ungulate prey as well as human factors. These results echo recent studies showing similar enhanced predictive performance in habitat and species distribution models when including biotic interactions such as predation for a wide range of carnivores (Burton et al., 2012; Hebblewhite et al., 2011; Keim et al., 2011). Moreover, our results, which clearly show the negative effects of human activity, including road density, distance to protected areas, and agricultural land-use on preferred ungulate prey species and on tigers themselves, confirm the widespread direct and indirect negative impacts of human activities on carnivores. This niche-based approach provides a clearer mechanistic understanding of the drivers of tiger habitat at regional scales that will be directly useful to Amur tiger conservation. The primary advantage of the hybrid model, in addition to improved model fit and predictive accuracy, is its more mechanistic insights about the importance of prey to shaping high-quality tiger habitat.

4.2. Resource selection by ungulates in the Russian Far East

There have been few studies of resource selection within ungulate communities in northeastern Asia. Therefore, analyses for our second objective, to model resource selection of ungulates in the Russian Far East, provide novel information themselves relevant to the ecology and conservation of large ungulates in the region. All ungulate species showed negative responses to human

Table 7
Classification success of tiger tracks as a function of differing cutpoint probabilities from the top Tiger-RSPF model for survey units occupied by tigers, as well as the corresponding area of predicted tiger habitat for each cutpoint probability. Classification success for both the extensive tiger survey data and intensive "simultaneous" tiger track survey are both shown. The preferred cutpoint is highlighted in bold at $p = 0.25$.

Cutpoint probability	# Tracks	% Extensive tiger tracks correctly classified	% Intensive tiger tracks correctly classified	% Classification success of non-habitat	Area tiger habitat (km^2)
0.21	5090	96.6	96.3	26.6	203,880
0.23	4880	92.8	95.3	29.7	168,557
0.25	**4753**	**90.2**	**93.0**	**32.0**	**155,230**
0.31	4082	77.6	87.9	40.72	114,968
0.37	3251	61.8	75.6	51.4	84,440
0.42	2142	40.7	68.8	61.74	56,130
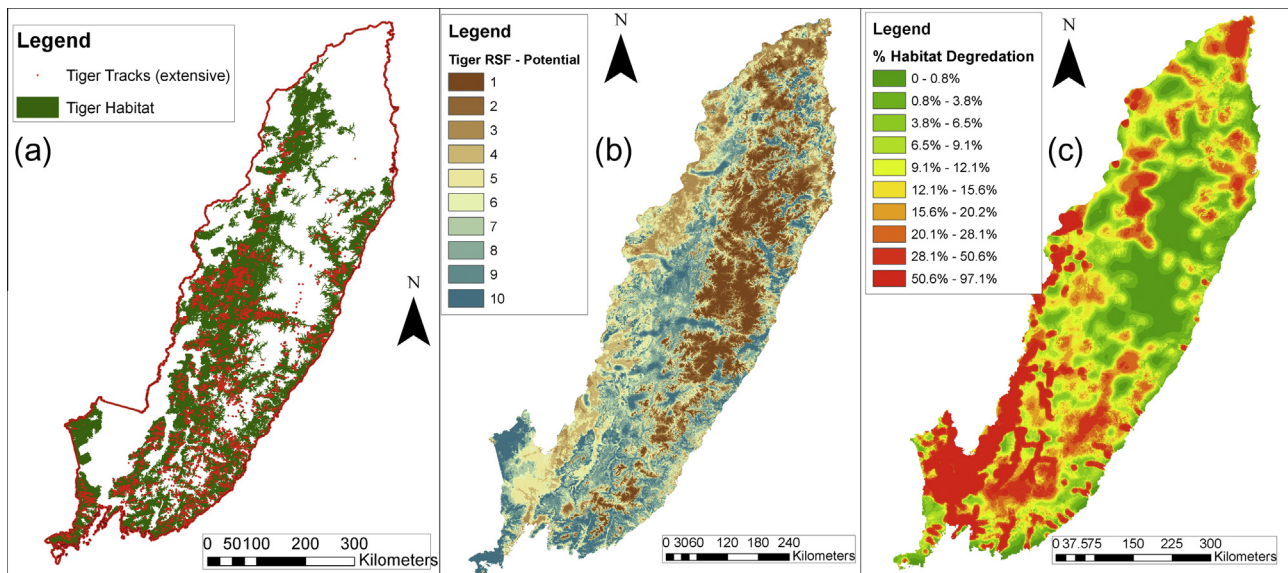
Fig. 6. Amur tiger habitat showing (a) evaluation of predicted discrete categories of winter tiger habitat and non-habitat based on the optimal cutpoint probability $P = 0.25$ that achieved 92% classification success of all tiger tracks observed during the entire 2004/2005 winter; (b) potential winter habitat for Amur tigers calculated from the environmental-covariate Tiger RSPF model assuming no human development, and (c) percent habitat loss calculated from the realized environmental model (e.g., Fig. 4) – potential tiger model.

disturbance measured by road density in a 10 km^2 radius, increased agriculture, areas closer to towns (except roe deer), and areas further from protected areas. It should be emphasized that these responses were measured at relatively large spatial scales (170 km^2). However, recent studies on sika deer in nearby Japan confirmed a tendency to avoid roads (Sakuragi et al., 2003), and moose in northeastern China avoided roads up to 3 km distant (Jiang et al., 2009). Though detailed demographic studies of ungulates explaining the mechanism for these negative relationships are rare in northeastern Asia, the intensity of legal hunting and high poaching rates in Russia is no doubt related to access, and therefore increases in areas with higher proximity to roads, settlements, and outside of protected areas (Frair et al., 2007; Maslov and Kovalev, 2013; Proffitt et al., 2013). While previous Eurasian studies have shown positive responses of roe deer, sika deer and wild boar to agricultural lands (Apollonio et al., 2010), the negative response we observed by all ungulates (except roe deer) to agriculture may be due in part to the large grain size of the tiger sampling units, but also to the pervasive prevalence of both legal and illegal hunting. Either way, this emphasizes that there may be differences in the overall distribution of ungulates and their conditional distribution in occupied tiger habitat. For example, in general, roe deer likely show strong selection at landscape scales for human agriculture. But, because Amur tigers avoid human dominated areas, within the distribution of tigers, roe deer resource selection will differ from roe deer resource selection across all of roe deer range.

Ungulate species showed strong selection for deciduous land-cover types including selection for oak by roe deer, sika deer, and wild boar, selection for birch by sika deer and overall preferences for deciduous forests by red deer and roe deer, similar to many previous studies (Andersen et al., 1998; Jedrzejewska and Jedrzejewski, 1998; McCullough et al., 2009; Sakuragi et al., 2003). Also, wild boar and sika deer both showed strong selection for mast-bearing Korean pine, a species of conservation concern because of overharvesting in the Russian Far East (Kondrashov, 2004). Fortunately, harvest of Korean pine was recently banned in Russia (http://www.ens-newswire.com/ens/nov2010/2010-11-19-01.html), but enforcement will be critical to ensure protection.

The probability of occurrence for all ungulate species declined with increasing snow cover, but showed some separation along an elevation gradient with sika deer and roe deer showing the strongest selection for low elevations, followed by red deer, wild boar who selected intermediate elevations and musk deer who selected both intermediate and high elevations (Table 3, Appendix B). Moose and sika deer showed opposing trends to latitude, consistent with potential effects of climate change. In both Russia and nearby China, moose appear to be declining in the southern portions of their range possibly in response to climate change (Dou et al., 2013; Zaumyslova and Yu, 2000). Conversely, sika deer are expanding northwards in the Russian Far East (Aramilev, 2009; Voloshina and Myslenkov, 2009). The clear preference of tigers for red deer over sika deer (Miquelle et al., 2010), suggests that the loss of red deer in southern Primorye may be detrimental to tigers. These results emphasize the latitudinal variation in the importance of prey to Amur tigers, highlighted by our fourth objective.

4.3. Zonal prey-based tiger RSPF models and the influence of scale

Our fourth objective was to test the implicit assumption of habitat models that include predator–prey interactions that prey selection is independent of scale. By using both zonal and regional models, our study provides a valuable test of this assumption, and indeed demonstrated substantial plasticity in tiger selection for prey across our large spatial gradient. Previous studies in six areas of the Russian Far East ranked occurrence of ungulate prey in Amur tiger diets as follows in the winter (Miller et al., 2013; Miquelle et al., 1996): red deer ⩾ wild boar > roe deer > sika deer > other prey, with wild boar and red deer also being the two preferred species. This qualitative ranking corresponds well to that predicted by the overall regional model for Amur tigers from our hybrid model. Nonetheless, recent observations suggest that sika deer have become the dominant item in the diets of tigers in southern Primorye (L. Kerley, *pers. comm.*), and this fact is reflected in the substantial spatial variation in the association of Amur tigers and different prey species across the three zones of our study area. While wild boar were consistently the most strongly selected across all zones, there was greater variation in selection for sika deer, red deer and roe deer, presumably because of variability in availability of these prey. Whether or not tigers show a functional response in selection (Mysterud and Ims, 1998) for different

ungulate prey species as a function of availability is an important but yet unanswered question for understanding spatial tiger-prey dynamics. Regardless, our results echo conclusions from a range wide review of tiger prey selectivity (Hayward et al., 2012) that showed tigers prefer prey closest to their own body size, which in most areas of Asia is represented by a large deer and wild boar. These results coincide with Miller et al.'s (2014) conclusion that large ungulates are essential for successful reproduction.

4.4. Human impacts

Our results confirm broader scale results of human influences as demonstrated in previous tiger habitat models. Across tiger range, humans negatively impact tiger habitat suitability or quality at large spatial scales (Seidensticker et al., 1999; Tilson and Nyhus, 2010). In some studies, human activity was the only consistent predictor of tiger absence, confirming its widespread and strong effect (Linkie et al., 2006), but not providing much information about tiger occurrence. Despite a recent claim in Nepal that tigers and humans could coexist at fine spatial scales (Carter et al., 2012), we found strong evidence for large landscape-scale (10 km^2) negative effects of human activity on both prey and tiger occurrence. This is consistent with both the prey depletion hypothesis for tiger declines (Karanth and Stith, 1999) and the impact of direct poaching of tigers, with both likely driven via the same mechanism– poaching. While the top 'hybrid' tiger RSPF model did not include a direct negative effect of roads, negative effects of roads were manifest on tigers through prey depletion because high road densities were associated with low occurrence of key ungulate species. This supports the prey depletion hypothesis. Moreover, there was evidence that tiger reproduction declined in areas of higher road densities. Although detailed studies documenting the effects of human activities on tigers are rare, the negative effect of roads (via poaching) on tiger survival rates and demography are clear (Goodrich et al., 2008; Kerley et al., 2002).

4.5. Tigers and prey

While some studies have used direct measures of density to demonstrate the close relationship between tiger and prey densities (Karanth et al., 2004; Miquelle et al., 2010), most habitat-related studies have used surrogates or proxies for relating tiger distribution, habitat and occurrence to the spatial distribution of prey (Harihar and Pandav, 2012; Kawanishi and Sunquist, 2004; Sunarto et al., 2012). Our results indicate that direct measures of ungulate prey occurrence will provide a more accurate evaluation of tiger habitat, as well as a better delineation of the drivers defining tiger habitat. Similarly, Karanth et al. (2011) used broad scale trail surveys in southern India to model prey effects on tiger occurrence across multiple reserves. In Nepal, Barber-Meyer et al. (2013) found that the probability of tiger occupancy increased from 0.04 in areas with high human activity and lower ungulate prey to 1.0 with lower human activity and the highest relative prey density. With the growing deployment of remote cameras, especially for tigers, there is an amazing wealth of data on large ungulate prey in many tiger conservation landscapes. The challenge with such data will be how to estimate relative density measures of ungulates (e.g., Rowcliffe et al., 2008), to tiger densities. In this study, we found the probability of ungulate occurrence from an RSPF was reasonably correlated with track counts of most ungulate prey species (e.g., Poisson generalized linear model of sika deer track count = $-1.41 + 3.99 *$ sika RSPF, $p < 0.0005$, $R^2 = 0.45$; red deer $R^2 = 0.17$, $p < 0.0005$; wild boar $R^2 = 0.22$, $p < 0.0005$; roe deer $R^2 = 0.19$, $p < 0.0005$; musk deer $R^2 = 0.01$, $p = 0.44$; moose $R^2 = 0.27$, $p < 0.05$, *unpubl. data*). Thus, one could relate tiger occurrence directly to changes in prey abundance in the Russian Far

East, though these results are certainly not exceptionally strong. We think one of the most important areas of research will be on occupancy-abundance relationships for key ungulate prey of tigers to help link changes in prey occurrence to tiger-prey density relationships. The absence of rigorous estimates of prey densities in habitat models risks over-predicting habitat quality in areas with low densities or absence of prey, as demonstrated for Amur tigers in Northeastern China (Hebblewhite et al., 2012). Nonetheless, to conserve large carnivores such as tigers, we clearly need to know more about the distribution and occurrence of ungulates, and more importantly, how to manage for increases in densities of preferred prey species. Focusing just on tigers, for instance, solely on eliminating tiger poaching, without efforts to recover populations of preferred prey species, will ultimately fail to recover tiger populations. Recent examples of on the ground, broad-scale policy changes to increase the density of ungulates specifically for tiger conservation (Kawanishi et al., 2013) should be expanded across tiger range if decision-makers are serious about doubling wild tiger numbers.

4.6. Modeling habitat for tiger reproduction

An implied assumption of habitat modeling is that preferred resources improve an individual's chances of survival and reproduction over time. For large carnivores, this is a challenging assumption to test, requiring long-term monitoring of individual animal's lifetime reproductive success. A long-term study of African lions (*Panthera leo*) showed that a 40-year average of female reproductive success was explained by prey vulnerability, whereas lion density and cub production was more closely related to functional vegetation characteristics (Mosser et al., 2009). Thus, lion density or counts may not necessarily reflect African lion habitat quality. No tiger studies have sufficient data for this kind of comprehensive test. Nonetheless, for our fifth objective, to determine if we can predict breeding habitat for tigers, we found that good tiger habitat seems to be good breeding tiger habitat; that is, there is a positive correlation between a coarse measure of fitness (females with cubs) and high quality habitat as predicted from our hybrid RSPF. However, the results also suggested that females with cubs were more sensitive to human disturbance and more strongly influenced by wild boar occurrence than other tigers. These results reaffirm the findings of previous smaller-scale telemetry-based studies that occurrence of roads is associated with low cub survival (Kerley et al., 2002; Miller et al., 2013). The importance of wild boar to tiger reproduction coincides with the strong preference for wild boar found by Miquelle et al. (2010), and may be related to greater vulnerability of wild boar to predation (Yudakov and Nikolaev, 1990). Given that a tigress must acquire more than double the energetic requirements of a non-breeding female to successfully rear two cubs to dispersal age (Miller et al., 2013), greater vulnerability of prey such as wild boar may be critical to acquiring sufficient prey biomass. In a more concrete sense, given the sensitivity of tigers to poaching, delayed age at first reproduction and longer inter-birth interval than other large carnivores (Chapron et al., 2008), enhancing survival and densities of preferred prey are critical conservation actions.

4.7. Priority areas of high risk for tiger habitat conservation

Our attempts to estimate degradation and risk in tiger habitat (Objective 6) suggest that there has been approximately only a 19% reduction in habitat quality in the Russian Far East. However, this reduction was by no means evenly distributed across tiger range. Our analysis suggests that areas along the western border of Primorskii Krai, and in the Lake Khanka area are most degraded. In fact, tigers are extremely rare in these regions, even though the

areas surrounding Lake Khanka were historically considered to have some of the highest densities of tigers in the region when Nikolai Przhevalsky traveled through Primorskii Krai in the 1860s (Przhevalskii, 1990). This emphasizes that our 'potential' habitat is probably an underestimate of historic distribution because of a wide-spread 'shift' of the niche of Amur tigers away from high human activity. While recovery of these abandoned regions like Lake Khanka is unlikely due to extensive anthropogenic conversion, the indication of habitat degradation of the southern Sikhote-Alin Mountains should be of concern. Tiger densities here should be some of the highest in the Russian Far East, given the lower latitude and higher densities of ungulates. Habitat degradation, primarily in the form of logging and associated road building, as well as land use conversion from forest to agriculture in southern areas, threatens the integrity of this region. These results echo the conclusions of Carroll and Miquelle (2006), whose simulations suggest that fragmentation was a greater danger in this same region. Efforts to reduce the impacts of road densities, infrastructure development, and continued timber extraction should be a priority in this region to prevent fragmentation and degradation.

5. Conclusions

The Global Tiger Initiative's (2010) goal of doubling wild tigers in existing Tiger Conservation Landscapes by 2022 is ambitious. Our prey-based tiger models along with existing information on causes of tiger mortality (Goodrich et al., 2010) provide some clear guidelines on how to increase tiger numbers in the Russian Far East. Increasing habitat quality will be largely equivalent to increasing ungulate densities and reducing risk to tigers, prey, and their habitat. The ever-increasing network of logging roads in the Russian Far East provides access for illegal activities on a scale that has never existed in the past. Our results show the negative influence of roads on tiger occurrence, through their prey, and provide strong evidence for the need to reduce road densities in tiger habitat. Closure of logging roads unnecessary for immediate timber exploitation would greatly decrease effective road density in forested habitat, thereby greatly reducing access for legal hunters and poachers, both of whom are likely responsible for the strong relationship between high road density and the low occurrence of ungulates and tigers. Closure of logging roads and strong enforcement of both road closures and hunting regulations will be critical to increasing prey densities, and reducing poaching pressures on both prey and tigers.

Reducing habitat degradation and fragmentation will also be critically important in southern and central Sikhote-Alin, where infrastructure projects must be designed to minimize impact on tiger habitat, and where logging must be tightly controlled. Increasing the size of protected areas by expanding buffer zones – a process already underway – will enhance habitat quality and the effective size of protected areas. But more effective management of lands adjacent to protected areas (via better law enforcement and habitat improvement projects) will be the most important mechanism of expanding the positive "protected area" effect on both tigers and their prey noted in our analyses. These results also provide useful guidelines for Northeast China, where efforts to recover Amur tiger populations are underway (Hebblewhite et al., 2012). Recovery of red deer, sika deer, and wild boar populations (Zhang et al., 2013) will require elimination of snares and reduction in cattle grazing (Soh et al., 2014). Reduction of human access to remaining forests will also be key for recovering existing forest ecosystems there.

In addition, longer-term protection of preferred vegetation communities (e.g., Korean pine and deciduous forests) may enhance the long-term conservation of Amur tigers in both

countries. The ban on logging by the Chinese government, and the more recent ban on harvest of Korean pine trees by the Russian government are important first steps. Further efforts to protect Mongolian oak, an important mast crop of wild boar and other ungulates, and continued efforts to reduce poaching and overall human access will be crucial to improving productivity and persistence of the Amur tiger in both Russia and China.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.07.013.

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