RESOURCE PARTITIONING AND DENSITY DRIVERS

OF TWO ENDANGERED LARGE FELIDS:

AMUR TIGER (*Panthera tigris altaica*) AND AMUR LEOPARD (*Panthera pardus orientalis*)

IN THE RUSSIAN FAR EAST

Dina Matiukhina

Acknowledgments

First of all, I would like to acknowledge Dale Miquelle, the Director of WCS Russia Program, as the person who made the most significant contribution to my professional development. Since the beginning of my career Dale encouraged me to pursue higher objectives. Without his support and motivation this research won't be possible. Dale set an example for me of true professionalism and passion for conserving our unique big cats.

I'm indebted to Professor Jacqueline Frair, my academic advisor, for accepting me as a graduate student, supporting my application at SUNY ESF and being enormously patient during my studies. It seemed risky to take me on, so I deeply appreciate all the opportunities she gave me. Her perfectionism and guidance helped me a lot to improve my critical thinking and scientific writing. Our weekly meetings and potluck seminars provided me with a wealth of knowledge and ideas. And I will always cherish memories about Dickens Christmas in Skaneateles and a wonderful Christmas eve. That was an unforgettable cultural experience!

I'm particularly grateful to my steering committee: Mark Hebblewhite for accepting me at HebLab, UM and guiding me through challenging times of learning habitat modeling, Brian Gerber for his willingness to share his time and expertise and teaching me SECR, Jonathan Cohen for his endless patience and responsiveness to my queries about R coding and principles of population biology.

My gratitude goes to my core field team (Sergey Gubin, Viktor Storozhuk, Alexey Titov, Gleb Sedash, Peter Sonin, Timofey Petrov) and other staff members of the Land of the Leopard National Park (Anna Vitkalova, Alyona Shevtsova, Ekaterina Blidchenko, Anna Utitzkikh, Julia Burkova, Evgeniya Somova, Oxana Lenevich, Tigran Ayrapetyan, Albina Lelikovich and many

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

D.S. Matiukhina. Resource partitioning and density drivers of two endangered large cats: Amur tiger (*Panthera tigris altaica*) and Amur leopard (*Panthera pardus orientalis*) in the Russian Far East, 105 pages, 9 tables, 8 figures, 2020. APA style guide used.

Abstract

In Russia, long-term conservation interventions have bolstered the critically endangered Amur leopard (*Panthera pardus orientalis*) as well as their dominant competitor, the endangered Amur tiger (*Panthera tigris altaica*). Within the Land of the Leopard National Park, I investigated the potential for tigers to displace or suppress leopards. I used data from winter track surveys to fit resource selection functions and camera trap surveys to both fit spatially-explicit capture-recapture models and document leopard productivity. I found no evidence of habitat displacement or numerical limitation of leopards by tigers in this region. Leopards resource selection was defined by landscape features and density was explained by the putative availability of sika deer rather than competition from tigers. Lastly, the number of observed leopard litters of all ages increased positively with local tiger density. This research lays an important foundation for conservation actions that prioritize minimizing human impacts on both felids rather than limiting tigers to benefit leopards.

Key words: Amur tiger, Amur leopard, density, habitat modeling, interspecific competition, Resource Selection Functions, Spatially Explicit Capture-Recapture.

D.S. Matiukhina
Candidate for the degree of Master of Science, December 2020
Jacqueline Frair, Ph.D.
Department of Environmental and Forest Biology
State University of New York College of Environmental Science and Forestry
Syracuse, NY

INTRODUCTION

The Russian Far East is the home of two iconic felids, the endangered Amur tiger (*Panthera tigris altaica;* Miquelle et al. 2011) and the critically endangered Amur leopard (*Panthera pardus orientalis;* Stein et al. 2020). Both species are of the highest national and international conservation priority and the subject of targeted conservation measures in recent decades. Historically occupying vast expanses of Northeast Asia, including China, Korean Peninsula, and southern portion of the Russian Far East, the two species experienced considerable range reduction during the end of the 19th and 20th centuries (Kucherenko 1985, Pikunov and Korkishko 1992). Most of the present global Amur tiger range is found in Russia and areas on the China side immediately adjoining the international border with Russia. In Russia they occur within the Sikhote-Alin Mountain Range and the lower reaches of Amur River, as well as the East Manchurian Mountains in Southwest Primorsky Krai (hereinafter, SWP). The sub-population of tigers in SWP is considered to be geographically and genetically isolated from the main population in Sikhote Alin (Henry et al. 2009, Sorokin et al. 2016). The range of the only wild population of Amur leopards in Russia is exclusively confined to the SWP and the bordering areas of Jilin and Heilongjiang Provinces of China. Thus, the geographic ranges of the two subspecies overlap only in this small transboundary region. Furthermore, both Amur tiger and leopard populations in SWP represent the sole source for the recovery of the two subspecies in Northeast China (Miquelle et al. 2015). The SWP is an important part of the Global Priority Tiger Conservation Landscape (Dinerstein et al. 2006), and is designated to act as a bridge for further Amur tiger recovery in the Changbaishan region of China. Thus, Russia has a responsibility for conserving both felids by implementing actions aimed at sustaining their populations and habitat.

The result of a long-term joint effort for saving Amur leopards from the brink of extinction has been a single range-wide protected area established in SWP in 2012, the Land of the Leopard National Park (hereinafter, LLNP), that has played an important role in recent increases of Amur tiger and leopard abundance. The LLNP and its buffer zone encompasses most of the Amur leopard range in Russia. Within the park, intensive law-enforcement has alleviated poaching problems and large-scale monitoring via camera traps has provided insights into promising population trends. For instance, population estimates indicated almost a threefold increase in both cats, from 11-13 tigers and 25-34 leopards estimated in 2007 (Pikunov et al. 2010) to 29 tigers and 84 leopards in 2018 (LLNP, unpublished data)

Despite the promising trends conservation challenges and knowledge gaps remain. The critically endangered Amur leopard is still under risk of immediate extinction due to its extremely low numbers and long-term inbreeding (Uphyrkina and O'Brien 2003). Remaining habitats for Amur tiger and leopard in SWP are surrounded by anthropogenic development on all sides, including developments in Hunchun River basin in Jilin Province, China. The rate of inland dispersal by Amur tigers to China has been low (Ning et al. 2019). Thus, apparently lacking the opportunity for rapid range expansion, leopard and tiger populations are forced to subsist on limited resources within the SWP and adjoining regions of China. Given the increasing densities of both felids, resource limitations might lead to hazardous consequences pushing them into more human-dominated areas or increasing inter-specific aggression. The outcomes might be more pronounced for the smaller-bodied Amur leopard, unless the necessary conditions for recolonization in China or connectivity corridors with the suitable habitats in Russia are established (Miquelle et al. 2015).

The observed simultaneous growth of tiger and leopard numbers in SWP might instill confidence that the conditions supporting such an increase are sufficient for both. In fact, the Amur leopard hasn't experienced the current level of tiger numbers in its range for decades, so the long-term consequences of interspecific competition for the leopard population are unknown. Interspecific competition between the two sympatric carnivores might become more acute as their densities increase, possibly inducing large-scale displacement in habitat use or reducing fitness of Amur leopard, as the subordinate competitor.

This thesis research examines two main hypotheses concerning possible limitations imposed by Amur tiger on Amur leopard, specifically changes in resource selection and density. First, I investigated whether resource selection by tiger, humans, or prey influenced resource selection by leopard. I tested this first hypothesis by fitting Resource Selection Functions (RSFs) to winter track surveys for tigers and leopards, three ungulate prey (sika deer [*Cervus nippon*], roe deer [*Capreolus pygargus*], wild boar [*Sus scrofa*]), and humans over three consecutive winter seasons (2015-2018). In the second chapter, I tested my second hypothesis on the degree to which tiger density or predicted relative resource selection by tigers, prey and humans explained leopard density. This analysis involved six years of photographic capture data and spatially explicit capture-recapture modeling (Borchers and Efford 2008). I also used photographic captures of leopard females with cubs to examine to what extent leopard reproduction might be suppressed by tiger space use or local density.

The results of this work will be particularly useful to government officials and LLNP managers as a basis for effective conservation planning for these two rare felids. Moreover, my analyses provide a status assessment for these two felids against which future studies can track the degree to which conservation interventions have been successful.

This thesis is divided into two publishable units, each a chapter formatted according to specifications for submission to the journal Ecology and Evolution.

CHAPTER 1: Resource partitioning between Amur tiger and Amur leopard in the Russian Far East

ABSTRACT

Interspecific competition between large carnivores may exacerbate conservation challenges, especially where these species are already at elevated risk of extinction. The recently observed population growth of endangered Amur tiger (*Panthera tigris altaica*) and critically endangered Amur leopard (*Panthera pardus orientalis*) within their current range in Southwest Primorye, Russia has raised the question about impacts of intraguild interaction on population persistence of the leopard. Over three winters (2015-2018) field teams collected winter track data to quantify habitat selection by Amur leopard in relation to landscape characteristics, ungulate prey, human activities and presence of a dominant competitor using Resource Selection Functions (RSFs). Resource selection by both species was best predicted by landscape features rather than prey resource selection. Leopards heavily selected steep slopes along major river and areas closer to settlements. I found that 43% of high-quality Amur leopard habitat not shared with tigers occurred outside protected areas, reflecting the expanding leopard range and their higher tolerance for human disturbance. Amur leopard did not demonstrate spatial avoidance of tigers, and female leopards with cubs were disproportionally observed in habitats selected by tigers. At present, coexistence with tigers in SWP does not induce fitness reduction in Amur leopards through large-scale habitat exclusion or suppression in reproduction implying that tigers cannot be considered as an immediate threat to the Amur leopard conservation.

INTRODUCTION

Interspecific competition can shape niche breadth and resource partitioning among mobile carnivores (Morse 1974). Specifically, the competition for shared prey is thought to structure carnivore guilds (Rosenzweig 1966, Fenchel and Christiansen 1977). Competitive pressure among carnivores is usually asymmetric, being greater on relatively smaller-bodied or less aggressive species. Efforts to avoid a dominant competitor in space or time might restrict access to critical resources – imposing higher energetic costs for resource acquisition (Gorman et al. 1998). Moreover, subordinate predators may suffer intraguild predation and kleptoparasitism (Palomares and Caro 1999, Caro and Stoner 2003). As a result, inter-specific competition may drive reductions in population density of subordinate competitors (Creel and Creel 1996, Durant 1998, Creel et al. 2001).

Throughout their range, tigers (*Panthera tigris,* Linnaeus, 1758) are the dominant predator while sympatric large felids, such as leopard (*Panthera pardus*, Linnaeus, 1758), are subordinate competitors. Yet, the leopard remains one of the most widespread and adaptable large felids on Earth (Jacobson et al. 2016). The leopard's ability to subsist on a broad range of prey (Hayward et al. 2006), and occupy human-dominated landscapes (Athreya et al. 2013, 2016), makes it less susceptible than other large felids to environmental variation, including varying competitor levels (Chapron et al. 2008, Lamichhane et al. 2019). Nonetheless, medium- to small-bodied prey dominate leopard diets, and sufficient density of prey in that size class is an important prerequisite for population persistence and sympatry with larger felids (Andheria et al. 2007, Hayward and Kerley 2008, Braczkowski et al. 2012). As with many large carnivores, habitat loss and fragmentation, along with illegal or unmanaged harvest of prey, have greatly reduced the amount and quality of habitat available to tigers and leopards (Dinerstein et al. 2006, Macdonald et al.

2010, Wikramanayake et al. 2010). Moreover, intraguild interactions are known to be mediated by direct and indirect human impacts (Steinmetz et al. 2013, Carter et al. 2015, Li et al. 2018). As their sympatric range becomes increasingly restricted, competition between tiger and leopard has increased and likely will continue to increase, exacerbating conservation challenges, especially where these species may already be at elevated risk of extinction (Rayan and Linkie 2016, Kumar et al. 2019).

Despite their coexistence for centuries, ever-changing environmental and land use conditions may abruptly shift the balance facilitating tiger and leopard coexistence (Wang and Macdonald 2009, Bhattarai and Kindlmann 2012), with potentially negative effects borne inordinately by the subordinate leopard (Wegge et al. 2009, Odden et al. 2010, Abishek Harihar et al. 2011). Whereas the negative effects of interspecific competition may be difficult to detect, competitive relationships have been honed by evolution and behavioral mechanisms to alleviate the impact of competition should be apparent (Creel et al. 2001). Across Asia, resource partitioning between tiger and leopard has been observed with respect to prey (Seidensticker 1976, Karanth and Sunquist 1995, Andheria et al. 2007, Mondal et al. 2012, Lovari et al. 2015), space, and time (Karanth, K. U.; Sunquist 2000, Steinmetz et al. 2013, Karanth et al. 2017, Kumar et al. 2019). Given that intraguild interactions are heavily mediated by environmental settings, there is no single or simple delineation of the relationship between tigers and leopards across their global range. Contemporary studies across their sympatric range are needed to better define competition and its consequences for populations dynamics.

Long-term persecution of tigers and leopards and habitat degradation have resulted in a remarkable reduction of their range across Northeast Asia (Miquelle 2015, Yang et al. 2016). Nowadays, the main population of Amur tigers occur within the Sikhote-Alin Mountain Range,

with a remaining sub-population occupying the East Manchurian Mountains in southwest Primorsky Krai or Province (hereinafter, SWP) and the bordering regions of Jilin and Heilongjiang Provinces of China. The range of the only wild population of critically endangered Amur leopard (*Panthera pardus orientalis*) (Stein et al. 2020) is confined exclusively to the SWP and adjoining areas of Northeast China. Thus, the geographic ranges of these two subspecies overlap only in this small transboundary region, with source populations occurring primarily on the Russia side of the border (Wang et al. 2017, Vitkalova et al. 2018). Long-term conservation efforts in the region, including establishment of the Land of the Leopard National Park (hereinafter, LLNP) in 2012, have resulted in a steady population growth in both species (Matiukhina et al. 2016, Wang et al. 2016, Xiao et al. 2016, Vitkalova et al. 2018). Although recent growth in the Amur leopard population remains auspicious, this critically small population will remain prone to extinction because of their geographic isolation; they lack the dispersal ability to naturally resettle their historic range in Russia (Miquelle et al. 2015) and expansion westward to the Changbaishan region of China has been slow (Wang et al. 2017, Ning et al. 2019). Within this context, it is also concerning that Amur leopards are co-existing with a growing number of tigers, at least since the 1970s when regular scientific observations began (Pikunov and Korkishko 1992). As a result, leopard behavior, demography, and habitat selection patterns may be changing, with the long-term consequences of interspecific competition as yet unknown. For instance, a rebounding population of Amur tigers in SWP may potentially drive Amur leopards to suboptimal habitats and suppress reproduction of the smaller felid. Potential implications of competition for Amur leopard reproduction might challenge the conservation of this critically endangered subspecies through increasing juvenile mortality and inducing risk effects altering spatial behaviour of breeding females (Laurenson 1995, Watts and Holekamp 2008, Fisher et al. 2014).

Evaluating these mechanisms requires an independent habitat assessment for each of the competitors. The most recent range-wide assessments of habitat use by Amur tiger and leopard were undertaken with data that are now fifteen-years old (Hebblewhite et al. 2011, 2012, 2014), predating establishment of the LLNP and related conservation actions that led to tiger and leopard resurgence in the region (Hötte et al. 2016). These large-scale investigations underscored the pre-dominance of prey as a major predictor of habitat suitability for both predators (Mitchell and Hebblewhite 2012). However, no study has considered potentially limiting effects imposed by tigers on habitat suitability and demographic responses of leopards. Following Hebblewhite et al. (2011), I used winter tracking data and resource selection functions (RSFs, Manly et al. 2002) to evaluate the degree to which contemporary resource selection by leopard is shaped by environmental covariates (i.e., terrain conditions and landcover type), the resource selection patterns of principle prey species (sika deer [*Cervus nippon*], roe deer [*Capreolus pygargus*], and wild boar [*Sus scrofa*]), human activity patterns, and potential encounters with Amur tiger. Although I anticipated both felids to exhibit similarities in habitat selection at a large scale, I expected leopards to select for landscape features that decreased their chance of encountering a tiger. I further hypothesized that tigers would impose demographic constraints by suppressing productivity of leopards, thus the encounter rate of female leopards with cubs should be lower in areas used more frequently by tigers.

METHODS

Study Area

The study area encompassed southwest Primorski Krai (SWP; 7,440 km^2), which extends southwest for 200 km from the Rasdolnaya River to the border with North Korea (Figure 1.1*a*).

The region is limited by the Sea of Japan to the east and by the Russia-China border to the west. Located in eastern spurs of the East Manchurian Mountains, the SWP rises from sea level to 800-900 m to the east. Average annual temperature in the region is +4 ℃, with January being the coldest month (average temperature -15.0℃). The precipitation regime is typical for a monsoonal climate (800-850 mm, annually), with the majority of precipitation (80%) occurring Apr-Oct. Winters are relatively mild, with a maximum average snow depth of 12 cm.

The region is 87.4% forested. The major forest type is deciduous (48%) with a predominance of Mongolian oak (*Quercus mongolica*) followed by mixed coniferous/broadleaved forest type (25.7%) with Korean pine (*Pinus koraiensis*), Ajan spruce (*Picea ajanensis*), Needle fir (*Abies holophylla*), Khingan fir (*Abies nephrolepis*) and various linden (*Tilia* spp.), ash (*Fraxinus* spp.), birch (*Betula* spp.) and maple (*Acer* spp.) species. Oak-dominated open woodland constitutes 10.6% of the area.

Four species of ungulates predominate in the area: sika deer (*Cervus nippon*), Siberian roe deer (*Capreolus pygargus*), wild boar (*Sus scrofa*) and musk deer (*Moschus moschiferus*). Amur goral (*Naemorhedus caudatus*) and water deer (*Hydropotes inermis)* recently discovered in SWP (LLNP, unpublished data, Darman et al. 2019) are extremely rare. Red deer (*Cervus elaphus xanthopygus*), one of the preferred prey of Amur tiger in the rest of its range in Russia (Miquelle et al. 1996, D. G. Miquelle et al. 2010, Yudakov and Nikolaev 2012), went locally extinct from this area in the 1990s. Sika deer are the most abundant ungulate species in the SWP (Miquelle et al. 2010, Aramilev et al. 2016) and are a dietary staple of Amur leopard (≈36% [Salmanova et al. 2013]) and Amur tiger (≈25% [Kerley et al. 2015]).

Nearly half of SWP, and most of Amur leopard range in Russia, is under protection within the Land of the Leopard National Park (2,619 km^2) with its surrounding buffer zone (823 km^2) and

Kedrovaya Pad State Nature Biosphere Reserve (180.4 km^2) (Figure 1.1). Approximately 259,000 people inhabit the region (71% urban) (Gorbatenko et al. 2012). The majority of settlements are located in the lower reaches of the rivers, near the coast or along the major roads. The two most high-traffic paved roads run through the entire region parallel to the coast to the south and along Razdolnaya River to the northwest, connecting the two biggest cities of Primorsky Krai, Vladivostok and Ussuriysk, with gravel roads connecting smaller settlements. Agriculture is concentrated primarily in Razdolnaya River basin in the north of the SWP, and sparsely (individual farms) in the central and southern parts of this region. Road density declines from the lowlands to the higher elevations of the region.

The focal area for this study (1,670 km^2) constituted nearly 1/4 of SWP and encompassed Kedrovaya Pad State Nature Biosphere Reserve, central and northeastern parts of the Land of the Leopard National Park plus the buffer zone and small portions of adjacent hunting leases (Figure 1.1*b*). The study area stretches north to south and covers most of the region's prevalent vegetation cover and land use types.

Sampling Design

Using winter track survey data, I employed a used-available design to fit RSFs (Boyce and McDonald 1999, Boyce et al. 2002) for Amur tiger, leopard, herbivores (primary prey), and humans (disturbance and poaching risk). Individuals were not known, so resource units were sampled across each population as a whole (Manly et al. 2002).

Track data were collected over three successive winter seasons from December 2015 to March 2018 (Table 1.1). During winters 2015/2016 and 2016/2017 data were gathered in two different ways. First, individual tiger and leopard were snow tracked on foot with their individual

paths considered a survey transect and any other tracks (tiger, leopard, prey, human) intercepted along this transect recorded as independent sightings. Secondly, field staff surveyed independent transects designed to capture a range of relief features, vegetation cover and land use types (during the final winter season 2017/2018 only independent transects were sampled). Transects were positioned predominantly across major watersheds in lower, middle and upper reaches of the rivers. Coastal areas within the study area were not surveyed presuming low probability of encountering tiger and leopard there. While conducting surveys, the geographic coordinates of all fresh tracks (<24 hours) of ungulates were recorded along with evidence of occurrence by tigers, leopards, and humans. For both felids, evidence of their occurrence included pawprints, prey kills, feces, and territorial markings (visual and scent). Evidence of human disturbances included footprints, logging, hunting debris (e.g., shell casings, skins and other parts), tracks from off-road vehicles (e.g., snowmobile), unattended vehicles, campfires, artificial salt licks, feeding grounds for ungulates, and presence of dogs (including feral dogs). All tracks belonging to the same individual or group of animals and humans within up to 10 m were recorded as a single observation. Tracks of ungulates, felids and humans were also recorded opportunistically across the study area whilst performing other daily routines, such as camera trapping, and were used as supplementary presence data for fitting RSFs. Field teams also recorded snow depth along both snow-tracking routes and independent transects, with measures taken systematically every kilometer and at every change of relief feature (e.g. slope, aspect, valley, ridge, plateau). On the independent transects the snow depth measurements were also taken at tiger and leopard track locations.

Overall, 3,574 animal and human track records were used for modelling resource selection, of which 272 (7.6%) tracks were collected opportunistically. For the purpose of ungulate model

validation, I used out-of-sample presence data collected over four winter seasons (2014/2015, 2016/2017, 2017/2018, and 2018/2019). In winter 2014/2015, these out-of-sample data stemmed from recording ungulate tracks opportunistically in the central and northern parts of the region both within and outside protected areas. Aerial surveys conducted by the LLNP each winter starting from November 2016 provided an additional out-of-sample data set. In total, 818 sika deer, 332 roe deer and 214 wild boar occurrence records were available for validation purposes.

Environmental Covariates

Terrain variables (elevation, slope, hillshade, and ruggedness) were calculated from an SRTM digital elevation model (Farr et al. 2007) with 90-m resolution (Appendix 1.1). The terrain ruggedness index (Riley et al. 1999) was quantified as the topographic heterogeneity in a neighborhood of 3×3 and 5×5 raster cells. Higher hillshade values indicated southern aspects that receive more solar illumination and were presumed to have less snow. For snow, I additionally used Normalized Difference Snow Index (NDSI; Hall and Riggs 2016, Riggs et al. 2017) data to calculate percent of the cold period (mid-Nov – mid-Apr) that each grid 500-m^2 cell was covered with snow in each study season. The NDSI snow cover metric was compared to snow measurements taken on the ground, using Pearson's correlation test and linear regression, to evaluate its ability to reflect differences in snow depth. A Wilcoxon signed-rank test was used to examine whether felids occurred in areas of shallower snowpack, or the degree to which leopard and tiger occurrence differed by snowpack values.

Measured biotic variables included vegetation cover type (nonforest, open woodland, oak, deciduous, mixed deciduous/coniferous) and percent tree cover (MODIS Vegetation Continuous Fields, DiMiceli et al. 2017). I further calculated distance to river (for larger rivers and their main

tributaries only). For measures of human disturbance, I calculated distance to settlement, distance to primary road, road density and distance to protected area. Acknowledging that the spatial scale at which explanatory variables are measured can affect inference about animal resource selection (DeCesare et al. 2012, McGarigal et al. 2016), I calculated road density within varying rectangular neighborhood of 5, 10, 15 km^2 in size.

Statistical analysis

For the used-available design, the relative probability of selection is acquired following Boyce et al. (2002) and Manly et al. (2002) as:

$$w(x) = \exp(\mathbf{x}\boldsymbol{\beta}),$$

where *w(x)* is the relative probability of selection as a function of explanatory variables, x_n, and $\boldsymbol{\beta}$ is a vector of estimated regression coefficients.

In selecting available points for comparison to the observed used points, I attempted to control for two key sampling issues: autocorrelation in the track production and detection process, and the ratio of used to available samples (Johnson et al. 2008, Beyer et al. 2010, Northrup et al. 2013). In the first case, collected track data were inherently autocorrelated, but its scarcity did not allow for thinning, as it could further reduce limited sample size. Therefore, I corrected for autocorrelation in the sample of available locations by drawing it so as to induce similar levels of autocorrelation as in the observed data assuming this would balance potential bias in the coefficients. To achieve this, I first generated three subsets of randomly located transects within the focal area (one subset for each year), with transect length drawn randomly from the distribution of surveyed transect lengths for the corresponding year. On each random transect, I then drew locations at random from a uniform distribution at a density set by the observed density of tracks

for a specific species and year, thus inducing the same level of spatial correlation as the observed data.

In the second case, whereas a large number of available points is generally considered ideal in the analysis of presence-only data (yielding reductions in variance estimates; (Fithian and Hastie 2013), the ratio of used to available units may affect the inferences drawn from RSF model coefficients (Northrup et al. 2013). I determined the optimal number of available units for each species based on overdispersion ($\hat{c}$; calculated as the model residual deviance over degrees of freedom; Fletcher 2012). For instance, a large number of available units (10,000) relative to a small sample of used units (range 291-1569) resulted in under-dispersion ($\hat{c}<1$) that can potentially result in overestimated standard errors and mislead inference (Sellers and Morris 2017). For each species, I increased or decreased availability samples until achieving $\hat{c} \approx 1.0$. Importantly, to retain the autocorrelation pattern in the data, increasing or decreasing the total number of available points was achieved by increasing or decreasing the number of random transects sampled, not the number of generated points along any given random transect. Overall, the chosen ratio of used to available units for any given species never exceeded 1:10.

Relatedly, Warton and Shepherd showed (2010) that logistic regression estimates converge to inhomogeneous Poisson process (IPP) estimates when the size of the presence-only data remains fixed and the background sample grows infinitely large. Since there is a limitation on using large background samples for a small sample of presence records (as demonstrated in the last paragraph), I adopted the infinitely weighted logistic regression (IWLR) approach described by Fithian and Hastie (2013), which assumes logistic regression to approximate an IPP regardless of the ratio of 1's to 0's as long as an appropriately large weight is added to the existing availability sample. I

determined the appropriate weight (e.g., 1000, 2000, or 3000) based on the expectation that $\boldsymbol{\beta}$ values would stabilize after the appropriate weight was applied.

To predict potential encounters with prey and anthropogenic risks across the landscape, I initially fit RSF models separately for humans and each of the three primary prey species (sika deer, roe deer, and wild boar). The resource selection for each species predicted across entire SWP at a 90 m scale were considered as explanatory variable in felid resource selection. In the predator models, I also tested individual prey RSF values against a combined metric of prey occurrence (averaged value of the three prey-based RSFs). Lastly, the best RSF model for tiger was likewise included as a covariate in the RSF for leopard. When RSFs were used as explanatory variables, values were averaged within defined rectangular neighborhoods of 0.5, 1, 2, and 3 km^2 to evaluate potential scale-dependent effects. Prior to model fitting all continuous variables were standardized using the z-score transformation (Schielzeth 2010). Spatial data were managed using ArcGIS 10.2 (Environmental Systems Research Institute 2013) and all statistical analyses were performed within the R environment (R Core Team 2019).

Candidate models first compared linear versus non-linear (polynomial) parameterizations of each covariate, as well as alternative scales for each covariate, as appropriate. To guard against multi-collinearity, multivariable models included only pairs of variables having a Pearson correlation coefficient ≤0.7. Additionally, I compared coefficients estimated in each of the candidate global models against univariate models. Where meaningful changes in coefficient estimates were observed (large effect size change or change in coefficient sign) then variables causing this changes were not used in the same model (Hosmer et al. 2013). For each species, I produced a candidate model set that included all possible combinations of uncorrelated and not confounded variables, with models ranked based on Akaike Information Criteria (AICc) corrected

for small sample size and Akaike weight (w_i; Burnham and Anderson 2002). From the top-ranked global model, backwards model selection proceeded to identify the most parsimonious subset of covariates (Hosmer et al. 2013). Final models were checked for issues of multi-collinearity by ensuring Variance Inflation Factors (VIF) ≤ 5 (O'Brien 2007).

Initially, I tested whether treating the categorical variable of year as a random effect would improve model fit. However, the prey and predator models captured the variation among years most effectively (in terms of AIC model support and coefficient stability) by including the temporally dynamic snow cover variable. In fact, when snow was included as a covariate, models including a random effect of year failed to converge, due to confounding. However, resource selection by humans did not support effects of snow conditions, and as such I included a random effect of year to account for inter-annual variation in the human RSF models only.

For each felid I built an array of model sets each representing a hypothesis on drivers of resource selection such as environmental, prey-only, human-only, and hybrid models. The latter included prey, human or tiger RSF and uncorrelated variables. Within each model set the best model was defined based on ΔAICc and AIC weight. Then these top models were further compared to define the ultimate top model. To evaluate predictive capacity of the top model for each species, I employed five-fold cross validation following Boyce et al. (2002). In addition to internal cross-validation, I adopted the approach of Johnson et al. (2006) to evaluate ungulate RSF models using out-of-sample data. I also used the same out-of-sample ungulate records to calculate kernel track density for each ungulate species and to test for correlation between the track density index (as a potential measure of prey density) and RSF spatial predictions.

To test for potential effects of competition on Amur leopard reproduction, I used photographic capture data on female leopards with cubs obtained within the same time frame

(2015-2018) from camera trap stations deployed across the LLNP. I compared the frequency at which leopard litters were observed with respect to ranked RSF values from the best leopard and tiger models predicted across entire SWP. For this comparison I binned RSF values into ten intervals based on quantiles. Ultimately, I reclassified RSF values into two major categories representing high versus low habitat quality to quantify spatial overlap in prime habitat for the two felids and examined the potential for a large-scale displacement of Amur leopard by tiger. High quality habitat was defined as the range of RSF bins comprising ≥90% of all used points of the target species.

RESULTS

Data collection

In any given year, the number of surveyed transects and length of snow tracking sessions varied depending on snow conditions. Over the winters, tiger tracks were encountered more often than leopard tracks with a mean of 0.31 versus 0.24 tracks/km, respectively (Table 1.1). For large herbivores, sika deer were encountered most, followed by roe deer and then wild boar. Additionally, 464 records of human presence and 1209 snow measurements were obtained.

Snow conditions

Snow depths measured at tiger (n=234, $\bar{x}$ =19.42±9.92 SD cm) and leopard (n=188, $\bar{x}$=18.3±10.72 SD cm) locations did not differ (W=23519, P=0.22). However, leopard occurrences were found at significantly lower snow depths than occurred at random based on Wilcoxon signed-rank test statistic (n=779, $\bar{x}$=21.10±12.52SD cm; W=82435, P<0.05) while tiger occurrences did not (W=96832, P=0.14). When combining records over three years, local snow depth was significantly

correlated with the snow metric derived from NDSI (r=0.56, P<0.001), although the relationship varied among years. Furthermore, a significant linear relationship existed between the percent of time each grid cell was covered with snow and the snow depth measured in centimeters (snow depth = 1.18 + 0.35*percent time; $F_{1,1207}$=544.5, P<0.001, adj-R^2=0.31), validating use of the NDSI variable for representing snow cover in RSF models.

Resource Selection Functions

Internal model validation for prey models indicated strong concordance between expected and observed values (within ranked bins of predicted RSF values) for sika deer (adj-R^2=0.91) and roe deer (adj-R^2=0.89), while low concordance for wild boar (adj-R^2=0.40) indicated low predictability of their space use patterns. χ^2 GOF tests indicated significant deviations mostly within the lower ranked bins where ungulate use was consistently underestimated. Mapped RSF predictions (Figure 1.2) were slightly-moderately correlated (r = 0.19-0.49) with kernel track density derived from out-of-sample data for these three ungulates, with wild boar exhibiting the lowest correlation (Table 1.3). Correlation strength increased somewhat with the scale over which RSF predictions were averaged, e.g. r = 0.65, 0.39 and 0.25 for sika deer, roe deer and wild boar, respectively, when RSF predictions were averaged within 3 km^2.

The best-supported model for human activity predicted higher probabilities of selection in areas closer to settlements and having a higher road density (Table 1.5). Further, human activities were predicted to occur disproportionately along south-facing aspects, on shallower slopes, and in areas having a higher percent tree cover. Exploring ungulate and predator responses to the human RSF in univariate models revealed differential responses among species and scales (Table 1.2). Sika deer generally avoided areas of high human activity (apparent strength of avoidance

increasing with spatial scale), whereas roe deer generally selected areas associated with human activity (strength of selection diminishing with increasing spatial scale). In contrast, wild boar selected areas associated with humans at fine spatial scales (≤ 1 km^2), while avoiding those areas at broader spatial scales (2-3 km^2). Despite being highly predictive of human activity ($r = 0.99$, Table 1.3), as an explanatory covariate the human RSF did not perform as well as anthropogenic landscape variables *per se* (e.g., proximity of a road or settlement), and was thus not retained in any of the final models.

For each of the prey species, a clear top model was observed given $\Delta \text{AIC}_c \geq 4.88$ for alternative models (Table 1.4). Although all three ungulates strongly avoided steep slopes, across species the top models varied in the contributing variables retained (Table 1.4). Sika deer and wild boar selected areas away from human settlements and closer to protected area boundaries (Table 1.5). To some degree, sika and roe deer responded differently to roads, with roe deer selecting areas of intermediate road density and sika deer avoiding areas of increasing road density at the 10 and 15-km^2 scale, respectively. Sika deer also selected for areas having higher tree and snow cover.

For tiger and leopard, models containing environmental variables received substantially more support than models that included prey RSFs or human RSF covariates, "hybrid" models that included as covariates prey RSFs and uncorrelated environmental covariates (Table 1.6). According to the best supported model, tigers selected areas having shallower slopes, lower overall road density (5-km^2 scale), higher percent tree cover, south-facing slopes, and intermediate snow cover (Table 1.5). For leopard, a positive association with topographical ruggedness (5×5 grid cells) was the main driver of resource selection, followed by an affinity for areas closer to settlements (Table 1.5). The leopard was the only species that responded positively to terrain ruggedness and slope (ruggedness was the stronger predictor). Moreover, leopards were the only

species to select areas close to rivers (other species appeared indifferent to rivers). However, like tigers, Amur leopards selected south-facing aspects and areas having a higher percent of tree cover with moderate snow cover. Importantly, the tiger RSF was not a useful predictor of resource selection by leopards (models containing tiger RSF AIC$_c$ ≥ 165.20 over top model; Table 1.6).

From the camera trap surveys 57 captures of leopard females with cubs, representing 32 different litters were documented. The majority of litter captures (77%) fell within the highest RSF values for leopard (i.e., bins 9 and 10 of the top leopard RSF; Figure 1.3b). Averaging RSF predictions over a rectangular neighborhood of 0.5-3 km^2 indicated that, regardless of scale, most litter occurrences were observed above mid-rank 5, e.g., at a scale of 3 km^2 88% of captures were found within habitat ranks 7-10. The same pattern was observed in comparison to Amur tiger habitat ranks, where 86% of leopard litter captures were recorded in ranks 8-10 of the top tiger RSF. On average, the correlation between the number of leopard litter captures and RSF bin rank was 0.83 for leopard models and 0.85 for tiger models ($P<0.05$).

I ultimately categorized Amur tiger and leopard habitat as high (equal area bins comprising ≥90% of all used points) versus low quality. Accordingly, bins 5-10 for tiger (89% of occurrences) and bins 6-10 for leopard (90% of occurrences) were considered to be of high habitat quality. The predicted amount of high-quality habitat for tigers (1648 km^2) was more than 2-fold greater that for leopards (778 km^2) in this region. Overlaying these two binary habitat depictions indicated 1897 km^2 of high-quality habitat shared by tiger and leopard, of which 81% of occurred within LLNP and its buffer zone, and 2926 km^2 of shared low-quality habitat (Figure 1.4). About 43% (338 km^2) of the Amur leopard habitat not shared with tigers fell outside protected areas. Nevertheless, inside and outside the Park, the ratio of tiger to leopard habitat (shared and not

shared) was approximately the same, with 23% of tiger and 27% of leopard habitat occurring outside protected area.

DISCUSSION

The results of this study did not indicate evidence of competitive exclusion of leopards by tigers and that competitive pressure may drive leopard space use patterns. Human activities have played a leading role in shaping the distribution of tiger and leopard in and around the Park. Foremost, leopards appeared considerably less sensitive than tigers to areas of higher human activity, with leopards selecting areas closer to human settlements while tigers avoided areas of increasing road density. This contrasts to some degree with Hebblewhite et al. (2011) who reported leopards selecting areas closer to protected area boundaries and away from roads. But the landscape and population context experienced by leopards in this region has changed following establishment of the Land of the Leopard National Park. Officials estimated approximately 11-13 tigers and 20-28 leopards in SWP in 2007 (Pikunov et al. 2010), whereas minimum counts derived from camera traps (within the protected areas only) indicated 18 tigers and 48 leopards in 2016, and 25 tigers and 84 leopards in 2018 (LLNP, unpublished report). Standardized track surveys likewise indicated increases in encounters and likely abundance of major prey species over this same period, particularly sika deer (increasing from 9.9 to 12.4 tracks/10 km) and wild boar (1.3 to 2.9 tracks/10 km), although no noticeable change was observed with respect to roe deer (4.6 to 5.0 tracks/10 km; Pikunov et al. 2010 and this study). Given these changes in population context, it is reasonable to expect that resource selection patterns and, by extension, the distribution of both tiger and leopard might also have changed. The differential tolerance for human activities that I observed may reflect a shift by leopards in attempt to avoid tigers (Odden et al. 2010, Lamichhane et al.

22

2019). But, importantly, predicted space use by tiger did not directly influence leopard resource selection in this study, providing evidence against the competitive displacement hypothesis. Rather, throughout the species' global range leopards are highly adaptable (Athreya et al. 2013, 2016), persisting in areas of higher human disturbance regardless of the presence of dominant competitor (Balme et al. 2010, Swanepoel et al. 2015). Thus, the selection patterns observed herein may simply reflect expanding Amur leopard range following recent population increases. Notably, roe deer – one of the most preferred prey for Amur leopard (Pikunov and Korkishko 1992, Sugimoto et al. 2016, Yang et al. 2018) – were likewise shown to select areas of higher rod density, predicting higher space use by roe deer outside of the protected areas. Thus, use of human-modified areas by leopard also may be driven by changes in prey availability, although here too predicted space use by prey was not as good a predictor of leopard resource selection as environmental covariates. Ultimately, the true processes underlying the observed selection patterns in leopards should be investigated further, especially given the elevated mortality risks for large cats outside protected areas (Woodroffe and Ginsberg 1998).

There is no doubt that prey is a vital component of carnivore habitat (Mitchell and Hebblewhite 2012), and carnivores gravitate to areas of higher prey biomass (Elbroch and Wittmer 2012). Yet, my results indicated that predators responded more directly to landscape features than to inferred space use based on selection of those same features by their prey (i.e., including prey RSF as a covariate). One possible explanation is that predicted resource selection maps do not effectively capture the dynamic changes in the local intensity of use by prey to which predators respond (Keim et al. 2011). My attempt to correlate RSF predictions to the intensity of local habitat use showed the greatest correspondence for sika deer, the most common species in the region, although even that correspondence was relatively low ($r = 0.49$). Predators also likely integrate

expectations of prey encounters across multiple prey, potentially weighting putative prey habitat by the relative abundance of different species and prey catchability (Hopcraft et al. 2005, Balme et al. 2007). Here, my treatment of each static prey map as having equal weight and additive effects may have oversimplified the predator search process. Moreover, while prey availability may fluctuate depending on natural forage and snow conditions, the prolonged data collection and pooling of data across seasons and years required to map resource selection patterns may not effectively capture these changes. On the other hand, predators may select for landscape conditions in which prey are more vulnerable rather than more prevalent (Petrunenko et al. 2016). In my study area, wild boar dominated Amur tiger diet despite their local rarity (Kerley et al. 2015). Yet, given the rarity of wild board detections, I was unable to effectively model boar habitat selection patterns and thus could not link tiger space use with that of its principle prey. Predators also may be less adept at tracking dynamic variation in prey populations than they are of judging the more immediate costs of moving over rugged terrain and the risks imposed by encounters with humans, which prey likewise respond fairly predictably to. Importantly, in this region, large felids and their prey are forced to share an insular area, compressed by anthropogenic developments, without much room for spatial segregation. As such, the link between predator resource selection patterns and prey resource selection patterns is not straightforward.

Ultimately, leopard appeared more habitat-restricted than tiger, with 25% less high-quality habitat predicted in SWP for leopard that for tiger. This can be partly explained by tigers being more likely to select for wide river valleys and plateaus at intermediate and higher altitudes, areas that accumulate deeper snow cover, and for which leopards appear less tolerant. Yet, despite being more habitat limited and exhibiting a high degree of spatial overlap with tiger, I did not detect suppression of leopard reproduction by tiger. In fact, leopard females with cubs were

disproportionately observed using high quality-tiger habitat. Moreover, given the varying age of the observed Amur leopard litters (juvenile to nearly sub-adult), I suggest that leopard recruitment to older age classes is occurring in areas of high tiger use, although via the current analysis I cannot say ultimately whether rates of recruitment vary spatially. That both tiger and leopard litters were most consistently observed in areas of high tiger habitat quality indicate both tigers and leopards generally select for the same habitat to rear their young. The same was observed in Africa, where leopards were typically found in the areas with higher chance of encountering lions and both felids selected the same habitat as den sites (Balme et al. 2017). The fact that the majority of that habitat is found within the LLNP boundaries underscores the importance of protected areas in conserving rare species.

Beyond the scope of this study, leopard also may separate from tiger behaviorally by employing a fine-scale spatiotemporal avoidance strategy even in the areas where habitat use by the larger predator intensifies (Swanson et al. 2016, Lamichhane et al. 2019). Across the international border, temporal separation between Amur tiger and leopard in China with no large-scale displacement was documented (Li et al. 2018). In my study, strong selection for rugged slopes along river valleys and declining selection with distance from rivers may indicate that leopards use local terrain features as escape cover. Rugged terrain can substantially decrease visibility, especially in the absence of foliage, and would thus minimize the chance for leopards being located by tiger (Vanak et al. 2013). This in turn may indicate, though indirectly, a reactive rather than predictive response of leopards towards tigers (Broekhuis et al. 2013). Previous studies on Amur leopard spatial ecology (Pikunov and Korkishko 1992) also emphasized the importance of rugged terrain as one of the major determinants of habitat quality.

Increasing density of competitors along with natural prey scarcity have a potential to exacerbate interspecific competition (Mondal et al. 2012*a*, Rayan and Linkie 2016, Kumar et al. 2019). Thus, a threshold of density of a dominant intraguild competitor should exist, beyond which a subordinate shifts its habitat use into suboptimal habitat rather than temporally separates at the home range level so that to avoid aggressive encounters (Harihar et al. 2011). This does not appear to be the case with tiger and leopard in SWP. The evidence from Southeast Asia suggests that the top-down effects imposed on leopards vanishes at densities below 1 tiger/100 km^2 (Steinmetz et al. 2013). Although the density of tigers in LLNP is among the highest recorded across the subspecies' range (ANO Amur Tiger Centre, unpublished report), it is still low (0.42/100 km^2) compared to other parts of the tiger global range (Bisht et al. 2019, Harihar et al. 2020). For comparison, Amur leopard density in LLNP over the six-year period was three times higher (1.38/100 km^2, see Chapter 2). Since we have been observing simultaneous increases in both tiger and leopard numbers in SWP, it is unlikely that tigers limit leopard numbers, though the joint analysis of the population growth rate is needed.

My findings agree with Li et al. (2018) who observed leopard site occupancy being unaffected by the presence of tigers. Still, on the China side of the border, tiger density was an order of magnitude lower than in SWP (Xiao et al. 2016). In looking to the future, the prey biomass at this northern limit of the two species' range is naturally low suggesting lower potential carrying capacity compared to contemporary tiger and leopard range in South and Southeast Asia (Miquelle et al. 2010). As such, I do not anticipate substantial density increases unless substantive inflation of ungulate numbers occurs. The greater concentration and intensity of human activities on both Russia and China side of Amur leopard range pose greater constraints on continued range expansion, resulting in locally higher densities of both tigers and leopards and, by extension,

greater potential for interspecific competition. Although we've observed increases in prey and predator numbers since formation of the protected area and related conservation measures, those increases may be unlikely to persist given that concentration and intensity of human activities on both the Russia and China side of Amur leopard range pose considerable constraints on continued range expansion. Thus, for the foreseeable future, I expect human activities to pose greater conservation concerns for Amur leopard than continued increases in Amur tiger within the region.

TABLES: CHAPTER 1

Table 1.1. Survey effort and amount of track data of Amur tiger, Amur leopard, their ungulate prey and humans collected for three winters 2015-2018 in Southwest Primorsky Krai, Russia.

Year	# of transects	Total length, km	Mean length (SD), km	Sika deer	Roe deer	Wild boar	Amur tiger	Amur leopard	Human
2015/ 2016	50	487.87	9.76 (4.73)	458	159	64	130	113	80
2016/ 2017	31	339.85	10.96 (4.39)	575	186	90	118	83	237
2017/ 2018	30	383.25	12.77 (3.75)	536	296	222	134	95	147
Total	**111**	**1210.97**		**1569**	**641**	**376**	**382**	**291**	**464**

Table 1.2 Effect of human disturbance expressed by human Resource Selection Functions (RSF) averaged at four scales on resource selection by three ungulates, Amur tiger and leopard based on winter track data from 2015-2018. Negative values indicate avoidance and positive values indicate selection, relative to the defined availability.

Species	β-coefficients				
	90 m	500 m^2	1 km^2	2 km^2	3 km^2
Sika deer	0.06*	-0.11*	-0.19*	-0.24*	-0.24*
Roe deer	0.38*	0.23*	0.16*	0.11*	0.11*
Wild boar	0.24*	0.11*	0.04	-0.02	-0.01
Tiger	0.14*	-0.02	-0.08	-0.12*	-0.11
Leopard	0.08	-0.08	-0.06	0.05	0.09

* - statistically significant coefficient at α=0.05

Table 1.3 Model diagnostics for the top ungulate, Amur tiger and Amur leopard RSF models based on winter track data collected in SWP for three winter seasons (2015-2018). A - indicates no external model validation due to lack of out-of-sample data.

Type	Model diagnostics	Sika deer	Roe deer	Wild boar	Humans	Amur tiger	Amur leopard
Internal	Spearman rank correlation	0.99	0.95	0.91	0.99	0.96	0.94
External	Out-of-sample data	818	332	214	-	-	-
	χ^2 GOF test, *p*-value	119.48, *p*<0.05	27.81, *p*<0.05	39.73, *p*<0.05	-	-	-
	Correlation with kernel track density	0.49	0.33	0.19	-	-	-

Table 1.4 Comparison of top three RSF models for sika deer, roe deer, and wild boar. Covariate definitions given in Appendix 1.1. Shown here are the number of estimated parameters (K), Akaike's Information Criterion with small-sample adjustment (AICc) and, by species, the difference in AICc value (ΔAICc) and AICc model weight (w_i).

Species	Model structure	K	ΔAICc	w_i
Sika deer	slope + slope^2 + hillshade + tree cover+ snow + snow^2 + dist to protected area + roadens15 + settl + settl^2	11	0.00	1
	slope + slope^2 + hillshade + tree cover+ snow + snow^2 + dist to protected area + roadens5	9	44.03	0
	slope + slope^2 + hillshade + tree cover+ snow + snow^2 + dist to protected area + settl + settl^2	10	63.82	0
Roe deer	slope + snow + snow^2 + roadens10 + roadens10^2	6	0.00	1
	slope + snow + snow^2 + tree cover+ mainroad + mainroad^2	7	64.38	0
	slope + snow + snow^2 + roadens15 + vegetation (mixed + decid + nonforest + oak)	8	69.10	0
Wild boar	slope + snow + dist to protected area + settl + settl^2	6	0.00	0.85
	slope + snow + dist to protected area + roadens15+ roadens15^2 + river	7	4.88	0.07
	slope + snow + dist to protected area + mainroad + mainroad^2 + river	7	4.91	0.07

Table 1.5 Estimated effects of fitted resource selection models (SE) from the top fixed-effect models for ungulates and predators, and the top mixed-effect model for humans. Standardized coefficients (β) of covariate effects along with standard error (SE). Covariates defined in Appendix 1.1. A - indicates the variable was not included in the most supported model.

Model parameter	Sika deer		Roe deer		Wild boar		Humans		Amur tiger		Amur leopard	
	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
Intercept	-8.04*	0.05	-8.63*	0.07	-8.48*	0.07	-8.99*	0.15	-9.00*	0.11	-9.09*	0.10
Slope	-0.33*	0.04	-0.42*	0.05	-0.35*	0.06	-0.88*	0.07	-0.48*	0.08	-	-
Slope^2	-0.03	0.03	-	-	-	-	-	-	0.08	0.04	-	-
Ruggedness (5×5)	-	-	-	-	-	-	-	-	-	-	0.65*	0.08
Hillshade	0.23*	0.03	-	-	-	-	0.28*	0.07	0.34*	0.07	0.28*	0.05
Distance to river	-	-	-	-	-	-	-	-	-	-	-0.20*	0.07
Tree cover	0.43*	0.04	-	-	-	-	0.36*	0.06	0.28*	0.09	0.33*	0.10
Snow cover	0.15*	0.03	-0.11*	0.04	-0.13*	0.05	-	-	0.06	0.06	0.02	0.07
Snow cover^2	-0.12*	0.03	-0.08	0.05	-	-	-	-	-0.21*	0.07	-0.32*	0.08
Dist. to protected area	-0.15*	0.04	-	-	-0.21*	0.07	-	-	-	-	-	-
Dist. to settlement	0.21*	0.04	-	-	0.21*	0.07	-0.36*	0.06	-	-	-0.43*	0.07
Dist. to settlement^2	-0.28*	0.03	-	-	-0.36*	0.06	-0.09	0.06	-	-	-	-
Road density, 5 km^2	-	-	-	-	-	-	-	-	-0.41*	0.07	-	-

Road density, 10 km^2	-	-	0.71*	0.07	-	-	-	-	-	-	-	-
(Road density, 10 km^2)^2	-	-	-0.34*	0.06	-	-	-	-	-	-	-	-
Road density, 15 km^2	-0.29*	0.04	-	-	-	-	0.28*	0.06	-	-	-	-

Random effect of season: variance (SD)	0.05 (0.22)

* - statistically significant coefficient at $\alpha=0.05$

Table 1.6 Model selection for Amur tiger and Amur leopard, showing only the top model for each component (e.g., the environmental component consisted of 20 candidate models for Amur leopard). Covariate definitions given in Appendix 1.1. Shown here are the number of estimated parameters (K), and the difference in AICc value (ΔAICc) and AICc model weight (w_i).

Species	Model set	K	ΔAICc	w_i
Amur leopard	Environmental	8	0.00	1
	Hybrid (prey RSFs + environmental)	9	30.74	0
	Individual prey RSFs (sika deer + wild boar 0.5 km^2)	3	100.94	0
	Averaged prey RSFs (1 km^2)	2	164.10	0
	Tiger RSF (hybrid)	2	165.20	0
	Tiger RSF (environmental)	2	172.44	0
	Human RSF (3 km^2)	2	193.30	0
	Null model	1	193.93	0
Amur tiger	Environmental	8	0.00	1
	Hybrid (prey RSFs + environmental)	6	26.87	0
	Individual prey RSFs	3	40.00	0
	Averaged prey RSF	2	145.28	0
	Human RSF	2	147.32	0
	Null model	1	152.93	0

FIGURES: CHAPTER 1
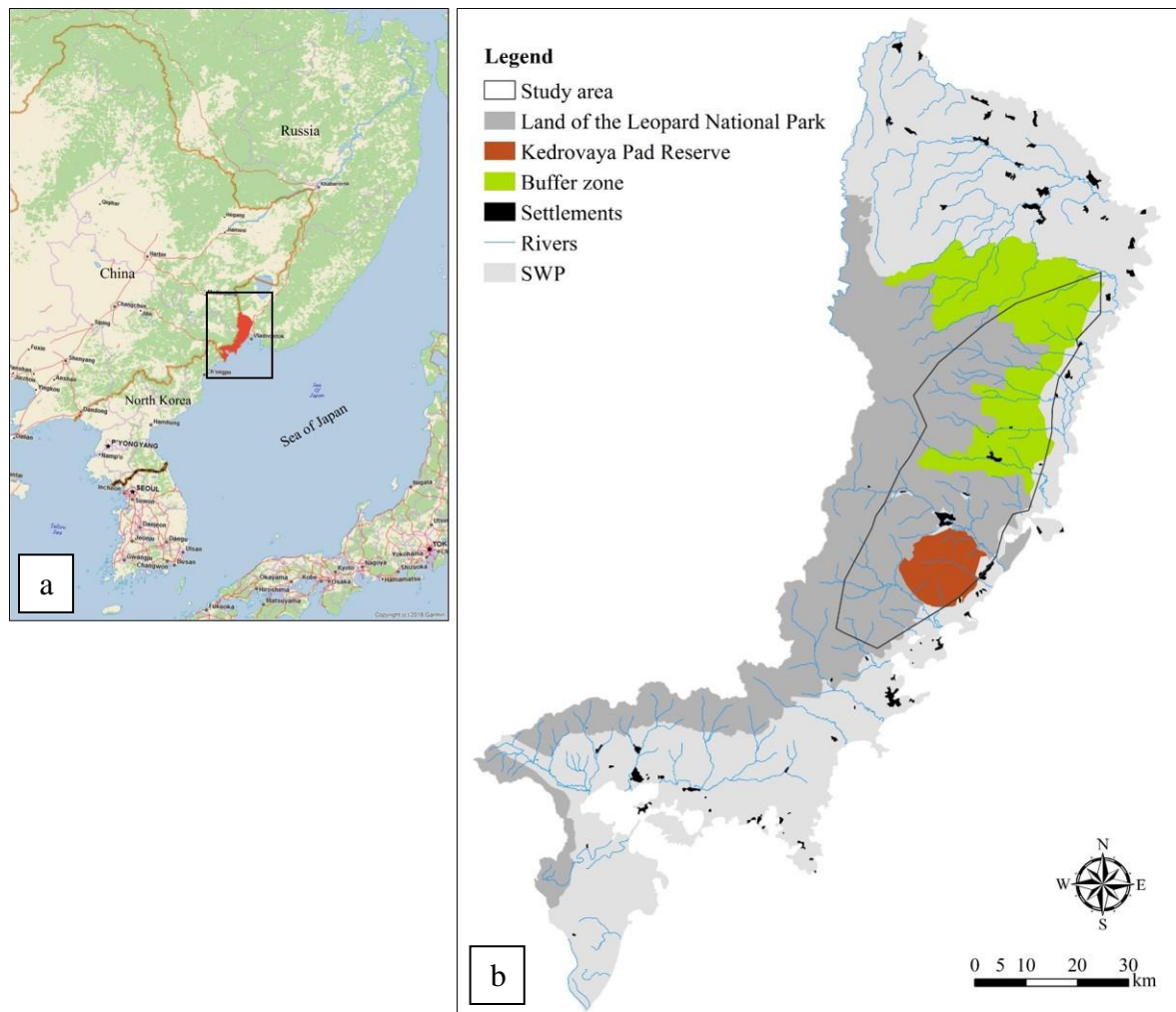
Figure 1.1. Location of focal study area for collection of Amur tiger, Amur leopard, ungulates (sika deer, roe deer, wild boar) and human winter track data during 2015-2018 (b) within southwest Primorsky Krai (SWP) (a).
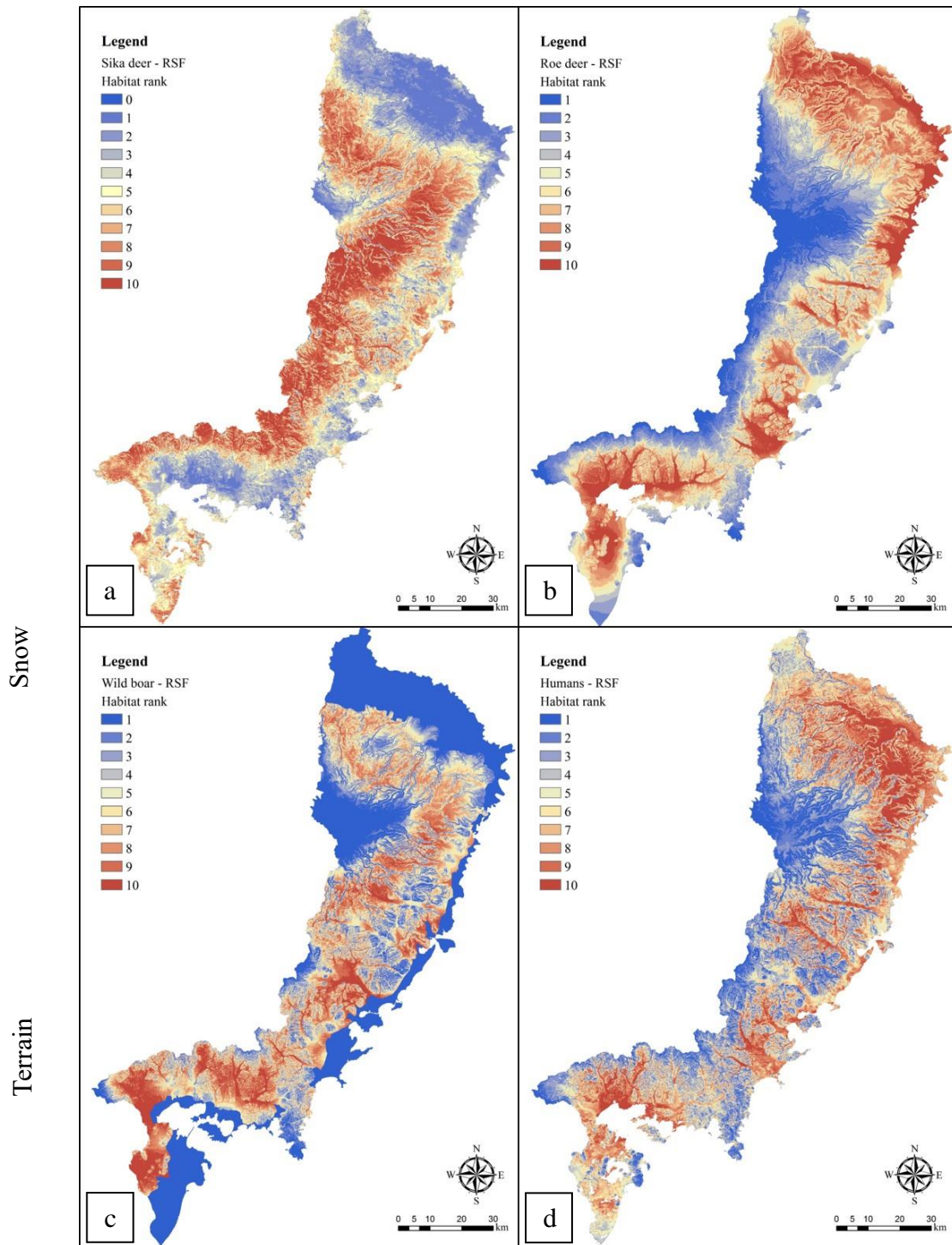
Figure 1.2 Relative probability of selection by (a) sika deer, (b) roe deer, (c) wild boar and (d) humans, predicted from the top model based on track data acquired winter 2015-16, 2016-17, and 2017-18, and with each bin corresponding to 10% of the predicted values across the landscape in ascending order of predicted probability.
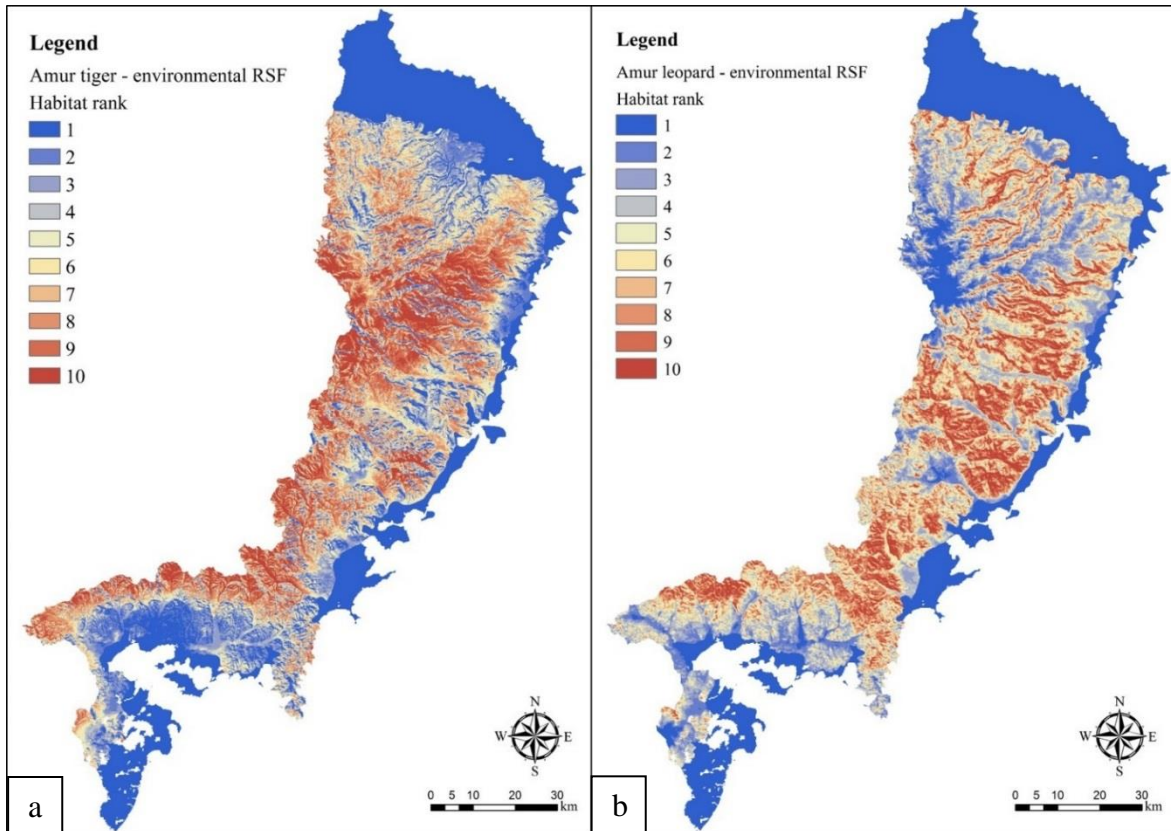
Figure 1.3. Relative probability of selection by (a) Amur tiger and (b) Amur leopard, predicted from the top model based on sign survey data acquired winter 2015-16, 2016-17, and 2017-18, and with each bin corresponding to 10% of the predicted values across the landscape in ascending order of predicted probability.
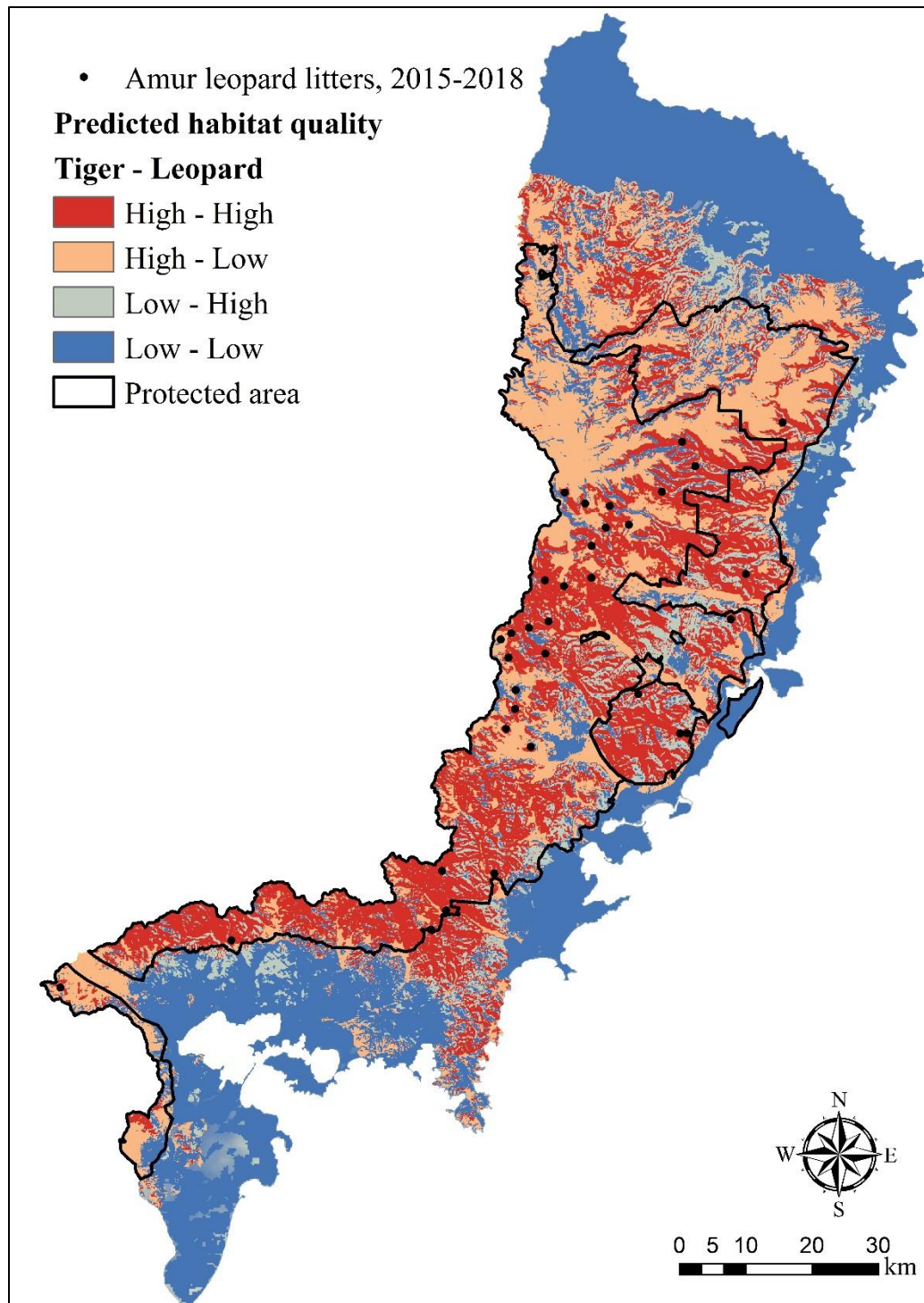
Figure 1.4 Overlap of Amur tiger and leopard habitat discretized in two major categories of high versus low quality based on the top environmental models for both felids. Overlaying this comparison is the location of leopard litters.

CHAPTER 2: Competition, prey and human drivers of Amur leopard density in the Russian Far East

ABSTRACT

Intraguild interactions among terrestrial carnivores can shape the distribution of subordinate competitors through such processes as spatial displacement and diminished recruitment. The factors governing coexistence of Amur tigers and leopards at their northern range, where both species are at risk of local extinction, are poorly understood. Here, I used photographic data obtained in the Land of the Leopard National Park, Russia during 2014-2019 to examine drivers of Amur leopard (*Panthera pardus orientalis*) and Amur tiger (*Panthera tigris altaica*) density with respect to prey, humans and each other. Densities of tiger and leopards were estimated at 0.42 and 1.38 adults/100 km^2, respectively. Tiger density was best predicted by putative habitat quality (based on resource selection patterns), while leopard density varied with the putative distribution of the most abundant prey – sika deer while appearing unaffected by tiger density. Amur leopard litters were also disproportionally observed in the areas of high tiger density. Despite tiger and leopard numbers being the highest since 1970s, I found no evidence for suppression of Amur leopard density or reproduction by the dominant tiger, likely owing to the highly adaptable behavior of leopards and the likelihood that populations of both felids may still remain below carrying capacity in the region.

INTRODUCTION

Holding all other considerations constant, areas providing greater amounts of a limiting resource are expected to maintain higher animal densities (Fretwell and Lucas 1969). It thus follows that comparing animal density to available resources, e.g. units of food, discrete habitat patches, or space, may reveal factors limiting population growth (Williams et al. 2002). For endangered large carnivores, density remains a key parameter used in population monitoring and conservation planning (Karanth and Nichols 1998, Silver et al. 2004, Jackson et al. 2006, Soisalo and Cavalcanti 2006, Walston et al. 2010, Tempa et al. 2019). However, the local density of predators will be mediated by, among other things, territoriality (Chanchani et al. 2018) and competition (Fedriani et al. 2000, Linnell and Strand 2000, Odden et al. 2010, Harihar et al. 2011, Steinmetz et al. 2013). As such, while density remains an important measure of population performance, it is likely insufficient on its own for identifying population drivers in heterogeneous landscapes shared by competitors.

Competing species may partition shared resources in space and time. In many sympatric carnivore dyads, competition limits the realized niche of the subordinate species with potentially deleterious consequences for population vital rates (Mills and Gorman 1997, Palomares and Caro 1999, Elbroch et al. 2015). For example, across the sympatric Asiatic range for tiger (*Panthera tigris*) and leopard (*Panthera pardus*) the apparent cost of coexistence is born inordinately by the smaller-bodied leopard (Rayan and Linkie 2016, Kumar et al. 2019). The spatio-temporal changes an individual makes in their resource use to mitigate one form of risk, e.g., to avoid a superior competitor, may lead to increases in another risk, e.g., exposure to human-caused mortality risk (Arjo and Pletscher 2004). For example, whereas protected areas play a fundamental role in the conservation of top carnivores (Balme et al. 2010, Wikramanayake et al. 2011, Farhadinia et al.

2019, Havmøller et al. 2019), larger-bodied or superior competitors (tiger) may displace smaller-bodied, inferior competitors (leopard) to peripheral areas where anthropogenic threats are elevated (Woodroffe and Ginsberg 1998, Naughton-Treves et al. 2005, Wittemyer et al. 2008, Odden et al. 2010). Yet, more generalist species like leopards (Hayward et al. 2006, Athreya et al. 2013) may demonstrate ecological plasticity by sustaining similar population densities across a gradient of tiger densities, prey biomass and human-caused risks (Swanepoel et al. 2015, Rosenblatt et al. 2016, Kafley et al. 2019). Nevertheless, given intensifying anthropogenic landscape changes occurring outside protected areas (Wittemyer et al. 2008), the conservation of so-called "plastic" species like leopards is increasingly of concern (Henschel et al. 2011).

This concern is perhaps most tangible for the critically endangered Amur leopard (*Panthera pardus orientalis,* Schlegel, 1857; Stein et al. 2020), which overlaps the endangered Amur tiger (*Panthera tigris altaica,* Temminck, 1984; Miquelle et al. 2011) in the transboundary region of southwest Primorye (SWP) of the Russian Far East and the adjacent provinces of Northeast China. Low overall abundances of tiger and leopard in China (Xiao et al. 2016, Vitkalova et al. 2018) may have minimized the degree to which competitive interactions might be evident. But given concerted conservation effort on the SWP side of their range, the Amur tiger population has increased ten-fold since 1972 when only three individuals were recorded (Pikunov and Korkishko 1992, FSBI Land of the Leopard, unpublished data). As a result, Amur leopard in the SWP have experienced relatively rapid and substantive increases in potential competition pressure from Amur tiger, which on top of changing prey availability and human pressures may be sufficient to suppress Amur leopard density. Moreover, increasing density of dominant competitor may impact Amur leopard productivity through juvenile mortality and changing

behaviour of breeding females that would tend to avoid areas of higher tiger density to protect their young (Laurenson 1995, Watts and Holekamp 2008).

Animal density usually connects to habitat use (Boyce et al. 2016). Given this, higher probability of habitat selection by tigers would predict higher density of the species. Therefore, it is reasonable to assume that leopard density would decline with increasing density of sympatric tigers. Although several studies demonstrated that incorporating information on resource selection (RSF; Manly et al. 2002) into spatial capture-recapture models improves density estimation (Royle et al. 2013, Proffitt et al. 2015, Loosen et al. 2019), this work represents the first attempt to do so for Amur tiger and leopard.

Therefore, the goals of this research were to a) evaluate the relative influences of prey availability, tiger density or habitat use, human disturbance, and habitat quality as drivers of Amur leopard density across SWP, b) contrast conditions that support higher densities of male versus female leopards – anticipating females to be prey-driven and males to be more sensitive to the availability of females and potential conflict with tigers, and c) gain insight into Amur leopard productivity in areas of relatively high versus low tiger abundance. This research relies on an extensive, six-year camera trap survey across the Land of the Leopard National Park (LLNP) – a protected area that, along with its buffer zone, encompasses more than a half of the entire range of Amur leopard in Russia. Using spatially explicit capture-recapture models (SECR; Borchers and Efford 2008, Efford and Fewster 2013), I expected density to correlate strongly with prey resources, but for leopard density to also be inversely related to tiger density. Further, I anticipated females with cubs to be more sensitive to potential encounters with tigers, and therefore for sightings of cubs to be higher in areas of relatively lower tiger density.

METHODS

Study area

Camera trapping for monitoring of Amur tigers and leopards was conducted in the Land of the Leopard National Park with its buffer zone and Kedrovaya Pad State Nature Biosphere Reserve (total area 3620 km^2). The study area is contiguous to the international border with China in the west and surrounded by the areas of various land use types such as hunting leases, state forestry enterprises, and private farms elsewhere (Figure 2.1). The border control fence stretching parallel to the international border with China at the distance of 1-12 km separates the Border Security Zone (BSZ, 1152 km^2) from the rest of the National Park. Thus, the BSZ represents a strip of land, where all economic activities as well as public access are highly restricted.

The Land of the Leopard National Park (hereafter, the Park) falls within the East Manchurian Mountain Range that divides Hunchun River in China and Amur Bay in Russia. The major rivers flowing into Amur bay run southward or eastward, while the main tributaries of Razdolnaya River (the largest river of SWP) run primarily northeastward. Altitudes range 800-900 m above sea level. The climate is monsoonal with precipitation totaling 800-850 mm annually. Winters are relatively mild with an average snow depth of 12 cm.

The SWP is characterized by various forest types, with oak-dominated (*Quercus mongolica*) deciduous forests covering 48% of the area. The mixed coniferous/broadleaved forest type with Korean pine (*Pinus koraiensis*), Ajan spruce (*Picea ajanensis*), Needle fir (*Abies holophylla*), Khingan fir (*Abies nephrolepis*) and various broadleaved tree species constitutes 25.7% of the area and is the most biodiversity rich forest type of the Russian Far East. The forests composed predominantly of birch, aspen and poplar together with mosaic riverine forests add up 12.7% of the area. The periphery areas of the Park have been exposed to wildfires and economic

development for decades and have been transformed into an open woodland, grassland and agricultural lands (13.6%).

The ungulate complex of the Park consists of four main species - sika deer (*Cervus nippon*), Siberian roe deer (*Capreolus pygargus*), wild boar (*Sus scrofa*) and musk deer (*Moschus moschiferus*). The recently discovered water deer (*Hydropotes inermis*; Darman et al. 2019) inhabits the southern portion of the Park and is believed to have recently arrived from adjacent China or North Korea. A few observations of Amur goral (*Naemorhedus caudatus*), close to the border with China, suggest this species is exceedingly rare in the region.

Most of the regions' settlements are situated outside the Park. The largest settlement located on the border of the Park does not exceed 6000 people. A main highway runs through the entire region north to south and bisects the Park in its central portion. Gravel roads connect smaller settlements to the main road. Most agricultural lands occur in the Razdolnaya River basin, with small individual farms are scattered in central and southern parts of the region.

Camera-trapping design and individual identification

Large-scale camera trap monitoring has been conducted annually in LLNP since 2013. The number of camera trap stations ranged 136-197 among years. Set-up of the seasonal camera trapping started in October and continued through January. All stations then operated simultaneously till May. This timing also known as intensive monitoring period allows a sufficient amount of tiger and leopard photographic data, as the peak numbers of tiger and leopard detections are observed from January till April (Matiukhina et al. 2016; Vitkalova, unpublished data).

Monitoring stations (each consisting of a pair of camera traps) were placed to maximize the probability of Amur leopard detection, specifically on animal trails, along ridges, and along

rocky edges of plateaus. Stations were approximately evenly spaced across the study area (Figure 2.1) at a minimum 2.5-3 km apart such that an area the size of the average Amur leopard female home range would contain 2-3 stations (Kostyria et al. 2003). At each station, cameras were positioned opposite each other to photograph both flanks of a passing animal. This camera trapping network also provided sufficient data on Amur tiger (*Panthera tigris altaica*), as both species tend to use similar movement corridors. However, tigers use roads more frequently than leopards (Yudakov and Nikolaev 2012) and from 2017 onwards extra stations were deployed on forest roads to augment the number of tiger detections.

Amur tigers and leopards were individually identified by stripe and rosette patterns, using ExtractCompare computer software (Conservation Research Ltd., Cambridge, UK). This software fits a 3D surface model to an animal image, extracts the pattern, and then compares the new pattern with those stored in the library to identify the most likely matches. Once the software makes a match, a human observer confirms or denies the match based on their visual comparison. During the whole period of study, two observers were responsible for animal identification – one for the tiger and one for the leopard. The sex of each animal was determined based on external genitalia visible on the images and other exterior features, such as shape of head and neck (e.g. mature males usually have a more massive neck with a dewlap below it compared to females). I treated a single photographic capture as an event of an animal presence at a station over one hour.

Spatially explicit capture-recapture modeling

The spatially explicit capture-recapture (SECR) approach has an advantage over conventional capture-recapture as it accounts for the spatial structure of a population as well as the spatial nature of the trapping process (Borchers and Efford 2008). The density of a studied population (D) is

defined as the intensity of a spatial point process that describes the distribution of home range centers. The observation process is commonly represented by a 2-parameter detection function having a baseline probability (g_0) that declines away from the home-range center over spatial scale sigma (σ; Efford 2004, Efford and Fewster 2013). As detection probability decays with increasing distance from home-range centers it is expected that at some point the area of integration (region over which the unknown activity centers are numerically integrated; Efford 2019) has a negligible effect on density estimates. Therefore, the area of integration is set up so that the animals that were exposed to the trap array during the sampling period have zero chance of having a home range center outside the area of integration.

The area of integration in this study was defined using the trapping grid during the 2019 sampling period, when the maximum number of stations were deployed. To each station, I applied a buffer having radius corresponding to 4σ, where σ was derived from the null model for males of the target species (Figure 2.2; Efford 2019). I clipped the resulting buffered grid to the boundary of Russia as I lacked landscape data for the neighboring region of China. To evaluate the degree to which the truncation of the buffer may have biased parameter estimation, I fit a null model (excluding spatial covariates) for the whole/untruncated buffer (including China) and compared the resulting density estimate to that estimated from the same model (excluding spatial covariates) fit to the truncated study area.

Within the truncated region of integration I masked areas of non-habitat such as sea, lakes, settlements, coastal marshlands, and agricultural lands using ArcGIS 10.2 (Environmental Systems Research Institute 2013). The region of integration was then overlaid with a gridded habitat mask having grid centroids spaced 2 km apart. The choice of spacing was a trade-off between the computational time and the precision of estimates, and further reduction of the

distance between the centroids had negligible effect on density estimates for both tigers and leopards.

I used six years of Amur tiger and leopard photographic data obtained 2014-2019. Within each intensive monitoring period (January – May), I selected a 120-day sampling period to satisfy the population closure assumption of no births, deaths or permanent immigration (Otis et al. 1978, Karanth et al. 2004*a*). Given the elusive nature of the focal species, the length of sampling period also allowed for more recaptures at multiple locations – a prerequisite for more robust density estimates (Tobler and Powell 2013). Transients were a potential source of bias because animals at the age of dispersal tend to make long-distance movements (without home range) or inversely stay close to the natal home range shortly after separation from their mothers (Pikunov and Korkishko 1992, Goodrich et al. 2010). To remove potential transients, I 1) excluded known cubs until they reach the age of reproduction (2.5-3 years) and 2) removed records of animals photographed at a single location only once over the six-year period. This resulted in excluding 10 tigers and 23 leopards from the analyses to follow.

Published resource selection functions (RSFs; Chapter 1) were included as covariates to test a set of hypotheses related to prey, humans, and competitors. As predator, prey and human RSFs were composed of common landscape covariates (see Chapter 1, Table 1.5), they were subject to multicollinearity if used together to model density. Therefore, candidate models for tiger and leopard density included one spatial covariate (a single RSF) only, representing a single hypothesis. RSF models were extrapolated to every 90 m resolution cell across the study area, averaged over rectangular neighborhoods of 1 and 3 km^2 yielding 3 scales of analysis (90 m cell + 2 higher levels of integration).

For the Amur tiger, I fit 24 candidate SECR models to test hypotheses related to prey availability (sika deer RSF, wild boar RSF, roe deer RSF alone or in combination, e.g. averaged RSFs for three species), anthropogenic disturbance (human RSF, road density at scales of 5 km^2 and 15 km^2, and distance to settlements), and habitat (tiger RSF). Next, for leopards, I fit the same series of models while further testing two additional hypotheses: the effects of competition (tiger presence [i.e., RSF] or density) and sexual segregation (density of male versus female leopards) on leopard density. To test the first hypothesis, I evaluated either tiger RSFs (3 levels: cell, 1 and 3 km^2) or the predicted tiger density surface (derived from a SECR fitted model) as covariates related to the density of leopards. For the second hypothesis, I split the data between male and female leopards to fit separate models following the same approach as above, but also included the predicted spatial density surface of one sex as a covariate in models for the other sex, i.e. males on females and vice versa.

I estimated density (D), g_0 and σ using maximum likelihood in R via package `secr` (v.4.2.2, Efford 2020, R Core Team 2019), applying a half-normal detection function. Individual heterogeneity was accounted for by including sex as a covariate on detection probability (g_0 and σ). Additionally, I allowed detection and density parameters to vary over time by including year as a covariate.

Each model was fit multiple times, each time starting with initial values from the preceding fit, until convergence was achieved as indicated by stable coefficients. I selected the top model based on Akaike Information Criterion (AIC; Burnham and Anderson, 2002) and AIC weights, with model selection uncertainty indicated where top models yielded ∆AIC <2.

RESULTS

Data collection and preparation

Both effort and the total number of leopards and tigers detected increased over time, with minimum numbers recorded in 2016 when a portion of the Park and the buffer zone were not surveyed (Appendix 2.1-2.2). A notable increase in detections was observed in 2017, when the number of captures of both tigers and leopards increased by 47% and 45%, respectively, compared to 2015 (the two years having similar levels of effort). While the number of tigers detected did not significantly change between 2015 and 2017, the number leopards was 25% higher in 2017. The proportion of stations visited by tigers had been steadily increasing over the course of the study from 23% in 2014 to 43% in 2019; the same was observed for the leopards which visited 17% more stations in 2019 than in 2014. The observed positive trend might be indicative of population expansion over time. The overall number of photographic captures of adult and sub-adult tigers and leopards between 2013-2019 was 1323 and 6025, respectively. From these records, researchers identified 72 and 228 individual Amur tigers and leopards, respectively. After narrowing to our 120-day sampling periods, 2411 captures of 172 leopards and 642 captures of 47 tigers were retained for SECR analysis.

The observed sex ratio in both species was skewed towards females, being more pronounced for tigers with 2-2.5 times more females than males since 2017 (Appendix 2.1-2.2). Female tigers were also photographed more often than males (mean 59%), whereas female leopards were less detectable (the number of female captures constituted roughly 27% on average of all leopard captures).

The area of integration totaled 6698 km^2 for tigers and 6060 km^2 for leopards. Comparison of density estimates for tigers between the null models based on the full and truncated buffers (that

included and excluded area in China, respectively) revealed that area truncation led to a 14% and 13% overestimation of density of tigers and leopards, respectively.

SECR model estimates

Of the 24 models considered for tiger, three were comparable given ΔAICc<2 (Appendix 2.3). Each of these top models included the tiger resource selection as a covariate on density, with model selection uncertainty based on the scale of integration for the RSF variable (90 m cell, 1 km^2, or 3 km^2). As a result, I opted to use the top model for inference rather than average model predictions. The top model (tiger environmental RSF averaged over 1 km^2) indicated a strong positive relationship (β=3.95, SE=0.75, Table 2.1) between tiger resource selection and tiger density (Figure 2.3), predicting a density of 0.42 tigers/100 km^2 (SD=0.35) across the region and a total abundance of 28 (23.43-33.63) tigers across the six-year study period (Table 2.2). Density was found not to vary annually, as a year covariate was not supported (Appendix 2.3). Based on the top model, the scale of movements (scaling parameter σ) for male tigers was ~48% greater than that of females, yet their detection probability (g_0) was ~55% lower than females (Table 2.2).

Of the 29 models considered for leopard, two were comparable in AIC (Appendix 2.4), with both including the sika deer RSF integrated over different scales as the sole predictor of leopard density. The top model included a positive relationship between leopard density and sika deer RSF values integrated over 1 km^2 (β=2.32, SE=0.36; Table 2.1, Figure 2.3*b*). Notably, the spatial scale at which density was best predicted was the same for both cats (1 km^2) despite the scales of movement being 1.6-1.8 times larger for males and female tigers, respectively, compared to leopards. The scale of movement by male leopards was 42% larger, and the detection probability 43.5% larger, than those estimated for female leopards (Table 2.2). As observed for tigers, models

including year as a predictor of density (alone or in combination with spatial covariates) were not supported (ΔAICc difference is 43.62). With data pooled across years, the best model estimated a density of 1.38 leopards/100 km^2 (SD=0.36) for an abundance of 83.83 (95% CI, 74.95-93.78) leopards across the region – roughly 3 times greater than observed for tiger. Tiger covariates (RSF or density) were not supported as explanatory variables for Amur leopard density. Nevertheless, predicted density surfaces from the top tiger and leopard SECR models were positively correlated (r=0.7, P<0.01).

I further failed to detect an effect of the density of the opposite sex as a local driver of density for the focal sex for leopards (Appendix 2.5-2.6). Yet, these models revealed that while female density was strongly related to spatial variation in resource selection by sika deer, the density of male leopards was negatively related to road density at the scale of 5 km^2 (Table 2.3, Figure 2.4) – potentially reflecting different limiting factors for females versus males (prey resources supporting reproduction versus areas safe from human-related risks). From the top model for each sex, I estimated 0.86 females/100 km^2 (SD=0.44; N = 52.92 females, 95% CI 44.56-60.48) compared to 0.49 males/100 km^2 (SD=0.20; N = 29.98, 95% CI 25.46-35.31).

A total of 118 photographic captures of 57 Amur leopard litters of various ages were recorded during this study (2013-2019). Contrasting the mean tiger density values across camera trap stations where leopard litters were detected (n=60) and not detected (n=161) indicated that leopards produced and reared cubs in areas of significantly higher tiger density (Wilcoxon signed-rank test, W=5602, P<0.001). The photographic capture rate of females with cubs was also significantly higher in the areas with increasing male leopard density (Wilcoxon test, W=6647, P<0.01).

DISCUSSION

As the first comprehensive consideration of major drivers of Amur leopard density in the Russian part of its global range, this work substantiated the role of primary prey as a critical resource affecting Amur leopard distribution and density. According to the results, the putative availability of sika deer, inferred from sika deer resource selection, was the main driver of Amur leopard density in SWP. Cervids constitute much of the Amur leopard prey base (Sugimoto et al. 2016), with roe deer long recognized as the most preferred prey (Pikunov and Korkishko 1992). Roe deer remains the most abundant ungulate species on the China side of Amur leopard range, driving leopard distribution and dominating local diets (Qi et al. 2015, Yang et al. 2018). On the Russian side of the range, sika deer outnumber all other ungulate species taken together (Aramilev et al. 2016, Darman et al. 2020), yet roe deer and sika deer contribute equally to Amur leopard diets in the SWP (Salmanova et al. 2013). Of note, roe deer in SWP tended to select habitats with higher levels of human disturbance (Table 1.5, Chapter 1), and the highest density of roe deer occurred in open habitats (Darman et al. 2020) such as the lower river valleys, meadows and swampy plains – areas considerably altered by the long-term effects of wildfire and agriculture (Miquelle et al. 2004). Although leopards are able to inhabit a wider range of human-modified landscapes than tiger (Athreya et al. 2013), the intensity of human use and landscape change in putative roe deer habitat in the SWP may exceed leopard tolerance levels – a question requiring targeted investigation beyond the available data.

Despite the fact that prey availability plays a vital role in tiger distribution globally and population persistence locally (Karanth et al. 2004*b*, Hebblewhite et al. 2014, Kafley et al. 2016), prey covariates as represented by individual or combined RSFs failed as potential predictors of tiger density in this study. Yet linking predator density to prey habitat in lieu of direct prey

availability can be fraught, as it assumes a stable availability of prey over time (Boyce and McDonald 1999). Should prey availability fluctuate, and data collection be stretched in time in a manner that fails to capture these changes, then density of the predator may appear decoupled from putative prey habitat *per se* (Keim et al. 2011, Elbroch and Wittmer 2012). Nonetheless, the sika deer RSF proved to be an adequate surrogate for sika deer abundance as opposed to the other two ungulate species (Chapter 1).

Wild boar and red deer (*Cervus elaphus xanthopygus*) dominate tiger diets across the subspecies' range in Russia (Miquelle et al. 1996). Even where sika deer are about 12 times more prevalent than boar, wild boar still comprise the highest percent biomass of tiger diets (Kerley et al. 2015). Whereas boar were about five times less abundant in SWP compared to sika deer (Darman et al. 2020), tiger distribution and density did not reflect sika deer distribution (Chapter 1 and this study). A similar pattern was observed in Sikhote-Alin, where tigers in the presence of their preferred prey – red deer and wild boar – avoided areas having higher density of sika deer (Petrunenko et al. 2016). Due to their relative rarity in the study region, the distribution of wild boar was poorly predicted by RSF models (Chapter 1). Importantly, selection for resources at a level finer than could be monitored given our broad-scale focus likely exerted important influences on the distribution of both prey and predators in this region. For example, a lack of precise and timely information on mast crop of Mongolian oak (*Quercus mongolica*) and Korean pine (*Pinus koraiensis*) as well as availability of other natural forage for wild boar precluded us from accurately predicting the species' habitat and therefore using it to model predator responses to distribution of its principle prey. The range-wide RSF models for Amur tiger (Hebblewhite et al. 2014), derived from extensive spatial data collected in a short period of time are probably more capable of capturing close relationships between tiger and its prey.

In contrast to the Amur leopard, the strongest predictors of Amur tiger density in SWP was tiger selection for areas of lower road density, moderate slopes facing south and southwest, greater percent tree cover and low-intermediate snow cover (see Chapter 1). Throughout tiger range elevated anthropogenic disturbance prevents individuals from settling in areas where conditions might otherwise be sufficient (Kerley et al. 2002, Barber-Meyer et al. 2013, Jiang et al. 2014). Tigers more than leopards are susceptible to poaching, requiring more extensive tracts of relatively intact habitats (Chapron et al. 2008, Miquelle et al. 2010). At the same time, road density and distance to settlement when taken alone did not prove to be the good predictors of tiger density in the present study. Therefore, habitat composed of a suite of both landscape and anthropogenic covariates appears to better define Amur tiger density in SWP with habitat quality driven primarily by lower human access.

Empirical studies suggest that in large carnivore guilds the dominant competitor affects the spatial distribution of subordinate, the latter at an extreme becoming limited to marginal and suboptimal habitats (Odden et al. 2010). For instance, in response to creation of protected areas and other conservation measures, an increasing density of tiger has been related to decreased density of leopards in some parts of the species' global range (Harihar et al. 2011, Mondal et al. 2012*a*). Although the population of tigers in Amur leopard range in Russia has recently undergone a substantial increase, I did not find evidence of a large-scale displacement of leopards by tigers, although finer spatial or temporal shifts in behavior would have gone unobserved in this study. Rayan and Linkie (2016) showed that leopards exhibit less behavioral avoidance of tiger where tiger densities remain below $1/100km^2$, as observed in this study. However, leopards may avoid tigers at fine-scale even at low tiger densities (Steinmetz et al., 2013). For instance, the density of Amur tigers in China (0.24-0.30 tigers/$100km^2$, Xiao et al. 2016) was even lower than that

estimated in this work (0.42 tigers/100km^2), yet fine-scale avoidance of tigers by leopards was observed (Li et al. 2018).

For many carnivores, reproduction parameters such as per capita reproductive output and neonate survival largely depends on prey abundance (Fuller and Sievert 2001). The energetic costs for a female Amur tiger raising an average litter has been estimated at nearly twice that of a non-breeding female (Miller et al. 2014), with previous studies documenting a higher density of breeding female tigers in prey-rich areas (Miquelle et al. 2010, Goodrich et al. 2010). By extension, breeding female leopards – the population segment most critical to population growth – may be especially vulnerable to local depression in prey numbers. Whereas leopard density in this study reflected a strong, positive association with resource selection by sika deer, that relationship appeared to be driven primarily by female leopards that responded directly to their principal prey rather than tiger density or habitat use. The results thus rebuked speculations about the potential suppression of the leopard population by increasing numbers of Amur tiger in the region – at least, under current conditions. In contrast, the density of male leopards appeared to be restricted by elevated anthropogenic pressure indicating that males might be less susceptible to variation in prey availability. Observed differences in density drivers between males and females may reflect unobserved variation in data or demography such as density-dependent dispersal of males and lowered territoriality (Goodrich et al. 2010, Chistopolova et al. 2018).

Ultimately, carrying capacity of the SWP for both leopard and tiger is presumably low compared to the other parts of their ranges across south and southeast Asia, which is typical of northern temperate forests. Given the geographic constraints imposed on large cats in this region of limited resources, it is hard to expect substantial population increase continuing into the future.

Yet, at current densities tigers and leopards appeared capable of coexistence without noticeable detrimental effect of interspecific competition being observed.

TABLES: CHAPTER 2

Table 2.1 Top SECR model output for Amur tiger and Amur leopard based on six-year photographic data (2014-2019) obtained in the Land of the Leopard National park, Russia. Density (D) and scale parameter (σ) are on the log-scale and baseline probability (g_0) and sex ratio (pmix) are on the logit scale.

Species	Parameter	β	SE	LCI	UCI
Amur tiger	D (Intercept)	-11.29	0.32	-11.91	-10.67
	D (Tiger RSF 1 km^2)	3.95	0.75	2.48	5.42
	g_0 (Intercept)	-4.72	0.08	-4.88	-4.56
	g_0 (Males)	-0.80	0.13	-1.05	-0.56
	σ (Intercept)	8.43	0.03	8.36	8.49
	σ (Males)	0.66	0.06	0.55	0.77
	pmix (Males)	-0.54	0.18	-0.89	-0.18
Amur leopard	D (Intercept)	-9.59	0.15	-9.88	-9.29
	D (Sika deer RSF 1 km^2)	2.32	0.36	1.61	3.03
	g_0 (Intercept)	-4.35	0.06	-4.47	-4.23
	g_0 (Males)	0.62	0.07	0.48	0.76
	σ (Intercept)	7.94	0.03	7.89	7.99
	σ (Males)	0.54	0.03	0.48	0.60
	pmix (Males)	-0.33	0.11	-0.54	-0.12

Table 2.2 Real parameter estimates from the top SECR model for Amur tiger and Amur leopard based on six-year photographic data (2014-2019) obtained in the Land of the Leopard Park, Russia.

Species	Parameter	Estimate	SE	LCI	UCI
Amur tiger	Abundance	28.07	2.59	23.43	33.63
	σ males (km)	8.83	0.40	8.09	9.65
	σ females (km)	4.58	0.15	4.28	4.89
	g_0 males	0.004	0.0004	0.003	0.005
	g_0 females	0.009	0.0007	0.008	0.01
Amur leopard	Abundance	83.83	4.79	74.95	93.78
	σ males (km)	4.83	0.07	4.68	4.98
	σ females (km)	2.80	0.07	2.66	2.96
	g_0 males	0.023	0.0008	0.022	0.025
	g_0 females	0.013	0.0008	0.011	0.014

Table 2.3 Top SECR model outputs for males and females Amur leopard based on six-year photographic data (2014-2019) obtained in the Land of the Leopard National park, Russia. Density (D) and scale parameter (σ) are on the log-scale and baseline probability (g_0) is on the logit scale.

Sex	Parameter	β	SE	LCI	UCL
Females	D (Intercept)	-10.24	0.21	-10.66	-9.82
	D (Sika deer RSF 1 km^2)	2.82	0.48	1.87	3.76
	g_0	-4.34	0.06	-4.47	-4.22
	σ	7.94	0.03	7.89	7.99
Males	D (Intercept)	-9.25	0.17	-9.57	-8.92
	D (Road density 5 km^2)	-1.15	0.30	-1.75	-0.55
	g_0	-3.73	0.04	-3.80	-3.66
	σ	8.48	0.02	8.45	8.51

FIGURES: CHAPTER 2
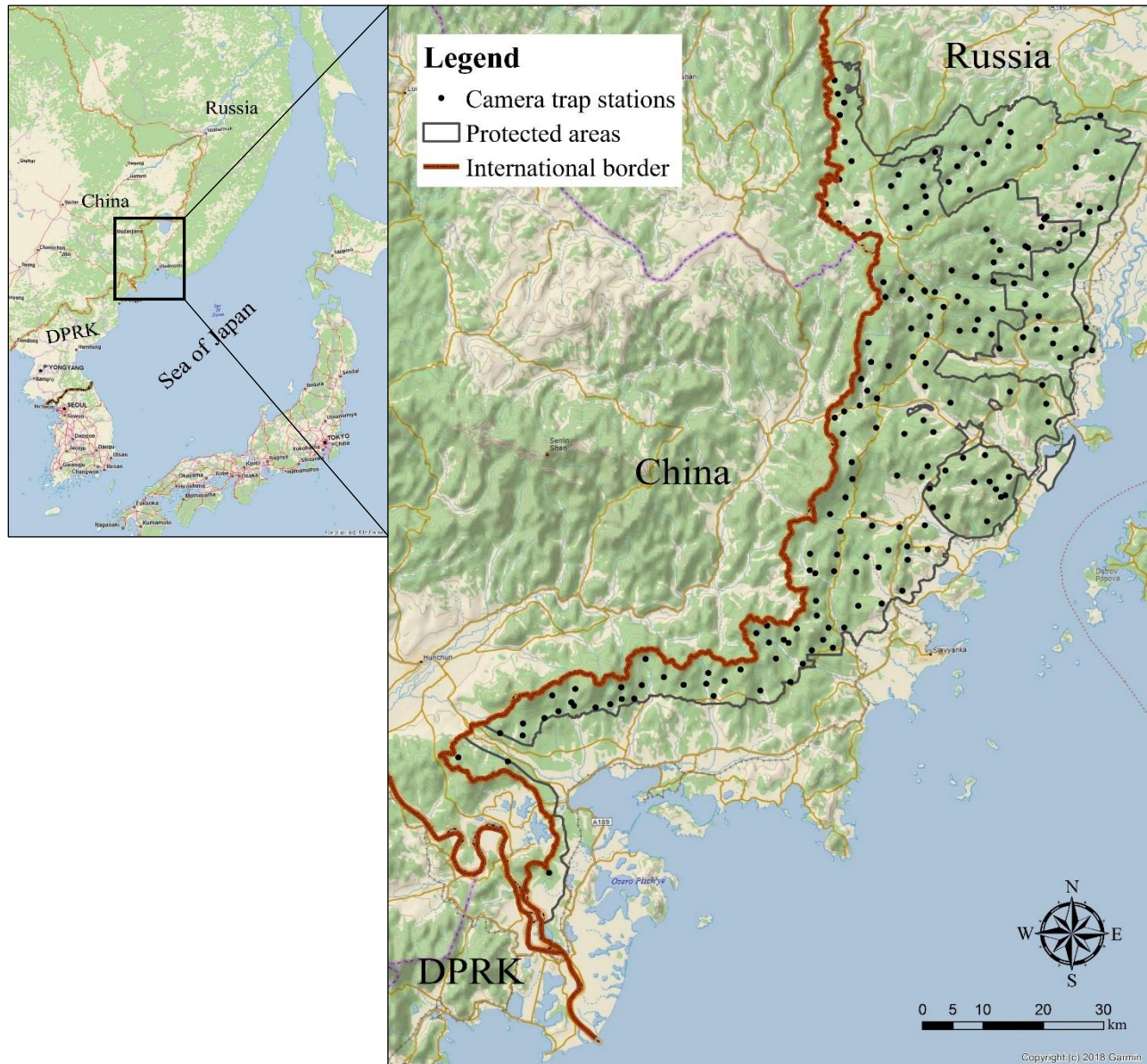
Figure 2.1 Location of the study area and the camera trap placement for Amur tiger and Amur leopard monitoring in the Land of the Leopard National Park in 2019
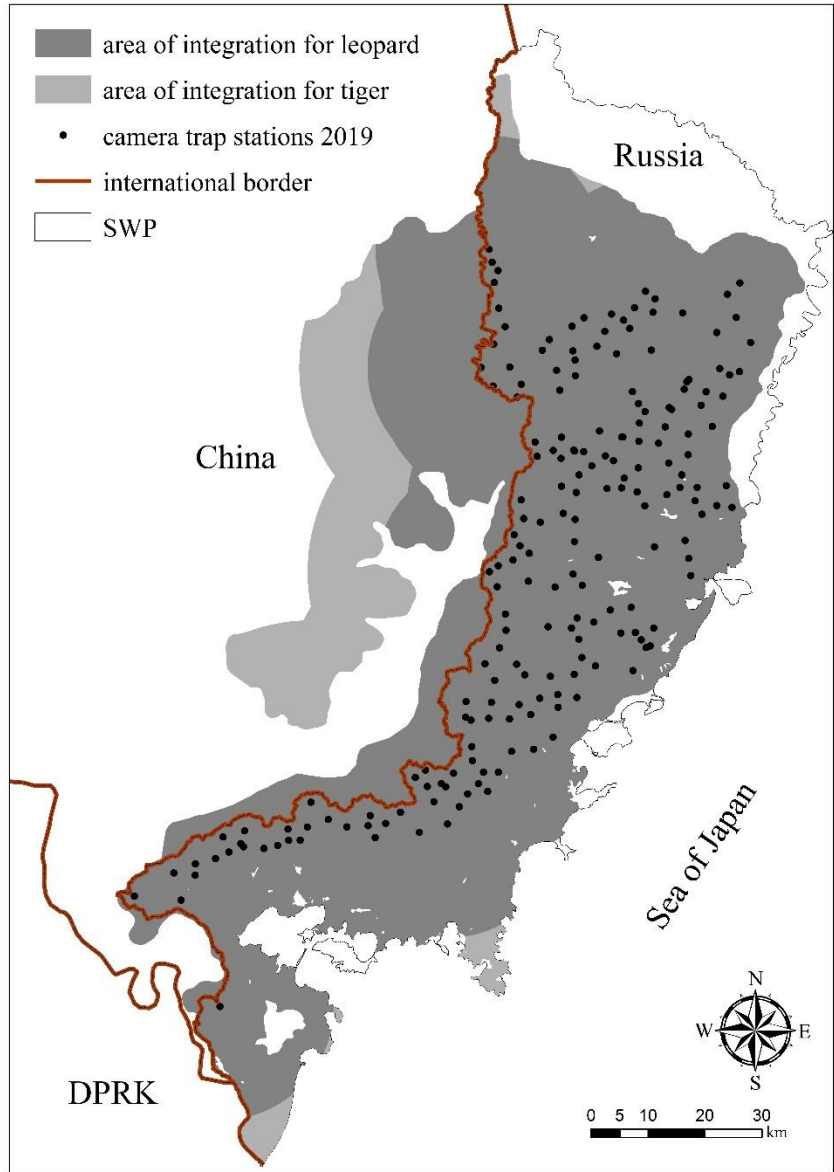
Figure 2.2 Area of integration for Amur tiger and Amur leopard defined as a buffer around camera trap grid 2019 with radius corresponding to 4σ for males of either species
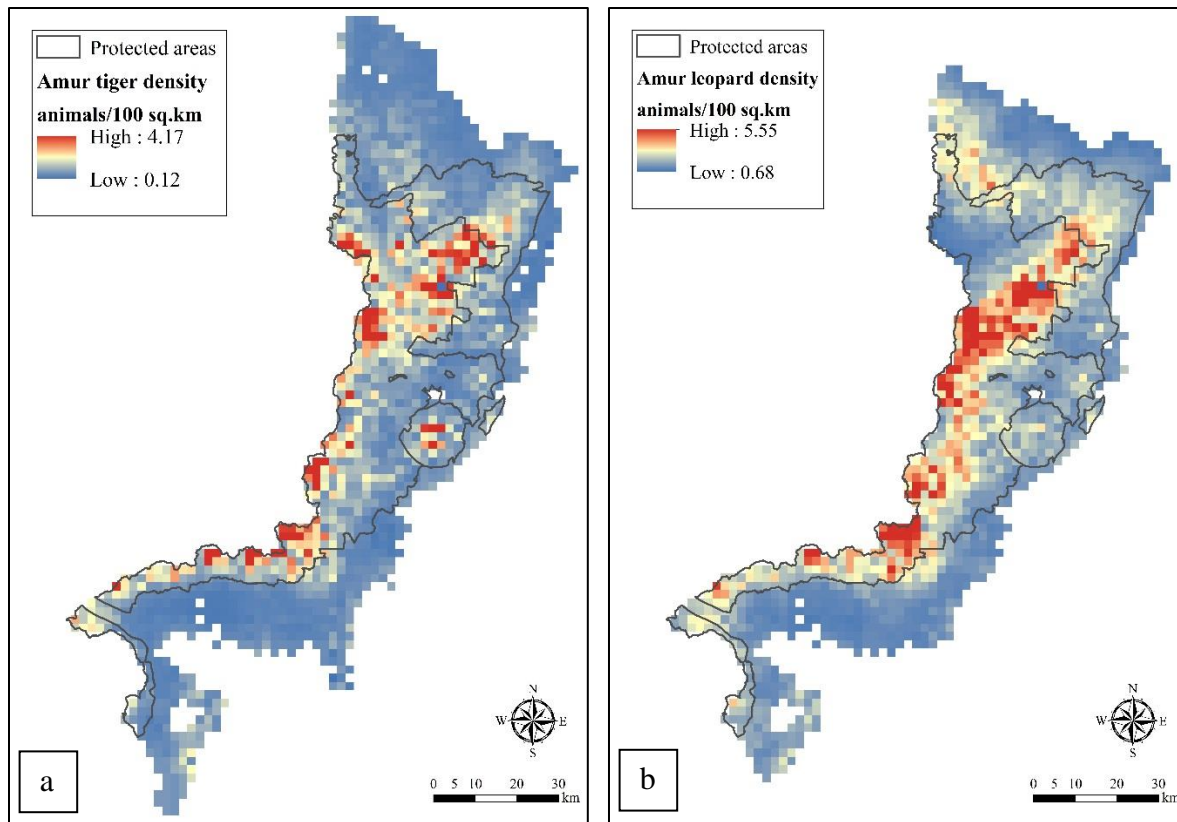
Figure 2.3 Density predictions from the top SECR models for Amur tiger and Amur leopard based on six-year (2014-2019) photographic data from the Land of the Leopard National Park, Russia.
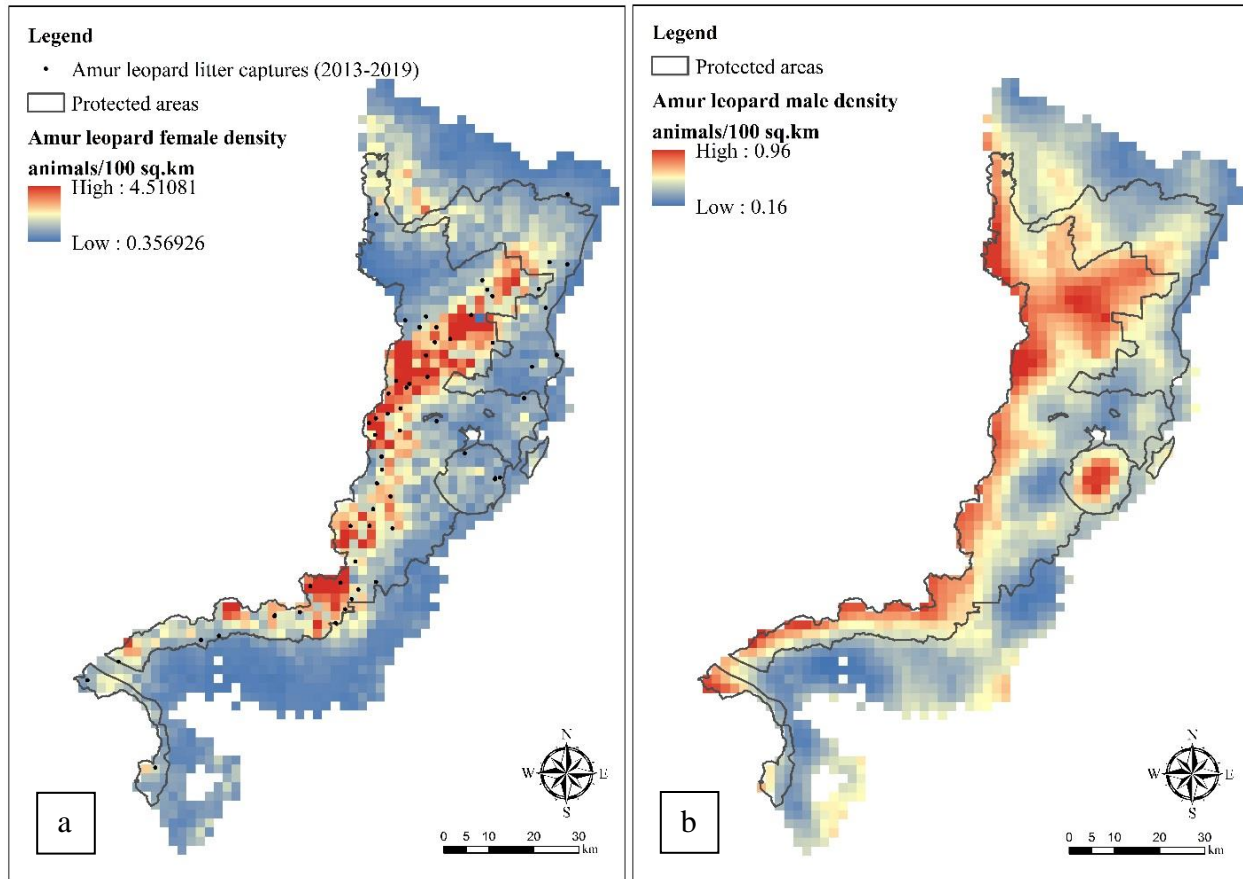
Figure 2.4 Density predictions from the top SECR models for female (a) and male (b) Amur leopard in Southwest Primorski Krai, Russia, 2014-2019

CONCLUSIONS

Land of the Leopard National Park on the Russia side of the global range of Amur leopard is considered to harbor the source population of this critically endangered subspecies and a small isolated sub-population of endangered Amur tiger. In the light of the recently documented growth of both species in the region, and amid public pressure, research on possible limitations of Amur leopard due to interspecific competition with tiger became increasingly important. At present, no immediate threats to the Amur leopard population, such as large-scale displacement or suppression of reproduction, were observed. Both tigers and leopards attain high densities within the Park. Capture rates of female leopard with cubs also increased in areas of high probability of habitat selection by tigers and, by relatedly, in areas of higher tiger density. Presumably evolutionarily-established plasticity allows leopards to persist in areas where their dominant competitor is abundant. On the other hand, the carrying capacity of either species in the region might not yet be achieved, facilitating their coexistence.

However, should tiger numbers within the current Amur leopard range continue to grow and opportunities for range expansion diminish, resilience of the leopard population may ultimately be constrained. Therefore, monitoring of population parameters of critically endangered subspecies such as Amur leopard and its habitat should continue, and interspecific interactions with sympatric Amur tiger revisited periodically. Nonetheless, improving habitat quality outside protected areas across the international border and establishing ecological corridors to ensure resettlement of leopards in Changbaishan region of China and southern Sikhote-Alin of Russia are an overarching conservation priority. Expanding buffer zone around LLNP to effectively guard against poaching and wildfires would also help secure habitat for the growing population of Amur leopard on Russia side.

LITERATURE CITED

Andheria, A. P., K. U. Karanth, and N. S. Kumar. 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. Journal of Zoology 273:169–175.

Aramilev, V. V., S. V. Aramilev, Y. M. Dunishenko, A. S. Batalov, V. M. Boltrushko, S. A. Vobly, A. M. Golub, A. V. Golynski, V. V. Dolinin, S. V. Kostomarov, A. V. Kostyria, M. N. Litvinov, V. F. Mitroshin, S. N. Naymushin, A. M. Panichev, G. P. Salkina, A. E. Samarin, I. V. Seryodkin, S. A. Sokolov, S. V. Sutyrina, P. V. Fomenko, and A. A. Murzin. 2016. The report on the Amur tiger survey in the southern Russian Far East, 2014-2015. Vladivostok. [in Russian]

Arjo, W. M., and D. H. Pletscher. 2004. Coyote and wolf habitat use in northwestern Montana. Northwest Science 78:24–32.

Athreya, V., M. Odden, J. D. C. Linnell, J. Krishnaswamy, and K. U. Karanth. 2016. A cat among the dogs: leopard (Panthera pardus) diet in a human-dominated landscape in western Maharashtra, India. Oryx 50:156–162.

Athreya, V., M. Odden, J. D. C. Linnell, J. Krishnaswamy, and U. Karanth. 2013. Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLOS ONE 8:1–8. Public Library of Science.

Balme, G. A., R. T. Pitman, H. S. Robinson, J. R. B. Miller, P. J. Funston, and L. T. B. Hunter. 2017. Leopard distribution and abundance is unaffected by interference competition with lions. Behavioral Ecology 28:1348–1358.

Balme, G. A., R. Slotow, and L. T. B. Hunter. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. Animal Conservation 13:315–323.

Balme, G., L. Hunter, and R. Slotow. 2007. Feeding habitat selection by hunting leopards
Panthera pardus in a woodland savanna: prey catchability versus abundance. Animal
Behaviour 74:589– 598.

Barber-Meyer, S. M., S. R. Jnawali, J. B. Karki, P. Khanal, S. Lohani, B. Long, D. I. MacKenzie,
B. Pandav, N. M. B. Pradhan, R. Shrestha, N. Subedi, G. Thapa, K. Thapa, and E.
Wikramanayake. 2013. Influence of prey depletion and human disturbance on tiger
occupancy in Nepal. Journal of Zoology 289:10–18.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J.
Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-
availability designs. Philosophical Transactions of the Royal Society B: Biological
Sciences 365:2245– 2254.

Bhattarai, B. P., and P. Kindlmann. 2012. Interactions between Bengal tiger (Panthera tigris) and
leopard (Panthera pardus): Implications for their conservation. Biodiversity and
Conservation 21:2075–2094.

Bisht, S., S. Banerjee, Q. Qureshi, and Y. Jhala. 2019. Demography of a high-density tiger
population and its implications for tiger recovery. Journal of Applied Ecology 56:1725–
1740. Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood
methods for capture–recapture studies. Biometrics 64:377–385.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource
selection functions. Trends in Ecology & Evolution 14:268–272.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource
selection functions. Ecological Modelling 157:281–300.

Boyce, M.S., C.J. Johnson, E.H. Merrill, S.E. Nielsen, E.J. Solberg, and B. van Moorter. 2016. Review: Can habitat selection predict abundance? Journal of Animal Ecology 85:11-20.

Braczkowski, A., L. Watson, D. Coulson, and R. Randall. 2012. Diet of leopards in the southern Cape, South Africa. African Journal of Ecology 50:377-380.

Broekhuis, F., G. Cozzi, M. Valeix, J. W. McNutt, and D. W. Macdonald. 2013. Risk avoidance in sympatric large carnivores: Reactive or predictive? Journal of Animal Ecology 82:1098–1105.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67–75.

Carter, N., M. Jasny, B. Gurung, and J. Liu. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. Global Ecology and Conservation 3:149–162.

Chanchani, P., B. D. Gerber, and B. R. Noon. 2018. Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes. Biological Conservation 227:275– 283.

Chapron, G., D. Miquelle, A. Lambert, J. Goodrich, S. Legendre, and J. Clobert. 2008. The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology 45:1667–1674.

Chistopolova, M. D., V. V Rozhnov, J. A. Hernandes-Blanco, S. V Naidenko, and P. A. Sorokin. 2018. A new analytical approach to the study of the spatial structure of the Amur leopard (Panthera pardus orientalis) population. Russian Journal of Ecology 49:534–542.

Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526–538.

Creel, S., G. Spong, and N. Creel. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Pages 33–60 in J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press, Cambridge.

Darman, Y. A., T. A. Petrov, A. Z. Purekhovsky, G. A. Sedash, and A. S. Titov. 2020. Aerial census of the wild ungulates in the Far Eastern leopard area. XIII Far Eastern Conference on Conservation in Protected Areas. Khabarovsk. [in Russian]

Darman, Yu. A., V. B. Storozhuk, and G. A. Sedash. 2019. Hydropotes inermis (Cervidae), a new species for the Russian fauna registered in the Land of the Leopard National Park (Russia). Nature Conservation Research 4:127–129. [in Russian]

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

DiMiceli, C. M., M. L. Carroll, R. A. Sohlberg, C. Huang, M. C. Hansen, and J. R. G. Townshend. 2017. Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2014, collection 5 percent tree cover, version 6. University of Maryland, College Park, MD, USA.

Dinerstein, E., C. Loucks, A. Heydlauff, E. Wikramanayake, G. Bryja, J. Forrest, J. R. Ginsberg, S. Klenzendorf, P. Leimgruber, T. G. O'Brien, E. Sanderson, J. Seidensticker, and M.

Songer. 2006. Setting priorities for the conservation and restoration of wild tigers: 2005-2015. A user's guide. Washington, D.C. - New York.

Durant, S. M. 1998. Competition refuges and coexistence: An example from Serengeti carnivores. Journal of Animal Ecology 67:370–386.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos 106:598–610.

Efford, M. 2019. Habitat masks in the package secr. https://www.otago.ac.nz/density/pdfs/secr-habitatmasks.pdf.

Efford, M. 2020. Package 'secr.' https://www.otago.ac.nz/density.

Efford, M., and R. M. Fewster. 2013. Estimating population size by spatially explicit capture–recapture. Oikos 122:918–928.

Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. J. Thompson. 2015. Recolonizing wolves influence the realized niche of resident cougars. Zoological Studies 54:41.

Elbroch, L. M., and H. U. Wittmer. 2012. Puma spatial ecology in open habitats with aggregate prey. Mammalian Biology 77:377–384.

Environmental Systems Research Institute. 2013. ArcGIS Release 10.2. Redlands, CA.

Ermoshin, V.V., A.A. Murzin, and V.V. Aramilev. 2011. Mapping habitat of large predators and ungulates of Primorski Krai. Apelsin, Vladivostok. [in Russian]

Farhadinia, M. S., B. T. McClintock, P. J. Johnson, P. Behnoud, K. Hobeali, P. Moghadas, L. T. B. Hunter, and D. W. Macdonald. 2019. A paradox of local abundance amidst regional rarity: the value of montane refugia for Persian leopard conservation. Scientific Reports 9:14622.

Farr, T. G., P. A. Rosen, E. Caro, R. Crippen, R. Duren, S. Hensley, M. Kobrick, M. Paller, E. Rodriguez, L. Roth, D. Seal, S. Shaffer, J. Shimada, J. Umland, M. Werner, M. Oskin, D.

Burbank, and D. Alsdorf. 2007. The Shuttle Radar Topography Mission. Reviews of Geophysics 45:RG2004.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fenchel, T. M., and F. B. Christiansen. 1977. Selection and interspecific competition. Pages 477– 498 in F. B. Christiansen and T. M. Fenchel, editors. Measuring Selection in Natural Populations. Springer Berlin Heidelberg, Berlin, Heidelberg.

Fisher, J. T., M. Wheatley, and D. MacKenzie. 2014. Spatial patterns of breeding success of grizzly bears derived from hierarchical multistate models. Conservation Biology 28:1249– 1259.

Fithian, W., and T. Hastie. 2013. Finite-sample equivalence in statistical models for presence-only data. Annals of Applied Statistics 7:1917–1939.

Fletcher, D. J. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. Biometrika 99:230–237.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. Pages 163–178 in J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore conservation. Cambridge University Press.

Goodrich, J. M., D. G. Miquelle, E. N. Smirnov, L. L. Kerley, and B. Howard. 2010. Spatial structure of Amur (Siberian) tigers (Panthera tigris altaica) on Sikhote Alin Biosphere Zapovednik, Russia. Journal of Mammalogy 91:737–748.

Gorbatenko, L. V., A. N. Kachur, and Y. A. Darman. 2012. The economic and ecological rationale for creating Land of the Leopard National Park. Vladivostok. [in Russian]

Gorman, M. L., J. R. Speakman, M. G. Mills, and J. P. Raath. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391:479–481.

Hall, D. K., and G. A. Riggs. 2016. MODIS/Terra Snow Cover Daily L3 Global 500m SIN Grid, Version 6. NASA National Snow and Ice Data Center, Boulder, Colorado USA.

Harihar, A., B. Pandav, M. Ghosh-Harihar, and J. Goodrich. 2020. Demographic and ecological correlates of a recovering tiger (Panthera tigris) population: Lessons learnt from 13-years of monitoring. Biological Conservation 252:108848.

Harihar, A., B. Pandav, and S. P. Goyal. 2011. Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. Journal of Applied Ecology 48:806–814.

Harihar, A, B. Pandav, and S. P. Goyal. 2011. Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. Journal of Applied Ecology 48:806–814.

Havmøller, R. W., S. Tenan, N. Scharff, and F. Rovero. 2019. Reserve size and anthropogenic disturbance affect the density of an African leopard (Panthera pardus) meta-population. PLOS ONE 14:1–17.

Hayward, M., and G. Kerley. 2008. Prey preferences and dietary overlap amongst Africa's large predators. South African Journal of Wildlife Research 38:93–108.

Hayward, M. W., P. Henschel, J. O'Brien, M. Hofmeyr, G. Balme, and G. I. H. Kerley. 2006. Prey preferences of the leopard (Panthera pardus). Journal of Zoology 270:298–313.

Hebblewhite, M., D. G. Miquelle, A. A. Murzin, V. V Aramilev, and D. G. Pikunov. 2011. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. Biological Conservation 144:2403–2413.

Hebblewhite, M., D. G. Miquelle, H. Robinson, D. G. Pikunov, Y. M. Dunishenko, V. V Aramilev, I. G. Nikolaev, G. P. Salkina, I. V Seryodkin, V. V Gaponov, M. N. Litvinov, A. V Kostyria, P. V Fomenko, and A. A. Murzin. 2014. Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biological Conservation 178:50–64.

Hebblewhite, M., F. Zimmermann, Z. Li, D. G. Miquelle, M. Zhang, H. Sun, F. Mörschel, Z. Wu, L. Sheng, A. Purekhovsky, and Z. Chunquan. 2012. Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China? Animal Conservation 15:579–592.

Henry, P., D. Miquelle, T. Sugimoto, D. McCullough, A. Caccone, and M. Russello. 2009. In situ population structure and ex situ representation of the endangered Amur tiger. Molecular Ecology 18:3173–3184.

Henschel, P., L. T. B. Hunter, L. Coad, K. A. Abernethy, and M. Mühlenberg. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. Journal of Zoology 285:11–20.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied Logistic Regression. Third edition. John Wiley & Sons, Inc., Hoboken, New Jersey.

Hötte, M., I. A. Kolodin, S. L. Bereznuk, J. C. Slaght, L. L. Kerley, S. V Soutyrina, G. P. Salkina, O. Y. Zaumyslova, E. J. Stokes, and D. G. Miquelle. 2016. Indicators of success for smart law enforcement in protected areas: A case study for Russian Amur tiger (Panthera tigris altaica) reserves. Integrative Zoology 11:2–15.

Jackson, R. M., J. D. Roe, R. Wangchuk, and D. O. Hunter. 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildlife Society Bulletin 34:772–781.

Jacobson, A. P., P. Gerngross, J. R. Lemeris Jr, R. F. Schoonover, C. Anco, C. BreitenmoserWürsten, S. M. Durant, M. S. Farhadinia, P. Henschel, J. F. Kamler, A. Laguardia, S. RostroGarcía, A. B. Stein, and L. Dollar. 2016. Leopard (Panthera pardus) status, distribution, and the research efforts across its range. PeerJ 4:e1974–e1974.

Jiang, G., H. Sun, J. Lang, L. Yang, C. Li, A. Lyet, B. Long, D. G. Miquelle, C. Zhang, S. Aramilev, J. Ma, and M. Zhang. 2014. Effects of environmental and anthropogenic drivers on Amur tiger distribution in northeastern China. Ecological Research 29:801–813.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use – availability data: theoretical motivation and evaluation methods. The Journal of Wildlife Management 70:347–357.

Johnson, D. S., D. L. Thomas, J. M. Ver Hoef, and A. Christ. 2008. A General Framework for the Analysis of Animal Resource Selection from Telemetry Data. Biometrics 64:968–976.

Kafley, H., M. E. Gompper, M. Sharma, B. R. Lamichane, and R. Maharjan. 2016. Tigers (Panthera tigris) respond to fine spatial-scale habitat factors: occupancy-based habitat association of tigers in Chitwan National Park, Nepal. Wildlife Research 43:398–410.

Kafley, H., B. R. Lamichhane, R. Maharjan, M. Khadka, N. Bhattarai, and M. E. Gompper. 2019. Tiger and leopard co-occurrence: intraguild interactions in response to human and livestock disturbance. Basic and Applied Ecology 40:78–89.

Karanth, K. U.; Sunquist, M. E. 2000. Behavioural correlates of predation by tiger (Panthera tigris) & leopard (Panthera pardus) in Nagarahole, India. Journal of Zoology 250:255–265.

Karanth, K. U., R. S. Chundawat, J. D. Nichols, and N. S. Kumar. 2004a. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. Animal Conservation 7:285–290.

Karanth, K. U., N. S. Kumar, J. D. Nichols, W. A. Link, and J. E. Hines. 2004b. 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.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Karanth, K. U., A. Srivathsa, D. Vasudev, M. Puri, R. Parameshwaran, and N. S. Kumar. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings. Biological sciences 284:20161860.

Karanth, K. U., and M. E. Sunquist. 1995. Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology 64:439–450.

Keim, J. L., P. D. Dewitt, and S. R. Lele. 2011. Predators choose prey over prey habitats: Evidence from a lynx - hare system. Ecological Applications 21:1011–1016.

Kerley, L. L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16:97–108.

Kerley, L. L., A. S. Mukhacheva, D. S. Matyukhina, E. I. Salmanova, G. P. Salkina, and D. G. Miquelle. 2015. A comparison of food habits and prey preference of Amur tiger

(Panthera tigris altaica) at three sites in the Russian Far East. Integrative Zoology 10:354–364.

Kostyria, A. V., A. S. Skorodelov, D. G. Miquelle, V. V. Aramilev, and D. McCullough. 2003. Results of camera trap survey of far eastern leopard population in southwest Primorski krai, winter 2002-2003. Vladivostok. [in Russian]

Kucherenko, S. P. 1985. The tiger. Agropromizdat, Moscow. [in Russian]

Kumar, U., N. Awasthi, Q. Qureshi, and Y. Jhala. 2019. Do conservation strategies that increase tiger populations have consequences for other wild carnivores like leopards? Scientific Reports 9:14673.

Lamichhane, B. R., H. Leirs, G. A. Persoon, N. Subedi, M. Dhakal, B. N. Oli, S. Reynaert, V. Sluydts, C. P. Pokheral, L. P. Poudyal, S. Malla, and H. H. de Iongh. 2019. Factors associated with co-occurrence of large carnivores in a human-dominated landscape. Biodiversity and Conservation 28:1473–1491.

Laurenson, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385–399 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. Chicago University Press, Chicago.

Li, Z., T. Wang, J. L. D. Smith, R. Feng, L. Feng, P. Mou, and J. Ge. 2018. Coexistence of two sympatric flagship carnivores in the human-dominated forest landscapes of Northeast Asia. Landscape Ecology 34:291–305.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

Loosen, A. E., A. T. Morehouse, and M. S. Boyce. 2019. Land tenure shapes black bear density and abundance on a multi-use landscape. Ecology and Evolution 9:73–89.

Lovari, S., C. P. Pokheral, S. R. Jnawali, L. Fusani, and F. Ferretti. 2015. Coexistence of the tiger and the common leopard in a prey-rich area: the role of prey partitioning. Journal of Zoology 295:122–131.

Macdonald, D. W., A. J. Loveridge, and K. Nowell. 2010. Dramatis personae: an introduction to the wild felids. Pages 3–58 in D. W. Macdonald and A. J. Loveridge, editors. Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht.

Matiukhina, D. S., A. V. Vitkalova, A. N. Rybin, V. V. Aramilev, E. I. Shevtsova, and D. G. Miquelle. 2016. Camera-trap monitoring of Amur tiger (Panthera tigris altaica) in southwest Primorsky Krai, 2013-2016: preliminary results. Nature Conservation Research 1:36–43.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

Miller, C. S., M. Hebblewhite, Y. K. Petrunenko, I. V Seryodkin, J. M. Goodrich, and D. G. Miquelle. 2014. Amur tiger (Panthera tigris altaica) energetic requirements: Implications for conserving wild tigers. Biological Conservation 170:120–129.

Mills, M. G. L., and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11:1397–1406.

Miquelle, D., Y. M. Dunishenko, D. A. Zvyagintsev, A. A. Darensky, A. M. Golyb, V. V. Dolinin, V. G. Shvets, S. V. Kostomarov, V. V. Aramilev, P. V. Fomenko, M. N. Litvinov, I. G. Nikolaev, D. G. Pikunov, G. P. Salkina, O. Y. Zaumyslova, and R. P. Kozhichev. 2010. A monitoring program for Amur tiger. Thirteenth-year report: 1998-2010. Vladivostok.

Miquelle, D. G. 2015. The Amur tiger in Northeast Asia: Conservation and ecology of an endangered subspecies. Integrative Zoology 10:311–314.

Miquelle, D. G., Y. A. Darman, and I. V. Seryodkin. 2011. Panthera tigris ssp. altaica. The IUCN Red List of Threatened Species 2011: e.T15956A5333650.

Miquelle, D. G., J. M. Goodrich, E. N. Smirnov, P. A. Stephens, O. Y. Zaumyslova, G. Chapron, L. Kerley, A. A. Murzin, M. J. Hornocker, and H. B. Quigley. 2010. Amur tiger: a case study of living on the edge. Pages 325–339 in D. W. Macdonald and A. J. Loveridge, editors. Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Miquelle, D. G., A. A. Murzin, and M. Hötte. 2004. An analysis of fires and their impact on leopards in Southwest Primorye. Dalnauka, Vladivostok. [in Russian]

Miquelle, D. G., V. V. Rozhnov, V. Ermoshin, A. A. Murzin, I. G. Nikolaev, J. A. Hernandez-Blanco, and S. V. Naidenko. 2015. Identifying ecological corridors for Amur tigers (Panthera tigris altaica) and Amur leopards (Panthera pardus orientalis). Integrative Zoology 10:389–402.

Miquelle, D. G., E. N. Smirnov, H. G. Quigley, M. J. Hornocker, I. G. Nikolaev, and E. N. Matyushkin. 1996. Food habits of Amur tigers in Sikhote-Alin Zapovednik and Russian Far East, and implications for conservation. Journal of Wildlife Research 1:138–147.

Mitchell, M. S., and M. Hebblewhite. 2012. Carnivore habitat ecology: integrating theory and application for conservation. Pages 218–255 in R. A. Powell and L. Boitani, editors. Carnivore Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford.

Mondal, K., S. Gupta, S. K. Bhattacharjee, Q. Qureshi, and K. Sankar. 2012a. Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. International Journal of Biodiversity and Conservation 4:228–236.

Mondal, K., S. Gupta, S. Bhattacharjee, Q. Qureshi, and K. Sankar. 2012b. Prey selection, food habits and dietary overlap between leopard Panthera pardus (Mammalia: Carnivora) and reintroduced tiger Panthera tigris (Mammalia: Carnivora) in a semi-arid forest of Sariska Tiger Reserve, Western India. Italian Journal of Zoology 79:607–616.

Morse, D. H. 1974. Niche breadth as a function of social dominance. The American Naturalist 108:818–830.

Naughton-Treves, L., M. B. Holland, and K. Brandon. 2005. The role of protected areas in conserving biodiversity and sustaining livelihoods. Annual Review of Environment and Resources 30:219–252.

Ning, Y., A. V Kostyria, J. Ma, M. I. Chayka, V. Y. Guskov, J. Qi, I. N. Sheremetyeva, M. Wang, and G. Jiang. 2019. Dispersal of Amur tiger from spatial distribution and genetics within the eastern Changbai mountain of China. Ecology and Evolution 9:2415–2424.

Northrup, J. M., M. B. Hooten, C. R. Anderson Jr., and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456–1463.

O'Brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality & Quantity 41:673–690.

Odden, M., P. Wegge, and T. Fredriksen. 2010. Do tigers displace leopards? If so, why? Ecological Research 25:875–881.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 3–135.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. The American Naturalist 153:492–508.

Petrunenko, Y. K., R. A. Montgomery, I. V Seryodkin, O. Y. Zaumyslova, D. G. Miquelle, and D. W. Macdonald. 2016. Spatial variation in the density and vulnerability of preferred prey in the landscape shape patterns of Amur tiger habitat use. Oikos 125:66–75.

Pikunov, D. G., and V. G. Korkishko. 1992. Leopard of the Far East. V. E. Sokolov, editor. Nauka, Moscow. Pikunov, D. G., I. V. Seryodkin, V. V. Aramilev, and I. G. Nikolaev. 2010. Results of the 2007 survey of far eastern leopard, amur tiger and ungulate populations in southwest Primorsky krai. Pages 353–356 in. The Amur Tiger in Northeast Asia: Planning for the 21st Century. Dalnauka, Vladivostok. [in Russian]

Proffitt, K. M., J. F. Goldberg, M. Hebblewhite, R. Russell, B. S. Jimenez, H. S. Robinson, K. Pilgrim, and M. K. Schwartz. 2015. Integrating resource selection into spatial capture-recapture models for large carnivores. Ecosphere 6:art239.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rayan, D. M., and M. Linkie. 2016. Managing conservation flagship species in competition: Tiger, leopard and dhole in Malaysia. Biological Conservation 204:360–366.

Riggs, G. A., D. K. Hall, and M. O. Román. 2017. Overview of NASA's MODIS and Visible Infrared Imaging Radiometer Suite (VIIRS) snow-cover Earth System Data Records. Earth System Science Data 9:765–777.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.

Rosenblatt, E., S. Creel, M. S. Becker, J. Merkle, H. Mwape, P. Schuette, and T. Simpamba. 2016. Effects of a protection gradient on carnivore density and survival: an example with leopards in the Luangwa valley, Zambia. Ecology and Evolution 6:3772–3785.

Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. Journal of Mammalogy 47:602–612.

Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013. Integrating resource selection information with spatial capture–recapture. Methods in Ecology and Evolution 4:520–530.

Salmanova, E. I., A. V. Kostirya, and D. G. Miquelle. 2013. Far Eastern leopard (Panthera pardus orientalis) diet composition in the Russian Far East. Proceedings of the Irkutsk State University. Biology and Ecology Series 6:84–89. [in Russian]

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Seidensticker, J. 1976. On the ecological separation between tigers and leopards. Biotropica 8:225– 234.

Sellers, K. F., and D. S. Morris. 2017. Underdispersion models: Models that are "under the radar." Communications in Statistics - Theory and Methods 46:12075–12086.

Silver, S. C., L. E. T. Ostro, L. K. Marsh, L. Maffei, A. J. Noss, M. J. Kelly, R. B. Wallace, H. Gomez, and G. Ayala. 2004. The use of camera traps for estimating jaguar (Panthera once) abundance and density using capture/recapture analysis. Oryx 38:148–154.

Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129:487–496.

Sorokin, P. A., V. V. Rozhnov, A. U. Krasnenko, V. S. Lukarevskiy, S. V. Naidenko, and J. A. Hernandez-Blanco. 2016. Genetic structure of the Amur tiger (Panthera tigris altaica) population: Are tigers in Sikhote-Alin and southwest Primorye truly isolated? Integrative Zoology 11:25–32.

Stein, A. B., V. Athreya, P. Gerngross, G. Balme, P. Henschel, U. Karanth, D. Miquelle, S. RostroGarcia, J. F. Kamler, A. Laguardia, I. Khorozyan, and A. Ghoddousi. 2020. Panthera pardus (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020.

Steinmetz, R., N. Seuaturien, and W. Chutipong. 2013. Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. Biological Conservation 163:68–78.

Sugimoto, T., V. V Aramilev, J. Nagata, and D. R. McCullough. 2016. Winter food habits of sympatric carnivores, Amur tigers and Far Eastern leopards, in the Russian Far East. Mammalian Biology 81:214–218.

Swanepoel, L. H., M. J. Somers, and F. Dalerum. 2015. Density of leopards (Panthera pardus) on protected and non-protected land in the Waterberg Biosphere, South Africa. Wildlife Biology 21:263–268.

Swanson, A., T. Arnold, M. Kosmala, J. Forester, and C. Packer. 2016. In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. Ecology and Evolution 6:8534– 8545.

Tempa, T., M. Hebblewhite, J. F. Goldberg, N. Norbu, T. R. Wangchuk, W. Xiao, and L. S. Mills. 2019. The spatial distribution and population density of tigers in mountainous terrain of Bhutan. Biological Conservation 238:108192.

Tobler, M.W., and G.V.N. Powell. 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biological Conservation 159:109–118.

Uphyrkina, O., and S. J. O'Brien. 2003. Applying molecular genetic tools to the conservation and action plan for the critically endangered Far Eastern leopard (Panthera pardus orientalis). Comptes Rendus - Biologies 326:93–97.

Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631.

Vitkalova, A. V., L. Feng, A. N. Rybin, B. D. Gerber, D. G. Miquelle, T. Wang, H. Yang, E. I. Shevtsova, V. V Aramilev, and J. Ge. 2018. Transboundary cooperation improves endangered species monitoring and conservation actions: A case study of the global population of Amur leopards. Conservation Letters 11:e12574.

Walston, J., J. G. Robinson, E. L. Bennett, U. Breitenmoser, G. A. B. da Fonseca, J. Goodrich, M. Gumal, L. Hunter, A. Johnson, K. U. Karanth, N. Leader-Williams, K. MacKinnon, D. Miquelle, A. Pattanavibool, C. Poole, A. Rabinowitz, J. L. D. Smith, E. J. Stokes, S.

N. Stuart, C. Vongkhamheng, and H. Wibisono. 2010. Bringing the tiger back from the brink – the six percent solution. PLOS Biology 8:1–4.

Wang, S. W., and D. W. Macdonald. 2009. Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. Journal of Zoology 277:275–283.

Wang, T., L. Feng, P. Mou, J. Wu, J. L. D. Smith, W. Xiao, H. Yang, H. Dou, X. Zhao, Y. Cheng, B. Zhou, H. Wu, L. Zhang, Y. Tian, Q. Guo, X. Kou, X. Han, D. G. Miquelle, C. D. Oliver, R. Xu, and J. Ge. 2016. Amur tigers and leopards returning to China: direct evidence and a landscape conservation plan. Landscape Ecology 31:491–503.

Wang, T., L. Feng, H. Yang, B. Han, Y. Zhao, L. Juan, X. Lü, L. Zou, T. Li, W. Xiao, P. Mou, J. L. D. Smith, and J. Ge. 2017. A science-based approach to guide Amur leopard recovery in China. Biological Conservation 210:47–55.

Warton, D. I., and L. C. Shepherd. 2010. Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. The Annals of Applied Statistics 4:1383–1402.

Watts, H., and K. Holekamp. 2008. Interspecific competition influences reproduction in spotted hyenas. Journal of Zoology 276:402–410.

Wegge, P., M. Odden, C. Pokharel, and T. Storaas. 2009. Predator-prey relationships and responses of ungulates and their predators to the establishment of protected areas: A case study of tigers, leopards and their prey in Bardia National Park, Nepal. Biological Conservation 142:189–202.

Wikramanayake, E., E. Dinerstein, J. Forrest, C. Loucks, J. Seidensticker, S. Klenzendorf, E. W. Sanderson, R. Simons, A. Heydlauff, J. Ginsberg, T. O'Brien, P. Leimgruber, M. Songer,

and G. Bryja. 2010. Roads to recovery or catastrophic loss: how will the next decade end for wild tigers? R. Tilson and P. J. Nyhus, editors. Tigers of the world: the science, politics, and conservation of Panthera tigris. Second edition. Elsevier Inc.

Wikramanayake, E., E. Dinerstein, J. Seidensticker, S. Lumpkin, B. Pandav, M. Shrestha, H. Mishra, J. Ballou, A. J. T. Johnsingh, I. Chestin, S. Sunarto, P. Thinley, K. Thapa, G. Jiang, S. Elagupillay, H. Kafley, N. M. B. Pradhan, K. Jigme, S. Teak, P. Cutter, M. A. Aziz, and U. Than. 2011. A landscape-based conservation strategy to double the wild tiger population. Conservation Letters 4:219–227.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Modeling, estimation, and decision making. Academic Press.

Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. Science 321:123–126.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science 280:2126–2128.

Xiao, W., L. Feng, P. Mou, D. G. Miquelle, M. Hebblewhite, J. F. Goldberg, H. S. Robinson, X. Zhao, B. Zhou, T. Wang, and J. Ge. 2016. Estimating abundance and density of Amur tigers along the Sino–Russian border. Integrative Zoology 11:322–332.

Yang, H., H. Dou, R. K. Baniya, S. Han, Y. Guan, B. Xie, G. Zhao, T. Wang, P. Mou, L. Feng, and J. Ge. 2018. Seasonal food habits and prey selection of Amur tigers and Amur leopards in Northeast China. Scientific reports 8:6930.

Yang, L., M. Huang, R. Zhang, L. Jiang, Y. Ren, Z. Jiang, W. Zhang, and X. Luan. 2016. Reconstructing the historical distribution of the Amur Leopard (Panthera pardus orientalis) in Northeast China based on historical records. ZooKeys 592:143–153.

Yudakov, A. G., and I. G. Nikolaev. 2012. Winter ecology of the Amur tiger based upon

observations in the west-central Sikhote-Alin Mountains, 1970-1973, 1996-2010. E. N.

Matyushkin, editor. Second rev. Dalnauka, Vladivostok.

APPENDICIES

Appendix 1.1 Summary on environmental covariates and assumptions related to their contribution to animals' habitat selection

Variable	Units	Assumption	Source
Elevation	meters	Large-scale proxy for vegetation cover types and human disturbance	SRTM DEM, NASA
Slope	degrees	Travel costs and escape cover	SRTM DEM, NASA
Hill shade	relative units	Proxy for snow cover	SRTM DEM, NASA
Ruggedness	relative units	Escape cover	SRTM DEM, NASA
Snow cover	percent	Food availability (ungulates) and travel costs (ungulates and predators)	MODIS Snow Cover Daily L3 Global 500m Grid, NASA
Distance to river	meters	Proxy for distance to valleys as movement corridors	GIS
Percent tree cover	percent	Landscape openness, wildfire frequency and risk	MODIS Vegetation Continuous Fields Yearly L3 Global 250m, NASA
Vegetation cover type	categories	Availability of hard mast and other potential food sources for ungulates	Ermoshin et al. 2011
Distance to settlement	meters	Human disturbance	GIS
Distance to primary road	meters	Human disturbance, risk of road collisions	GIS
Road density	km/km^2	Human disturbance and increased area accessibility	GIS
Distance to protected area	meters	Human disturbance	GIS

Appendix 2.1 Summary of Amur tiger camera-trapping in the Land of the Leopard National Park, 2014-2019

Parameter	2014	2015	2016	2017	2018	2019
Dates (MM/DD)	02/01-05/31	01/03-05/02	01/22-05/20	01/16-05/15	01/23-05/22	01/06-05/05
Trap-nights	13518	16316	11936	17749	20010	20332
No. stations	145	169	133	163	177	184
No. stations visited	33	45	41	56	57	79
No. captures	51	89	55	169	108	177
No. individuals	18	23	17	21	24	28
No. females	11	12	10	14	16	20
No. males	7	11	7	7	8	8
Sex ratio (F/M)	1.6	1.1	1.4	2	2	2.5

Appendix 2.2 Summary of Amur leopard camera-trapping in the Land of the Leopard National Park, 2014-2019

Parameter	2014	2015	2016	2017	2018	2019
Dates (MM/DD)	01/14-05/13	01/15-05/14	01/23-05/21	01/13-05/12	01/20-05/19	01/24-05/23
Trap-nights	12517	17122	11968	17677	19999	20904
No. stations	144	169	133	163	177	184
No. stations visited	87	95	73	117	127	142
No. captures	257	289	226	525	515	599
No. individuals	48	46	47	61	77	70
No. females	26	27	28	30	49	39
No. males	22	19	19	28	28	30
No. of individuals of unidentified sex	-	-	-	3	-	1
Sex ratio (F/M)	1.2	1.4	1.5	1.1	1.7	1.3

Appendix 2.3 Model selection for SECR models for Amur tiger

Model	K	AICc	ΔAICc	w_i
D ~ tiger RSF 1 km^2, g_0 ~ sex, σ ~ sex	7	3882.98	0	0.4671
D ~ tiger RSF, g_0 ~ sex, σ ~ sex	7	3883.74	0.76	0.3201
D ~ tiger RSF 3 km^2, g_0 ~ sex, σ ~ sex	7	3884.55	1.57	0.2128
D ~ road density 5 km^2, g_0 ~ sex, σ ~ sex	7	3892.98	10.00	0
D ~ roe deer RSF 3 km^2, g_0 ~ sex, σ ~ sex	7	3896.56	13.58	0
D ~ roe deer RSF 1 km^2, g_0 ~ sex, σ ~ sex	7	3897.06	14.08	0
D ~ roe deer RSF, g_0 ~ sex, σ ~ sex	7	3897.27	14.29	0
D ~ road density 15 km^2, g_0 ~ sex, σ ~ sex	7	3897.85	14.87	0
D ~ sika deer RSF 1 km^2, g_0 ~ sex, σ ~ sex	7	3899.56	16.58	0
D ~ settlements, g_0 ~ sex, σ ~ sex	7	3899.96	16.98	0
D ~ sika deer RSF, g_0 ~ sex, σ ~ sex	7	3900.01	17.03	0
D ~ sika deer RSF 3 km^2, g_0 ~ sex, σ ~ sex	7	3900.14	17.16	0
D ~ combined prey RSF 3 km^2, g_0 ~ sex, σ ~ sex	7	3903.24	20.26	0
D ~ human RSF 2 km^2, g_0 ~ sex, σ ~ sex	7	3903.40	20.42	0
D ~ combined prey RSF, g_0 ~ sex, σ ~ sex	7	3903.61	20.63	0
D ~ combined prey RSF 1 km^2, g_0 ~ sex, σ ~ sex	7	3903.87	20.89	0
D ~ tiger RSF 3 km^2 * year, g_0 ~ sex, σ ~ sex	17	3904.46	21.48	0
D ~ 1, g_0 ~ sex, σ ~ sex	6	3904.75	21.77	0
D ~ wild boar RSF 3 km^2, g_0 ~ sex, σ ~ sex	7	3904.88	21.90	0
D ~ wild boar RSF 1 km^2, g_0 ~ sex, σ ~ sex	7	3905.05	22.07	0
D ~ wild boar RSF, g_0 ~ sex, σ ~ sex	7	3905.07	22.09	0
D ~ sika deer RSF 3 km^2 * year, g_0 ~ sex, σ ~ sex	17	3922.64	39.66	0
D ~ year, g_0 ~ sex, σ ~ sex	11	3924.61	41.63	0
D ~ road density 15 km^2 * year, g_0 ~ sex, σ ~ sex	17	3933.82	50.84	0

Appendix 2.4 Model selection for SECR models for Amur leopard

Model	K	AICc	ΔAICc	w_i
D ~ sika deer RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9444.59	0.00	0.52
D ~ sika deer RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9444.73	0.15	0.48
D ~ sika deer RSF, g$_0$ ~ sex, σ ~ sex	7	9453.46	8.87	0.01
D ~ tiger RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9456.79	12.20	0.00
D ~ tiger RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9457.18	12.59	0.00
D ~ road density 5 km^2, g$_0$ ~ sex, σ ~ sex	7	9457.25	12.67	0.00
D ~ tiger RSF, g$_0$ ~ sex, σ ~ sex	7	9460.06	15.47	0.00
D ~ roe deer RSF, g$_0$ ~ sex, σ ~ sex	7	9463.79	19.20	0.00
D ~ roe deer RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9464.17	19.58	0.00
D ~ sika deer RSF 3 km^2 * year, g$_0$ ~ sex, σ ~ sex	17	9464.43	19.85	0.00
D ~ roe deer RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9466.28	21.69	0.00
D ~ road density 15 km^2, g$_0$ ~ sex, σ ~ sex	7	9467.27	22.69	0.00
D ~ leopard RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9472.99	28.41	0.00
D ~ human RSF 2 km^2, g$_0$ ~ sex, σ ~ sex	7	9476.44	31.86	0.00
D ~ leopard RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9477.28	32.70	0.00
D ~ leopard RSF, g$_0$ ~ sex, σ ~ sex	7	9478.46	33.88	0.00
D ~ 1, g$_0$ ~ sex, σ ~ sex	6	9480.46	35.88	0.00
D ~ settlement, g$_0$ ~ sex, σ ~ sex	7	9481.24	36.65	0.00
D ~ wild boar RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9481.94	37.36	0.00
D ~ wild boar RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9482.44	37.86	0.00
D ~ tiger density, g$_0$ ~ sex, σ ~ sex	7	9482.50	37.92	0.00
D ~ combined prey RSF 1 km^2, g$_0$ ~ sex, σ ~ sex	7	9482.52	37.94	0.00
D ~ wild boar RSF, g$_0$ ~ sex, σ ~ sex	7	9482.52	37.94	0.00
D ~ combined prey RSF, g$_0$ ~ sex, σ ~ sex	7	9482.55	37.96	0.00
D ~ combined prey RSF 3 km^2, g$_0$ ~ sex, σ ~ sex	7	9482.81	38.23	0.00
D ~ year, g$_0$ ~ sex, σ ~ sex	11	9488.21	43.62	0.00
D ~ tiger density * year, g$_0$ ~ sex, σ ~ sex	12	9488.21	43.62	0.00
D ~ leopard RSF 1 km^2 * year, g$_0$ ~ sex, σ ~ sex	17	9498.14	53.56	0.00
D ~ combined prey RSF 1 km^2 * year, g$_0$ ~ sex, σ ~ sex	17	9507.52	62.94	0.00

Appendix 2.5 SECR model selection for females Amur leopard

Model	K	AICc	ΔAICc	w_i
D ~ sika deer RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3132.40	0.00	0.56
D ~ sika deer RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3132.92	0.52	0.43
D ~ sika deer RSF, g_0 ~ 1, σ ~ 1	4	3139.89	7.49	0.01
D ~ tiger RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3148.33	15.93	0.00
D ~ tiger RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3150.04	17.65	0.00
D ~ tiger RSF, g_0 ~ 1, σ ~ 1	4	3150.96	18.57	0.00
D ~ road density 15 km^2, g_0 ~ 1, σ ~ 1	4	3151.72	19.32	0.00
D ~ road density 5 km^2, g_0 ~ 1, σ ~ 1	4	3152.93	20.53	0.00
D ~ roe deer RSF, g_0 ~ 1, σ ~ 1	4	3152.99	20.60	0.00
D ~ roe deer RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3153.46	21.06	0.00
D ~ roe deer RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3154.07	21.67	0.00
D ~ male density, g_0 ~ 1, σ ~ 1	4	3154.23	21.83	0.00
D ~ human RSF 2 km^2, g_0 ~ 1, σ ~ 1	4	3159.10	26.70	0.00
D ~ tiger density, g_0 ~ 1, σ ~ 1	4	3159.31	26.91	0.00
D ~ leopard RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3160.44	28.04	0.00
D ~ 1, g_0 ~ 1, σ ~ 1	3	3161.69	29.29	0.00
D ~ wild boar RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3162.65	30.25	0.00
D ~ leopard RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3162.70	30.31	0.00
D ~ wild boar RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3162.86	30.47	0.00
D ~ leopard RSF, g_0 ~ 1, σ ~ 1	4	3162.99	30.60	0.00
D ~ combined prey RSF 1 km^2, g_0 ~ 1, σ ~ 1	4	3163.26	30.86	0.00
D ~ combined prey RSF, g_0 ~ 1, σ ~ 1	4	3163.32	30.92	0.00
D ~ settlements, g_0 ~ 1, σ ~ 1	4	3163.38	30.98	0.00
D ~ combined prey RSF 3 km^2, g_0 ~ 1, σ ~ 1	4	3163.47	31.07	0.00
D ~ wild boar RSF, g_0 ~ 1, σ ~ 1	4	3163.48	31.08	0.00

Appendix 2.6 SECR model selection for males Amur leopard

Model	K	AICc	ΔAICc	w_i
D ~ road density 5 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6274.80	0.00	0.64
D ~ tiger RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6278.29	3.49	0.11
D ~ tiger RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6279.56	4.76	0.06
D ~ tiger RSF, $g_0 \sim 1$, $\sigma \sim 1$	4	6280.02	5.22	0.05
D ~ roe deer RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6281.02	6.22	0.03
D ~ roe deer RSF, $g_0 \sim 1$, $\sigma \sim 1$	4	6281.31	6.51	0.02
D ~ sika deer RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6281.41	6.60	0.02
D ~ sika deer RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6281.63	6.83	0.02
D ~ roe deer RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6281.92	7.12	0.02
D ~ leopard RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6282.90	8.10	0.01
D ~ sika deer RSF, $g_0 \sim 1$, $\sigma \sim 1$	4	6283.43	8.63	0.01
D ~ leopard RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6284.46	9.66	0.01
D ~ tiger density, $g_0 \sim 1$, $\sigma \sim 1$	4	6285.19	10.39	0.00
D ~ leopard RSF, $g_0 \sim 1$, $\sigma \sim 1$	4	6285.87	11.06	0.00
D ~ road density 15 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6286.27	11.47	0.00
D ~ female density, $g_0 \sim 1$, $\sigma \sim 1$	4	6286.55	11.74	0.00
D ~ 1, $g_0 \sim 1$, $\sigma \sim 1$	3	6288.04	13.24	0.00
D ~ human RSF 2 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6288.41	13.61	0.00
D ~ combined prey RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6288.46	13.66	0.00
D ~ combined prey RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6288.85	14.05	0.00
D ~ combined prey, $g_0 \sim 1$, $\sigma \sim 1$	4	6288.85	14.05	0.00
D ~ settlements, $g_0 \sim 1$, $\sigma \sim 1$	4	6289.03	14.23	0.00
D ~ wild boar RSF 3 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6289.80	15.00	0.00
D ~ wild boar RSF, $g_0 \sim 1$, $\sigma \sim 1$	4	6289.88	15.08	0.00
D ~ wild boar RSF 1 km^2, $g_0 \sim 1$, $\sigma \sim 1$	4	6289.95	15.15	0.00

RESUME

Dina Matiukhina

127, 100 Let Vladivostoku Ave.

Vladivostok, Primorski Krai

Russia, 690068

Mobile phone: +7 914 0751559

dina.matyukhina@gmail.com

EDUCATION

September 2000 – June 2005

Far Eastern State University

Academy of Ecology, Marine Biology and Bioengineering

Degree: Specialist in Ecology

Graduate work: The ecological and economic fundamentals of optimizing forest management in Primorski Krai, Russian Far East

September 2007 – May 2010

Far Eastern State Technical University

Department of Education

Major: English language

Degree not completed

February 2011 – September 2011

Postgraduate Diploma in International Wildlife Conservation Practice

Wildlife Conservation Research Unit

Department of Zoology, University of Oxford

Oxford, UK

November 2011 – Present

Federal State Budgetary Institute United Administration of Kedrovaya Pad Reserve and Land of the Leopard National Park

Position: Senior Research Scientist

December 2008 – January 2012

Amur leopard project - Wildlife Conservation Society Russia Program

Position: Field technician

COURSES

December 2008

First Aid

Wildlife Conservation Society Russia Program

Terney, Russia

August 2012

Population Viability Analysis

Wildlife Conservation Society Russia Program

Terney, Russia

March 2013

Statistics for Biologists

Wildlife Conservation Society Russia Program

Terney, Russia

July 2015

ESRI certified training

ArcGIS I: Introduction to GIS, v. 10.2.

ArcGIS II: Essentials Workflows, v. 10.2.

ArcGIS III: Performing Analysis, v. 10.2.

ESRI CIS

Moscow, Russia

March 2016

Scientific and grant application writing

Wildlife Conservation Society Russia Program

Sikhote-Alin Biosphere Reserve

Terney, Russia

TEACHING

Summer 2014, 2015

Teaching assistant in student field practice

Far Eastern Federal University, School of Natural Sciences

Land of the Leopard National Park, Russia

STUDENTS ADVISED

2014 – 2015

Anna Polinovskaya, BSc (Far Eastern Federal University)

Graduation project title: Seasonal variations in Amur tiger abundance estimates and daily activity in the Land of the Leopard National Park based on camera-trap monitoring.

GRANTS AND AWARDS

2015

WCS Research Fellowship Program

Project title: Investigating distribution patterns of Amur tiger in southwestern Primorski Province using species distribution modeling approach

Amount: $ 15 000

2016

WCS Graduate Scholarship

C.V. Starr Tiger Conservation Fellowship

Funding of two years of graduate level studies

2017

Tuition Scholarship Award

State University of New York, College of Environmental and Forestry Biology

Support of graduate studies in academic year 2017-2018

2019

Tuition Scholarship Award

State University of New York, College of Environmental and Forestry Biology

Support of graduate studies in Spring semester 2019