Conservation implications of sex-specific landscape suitability for a large generalist carnivore

Mariela Gantchoff1 | Laura Conlee2 | Jerrold Belant1

1Camp Fire Program in Wildlife Conservation, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA
2Missouri Department of Conservation, Columbia, Missouri, USA

Correspondence
Mariela Gantchoff, 1 Forestry Dr., Syracuse NY, 13210. Email: m.gantchoff@gmail.com

Funding information
State University of New York College of Environmental Science and Forestry; Missouri Department of Conservation; Federal Aid in Wildlife Restoration

Editor: Luca Santini

Abstract

Aim: Terrestrial mammal distribution models typically do not differentiate between sexes when making spatial predictions, which could have important conservation implications. As male carnivores are usually more risk tolerant and travel longer distances, male potential range should be larger and include more human-modified areas than female range. To evaluate if differences between females and males could influence their conservation planning, we quantified sex-specific suitable range for a recolonizing population of American black bears (Ursus americanus).

Location: We applied this method in Missouri, USA.

Methods: We collected telemetry data from 57 females and 43 male bears from 2010 to 2018. We used three machine-learning methods (generalized boosted regression, random forest and maximum entropy) to develop sex-specific distribution models, which were combined into a weighted average ensemble model and converted into a binary (presence/absence) model using an optimized threshold. We used 80% of individuals for each sex as training data, and 20% as evaluation data.

Results: All models had high predictive performance; the greatest uncertainty in model predictions corresponded with the periphery of the distributions, whereas there was high agreement in the core distribution. Male suitable range was 66% larger than female range, and males were predicted to occur in more human-modified areas and more likely to be present in developed land and agriculture.

Main conclusions: Distribution models based on data from both sexes, or that is male-biased, could overestimate the female (i.e., reproductive) range and potentially misrepresent the biologically relevant species distribution. This bias can potentially lead to misguided decisions and suboptimal use of resources. By improving models when sex-specific data are available, we can better focus resources in areas where there is reproductive potential, leading to more accurate assessments of species' conservation status and better identifying areas vital for species persistence.

KEYWORDS
carnivore, habitat suitability, mammal, range, sex-specific, spatial ecology, species distribution model, ursid
1 | INTRODUCTION

Many vertebrate taxa exhibit sex-based differences in ecology and behaviour (Ruckstuhl & Neuhaus, 2006; Shine, 1989). Among mammals, females are typically smaller than males yet have high-energy requirements during gestation and lactation, which can influence mating strategies, social organization and movements (Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999; Shine, 1989; Trivers, 1972). Though sexual dimorphism usually refers to physical attributes (e.g., body size, coloration, or ornaments), the term can also encompass other traits (Ruckstuhl & Neuhaus, 2006), such as prey selection (White, Koehler, Maletzke, & Wielgus, 2011), tolerance to human disturbance (Gaines, Lyons, Lehmkuhl, & Raedeke, 2005; Kerley et al., 2002; Mace, Waller, Manley, Lyon, & Zuuring, 1996; Maehr, 1997), foraging strategies (Breed, Bowen, McMillan, & Leonard, 2006; Koike et al., 2012) or space use (Ruckstuhl & Neuhaus, 2006). At smaller scales, differences in space use are most evident when males and females live in separate groups outside the mating season (Bowyer, 2004), yet subtler differences can also result in divergent foraging behaviours and nutritional requirements (Breed et al., 2006; van Toor, Jaberg, & Safi, 2011), even in generalist species (Bowyer, 2004; Rubin & Bleich, 2006). At broader scales, mammalian males usually display larger exploratory and mate-seeking movements (Lindstedt, Miller, & Buskirk, 1986), which could result in larger male ranges at the population level.

Differing body sizes and reproductive strategies can influence space use of mammalian females and males independently or interactively (Rode, Farley, & Robbins, 2006; Rubin & Bleich, 2006). For example, large carnivore males can be more tolerant of human-modified areas (Riley et al., 2003), are often involved in more vehicle collisions (Maehr, 1997) and are more likely to cause human–wildlife conflicts (Ditmer, Garshelis, Garshelis, Noyce, Haveles, & Fieberg, 2015; Odden, Smith, Aanes, & Swenson, 1999). When differences between sexes exist, lack of discrimination could result in underestimating important variables for one sex while overestimating them for the other (Da Conde et al., 2010), and loss or modification of a particular land cover may affect one sex more than the other, which in turn can influence population structure and growth (Bowyer, Pierce, Duffy, & Haggstrom, 2001; Kie & Bowyer, 1999). If land use differentially influences male and female mortality risk and sex ratios of a population (Reid & Peery, 2014; Rubin & Bleich, 2006), female decline could be masked by stable species occurrence. In ursids, an increased number of young males can be mistaken as population growth, even when female population is low and declining (Wielgus & Bunnell, 1994). Additionally, distribution models based on data from both sexes (or male-biased) could overestimate the female (i.e., reproductive) range (Fernández, Selva, Yuste, Okarma, & Jakubiec, 2012) and potentially misrepresent the species distribution range.

Representing a species or population suitable range considering only their reproductive or breeding range is frequent for some vertebrate taxa, such as birds (Hitch & Leberg, 2007), yet this approach appears uncommon in other taxa. Typically, terrestrial mammal distribution models do not differentiate between sexes when making spatial predictions (Ahmadi et al., 2017), often because the type of data available (e.g., tracks, scats, sightings) prevents sexing of individuals (Dempsey, Gese, Kluever, Lonsinger, & Waits, 2015), but too when such data are available (e.g., telemetry; Duncan, Kahl, Gray, Salice, & Stevens, 2016; Claessen & Broekhuis, 2018). This bias is often overlooked when managing wild mammal populations (Gordon, Hester, & Festa-Bianchet, 2004; Rubin & Bleich, 2006), which is particularly important for species where dispersal behaviour and movement can vary with sex, such as in large carnivores (Zeller et al., 2018). Species distribution maps are a key component of many studies, such as analysing species range shifts and contractions, or species richness patterns (Ceballos, Ehrlich, Soberón, Salazar, & Fay, 2005; Channell & Lomolino, 2000). Additionally, species distribution ranges (IUCN, 2010) are important criteria when assessing global conservation status (Akçakaya et al., 2018; Crees et al., 2016), and spatial prioritization of conservation areas (Brum et al., 2017; Rosauer, Pollock, Linke, & Jetz, 2017); therefore, this misrepresentation could have important implications.

Species distribution models (SDMs), also referred to as habitat suitability models (Hirzel & Le Lay, 2008), combine species occurrence data with environmental variables to predict distributions usually across large spatial scales (Franklin, 2010; Shabani, Kumar, & Ahmadi, 2016). Species distribution models can be used to predict suitable conditions for species survival and to extrapolate areas where the species could occur based on known locations (Franklin 2010). A promising tool within SDMs is machine-learning methods, due to their nonparametric approaches and ability to overcome difficulties such as multicollinearity (Farrell et al., 2019). Through the framework of machine learning and SDMs, we aim to quantify sex-specific distribution range for a low-density re-colonizing population of American black bears (Ursus americanus; Family: Carnivora), evaluating if differences between females and males could influence their conservation planning. Black bears are large opportunistic omnivores that exhibit sexually dimorphic body size; males typically weight 50%-100% more than females (Hunter & Barrett, 2011). As sex ratio can strongly influence population growth (Caughley, 1977; Milner, Nilsen, & Andreassen, 2007), quantifying the occurrence of sex-specific distribution would be key in developing state-wide strategies to manage female black bear establishment, reproduction and recolonization. In addition, as male bears are more likely to occur in human-modified areas (Ditmer, Noyce, Fieberg, & Garshelis, 2018; Merkle, Robinson, Krausman, & Alaback, 2013) and involved in human-bear conflicts (Ditmer, Burk, & Garshelis, 2015; Ditmer, Garshelis, et al., 2015), by mapping male distribution we can better inform decision-makers concerning locations for outreach and conflict prevention.

2 | METHODS

2.1 | Study area

The study area was the state of Missouri, USA, where the re-colonizing black bear population occurs primarily in the southern
Ozark Highlands (Wilton, Belant, & Beringer, 2014). This ecoregion is characterized by karst topography, with elevation ranging from 76 to 274 m (Karstensen, 2010). Agriculture (e.g., corn, cattle) is more prevalent in the western region, while forest is more prevalent in the eastern region (Karstensen, 2010). The state has a humid temperate continental climate, with a mean daily minimum temperature (January) of −8 to −4°C, mean daily maximum temperature (July) of 29 to 32°C, and mean annual precipitation of 102 to 132 cm (National Oceanic and Atmospheric Administration, 2013).

2.2 Data collection

Black bears were captured in the southern Ozark Highlands using modified Aldrich foot snares (Johnson and Pelton, 1980) and curl vert traps. Captured individuals were immobilized with tiletamine and zolazepam (Telazol; A. H. Robins Company) at a dosage of 4–7 mg/kg of estimated body weight and administered with a syringe pole or dart syringe fired from a CO₂-powered pistol or rifle, or cartridge fired dart guns. Each bear received a GPS radiocollar (Northstar RASSL Globalstar, King George, Virginia, USA; Advanced Telemetry Systems M2610B, Isanti, Minnesota, USA; Lotek Wireless 7000MU, Newmarket, Ontario, Canada). The collar battery lasts about 24–36 months, and collars are typically replaced every 1–4 hr. All collars had leather breakaway links (Garshelis & McLaughlin, 1998), and all capturing and handling of bears conform with the American Society of Mammalogists guidelines (Sikes & Gannon, 2011).

2.3 Species distribution modelling

We used black bear telemetry data spanning from September 2010 to October 2018. To decrease spatial and temporal autocorrelation, we randomly subsampled telemetry locations to no more than one location per day per individual (Hiller, Belant, Beringer, Tyre 2015, Gantchoff, Wang, Beyer, & Belant, 2018). To minimize overrepresentation of individuals with greater number of telemetry locations (Edrén, Wisz, Teilmann, Dietz, & Söderkvist2010), we first calculated the median number of locations separately for females and males (371 and 92, respectively). For individuals with more than the median value, we randomly subsampled the median number of locations from the total for that individual and used the subsample for subsequent modelling.

We considered 11 variables: land cover (four categories), Shannon diversity index for land cover, vegetation productivity (mean and maximum), elevation, human density and distance to roads (minor and major). For land cover, we used data from the National Land Cover Database (NLCD; USGS, 2011). To reduce the number of variables for modelling, we re-grouped the 15 original land covers in four categories: forest cover, other natural cover (e.g., herbaceous, shrub), agriculture cover (crops and livestock) and developed cover. We modified the 30-m cell size of NLCD data to fit the 250-m spatial resolution of other variables. We calculated the Shannon diversity index (Shannon & Weaver, 1949) at the 250-m spatial resolution using the original 15 land covers at the original 30-m spatial resolution (USGS, 2011). We obtained Normalized Difference Vegetation Index (NDVI) data from the Earth Resources Observation and Science (EROS) Center’s Moderate Resolution Imaging Spectroradiometer (MODIS) from 2010 to 2017 (latest data available) with a spatial resolution of 250-m and a 16-bit radiometric resolution (USGS, 2017). We used NDVI as a proxy for vegetation productivity (Bojarska & Selva, 2012; Pettorelli et al., 2006). We calculated the mean and maximum NDVI values for each cell in the study area during bear activity period (March to November). We obtained digital elevation models acquired by the Advanced Spaceborne Thermal Emission and Reflection Radiometer to extract elevation and modified the cell size to meet the 250-m spatial resolution (NASA Jet Propulsion Laboratory, 2009). We used 2010 human population and road data from the U. S. Census Bureau (2010, 2012, respectively) as additional anthropogenic variables. As human population data are provided as number of people per block and blocks varied in area, we calculated the density of people by block and modified the cell size by density to a raster with 250-m spatial resolution. We developed two distance to road layers: major roads (i.e., interstates and highways) and minor roads (i.e., local roads, rural roads and city streets). By estimating distance to nearest road from the centroid of each cell, we created a 250-m raster for each layer.

We used three machine-learning algorithms for SDMs: generalized boosting models (GBM), based on boosted regression tree (Friedman, 2001; Ridgeway, 1999), random forest (RF), based on Breiman’s random forest algorithm (Breiman, 2001), and maximum entropy (Maxent; Phillips, Anderson, & Schapire, 2006; Phillips, Anderson, Dudík, Schapire, & Blair, 2017). As different modelling methods can yield varying results, we developed an ensemble model to achieve more accurate and robust predictions (Marmion, Parviainen, Luoto, Heikkilä, & Thuiller, 2009) and obtain an integrative prediction of black bear potential distribution in Missouri. We used the biomod2 package (Thuiller, Lafourcade, Engler, & Araújo, 2009) in R v. 3.5.1 (R Core Team, 2014), for the GBM, RF and Maxent modelling as well as the development of the ensemble model (Ahmadi et al., 2017; Thuiller et al., 2009; Zeller et al., 2018). We performed the following steps to develop sex-specific models of potential black bear distribution. We used the Spatial Analyst tool in ArcGIS Desktop (Environmental Systems Research Institute, Redlands, CA) to calculate a correlation matrix among all independent variables. No pair comparison had $|r| > 0.70$ (Dormann et al., 2013); therefore, we assumed multicollinearity did not compromise models results. As models require background data (e.g., pseudo-absence points), we generated a randomly drawn sample of background points for the extent of study area equal to the number of black bear locations. We developed three single distribution models (GBM, RF and Maxent) using the 11 spatial variables previously described (the specific modelling parameters and values used by biomod2 for GBM, RF and Maxent can be found in Appendix S1: Table S1.1). Models were calibrated using the locations of 80% of individuals as training...
data and 20% of individuals as test data. Models were evaluated using the area under the curve (AUC) of a receiver operating characteristic plot (ROC) and the true skill statistic (TSS) because of their independence from prevalence in the species data (Allouche, Tsoar, & Kadmon, 2006). The ROC is a curve of true positive rate (i.e., sensitivity) against false positive rate (i.e., 1-specificity), and values range from 0 to 1, with 0.5 being equivalent to random predictions (Hilden, 1991). The true skill statistic (TSS; traditionally used for assessing the accuracy of weather forecasts) ranges from 1 to −1, a value of 1 indicating perfect agreement and values ≤0 equivalent to random predictions (Allouche et al., 2006). We created an ensemble model by weight-averaging all single models (GBM, RF, Maxent) proportionally to their evaluation metrics scores (Thuiller et al., 2009) which resulted in a final ensemble model representing a continuous likelihood of presence (because we used presence-only data, we were unable to calculate probability of presence; Franklin 2010). To compare distribution ranges for females and males, we transformed the ensemble model to a binary format (presence/absence) by defining a likelihood threshold to differentiate between cells predicted to be occupied and cells predicted to be unoccupied. We used an optimized threshold that resulted in maximum sensitivity (the ratio of presence sites correctly predicted over the number of positive sites in the sample; Thuiller et al., 2009). Finally, we developed a committee-averaged model in which each model had a vote (1 = presence or 0 = absence of the species for each cell) and the resulting map highlights model agreement and overall prediction uncertainty (Thuiller et al., 2009).

## RESULTS

We obtained 16,105 locations from 57 females and 2,976 locations from 43 males that were adequate for analysis (Appendix S2: Figure S2.3). For females, 46 random individuals were used for developing models (13,562 locations) and 11 individuals for validation (2,543 locations). For males, 35 random individuals were used for modelling (2,335 locations) and 8 for validation (641 locations).

All female species distribution models had strong predictive performance; ROC and TSS values for testing data were 0.972 and 0.83, respectively, for GBM, 0.98 and 0.88 for RF, and 0.97 and 0.83 for Maxent (Appendix S2: Figure S2.1). The final weights for the ensemble model were 0.33, 0.34 and 0.33 for GBM, RF and Maxent, respectively. The female ensemble model (Figure 1) had a ROC score of 0.87 and TSS score of 0.86. The binary map (presence–absence) developed from the ensemble model had a sensitivity (correctly predicted presences) of 95.3% and specificity (correctly predicted absences) of 90.7%. Variables most influential for females were forest cover (50%), elevation (19%), max NDVI (13%) and agriculture cover (8%; Appendix S3: Table S3.1). Females were more likely to occur in forest cover, in areas with greater elevation and greater mean NDVI values, and less likely in agriculture cover (Appendix S3: Figure S3.1).

Male models had good but slightly lower performance; ROC and TSS values for testing data were 0.93 and 0.79 for GBM, 0.95 and 0.72 for RF, and 0.92 and 0.74 for Maxent (Appendix S2: Figure S2.1). The final weights for the ensemble model were 0.33, 0.34 and 0.33

**FIGURE 1** Ensemble distribution model for recolonizing female (left) and male (right) American black bears (*Ursus americanus*) in Missouri, USA. Top row (a and b) final ensemble model based on three weighted average species distribution models. Bottom row (c and d), binary model (presence = green, absence = grey) derived from the weighted average model applying an optimized classifying threshold (see Methods)
for GBM, RF and Maxent respectively. The male ensemble model (Figure 1) had a ROC score of 0.78 and TSS score of 0.77. The binary map developed from the ensemble model had a sensitivity of 90.1% and specificity of 87.8%. Variables most influential for males were forest cover (36%), max NDVI (21%), agriculture cover (20%) and elevation (12%; Appendix S3: Table S3.1). Similar to females, male locations were more likely to occur in forest cover, in areas with greater elevation, and in areas with greater mean and max NDVI values, and less likely in agriculture cover (Appendix S3: Figure S3.2). Variable permutation scores were greatest for elevation for males and females (Appendix S3: Table S3.2, Table S3.3).

The committee-averaged model for both sexes indicated greatest uncertainty in model prediction corresponded to the periphery of the potential distribution, whereas there was high agreement in the interior of the potential distribution (Appendix S2: Figure S2.2). The threshold value to transform the continuous presence likelihood to a binary map was 0.53 for females (94% sensitivity) and 0.47 for males (89% sensitivity). The overlap of female and male binary models (Figure 2) suggests that male distribution range (22,359.5 km²) was 66.8% larger than female distribution range (14,939.6 km²). For both sexes, >90% of their distribution range consisted of forest cover (Table 1), and use of non-forested areas was relatively low. However, the larger male range included 85% more developed areas and 54% more agriculture than female range (total area, Table 1). Proportionally, males were 23% more likely to be present in developed areas, 11% more likely in cultivated crops and 56% more likely in non-forested natural areas (Table 1).

### DISCUSSION

Our black bear sex-specific distribution models indicated that the distribution male range in Missouri was considerably larger than for females, and males were predicted to occur in more human-modified

| Land cover          | F area | M area | Male/female | F prop. | M prop. | Male/female |
|---------------------|--------|--------|-------------|---------|---------|-------------|
| Forest              | 14,192.94 | 21,051.88 | 1.48       | 0.95    | 0.93    | 0.99        |
| Other natural cover | 257.44  | 603.06  | 2.34       | 0.02    | 0.03    | 1.56        |
| Agriculture         | 311.38  | 479.06  | 1.54       | 0.02    | 0.02    | 1.11        |
| Developed           | 208.13  | 385.19  | 1.85       | 0.01    | 0.02    | 1.23        |

Note: Suitable range = weighted average species distribution model based on telemetry data from 2010 to 2018. Abbreviations: F: female; M: male.
areas and more likely to be present in developed land and agriculture. In contrast, female range (i.e., reproductive range) was more constrained and included less human-modified areas. Since our study population is recolonizing and therefore below carrying capacity, it is possible that individuals, mostly females, are free of strong competition and only use the most suitable areas, a pattern that could change as these areas become saturated (Dupré, Genovesi, & Pedrotti, 2000). Selecting the most suitable areas could result in mapping a more restricted predicted range; however, similar to our results, the modelled distribution range for reproductive female brown bears (U. arctos) in Poland was smaller than the range based on occurrence of both sexes (Fernández et al., 2012), suggesting a general pattern may occur that is independent of density. Sex-specific behaviour has been observed in several ursid species, such as foraging behaviour in Asiatic black bears (U. thibetanus; Koike et al., 2012), road tolerance in black bears (Loosen, Morehouse, & Boyce, 2019) and brown bears (Mace et al., 1996), and spatial segregation in brown bears (Rode et al., 2006). Highlighting the importance of sex-specific modelling, a habitat-based conservation framework for brown bears in Canada was based on adult female habitat, as they are the most sensitive sex-age class for population trajectories and their habitat use differed from males (Nielsen, Stenhouse, & Boyce, 2006). A follow-up study, conducted in the same area but at a larger scale, focused on female-specific spatial management of the impact of roads on bear demographics (Boulanger & Stenhouse, 2014).

Modelling species distribution without considering potential differences between females and males, or the use of male-biased data, could result in the assumed species' reproductive range to be overestimated. This overestimation could lead to inaccurately assigning a species a better conservation status, overestimating a region's species richness or underestimating species range contractions and shifts.

Another potential problem from not differentiating between sexes is over- or underestimation of smaller scale presence–environment relationships. Previous species distribution models developed in Missouri from citizen reported black bear sightings found a strong positive effect of roads and negligible effect of forested areas (McFadden-Hiller & Belant, 2018), which contrasts with our results. Missouri bear sightings are likely male-biased due to males moving larger distances (Gantchoff et al., 2018) and more likely to occur in human-modified areas (this study). Additionally, wildlife sightings are more likely to occur closer to human-modified areas due to higher human density. Even when multiple measures are taken to reduce sampling bias, the data available to develop species distribution models (e.g., sightings, tracks, museum specimens) can have constraints that cannot be completely eliminated; it is important to acknowledge those limitations as well as the potential for biased results. Not all data types or species distribution model approaches are valid for all applications, and using inadequate species distribution results may lead to misguided decisions and suboptimal use of resources (Guillera-Arroita et al., 2015).

Black bears are forest obligate species, and as expected, their distribution in this study was strongly associated with the distribution of forest cover (Sollmann, Gardner, Belant, Wilton, & Beringer, 2016; Wilton et al., 2014). The proportion of forest in the potential distribution range for both sexes (93%–95%) was similar to the individual proportion of forest within annual and seasonal home ranges for this same study area (93% F, 89% M; Gantchoff et al., 2018), which suggests non-forested land covers are a small but consistent and scale independent fraction of areas used by black bears in Missouri. Second to land cover, elevation and vegetation productivity where most influential, suggesting areas of higher elevation and more productive are preferred likely because they offer more food resources and less human disturbance; human activity is often higher in areas of low elevation with less topographic relief (e.g., agriculture; Napton, Auch, Headley, & Taylor, 2010). Though the predicted range including human-modified areas was low for both sexes, the total area for males was considerably larger and males were more likely to use them, supporting with our predictions. Male black bears are more likely to use human-modified landscapes (Ditmer et al., 2018), use anthropogenic resources (Merkle et al., 2013) and are the primary crop depredators (Garshelis, 1989; Ditmer, Burk, et al., 2015). Female black bears could occupy smaller areas and areas with adequate, but poorer, resources than males because of high dietary and physiological plasticity (Hilderbrand et al., 2018; McDonald & Fuller, 2005). For example, adult female black bears can compensate for changes in food availability, producing milk of adequate quality for their cubs, regardless of spring diet (McDonald & Fuller, 2005).

As we determined with black bears, other mammalian taxa could have important differences based on their reproductive strategies, social structures and body size differences, which can influence whether use of sex-specific data is important for SDM development. For example, male African elephants (Loxodonta africana), being more mobile and risk tolerant, have access to areas and resources that are not available to females or mixed groups to use (Smit, Grant, & Whyte, 2007), and the distribution range for male parti-coloured bats (Vespertilio murinus) was larger than for females, who had a patchier and more restricted distribution (van Toor et al., 2011). However, selecting the reproductive range to represent the species range would not be appropriate for certain species, for example if maternal females segregate from all other sex and age classes (e.g., humpback whales Megaptera novaeangliae; Clapham, 1996) or when strong spatial segregation between sexes occurs for most of the year (e.g., grey seal Halichoerus grypus; Austin, Bowen, & McMillan, 2004).

Sex-specific space use and distribution range is possibly a widespread phenomenon that, while documented and acknowledged to exist, is often not explicitly incorporated in applied ecology projects, particularly for terrestrial carnivores (Ahmadi et al., 2017; Klaassen & Broekhuis, 2018, but see Nielsen et al., 2006). By developing separate spatial models for each sex, we have identified this limitation for black bears and therefore suggest that traditional SDMs might be overestimating the biologically relevant distribution range of many species, particularly if both sexes have similar overall requirements but different tolerances to disturbance. In addition, models used to predict ranges, particularly for endangered species, are possibly not conservative, which in turn suggests that the
conservation status of many species could be worse than currently believed or have different relationships with their environment than currently understood. Particularly for threatened and endangered species, not considering the distribution or needs of reproductive individuals could adversely affect long-term persistence of populations. As spatially explicit models of conservation priorities are becoming increasingly important (Brum et al., 2017; Rosauer et al., 2017), by acknowledging these limitations and developing improved models when data are available, we can improve our efforts to better focus resources in areas where population growth can occur, more accurately assess species’ conservation status, and better identify areas vital for species persistence.

ACKNOWLEDGEMENTS

Financial support was provided by the Federal Aid in Wildlife Restoration, the Missouri Department of Conservation and the State University of New York College of Environmental Science and Forestry. We thank all state biologists and field technicians who participated in fieldwork and data collection. We are grateful to reviewers M. van Toor and A. Scharf for helpful suggestions that improved our manuscript.

DATA ACCESSIBILITY

Data used in this manuscript will be available in Dryad: https://doi.org/10.5061/dryad.j5b27q3.

ORCID

Mariela Gantchoff https://orcid.org/0000-0002-7098-8072

REFERENCES

Ahmadi, M., Nezami Balouchi, B., Jowkar, H., Hemami, M. R., Fadakar, D., Malakouti-Khah, S., & Ostrowski, S. (2017). Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia. Diversity and Distributions, 23, 592-603. https://doi.org/10.1111/ddi.12560
Açıkçay, H. R., Bennett, E. L., Brooks, T. M., Grace, M. K., Heath, A., Hedges, S., ... Young, R. P. (2018). Quantifying species recovery and conservation success to develop an IUCN Green List of Species. Conservation Biology, 32, 1128-1138. https://doi.org/10.1111/cobi.13112
Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43, 1223-1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x
Austin, D., Bowen, W. D., & McMillan, J. I. (2004). Intraspecific variation in movement patterns: Modeling individual behaviour in a large marine predator. Oikos, 105, 15-30. https://doi.org/10.1111/j.0030-1299.1999.12730.x
Bojarska, K., & Selva, N. (2012). Spatial patterns in brown bear Ursus arctos diet: The role of geographical and environmental factors. Mammal Review, 42, 120-143. https://doi.org/10.1111/j.1365-2907.2011.00192.x
Boulanger, J., & Stenhouse, G. B. (2014). The impact of roads on the demography of grizzly bears in Alberta. PLoS ONE, 9, e115535. https://doi.org/10.1371/journal.pone.0115535
Bowyer, R. T. (2004). Sexual segregation in ruminants: Definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy, 85, 1039–1052. https://doi.org/10.1644/BBL-002.1
Bowyer, R. T., Pierce, B. M., Duffy, L. K., & Haggstrom, D. A. (2001). Sexual segregation in moose: Effects of habitat manipulation. Alces, 37, 109–123
Breed, G. A., Bowen, W. D., McMillan, J. I., & Leonard, M. L. (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proceedings of the Royal Society B: Biological Sciences, 273, 2319–2326. https://doi.org/10.1098/rspb.2006.3581
Breiman, L. (2001). Random Forests. Machine Learning, 45, 5–32.
Brum, F. T., Graham, C. H., Costa, G. C., Hedges, S. B., Penone, C., Radeloff, V. C., ... Davidson, A. D. (2017). Global priorities for conservation across multiple dimensions of mammalian diversity. Proceedings of the National Academy of Sciences of the United States of America, 114, 7641–7646. https://doi.org/10.1073/pnas.1706461114
Caughley, G. (1977). Analysis of vertebrate populations. Chichester, UK: John Wiley & Sons.
Ceballos, G., Ehrlich, P. R., Soberón, J., Salazar, I., & Fay, J. P. (2005). Global mammal conservation: What must we manage? Science, 309, 603–607. https://doi.org/10.1126/science.1114015
Channell, R., & Lombolino, M. V. (2000). Dynamic biogeography and conservation of endangered species. Nature, 403, 84–86. https://doi.org/10.1038/47487
Clapham, P. J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. Mammal Review, 26, 27–49. https://doi.org/10.1111/j.1365-2907.1996.tb00145.x
Crees, J. J., Collins, A. C., Stephenson, P. J., Meredith, H. M., Young, R. P., Howe, C., ... Turvey, S. T. (2016). A comparative approach to assess drivers of success in mammalian conservation recovery programs. Conservation Biology, 30, 694–705. https://doi.org/10.1111/cobi.12652
Da Conde, D. A., Colchero, F., Zarza, H., Christensen, N. L. Jr, Sexton, J. O., Manterola, C., ... Ceballos, G. (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation, 143, 1980–1988. https://doi.org/10.1016/j.biocon.2010.04.049
Dempsey, S. J., Gese, E. M., Kluiver, B. M., Lonsinger, R. C., & Waits, L. P. (2015). Evaluation of scat deposition transects versus radio telemetry for developing a species distribution model for a rare desert carnivore, the kit fox. PLoS ONE, 10(10), e0138995. https://doi.org/10.1371/journal.pone.0138995
Ditmter, M. A., Burk, T. E., & Garshelis, D. L. (2015). Do innate food preferences and learning affect crop raiding by American black bears? Ursus, 26, 40–52. https://doi.org/10.2192/URSUS-D-14-00028.1
Ditmter, M. A., Garshelis, D. L., Noyce, K. V., Haveles, A. W., & Fieberg, J. R. (2015). Are American black bears in an agricultural landscape being sustained by crops? Journal of Mammalogy, 97, 54–67.
Ditmter, M. A., Noyce, K. V., Fieberg, J. R., & Garshelis, D. L. (2018). Delineating the ecological and geographic edge of an opportunist: The American black bear exploiting an agricultural landscape. Ecological Modelling, 387, 205–219. https://doi.org/10.1016/j.ecolmodel.2018.08.018
Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecosphere, 36, 27–46. https://doi.org/10.1642/1179-6639.2012.07348.x
Duncan, N. P., Kahl, S. S., Gray, S. S., Salice, C. J., & Stevens, R. D. (2016). Pronghorn habitat suitability in the Texas Panhandle. The Journal of Wildlife Management, 80, 1471–1478. https://doi.org/10.1002/jwmg.21139
Dupré, E., Genovesi, P., & Pedrotti, L. (2000). A feasibility study on the reintroduction of the brown bear (Ursus arctos) in the Central Alps. Biologia E Conservazione Della Fauna, 105, 3–89.
Biosketches

Mariela Gantchoff is Postdoctoral Research Associate at the Camp Fire Program in Wildlife Conservation, SUNY College of Environmental Science and Forestry. Her research focuses on carnivore ecology and behaviour, spatial ecology and applied conservation.

Laura Conlee is Black Bear and Furbearer Biologist for the Missouri Department of Conservation. She focuses on black bear management, ecology and conflict resolution.

Jerrold Belant is Camp Fire Conservation Fund Professor at SUNY College of Environmental Science and Forestry in Syracuse, NY. His research emphasizes ecology of carnivores and ungulates, human–wildlife conflict resolution and international conservation.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Gantchoff M, Conlee L, Belant J. Conservation implications of sex-specific landscape suitability for a large generalist carnivore. Divers Distrib. 2019;25:1488-1496. https://doi.org/10.1111/ddi.12954