SPATIAL ECOLOGY OF GRAY WOLVES (*CANIS LUPUS*) IN THE WESTERN GREAT LAKES REGION IN RESPONSE TO ANTHROPOGENIC DISTURBANCE

By

Merijn van den Bosch

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

Fisheries and Wildlife — Doctor of Philosophy

ABSTRACT

Large carnivores tend to avoid humans and their activities spatially and temporally, yet often experience high rates of anthropogenic mortality and their conservation frequently depends on coexistence with humans. I investigated how human landscape disturbances influences landscape use by gray wolves (*Canis lupus*) in the western Great Lakes region of the United States. Specifically, I investigated whether landscape use by wolves has changed temporally, whether it differs among individuals, and how human disturbances may affect the future distribution of gray wolves. I characterized wolf recolonization of the western Great Lakes region during 1989–2020 by investigating whether the relationship between wolf habitat suitability and two indices of human disturbance, human population density and proportions of agricultural land cover, has changed during this period. I also modeled habitat selection for the western Great Lakes region, distinguishing between territorial and non-territorial wolves and conducted a subsequent connectivity analysis. Finally, I assessed wolf recolonization potential throughout their former range in the eastern USA by modeling habitat suitability and connectivity potential. During 1989–2020, wolves occupied areas with progressively higher levels of human disturbance, resulting in an estimated 35% increase in wolf habitat across Minnesota, Wisconsin, and Michigan, though range expansion appeared to slow over time. Habitat selection of territorial and non-territorial wolves was similar and connectivity analysis suggested limited habitat connectivity due to human landscape disturbance, constrained recolonization of suitable areas within the western Great Lakes region. I estimated 65.3% of former range in the eastern USA is currently unsuitable for wolves, but identified five unoccupied areas in the eastern USA that could maintain viable wolf populations. However, connectivity between current and potential wolf range appears limited due to high human disturbance and the presence of the Great Lakes. This work demonstrates an apparent range stabilization of wolves in the Great Lakes region, where little unoccupied habitat remains available, but there appears limited potential for further natural recolonization of unoccupied habitat throughout the eastern United States. This can inform policy discussions such as the desirability of human-assisted recolonization of additional historical range, and the accomplishment of targets set when wolves received federal protection.

ACKNOWLEDGEMENTS

I am deeply indebted to my supervisor, Dr. Jerry Belant, for granting me an opportunity beyond my wildest imaginations, for his extensive support in the form of invaluable advice and insights, and moreover, for his unwavering belief in my abilities to successfully complete the trajectory resulting in this dissertation. I would also like to extend my sincere thanks to those serving as my committee members: Dr. Mariela Gantchoff, Dr. Brent Patterson, Dr. Thomas Getty, and last but not least, Dr. Ken Kellner, whose abilities to provide analytical support in an accessible and pedagogic manner are unmatched.

This research was made possible by cooperation among the Minnesota, Wisconsin, and Michigan Departments of Natural Resources, the USDA, and various tribal agencies. I will not attempt individual recognitions but want to thank everyone involved with this gargantuan effort, from the wildlife professionals I have had the pleasure of working with directly to the many members of the public volunteering their time to collect data upon which most of my analyses relied. Funding was provided by the U.S. Fish and Wildlife Service through the Great Lakes Fish and Wildlife Restoration Act and the Boone and Crockett Program at Michigan State University.

I gratefully acknowledge the support I received from my peers, both past and present members of our lab, as well as other friends I made along the way.

I would also like to thank my friends back in Veusseleir and Antwaarpe, who have been important to me for many years already and provided me with remote friendship as well as revitalizing good times upon my visits home. I will be eternally grateful to my family, particularly my parents, for their unconditional love and support, despite my having placed the Atlantic Ocean between us. I therefore dedicate this dissertation to them. Finally, though he will never know, I thank my very own "Tennessee stud", Tucker, for coming into my life and being my pride and joy ever since he did.

iii

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION
CHAPTER 2: HUMAN DISTURBANCE LIMITS GRAY WOLF RANGE EXPANSION IN THE GREAT LAKES REGION, USA
CHAPTER 3: HABITAT SELECTION OF RESIDENT AND NON-RESIDENT GRAY WOLVES: IMPLICATIONS FOR HABITAT CONNECTIVITY
CHAPTER 4: IDENTIFYING POTENTIAL GRAY WOLF HABITAT AND CONNECTIVITY IN THE EASTERN USA
LITERATURE CITED
APPENDIX

CHAPTER 1: INTRODUCTION

The overarching goal of this research is to contribute to knowledge on the spatial ecology of gray wolves (*Canis lupus*) in the western Great Lakes region of the United States. The recurring theme is how human landscape disturbances influence landscape use by wolves. Large carnivores tend to avoid humans and their activities spatially (Laundre et al., 2010) and temporally (Gaynor et al., 2018), yet experience high rates of anthropogenic mortality (Ripple et al., 2014; Hill et al., 2022) and their conservation often depends on coexistence with humans (Oriol-Cotterill et al., 2015).

While expanding wolf populations may initially occupy high-quality territories, saturation of these areas can lead to occupation of lower quality territories, potentially with more human disturbance (Guisan and Theurillat, 2000). This variation in occupied space use should be accounted for to accurately forecast distributions of recolonizing carnivores (Guisan and Thuiller, 2005). In Chapter 1, I used long-term winter survey data on gray wolves in Minnesota, Wisconsin, and Michigan to study changes in the relationship between wolf presence and human disturbance during recolonization. The prediction of a negative relationship between gray wolf habitat suitability and two indices of human disturbance, human population density and proportions of agricultural land cover, was supported. The prediction of wolves expanding their range to include areas with higher human disturbance was also supported. I estimated a 35% increase in occupied habitat from 1989–1994 to 2016–2020. However, wolf range expansion into areas with higher human disturbance appeared to decline over time. Further wolf recolonization of the western Great Lakes region appears largely constrained by human disturbances, resulting in a stabilization of current range.

Assessing the spatial ecology of wolves requires understanding movements of dispersing individuals, an important biological stage in the life of wolves (Mech and Boitani, 2003). Studies generally consider habitat selection across individuals as being equivalent, which can affect the accuracy of habitat selection and connectivity analyses. In Chapter 2, I modeled habitat selection for the western Great Lakes distinct population segment of gray wolves and assessed habitat connectivity between current range and potential areas for range expansion. Using GPS data facilitates distinction between wolves established in a territory from those that are dispersing (Bunnefeld et al., 2011), and I used a step-selection function (Thurfjell et al., 2014) to test for differences between habitat selection of resident and dispersing wolves. I based a connectivity

analysis on the latter if differences were found. The prediction wolves would select against areas of greater human disturbance was supported, but the prediction that selection against disturbance would be greater for resident wolves (Rio-Maior et al., 2019) was not supported. I therefore conducted connectivity analysis on combined resident and disperser movements and concluded limited landscape permeability due to wolf avoidance of human landscape disturbance has constrained recolonization of suitable areas within current range and bordering states.

Increased legal protection and shifting human attitudes has allowed wolves to partially reoccupy former range in the USA (Gompper et al., 2015) and Europe (Chapron et al., 2014), yet it is unknown to what extent recolonization could continue. As wolf persistence and recolonization depends on human tolerance, estimating the potential for further recolonization of former range can facilitate the development of management and policy strategies before further recolonization occurs (Treves et al., 2004). In Chapter 3, I assessed recolonization potential throughout former wolf range in the eastern USA (Novak, 1995), by modeling habitat suitability and connectivity potential. I used recent winter survey data to develop an ensemble species distribution model for current wolf range in the western Great Lakes region and projected this model throughout former wolf range in the eastern USA and current wolf range in southern Canada. I estimated 65.3% of former range in the eastern USA is currently unsuitable for wolves but identified 6 core areas in the eastern USA that could maintain viable wolf populations, of which only the Great Lakes core area is currently occupied. Large areas of wolf habitat remain available throughout the eastern USA, but connectivity between current and potential wolf range appears limited due to extensive agriculture, high human populations, and presence of the Great Lakes.

Overall, I have demonstrated how recolonizing gray wolves have adapted to human disturbance and may further adapt in space and time. There is an apparent range stabilization of wolves in the Great Lakes region, where little unoccupied habitat remains available, but there appears limited potential for further natural recolonization of unoccupied habitat throughout the eastern United States. This can inform policy discussions, such as the desirability of human-assisted recolonization of additional historical range, and the accomplishment of targets set when wolves received federal protection.

CHAPTER 2: HUMAN DISTURBANCE LIMITS GRAY WOLF RANGE EXPANSION IN THE GREAT LAKES REGION, USA

2.1 ABSTRACT

Species distribution models can facilitate conservation planning and action but presume species-environment relationships are stable, which is not the case for invasive or recolonizing species only partially occupying their potential distributions. This complicates our understanding of colonization and recolonization processes and their effects on species distributions. We grouped snow tracking data collected during gray wolf (Canis lupus) recolonization of the western Great Lakes region into six periods spanning 1989–2020 and used a species distribution model to assess temporal variation in wolf distribution in response to two indices of human landscape disturbance: human population density and proportion of agricultural land cover. We found consistent negative relationships between these covariates and wolf habitat suitability, whereby the strength of these negative relationships decreased over time. Increases in habitat area decreased over time and our model estimated about 148 500 km² of wolf habitat in our study area in the first (1989–1994) period, increasing 35% to about 201 000 km² by the last (2016–2020) period. Wolves increasingly occupied areas with higher levels of human disturbance during recolonization, demonstrating temporal dynamics in the relationship between wolves and indices of human disturbance. The western Great Lakes wolf population may now occupy most areas currently suitable and is limited by human landscape disturbances, resulting in apparent stabilization of regional wolf range.

2.2 INTRODUCTION

The 21st century is characterized by an ongoing anthropogenic mass extinction event, with vertebrate extinctions having accelerated up to one hundredfold (Ceballos et al., 2015). Species distribution models facilitate conservation planning and action (Guisan and Thuiller, 2005) by predicting how species ranges shift in response to anthropogenic factors including habitat loss and fragmentation (Fahrig et al., 2003) or climate change (Thomas et al., 2004). Range shift studies are also crucial to assess the spread of recolonizing, reintroduced, or invasive species, whether these promote biodiversity (Ripple and Beschta, 2012) or degrade it (Clavero and García-Berthou, 2005; Lockwood et al., 2013). Accurate forecasts of species colonization processes are therefore prerequisite to mitigate or effectuate range shifts (Mladenoff and Sickley, 1998; Jiménez-Valverde et al., 2011).

Unraveling mechanisms influencing colonization or recolonization includes understanding the species' realized niche through modeling relationships between species occurrences and environmental variables (Guisan et al., 2017). However, these models presume species-environment relationships are stable (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009), which rarely occurs for invasive (Václavík and Meentemeyer, 2012) or recolonizing species (Svenning and Skov, 2004) that often only partially occupy their potential distribution and are not in spatial equilibrium with their environment (Guisan and Thuiller, 2005). Using species distribution models developed from presence data that do not represent the full range of suitable conditions in an area can reduce model accuracy and usefulness (Václavík and Meentemeyer, 2012).

Large carnivores are recolonizing parts of their historical range in North America (Gompper et al., 2015) and Europe (Chapron et al., 2014). Partial recolonizations of historical carnivore ranges resulted from increased legal protection of carnivores and their habitat, and changing public perception (Chapron et al., 2014; Gompper et al., 2015). However, human disturbance remains the most limiting factor driving large carnivore distributions in human-dominated landscapes, such as Eurasian lynx (*Lynx lynx*, Ripari et al., 2022), brown bears (*Ursus arctos*; Lamb et al., 2018), and mountain lions (*Puma concolor*, Suraci et al., 2019). Gray wolves (*Canis lupus*) occupied most of the conterminous United States but were largely extirpated from this area by 1970 (Boitani, 2003). Following federal protection in 1974 through the Endangered Species Act (ESA), wolves recolonized large portions of the western Great Lakes region of the USA (Ruid et al., 2009). The western Great Lakes population has recently stabilized at around 4,200 wolves, more recently for Michigan (2011) and Wisconsin (2017) than for Minnesota, where stability has been suggested since 2005 or earlier (USFWS, 2020a).

Wolf recolonization may be spatially constrained by anthropogenic disturbance and mortality risk (Mech, 2017; Hill et al., 2022). Earlier research found consistently negative relationships between wolf habitat suitability and indices of human disturbance (Mladenoff et al., 1995; Carroll et al., 2003; Martínez-Meyer et al., 2021), but may have underestimated limits of wolf tolerance for human disturbance (Mladenoff et al., 1995; Mladenoff and Sickley, 1998, Carroll et al., 2003) by not accounting for wolves occupying an incomplete realized niche (Mladenoff et al., 2009; O'Neil et al., 2019). For example, in Minnesota (Mech, 1989) and

Wisconsin (Mladenoff et al., 2009) wolves occupied areas with higher road densities than earlier in recolonization (Thiel, 1985). Landscape use of the western Great Lakes region wolf population appears dynamic during recolonization which complicates our understanding of their potential distribution.

We used snow tracking data collected during 1989–2020 to assess temporal variation in wolf distribution in response to landscape characteristics of the western Great Lakes region, USA. We predicted wolves would increasingly occupy areas with greater human disturbance during recolonization and range expansion. We also predicted a decline in the rate of recolonization, and that wolves currently occupy most accessible suitable areas suggesting wolves are approaching a local equilibrium.

2.3 METHODS

Study area

The western Great Lakes region (Figure 2.1) comprises the states of Minnesota (220,185 km²), Wisconsin (145,594 km²), and Michigan (150,648 km²), USA. This region is dominated by forest (44%) in the north, and agricultural land (37%) in the south, with 86% of the area within 10 km of natural water features (NLCD, 2016; Gantchoff et al., 2021). Elevations are 174–701 meters above sea level (USGS, 1996). Human populations are concentrated in the southern part of each state, with densities > 100 km², and declining sharply across a northern gradient (US Census Bureau, 2010; NLCD, 2016).

When wolves were protected in 1974 through the ESA, the regional population comprised about 750 individuals in northeastern Minnesota and a small, isolated population on Isle Royale, Michigan (Erb and DonCarlos, 2009). Legal protection facilitated population growth in Minnesota, resulting in the recolonization of northern Wisconsin by 1975 (Wydeven et al., 2009) and the Upper Peninsula of Michigan by 1989 (Beyer et al., 2009). Recent estimates of population size are about 4,200 individuals, with 2,600 in Minnesota, 900 in Wisconsin, and 700 in the Upper Peninsula of Michigan (USFWS, 2020a).

Data collection

We used long-term winter track survey data on gray wolves collected by the Departments of Natural Resources (DNR) of Minnesota, Wisconsin, and Michigan during 1989–2020. In Minnesota, trained natural resource officers were instructed to record locations of all wolf

sightings and signs (e.g., tracks, scat) observed during work hours from November until snowmelt, usually around mid-May (Gantchoff et al., 2022). Participants could record locations on forms or maps, but more recently primarily used a web-based GIS application. The final dataset was combined with other presence data recorded during other surveys coordinated by the DNR (e.g., furbearer survey, carnivore scent station survey). In Wisconsin, staff and trained volunteers conducted surveys throughout known wolf range, primarily during December-April (Stauffer et al, 2020). The survey area included 164 survey blocks of about 500 km²; delineated using waterways, roads, and state boundaries; ensuring each block could be surveyed within a day. Employees of the DNR, tribal biologists, and trained volunteers attempted to survey most snow-covered roads within a block 1–3 days after snowfall. In the Upper Peninsula of Michigan, surveys are conducted along roads and trails using truck or snowmobile (Michigan Department of Natural Resources, 2008). Efforts to estimate wolf abundance began in 1989 and initially focused on following up on reports of wolf sign observed by MDNR staff and the public and searching areas where the last wolf packs occurred in the 1940s-1950s. By 1995, staff surveyed suitable habitat across the Upper Peninsula and during 2000–2006, at least 25% of available roads and trails were surveyed at least once annually. Since 2007, due to increasing wolf abundance, the Upper Peninsula was divided into 21 survey units of which 12–13 were randomly selected and surveyed annually during 2007–2011 and 2013–2014, then every other year starting 2016, ensuring \geq 60% coverage of the Upper Peninsula. Portions of the Lower Peninsula of Michigan were periodically monitored for wolf occurrence based on reported sightings, but there are no systematic surveys as wolves have not established there (Beyer et al., 2009). Sampling area and methodology varies between states and over the three decades of data collection, though we are confident sampling consistently covered the approximate distribution of wolves in each state. Monitoring in Minnesota was well-established in 1989 as wolves were not extirpated, while the approximate distribution of wolves in Wisconsin and Michigan was well-known in early years of data collection, based on public sightings and extensive agency work resulting from high public interest in wolves.

Data selection and processing

Because areas states surveyed varied across years, we grouped data into six periods (1989–1994, 1995–2000, 2001–2005, 2006–2010, 2011–2015, and 2016–2020) that represented the shortest intervals of complete spatial coverage. To account for spatial autocorrelation, we

filtered each dataset to a maximum of one presence point per 3-km cell (Guisan et al., 2017 van den Bosch et al., 2022) and randomly generated two pseudo-absence points for each presence point, ensuring presence and pseudo-absence points grouped by period did not co-occur within a cell. We excluded Isle Royale National Park, Michigan, as we had no survey data available for this area. We chose random sampling despite potential sampling bias (Phillips et al., 2009) because the regional distribution of wolves was well-known from monitoring during the period of data collection.

Modeling

To model temporal dynamics in the relationship between wolf habitat suitability and human landscape disturbance, we used the National Land Cover Database (30-m resolution) (Yang et al., 2016; Dewitz, 2019; NLCD, 2001; 2006; 2008; 2011; 2016; 2020) to derive proportion of agricultural land cover (classes planted/cultivated and pasture/hay) (Figure 2.1), and layers of human population density (per km²) from 5 yearly Gridded Population of the World V4.11 (30 arc-second resolution) datasets (CIESIN, 2000; 2005; 2010; 2015; 2020). We extracted these variables from the datasets most temporally aligned with each period of data collection. As the earliest and most recent datasets were highly correlated for proportion of agricultural land cover (r = 0.97) and human population density (r = 0.98), we assumed similarity of these metrics in earlier years and used values from the 2000 dataset for periods for which data were unavailable. We rescaled covariates to 3-km resolution to reduce spatial mismatch between species data and our covariates (Guisan and Thuiller, 2005). This was the finest possible resolution as data contained presence points collected with accuracy to the nearest mile (1.61 km). We removed cells classified as water from analysis then scaled continuous variables (-1 to 1) to facilitate effect comparison. We did not use variables related to developed land cover (e.g. road density, proportion of developed cover, etc.) as surveys were conducted along roads which causes positive bias between wolf presence and such variables (van den Bosch et al., 2022). We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity between variables. We created two models for pairwise correlation > 0.70, each with one of the correlated variables, and removed the variable which resulted in greater AIC from the final model (Burnham and Anderson, 2003; Guisan et al., 2017).

We used a binomial generalized linear model in program R 3.6.2 (R Core Team, 2020), with proportion of agricultural land cover and human population density as continuous variables

which were not correlated (r = -0.09 - -0.10 across six periods), and interactions with the six periods of data. We used the area under the curve (AUC) of the receiver-operating characteristic (ROC), along with associated sensitivity and specificity scores, to evaluate model performance. We considered scores of AUC ≥ 0.90 as excellent, $0.90 > x \ge 0.80$ as good and $0.80 > x \ge 0.70$ as fair (Araújo et al., 2005). We used the DHARMa package in R (Hartig et al., 2017) to assess model fit diagnostics by testing for data dispersion, distribution, and outliers.

To assess temporal dynamics in wolf distribution we created binary habitat predictions for each period. We transformed habitat suitability maps for each period to binary format by defining a threshold suitability that maximized sensitivity and specificity with the ROCR package in R (Sing et al., 2005; Guisan et al., 2017). We then estimated total habitat area for each period. To quantify uncertainty associated with habitat area estimates, we used a bootstrap approach which incorporated random variability in the selection of pseudo-absence points and uncertainty around the model parameter estimates. We ran 1,000 bootstrap simulations, whereby each simulation fit a model using a randomly generated set of pseudo-absence points. From each fitted model, we randomly sampled a set of parameter estimates based on the point estimates and associated variance-covariance matrices. We used these estimates to predict habitat suitability. This bootstrap approach yielded a distribution of total habitat area for each period, from which we calculated a 95% confidence interval.

We used response curves of the continuous variables to indicate effects on habitat suitability for each period (Elith et al., 2005), and binary maps from the previous step to calculate changes in estimated habitat area between the bootstrapped predictions for all periods (Thuiller et al., 2009). An overall decline in increases of estimated wolf habitat would suggest the wolf population is approaching spatial equilibrium. We conducted a post-hoc evaluation of mean road density in gained or lost wolf habitat between periods to compare our results to previous studies (Thiel, 1985; Mech, 1989, Mladenoff et al., 2009).

2.4 RESULTS

The number of presence points for the six periods were 542 (1989–1994), 1,253 (1995–2000), 1,163 (2001–2005), 1,584 (2006–2010), 1,608 (2011–2015), and 1,588 (2016–2020). Our species distribution model had good model performance (AUC = 0.82). There were no indications of poor model fit relating to data dispersion, distribution, or outliers (Appendix: figure A).

Our model indicated a negative relationship between wolf habitat suitability and human population density, as well as proportional agricultural land cover (Table 2.1, Figure 2.2). This negative relationship between habitat suitability and human population density was stronger in the first (1989–1994) period than in the fourth (2006–2010), fifth (2011–2015), and sixth (2016–2020) periods. The negative relationship between habitat suitability and proportional agricultural land cover was stronger in the first (1989–1994) period than in the first (1989–1994) period than in the fifth (2011–2015) and sixth (2016–2020) periods. Overall, the strength of the negative relationships between habitat suitability and our environmental variables decreased over time, particularly for human population density.

Our binary habitat classification estimated about 148 500 km² of wolf habitat in the first (1989–1994) period, increasing 35% to about 201 000 km² by the last (2016–2020) period (Figure 2.3). Estimated wolf habitat increased between periods except between the second (1995–2000) and third (2001–2005) periods and increases in habitat overall declined across periods. Habitat gains occurred primarily in peripheral occupied wolf range, whereas habitat losses (500 km²; 0.003%) were dispersed throughout wolf range (Figure 2.4). Finally, mean road densities were greater (1.44 km/km²) in predicted habitat gained between the fifth (2011–2015) and last (2016–2020) period than in habitat present in the first period (1989–1994; 0.87 km/km²).

2.5 DISCUSSION

We identified a negative relationship between gray wolf habitat suitability and two indices of human disturbance, human population density and proportions of agricultural land cover, supporting our prediction. Our prediction of wolves expanding their range to include areas with higher human disturbance was also supported. We estimated a 35% increase in occupied habitat between the first (1989–1994) and last (2016–2020) periods. However, wolf range expansion into areas with more human disturbance appeared to slow during more recent periods, most notably in response to human population density, indicating wolves may be approaching spatial equilibrium within the study area. If wolves have neared spatial equilibrium, we can infer the approximate upper thresholds of human disturbance that wolves can occur in the western Great Lakes region. For example, using wolf presence locations from habitat gained between the last period (2016–2020) and the previous period (2011–2015), mean proportions of agriculture and human population densities were 20.73 and 11.40/km², respectively.

Gray wolves in the Great Lakes region have expanded their range from relatively undisturbed areas of northeastern Minnesota to include areas of the Great Lakes region with higher human landscape disturbance, where maximum road densities of occupied areas increased from 0.53 km/km² during 1926–1960 (Thiel, 1985) to 0.73 km/km² during 1969–1986 (Mech, 1989) and 0.93 km/km² in 2007 (Mladenoff et al., 2009). This increased use of areas with higher human disturbance has continued, given the greater mean road densities in habitat gained during 2016–2020 (1.44 km/km²).

We note several limitations of our study. We omitted cells classified as water from analysis, as the suitability of water can vary spatially and temporally. The suitability of waterbodies depends on their size, as wolves can cross waterbodies up to 2 km by swimming (Darimont and Paquet, 2002), while the extent and duration of freeze-over of larger waterbodies determines whether they are permeable to wolves (e.g., Orning et al., 2020). Our model predicted a decrease in wolf habitat in the third (2001–2005) period compared to the second (1995–2000), apparently relating to a temporarily increased negative relationship between habitat suitability and proportions of agricultural land cover. This was presumably caused by an unknown bias related to sampling effort or changes in sampling protocol, as the strength of the negative relationship between habitat suitability and human population density consistently decreased across periods.

The western Great Lakes region wolf population expanded rapidly in numbers from its legal protection in 1974 to about 2010, after which population growth decreased markedly (USFWS, 2020a). Though our estimates of wolf habitat area increased with each period after 2010, lower increases between recent periods compared to increases between earlier periods suggest that along with lower wolf population growth, wolf range expansion within the Great Lakes region has declined. Most areas currently estimated to be unsuitable for wolves have markedly higher levels of human disturbance than currently occupied areas except the northern Lower Peninsula of Michigan, which has not been recolonized as the Straits of Mackinaw limit dispersal, due to periods of limited or no ice formation or when ships have disrupted ice formation (Stricker et al., 2019; van den Bosch et al., 2022). The next closest area suitable for recolonization in the USA is in western North Dakota and South Dakota, but connectivity to this area is limited due to high human disturbance surrounding current wolf range in Minnesota (van den Bosch et al., 2022). While the upper thresholds of human disturbance wolves can co-exist

with are ultimately unknown, most areas suitable for recolonization within the western Great Lakes region appear occupied, suggesting the wolf population is approaching spatial equilibrium. This stage of equilibrium occurred about 30 years following initial wolf recolonization in the region, demonstrating the importance of long-term planning in wolf and other large carnivore management during recolonization of historical range.

2.6 CONCLUSIONS

Gray wolves have increasingly occupied areas with higher levels of human disturbance during recolonization, but the extent of areas reoccupied has declined since about 2010. Due to temporal variation in the relationship between environmental variables and the occurrence of a recolonizing species, dynamic landscape use of recolonizing species needs to be considered during development and interpretation of species distribution models. Further wolf recolonization of the western Great Lakes region appears largely constrained by human disturbances, resulting in a probable stabilization of current range. This information can aid policymakers and managers to determine the course of wolf conservation and management within and beyond the western Great Lakes region.

TABLES AND FIGURES

<u>Table 2.1</u> Model results from a binomial generalized linear model comparing presences and pseudo-absences within the western Great Lakes distinct population segment of gray wolves (*Canis lupus*), USA, 1989–2020. Variables included proportion of agricultural land cover (Prop. agriculture), human population density (Human pop. dens., per km²), and their interaction with six periods of data (reference level: first period = 1989–1994). Continuous variables were scaled (-1 to 1), parameter estimates are reported with standard error (SE) and p-values ($\alpha < 0.05$).

Parameter	Estimate	SE	P-value
Intercept	-2.254	0.168	< 0.001
Prop. agriculture	-2.043	0.155	< 0.001
Prop. agriculture : 1995–2000	0.188	0.184	0.306
Prop. agriculture : 2001–2005	-0.133	0.196	0.498
Prop. agriculture : 2006–2010	0.264	0.173	0.126
Prop. agriculture : 2011–2015	0.515	0.167	0.002
Prop. agriculture : 2016–2020	0.611	0.167	< 0.001
Human pop. dens.	-2.241	0.435	< 0.001
Human pop. dens. : 1995–2000	0.304	0.499	0.542
Human pop. dens. : 2001–2005	0.913	0.472	0.053
Human pop. dens. : 2006–2010	1.464	0.446	0.001
Human pop. dens. : 2011–2015	1.503	0.441	< 0.001
Human pop. dens. : 2016–2020	1.608	0.442	< 0.001

<u>Figure 2.1</u> Land cover in Minnesota, Wisconsin, and Michigan, USA including adjacent parts of the Great Lakes (from National Land Cover Database 2019).



<u>Figure 2.2</u> Relationship between predicted habitat suitability for gray wolves (*Canis lupus*) and human population density (per km², left panel) and proportion of agriculture (%, right panel) in Minnesota, Wisconsin, and Michigan, USA, 1989–2020, including 95% confidence intervals (shaded).



<u>Figure 2.3</u> Predicted change in estimated habitat area for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA, 1989–2020. The figure indicates predicted change in estimated habitat area (km²). Confidence intervals were obtained using a bootstrap approach.



<u>Figure 2.4</u> Predicted change in estimated habitat for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA, 1989–1994 to 2016–2020.



CHAPTER 3: HABITAT SELECTION OF RESIDENT AND NON-RESIDENT GRAY WOLVES: IMPLICATIONS FOR HABITAT CONNECTIVITY

3.1 ABSTRACT

Habitat selection studies facilitate assessing and predicting species distributions and habitat connectivity, but habitat selection can vary temporally and among individuals, which is often ignored. We used GPS telemetry data from 96 gray wolves (Canis lupus) in the western Great Lakes region of the USA to assess differences in habitat selection while wolves exhibited resident (territorial) or non-resident (dispersing or floating) movements and discuss implications for habitat connectivity. We used a step-selection function (SSF) to assess habitat selection by wolves exhibiting resident or non-resident movements, and modeled circuit connectivity throughout the western Great Lakes region. Wolves selected for natural land cover and against areas with high road densities, with no differences in selection among wolves when resident, dispersing, or floating. Similar habitat selection between resident and non-resident wolves may be due to similarity in environmental conditions, when non-resident movements occur largely within established wolf range rather than near the periphery or beyond the species range. Alternatively, non-resident wolves may travel through occupied territories because higher food availability or lower human disturbance outweighs risks posed by conspecifics. Finally, an absence of differences in habitat selection between resident and non-resident wolf movements may be due to other unknown reasons. We recommend considering context-dependency when evaluating differences in movements and habitat use between resident and non-resident individuals. Our results also provide independent validation of a previous species distribution model and connectivity analysis suggesting most potential wolf habitat in the western Great Lakes region is occupied, with limited connectivity to unoccupied habitat.

3.2 INTRODUCTION

Understanding how animals select habitat is necessary to explain and predict species distributions, facilitating population management and species conservation (Rodríguez et al., 2007, Guisan et al., 2013). Characterizing species-habitat relationships can inform where populations can establish (Fahrig et al., 2003) and identify linkages between habitat patches suitable for dispersal (Correa Ayram et al., 2016). Whereas habitat selection and associated connectivity studies are valuable (Guisan et al., 2013, Correa Ayram et al., 2016), processes

underlying habitat selection are often poorly understood (McLoughlin et al., 2010). Drivers of habitat selection can differ among life stages or individuals and understanding these differences can improve our understanding of habitat selection and connectivity (McLoughlin et al., 2010; Benz et al., 2016).

Mismatches between landscape connectivity analyses and focal species ecology can be mitigated by accounting for behavioral aspects that can influence movement (Chetkiewicz et al., 2006; Benz et al., 2016). Processes underlying animal movements are relevant to connectivity analyses as they influence the behavior and movement patterns of dispersing animals (Laundré et al., 2010). Human landscape disturbances, including high human population densities and associated activities, can substantially alter large carnivore movements (Oriol-Cotterill et al., 2015; Smith et al., 2016), but avoidance of human disturbance can be lower for non-resident individuals than for residents (Rio-Maior et al., 2019). This can affect accuracy of connectivity models, as studies generally consider habitat selection across individuals as being equivalent (Vasudev et al., 2015, Abrahms et al., 2016).

Reduced avoidance of human disturbance by non-resident animals has been documented for dispersing red wolves (*Canis rufus*; Hinton et al., 2016) and lions (*Panthera leo*; Elliot et al., 2014), which avoided areas near roads and with higher human population densities less strongly than residents. Non-resident gray wolves (*C. lupus*) similarly displayed lower selection against human disturbance compared to resident wolves (Dondina et al., 2022; Morales-González et al., 2022). Alternatively, dispersers may not avoid higher human disturbance at all; resident brown bears (*Ursus arctos*) avoided public roads and resident Iberian lynx (*Lynx pardinus*) avoided low-traffic roads, while dispersers did not (Gastón et al., 2016; Thorsen et al., 2022).

Gray wolves historically occupied the Northern Hemisphere north of 11–20° N, though by 1970 wolves were extirpated from most of their historical range in the contiguous USA (Boitani et al., 2003). Following federal protection in 1974, wolves recolonized additional areas of Minnesota, and former range in Wisconsin (Wydeven et al., 2009) and the Upper Peninsula of Michigan (Beyer et al., 2009). The western Great Lakes population appears to have stabilized at around 4,200 wolves (USFWS, 2020a). Unoccupied habitat within former wolf range has been identified in the eastern USA, with apparent limited connectivity to current wolf range in the Great Lakes region (van den Bosch et al., 2022). However, estimates of habitat availability and connectivity should further consider factors underlying habitat selection including potential

differences between resident and non-resident movements.

Gray wolves are territorial, though most wolves disperse from their natal territory and become residents of different territories (Mech and Boitani, 2003). Other wolves do not establish new territories or join existing territories and remain nomadically "floating" across the landscape, constrained by conspecific territories (Boitani, 2003; Mancinelli et al., 2018). Preceding dispersal, wolves can make extraterritorial excursions (i.e., predispersal movements) of varying distance and duration (Messier 1985; Mech, 2020). Lower avoidance of human disturbance by wolves when dispersing or floating could result from avoiding existing wolf territories in less human-disturbed areas or decreased site familiarity that reduces their ability to avoid human disturbances, compared to when they are resident of a territory (Laundré et al., 2010; Imbert et al., 2016). Alternatively, disturbances such as roads may facilitate efficient travel for non-residents (Hill et al., 2021), while areas with high livestock densities may provide food when lower site familiarity or prey abundance limits acquisition of wild prey (Imbert et al., 2016).

We investigated habitat use by gray wolves in the western Great Lakes region exhibiting resident (territorial) or non-resident (dispersing or floating) movements relative to human disturbance. We predicted wolves would select for areas with greater natural land cover and against areas of greater human disturbance as indexed by road densities and proportions of agricultural land cover, with stronger selection during resident than non-resident movements. We also quantified habitat selection and connectivity throughout the western Great Lakes region and evaluated these results against an existing connectivity map for wolves in the eastern USA. We expected a strong correlation between a previous connectivity map developed using winter track surveys (van den Bosch et al., 2022) and one resulting from this habitat selection analysis based on telemetry data.

3.3 METHODS

Study area

The study area (Figure 3.1) included the area representing the western Great Lakes distinct population segment of gray wolves (hereafter, western Great Lakes region; USFWS, 2008), including Minnesota (220,185 km²), Wisconsin (145,593 km²), and Michigan (151,279 km²), and parts of North Dakota (108,193 km²), South Dakota (93,571 km²), Iowa (99,971 km²), and Illinois (27,190 km²).

The study area also included southern Ontario, Canada (515,966 km²), delineated by the Area of the Undertaking (the area in Ontario under forest management; Ouellette et al., 2020), and southern Manitoba (84,920 km²). The climate is predominantly humid continental, with warm summers and cold winters (Beck et al., 2018). Average summer (June–September) minima are 7–17° C and maxima are 17–30° C while average winter (December–March) minima are - 25– -6° C and maxima are -10–4° C (Scott and Huff, 1996). Elevations are 30–757 m above sea level (USGS, 1996). The study area, excluding the Great Lakes, contains 46% natural land cover (primarily various forest types and wetlands) and 18% water, while agricultural and urban areas comprise 32% and 4%, respectively (Homer, 2017).

Data collection and processing

We used gray wolf GPS telemetry data collected during 2017–2021 by state, federal, and tribal agencies of Minnesota, Wisconsin, and Michigan, following their respective animal capture and handling protocols. We excluded the first five days of post-capture data from each wolf to reduce potential capture effects (Powell et al., 2003). We created a dataset of 96 wolves (51 males, 39 females, 6 unknown) collared in Michigan (44), Wisconsin (31), and Minnesota (21), with 13- or 16-hour relocation intervals. We compared two preliminary models using datasets with 13- or 16-h relocation intervals, found no notable differences, and pooled these datasets for analysis.

We separated resident (territorial) from non-resident (dispersing or floating) annual wolf movements by calculating relative net squared displacement (rNSD), which represents the squared Euclidian distance between consecutive locations, where a change from low to high rNSD values implies dispersal from a territory (Bunnefeld et al., 2011). For each wolf during each biological year (starting 15 April), we used the MigrateR package (Spitz et al., 2017) in program R (R Core Team, 2021) to fit data to three a priori non-linear models representing resident, dispersing, and floating (named 'nomadic' in the MigrateR package) movements (Bunnefeld et al., 2011). We selected the best supported movement type based on the lowest AIC score (Burnham and Anderson, 2004).

We further separated data by movement type when individual wolves displayed multiple movement categories within a biological year, based on visual inspection of the rNSD-plots and raw GPS data (Spitz et al., 2017). Visual inspection of movement data to confirm rNSD classifications is recommended to override rNSD classifications when suspected to be incorrect

(Spitz et al. 2017). We then calculated 90% bivariate normal kernel utilization distributions to approximate annual range size using the 'kernelUD' function in AdehabitatHR package (Calenge, 2011). We used an independent source to set the maximum annual range size for wolves to be considered resident and the associated annual range to be considered a territory from state reports during 2017–2021 (561 km²; Erb and Humpal, 2020). We classified movements within annual ranges \leq 561 km² as resident and reclassified movements within larger annual ranges initially classified as resident movements as floating movements. We classified extraterritorial movements between a territory and a non-overlapping territory as dispersal movements, from the first movement beyond the initial territory to the last movement before entering the subsequent territory. We included potential predispersal movements (Messier, 1985; Mech, 2020) as dispersal movements by including extraterritorial movements leaving from and returning to the same territory, with a duration \geq 10 days, based on visual inspection.

Modeling landscape use

We used step-selection functions (SSF), linking consecutive animal locations and contrasting each observed step with three random available steps (Thurfjell et al., 2014). To obtain random steps, we pooled individual movements by movement type (Thurfjell et al., 2014) then randomly sampled the length and angle of random steps from the distribution of observed steps for each type. We used road density, proportion of natural land cover, and proportion of agricultural cover as continuous variables, whereby proportional land covers were calculated as the percentage of respective land cover types within a cell. We used road data from TIGER/line shapefiles (50-m resolution; US Census Bureau, 2020) and the Canadian National Road Network (5-m resolution; Statistics Canada, 2020), the most comprehensive road databases for these countries including categories ranging from highways to service roads, and roads only accessible by four-wheel drive vehicles. We used the North American land change monitoring system (NALCMS; 30-m resolution) (Homer, 2017) to calculate proportional land cover. We reclassified land covers as natural (managed and unmanaged 'forest' classes, 'shrubland', 'grassland', 'barren land', and 'wetland'), agricultural (class 'cropland'), developed, and water (Figure 3.1). We resampled rasters to 300-m resolution to reduce spatial mismatch between species and environmental data (Guisan and Thuiller, 2005), and rescaled continuous variables (-1 to 1) to facilitate effect comparison.

We fit the SSF using a conditional Poisson regression model, which yields equivalent

estimates to the conditional logistic regression model typically used for SSFs (Muff et al., 2020). We included random slopes for the continuous variables (Muff et al., 2020) to account for individual variation among wolves. We fit the model using the glmmTMB package (Brooks et al., 2017) in program R. We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity of variables with thresholds of 10 and 0.70, respectively (Dormann et al., 2013). We selected from two candidate models based on the lowest AIC, or the competing model ($\Delta AIC < 2$) with fewer terms (Burnham and Anderson, 2004): one model contained road density and proportion of natural land cover, and another model contained these variables interacting with movement type. We created used-habitat calibration plots (UHC) to visualize how well model predictions characterize used locations by plotting the distribution of an explanatory variable at used locations and overlaying this with the distribution of explanatory variable values predicted by the model (Fieberg et al., 2018). As a measure of ecological importance of statistical estimates, we spatially predicted relative strength of selection (RSS; Avgar et al., 2017) throughout the study area by calculating RSS as the probability of selecting a given point over a point with average variable values in our study area, scaling probabilities from 0 to 1.

Modeling connectivity

To assess landscape-level connectivity without the assumption of animals having landscape knowledge, we used Circuitscape software (McRae and Shah, 2009). We inverted the RSS surface raster to obtain an estimate of movement resistance (Buchholtz et al., 2020) and then replaced each cell from the movement resistance surface with nodes connected by resistors, translating connectivity to 'current flow'. We limited connectivity analysis to non-resident movements if the results of our SSF indicated significant differences ($\alpha < 0.05$) in habitat selection for resident and non-resident wolf movements. We incorporated part of Indiana (8 795 km²) into the study area to avoid a spatial interruption that would bias the circuit connectivity model. We assigned 154 points at about 40-km intervals along the perimeter of the study area and calculated connectivity between all pairs of points, providing an omnidirectional connectivity map for animals moving randomly through the landscape (McRae and Shah, 2009). Connectivity between perimeter points is prone to edge effects as connectivity increases near these points. We therefore placed perimeter points at the midpoint of a 15-km buffer bordering the study area edge, filled cells within this buffer with the average movement resistance value of

the study area, and removed this buffer after analysis (Buchholtz et al. 2020). To assess how the connectivity map compared to a previous species distribution model (SDM) and circuit connectivity analysis for gray wolves in the eastern USA and southern Canada (van den Bosch et al., 2022), we resampled our RSS and circuit connectivity maps to 1-km resolution and calculated Pearson's correlation coefficients between the RSS and SDM rasters and their respective circuit connectivity rasters.

3.4 RESULTS

We retained 24,540 steps, with a median of 878 steps per wolf (range = 156-3,811 steps). Of these steps, 16,668 were classified as resident, 1,656 as dispersing, and 6,216 as floating movements, with median step-lengths of 609, 1,011, and 655 meters for resident, dispersing, and floating movements, respectively. Resident, dispersing, and floating movements were found for 72, 20, and 24 wolves, respectively, and 17 of 96 wolves displayed multiple movement types. We used a maximum annual range size of 561 km² for resident wolves to support movement type classification using the NSD-method and visual inspection, though average estimated annual range sizes were smaller for wolves classified as resident (mean = 195 km^2 , StDev = 116) than for dispersers (9,294 km², StDev= 15,065) or floaters (8,608 km², StDev= 11,119). Short-distance dispersal events occurred (n = 16, median = 54 km), with the longest dispersal 615 km. Proportions of natural (VIF = 3.36) and agricultural (VIF = 3.03) cover were correlated (*r* = -0.80), and we retained proportion of natural cover as it is inverse to the combined proportions of agricultural and urban cover, thus a stronger proxy of human disturbance.

The model retaining movement type as a factor interacting with proportion of natural land cover and road density indicated no habitat selection differences among resident, dispersing, and floating wolves (Table 3.1), due to high overlap in used habitat characteristics (Figure 3.2).

Our final model included road density and proportion of natural cover without interactions with movement type, and had a lower AIC value than the model including these interactions (Δ AIC = 5.2). This final model suggested wolves avoided areas with greater road density and selected for areas with greater proportions of natural cover (Figure 3.3). Calibration of our top-ranked model was successful for road density and reasonable for proportions of natural cover, based on visual inspection of overlap between predicted and used values in the UHC plots (Figure 3.4). The resampled RSS raster (Figure 3.5) was positively correlated (*r* = 0.78) with a previous habitat suitability raster (van den Bosch et al., 2022).

Areas previously estimated suitable that were not selected by wolves in this study included parts of the Lower Peninsula of Michigan, and isolated and fragmented areas east of the Missouri river in North and South Dakota. Non-resident movements in our dataset were limited to established wolf range. Because we detected no differences in habitat selection between resident and non-resident movements, we retained all data for connectivity analysis. Our circuit connectivity map indicated highest connectivity for wolves in the northern and eastern parts of Ontario and was positively correlated (r = 0.75) with the circuit connectivity raster of the SDM (Figure 3.6).

3.5 DISCUSSION

Our estimate of gray wolf habitat selection in the western Great Lakes region of the USA and southern Ontario and Manitoba, Canada, supported our prediction that wolves avoid areas with high road densities and select for areas with high proportions of natural cover. Contrary to our prediction, we found no differences among habitat selection of wolves exhibiting resident, dispersing, or floating movements. We also confirmed unoccupied habitat in the western Great Lakes region is limited, and connectivity between occupied and unoccupied habitat is constrained by the Great Lakes, areas of extensive agriculture, and urban areas.

Habitat selection of resident and non-resident wolves in our study was similar, though previous studies found it can differ by disturbance type. Gray wolves in Portugal displayed increased tolerance toward roads and settlements during dispersal, but not towards areas with higher livestock densities or windfarms (Rio-Maior et al., 2019). The absence of increased tolerance for high road densities or proportions of urban or agricultural land cover during non-residency may be due to non-resident movements in our study occurring within established wolf range, causing high similarity or overlap in habitat characteristics to which residents and non-residents are exposed. Only four dispersing wolves exceeded estimated mean dispersal distances (range = 29–148 km) for the western Great Lakes region (Treves et al., 2009). The prevalence of short-distance dispersals (median = 54 km), and dispersal and floating movements being largely limited to established wolf range, may be caused by increased opportunities for non-residents to join existing packs due to high pack densities (Brainerd et al., 2008; Jimenez et al., 2017). Alternatively, with little unoccupied habitat available, non-residents may traverse conspecific territories when higher prey availability or lower human disturbance in occupied habitat outweighs risks of encountering conspecifics (Morales-González et al., 2022).

The relative selection strength (RSS) map was positively correlated with a habitat suitability map for the same area based on wolf winter track surveys (van den Bosch et al., 2022), while derived connectivity maps were also positively correlated. This similarity provides validation of current wolf range and habitat connectivity throughout the western Great Lakes region from independent data. Our results also suggest that accounting for differences between resident and non-resident movements using data transformations (Keeley et al., 2016), or by limiting connectivity analyses to non-resident movement data (Elliot et al., 2014; Dondina et al., 2022), may be unnecessary when non-resident movements are largely limited to established range or otherwise similar to resident individuals.

We note several limitations to our study. Similar to how movement resistance rasters are calculated from habitat suitability maps (van den Bosch et al., 2022), we calculated a resistance raster by inverting the RSS map resulting from our SSF (Osipova et al., 2019). This is not ideal because RSS values are conditional probabilities (Avgar et al., 2017), though no alternative approach is available. Similarly, an entirely mechanistic approach to classifying movement types is unavailable, and the migrateR package was developed primarily for migratory animals, so classification depends in part on visual interpretation of data (Spitz et al., 2017). Also, wolves can swim up to 2 km (Darimont and Paquet, 2002) but can cross larger waterbodies during freeze-over (Orning et al., 2020). Our approach resulted in waterbodies having above average resistance to movement due to low natural, terrestrial cover, but as the Great Lakes are roadless they have a lower resistance than areas with low natural cover and high road density. Year-round estimates of connectivity are imperfect due to seasonal changes in movement resistance of water. Using GPS locations collected at shorter intervals could be used to assess finer-scale wolf movements, and may reveal differences in habitat selection among movement types (Rio-Maior et al., 2019). Analysis including non-resident movements beyond established range also is needed to confirm whether differences in habitat use between resident and non-resident wolves depend on differences in the range of conditions they occur in. Finally, wolves generally avoid higher road densities but can select for minor, lower traffic roads for efficient travel (Zimmermann et al., 2014). The road databases used here generally group unpaved rural roads, that wolves are known to use, with roads in suburban areas that wolves would likely avoid, thus testing the response to road densities classified by road type was not possible. We suggest potential for further recolonization of the western Great Lakes region is low as

unoccupied habitat and habitat connectivity are limited. The Straits of Mackinac can connect current range in the Upper Peninsula of Michigan with the Lower Peninsula during freeze-over, though recent crossings of the straits have been too infrequent for population establishment (Stricker et al., 2019). Recolonization of potential habitat in North and South Dakota is limited by low dispersal frequencies and high anthropogenic mortality (Licht and Fritts, 1994), and connectivity with current range may be higher through Manitoba than through Minnesota.

3.6 CONCLUSIONS

We offer further support that gray wolves in the western Great Lakes region select for areas with high proportions of natural cover, and against human disturbance as indexed by road densities. We found no differences in habitat selection among wolves that were resident, dispersing, or floating., suggesting the need to limit connectivity analyses to non-resident movements, or to apply transformations to data of primarily resident wolf movements, depends on the magnitude of differences in habitat characteristics experienced by resident and nonresident individuals. As most wolf habitat in the western Great Lakes region appears occupied and because limited habitat connectivity between currently occupied range and limited unoccupied range in the USA part of the western Great Lakes region, further recolonization appears most likely through Canada to connect with wolf habitat in North Dakota, and across the Straits of Mackinaw to connect with habitat in the Lower Peninsula of Michigan. Interjurisdictional cooperation will be important to improve landscape connectivity for gray wolves between Canada and the USA. If recolonization of areas beyond current wolf range in the Great Lakes region is desired, promoting human-wolf co-existence in areas most likely to be recolonized is pertinent, though further natural recolonization within and beyond the Great Lakes region appears limited by the dominance of urban and agricultural areas surrounding current range.

TABLES AND FIGURES

<u>Table 3.1</u> Model selection results comparing used and available steps within the western Great Lakes distinct population segment of gray wolves (*Canis lupus*), USA and southern Ontario and Manitoba, Canada, 2017–2021. Models were ranked using AIC; variables included road density (km/km²) and proportion of natural cover, and their interactions with movement type (reference level: Resident). Continuous variables were scaled (-1 to 1) and included random slopes for continuous variables to account for individual variation among wolves. Parameter estimates are reported with standard error (SE) and p-values ($\alpha < 0.05$).

Top model	AIC = 454,149.5			
Parameter	Estimate	SE	P-value	
Prop. natural cover	0.335	0.033	< 0.001	
Road density	-0.175	0.025	< 0.001	
Second model	$\Delta AIC = +$	5.2		
Parameter	Estimate	SE	P-value	
Prop. natural cover	0.335	0.033	< 0.001	
Road density	- 0.175	0.025	< 0.001	
Road density x Floating	0.031	0.052	0.557	
Prop. natural cover x Floating	- 0.069	0.064	0.275	
Road density x Dispersing	0.037	0.061	0.548	
Prop. natural cover x Dispersing	0.017	0.050	0.734	

<u>Figure 3.1</u> Land cover within the western Great Lakes distinct population segment of gray wolves (*Canis lupus*), USA and southern Ontario and Manitoba, Canada.



<u>Figure 3.2</u> Characteristics of used and available steps for road density (km/km², top panel) and proportion of natural cover (0–100, bottom panel) for 96 gray wolves (*Canis lupus*) in the western Great Lakes region, USA, and southern Ontario and Manitoba, Canada, 2017–2021. Circles represent average selection of wolves by movement type, and error bars are 95% confidence intervals of these averages.



<u>Figure 3.3</u> Predictions from a step-selection function for gray wolves (*Canis lupus*) in the western Great Lakes region, USA, and southern Ontario and Manitoba, Canada, 2017–2021. Predicted values are probabilities of selection relative to the average variable value of used and available steps (dashed lines, average proportion of natural land cover = 90.42%, average road density = 0.83 km/km^2).



<u>Figure 3.4</u> Used-habitat calibration plots for proportion of natural cover (top panel) and road density (km/km², bottom panel) used in a step-selection function for gray wolves (*Canis lupus*) in the western Great Lakes region, USA, and southern Ontario and Manitoba, Canada, 2017–2021.



<u>Figure 3.5</u> Predicted relative selection strength (RSS) for the western Great Lakes distinct population segment of gray wolves (*Canis lupus*), USA and southern Ontario and Manitoba, Canada based on a step-selection function, along with an approximate southern border of wolf range.


<u>Figure 3.6</u> Circuit connectivity for the western Great Lakes distinct population segment of gray wolves (*Canis lupus*), USA and southern Ontario and Manitoba, Canada, 2017–2021. Figure based on a step-selection function (main figure) and circuit connectivity map derived from the same study area based on snow track data (van den Bosch et al., 2022; inset).



CHAPTER 4: IDENTIFYING POTENTIAL GRAY WOLF HABITAT AND CONNECTIVITY IN THE EASTERN USA

4.1 ABSTRACT

Following federal protection in 1974, gray wolves (Canis lupus) partially recolonized former range in the western Great Lakes region, USA, yet remain absent from most of the eastern USA. Understanding potential for further recolonization requires quantifying remaining wolf habitat and habitat connectivity. We used recent snow tracking data from the western Great Lakes region to create an ensemble distribution model to estimate areas of habitat large enough to support gray wolf populations in the eastern USA. We then modeled cost-weighted distances between these areas and circuit connectivity to identify potential linkages. Our final distribution model had good performance (Receiver Operator Characteristic = 0.87) and suggests wolves selected against areas with greater human population densities and proportions of agricultural land. Gray wolves currently occupy about 4% of their historical range in the eastern USA, which represents 12% of the area estimated to remain suitable. We estimated 35% of range is currently suitable for wolves, and 18% of these suitable areas are protected, mostly under state and federal jurisdictions. We identified five unoccupied areas where wolves could establish viable populations ranging from 18,110 to 725,488 km². Connectivity between these areas and current wolf range is limited primarily by the Great Lakes and extensive agriculture in the Midwest USA. Most core habitat areas and priority linkages cross state or country borders, highlighting the importance of interjurisdictional cooperation. Our estimates of remaining suitable range and the potential for recolonization provide a baseline for the development of policies on gray wolf conservation in the eastern USA.

4.2 INTRODUCTION

Worldwide, geographic ranges of large carnivores have contracted markedly since the 1700s due to anthropogenic causes (Ripple et al., 2014; Wolf and Ripple, 2017), primarily persecution (Musiani and Paquet, 2004) and habitat and connectivity loss (Crooks et al., 2011), which are linked to increases in human populations and land use change (Woodroffe, 2000). Range contractions of over 20% have occurred for 80% of large carnivore species, particularly in regions with high livestock densities (Wolf and Ripple, 2017). Human encroachment on large carnivore habitat also increases potential for conflict with humans (Boudreau et al., 2021), which

can result in direct carnivore mortality and reduce public support for their conservation (Treves and Karanth, 2003; Treves and Bruskotter, 2014).

A better understanding of ecological top-down effects has increased recognition of the importance of large carnivores (Ripple et al., 2014). Together with improvements in public perceptions (Chapron et al., 2014; Gompper et al., 2015), policymaking has shifted and coexistence has become a more prevalent management objective (Linnell et al., 2001). Improved coexistence with large carnivores has contributed to partial reoccupation of former ranges in the United States (Gompper et al., 2015) and Europe (Chapron et al., 2014), though range contractions continue for many species, particularly in Africa and Asia (Wolf and Ripple, 2017). Recolonization of former range by large carnivores depends in part on habitat connectivity (Hemmingmoore et al., 2020). However, connectivity can be reduced by habitat fragmentation (Crooks et al., 2017), to which these species are especially vulnerable due to their low densities and large territories (Crooks et al., 2011). Maintaining viable populations of large carnivores requires large areas, often thousands of square kilometers (USFWS, 1992; Wielgus, 2002), yet only 5.2% of their habitat worldwide is estimated to have protected status (Crooks et al., 2011), requiring dispersal through, or persistence in, non-protected landscapes with high human disturbance (Boron et al., 2016). This suggests that land sparing, by protecting areas relatively free from human disturbance, but also land sharing, by tolerating large carnivores in unprotected areas, are critical for recolonization of former range by large carnivores (Chapron et al, 2014; Gompper et al, 2015).

In Europe and North America, species such as gray wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), and American black bear (*Ursus americanus*) have recolonized former range following increased legal protection of large carnivores and their habitat (Linnell et al., 2001; Smith et al., 2016). Since 1974 gray wolves have received federal protection in the contiguous USA through the Endangered Species Act (ESA) (Ruid et al., 2009), with periods wherein protection was removed for some populations (Bergstrom et al., 2009; Olson et al., 2015). Currently, the largest wolf population in the contiguous USA is the western Great Lakes distinct population segment, which occurs in portions of Minnesota, Wisconsin, and Michigan, and contained around 4,200 gray wolves in 2020 (USFWS, 2020a). Wolf habitat in other eastern USA states has been identified in New York, Vermont, New Hampshire, and Maine (Mladenoff et al., 1998), and 15 states in the Midwest region (Smith et al. 2016), but there are no

assessments of remaining habitat throughout former range across the eastern USA (Nowak, 1995; USFWS, 2009). Gray wolf populations are estimated to require 25,600 km² or 12,800 km² for viable independent or immigration-dependent populations, respectively (USFWS, 1992). However, there has been no assessment of where natural recolonization of former range is plausible, considering habitat availability and landscape connectivity.

Most gray wolf mortality in the USA is human-caused (Hill et al., 2022), and recolonization of former range in the eastern USA may depend largely on human tolerance, highlighting the need for conflict prevention and mitigation (Treves et al., 2004). Estimating habitat for gray wolf establishment and identifying linkages that might facilitate movement could assist development of management strategies and policy. Assessing the role of protected and non-protected areas in wolf recolonization is particularly important to management and policy planning, as human-wildlife conflicts are more likely in non-protected areas with greater human disturbance (Treves and Karanth, 2003, but see Reinhardt et al., 2019). Additionally, evaluating natural recolonization potential can help identify areas where re-establishment within former range is unlikely without human assistance, or where former range has become unsuitable.

We developed a distribution model to estimate current wolf range in the western Great Lakes region and used it to predict habitat availability throughout former wolf range in the eastern USA, expecting wolf habitat to occur mostly in areas with low human disturbance and greater proportions of natural land cover. We also estimated habitat connectivity, including southern Canada, to identify potential linkages that could connect unoccupied areas with currently occupied areas. Finally, we evaluated the ownership status of protected suitable areas, potential linkages, and identified areas likely suitable to maintain viable wolf populations.

4.3 METHODS

Study area

Our study included the former range of wolves in the eastern USA (Nowak, 1995), and adjacent southern Canada of which most is currently occupied by wolves (Wolf and Ripple, 2017). We used the Area of the Undertaking of Ontario (Hunt et al., 2005), the zone where forests are managed by the province, as the northern limit of the study area (Figure 4.1). The overall area excluding water is 4,187,681 km², of which about 60% is natural land cover (e.g. forests, grasslands, shrubland), 33% is agricultural land, and 7% developed (Homer, 2017).

Elevations are 1–2,436 meters above sea level (USGS, 1996), with higher elevations in the western part of the study area and the Appalachian range in the east.

Data collection and processing

We used winter wolf track survey data collected by the Departments of Natural Resources (DNR) of Minnesota (2018), Wisconsin (2018–2020), and Michigan (2018, 2020). In Minnesota, trained natural resource professionals were instructed to record locations of all wolf sightings and signs (e.g. tracks, scat) observed from November until snowmelt, usually mid-April (Erb and Sampson, 2013). Participants could record locations on forms or maps, but most used a web-based GIS application. The final dataset was combined with presence data recorded during other surveys coordinated by the DNR (e.g. furbearer survey, carnivore scent station survey). In Wisconsin, DNR staff, tribal biologists, and trained volunteers conducted surveys throughout known wolf range, primarily during December–April (Stauffer et al, 2020). The survey area included 164 survey blocks of approximately 500 km² each, delineated using waterways, roads, and state boundaries, ensuring each block could be surveyed within a day. Surveyors attempted to survey most snow-covered roads within a block 1–3 days after snowfall and blocks were surveyed on average 2.8 times. In Michigan, the Upper Peninsula is divided into 21 survey blocks from which a stratified random sample of 12–13 survey blocks are selected for surveys every other year, representing $\geq 60\%$ of the total area (Michigan Department of Natural Resources, 2008). Michigan Department of Natural Resources staff were assisted by US Department of Agriculture Wildlife Services personnel, and surveys occurred during December-April. Searches for wolf tracks and other sign occurred along trails and roads by truck or snowmobile. Only the Upper Peninsula was surveyed as wolves are not established in the Lower Peninsula of Michigan (Michigan Department of Natural Resources, 2008).

We filtered snow tracking data to one presence point per 1 km² across all years to reduce spatial autocorrelation (Gantchoff et al., 2021), resulting in 3 689 presence points. Within the entirety of each state, we randomly generated twice as many pseudo-absence points as there were presence points (Barbet-Massin et al., 2012; Figure 4.2). Assigning pseudo-absences throughout former range would imply a mismatch between the environment currently unoccupied and the ecological niche of wolves, yet wolf absence in most former range is thought to be primarily a consequence of historic anthropogenic activities (Wolf and Ripple, 2017) rather than a consequence of differences in physical landscape features (Nowak, 1995). We then removed

duplicate points, pseudo-absence points located in water, and pseudo-absence points on Isle Royale National Park, Michigan (USA), where wolves are present but we did not have survey data.

Ensemble modeling

We used six variables to model wolf presence in the western Great Lakes region. We used the North American Land Change Monitoring System (30-m resolution; Homer, 2017) to derive proportions of, and distances to, agricultural land (class cropland), and natural land (all other classes except water and ice and snow) (Figure 4.1). We excluded areas of the land cover class water from the model, as water bodies are typically not considered wolf habitat. We combined all natural land covers into a single class, because vegetation types in current wolf range, where presence points for the model originate, differ from parts of former wolf range. This mismatch could result in former range being estimated unsuitable based on vegetation differences, despite wolves being adaptable to most ecoregions (Nowak et al, 1995). For human population density we used the Gridded Population of the World (v4.11) database (30 arcseconds resolution; CIESIN, 2020). We used the USGS GTOPO30 digital elevation model for elevation (30 arc-seconds resolution; USGS, 1996). Before calculating proportional land cover variables, we rescaled variables to 1-km resolution to reduce spatial mismatch between species data and environmental data (Guisan and Thuiller, 2005). Because wolf surveys were mostly conducted along roads, leading to positive bias between wolf presence and variables related to developed land cover and road density, we did not include distance to, and proportion of, developed land cover, or road density (Gantchoff et al., in revision). As road density has been found negatively related to wolf habitat selection in distribution models (Jędrzejewski et al., 2008; Mladenoff et al., 2009), we used alternative variables relating to human populations and agricultural activities as proxies for human landscape disturbance (Smith et al., 2016). We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity of variables. For variables with pairwise correlation > 0.70, we created test models with only one of the correlated variables, and removed the variable which resulted in lower fit from the final model. This was done until all pairwise correlations were < 0.70 and VIF scores were < 10(Guisan et al., 2017).

To reduce potential for overprediction of wolf habitat using single models (Marmion et al, 2009), we developed an ensemble model with 10 submodels (Thuiller et al, 2009): artificial

neural network (ANN), random forest (RF), mixture discriminant analysis (MDA), maximum entropy (MaxEnt), generalized linear model (GLM), generalized additive model (GAM), generalized boosted model (GBM), multivariate adaptive regression splines (MARS), surface range envelope (SRE), and classification tree analysis (CTA). We created the ensemble model and extrapolation beyond current range using the biomod2 package (Thuiller et al, 2009) in program R 3.6.2 (R Core Team, 2020). We used 70% of data to calibrate the model and the remaining 30% to evaluate model performance, repeating this procedure three times (Guisan et al., 2017). We used the area under the curve (AUC) of the receiver-operating characteristic (ROC) and the True Skill Statistic (TSS), and their associated sensitivity and specificity scores, as evaluation metrics (Allouche et al., 2006). We considered AUC scores > 0.90 as "excellent", 0.90 > x > 0.80 as "good" and 0.80 > x > 0.70 as "fair" (Araújo et al, 2005) and limited the ensemble model to submodels with a TSS score ≥ 0.5 (Gantchoff et al., 2021). We assigned weights to submodels that were retained, proportional to their respective evaluation scores, and averaged them using an ensemble model for the western Great Lakes region, and a projection to former wolf range in the eastern US. We assessed variable importance by calculating correlations between fitted values and three randomly permutated values of each variable (Thuiller et al, 2009). As resulting values are automatically inverted, low correlation numbers imply low contribution of each variable to the model. We used response curves of the variables with greatest importance to assess their effects on likelihood of wolf presence (Elith et al, 2005).

Estimating connectivity

We first classified core areas of habitat by transforming the landscape suitability map to a binary format, using an optimized probability threshold resulting in maximized TSS scores in Biomod2 (Thuiller et al., 2009). We defined core areas as habitat patches $\geq 100 \text{ km}^2$, representing the smallest plausible annual home range (Stauffer et al., 2020). Patches separated \leq 2 km were merged (Gantchoff et al., 2020), considered reasonable as wolves can travel up to 72 km in 24 hours (Mech and Boitani, 2003). Because wolves might use lower-quality habitat than residents (Keeley et al., 2016), we created a resistance surface raster using a c8 exponential transformation (Zeller et al. 2018) rather than assuming an inverse relationship between habitat suitability and landscape resistance. Though wolves cross frozen lakes and rivers during winter (Orning et al., 2020), these conditions occur only several months each year in northern portions of our study area. We therefore assigned maximum resistance scores to 1-km cells classified as water to better represent overall natural barriers to dispersal, as the maximum distance recorded for swimming wolves is about 2 km (Darimont and Paquet, 2002).

To map linkages, we calculated least-cost paths (LCP) between core areas using the LinkageMapper toolbox in ArcGIS (McRae and Kavanagh, 2011), and created linkages by buffering 1 km on either side of LCPs. We calculated cost-weighted distances (CWD) of linkages by summing resistance values we derived from the resistance surface raster, using cells that intersected with linkages (Zeller et al, 2018, Gantchoff et al. 2021). Linkages between core areas are categorized as having low, medium or high connectivity using equal intervals of their total CWD, whereby a lower CWD implies higher landscape connectivity. We used the Linkage Priority tool to assign linkage importance, equally weighted using linkage permeability, and the proximity and value of core areas connected by this linkage (Gallo and Greene, 2018). We calculated core area values based on area size, centrality, landscape resistance, and area/perimeter ratio. To further assess landscape-level connectivity without the assumption of animal landscape knowledge, we used Circuitscape software (McRae and Shah, 2020). We assigned 310 points at 40-km intervals around the perimeter of the study area and calculated connectivity between all pairs of points, providing an omnidirectional connectivity map for animals moving randomly through the landscape (Gantchoff et al., 2021)

Core area protection status and size

We assessed the ownership of core areas and linkages with protection status using the Protected Areas Database of the United States (USGS, 2018) and the Canadian Protected and Conserved Areas Database (Environment Canada, 2020), which include private conservation lands and public lands at all jurisdictional levels (Table 4.1; Table 4.2). Only terrestrial parts of protected areas were used in analyses. We examined core area size to estimate their potential to maintain a viable population alone or with immigration, using areas of > 25,600 and 12,800–25, 600 km², respectively (USFWS, 1992), and defined these as population-sized core areas (PCAs). 4.4 RESULTS

From the initial 3,238 presence points (1,601 in Minnesota, 1,002 in Wisconsin, and 635 in Michigan) we created a filtered dataset of 2,832 wolf presence points (1,095, 1,141, and 596, respectively) and 6,928 pseudo-absence points (Figure 4.2). The proportion of natural land cover (VIF = 13.06) and agricultural land cover (VIF = 12.07) were correlated (r = -0.92) and we retained proportion of agriculture due to better model fit. No variables used in analyses had VIF

> 1.82 or pairwise correlation > 0.57.

All submodels except the SRE had TSS scores ≥ 0.5 and were included in the ensemble model. The ensemble model had ROC and TSS scores of 0.87 and 0.59, respectively, and the suitability map had a sensitivity and specificity of 90.7 and 68.3, respectively. Averaged variable importance suggested proportion of agricultural cover as most influential (0.32), followed by human population density (0.22), and distance to agricultural land cover (0.15). Elevation (0.05) and distance to natural land cover (0.03) were of least importance. Our model estimated a strong decline in wolf presence likelihood at human population densities 50–75/km², and an inverse relationship with proportions of agricultural land (Figure 4.3).

Overall, we estimated 1,174,839 km², or 34.7% of former range in the eastern USA (3,385,780 km²) as potential wolf habitat. Wolves currently occupy 4.1%, or 139,462 km², of their former range, which is 11.9% of the area we estimated suitable. We identified 161 core areas comprising 1,760,835 km² overall, with the largest 5 comprising 94.8% of the total (Figure 4.4). We identified 6 population-sized core areas (PCAs) including the currently occupied Great Lakes PCA (135,060 km²). The 5 unoccupied PCAs (18,110 to 725,488 km²) included 3 which could maintain independent populations and 2 estimated as immigration-dependent (Figure 4.5). Among core areas, 308,028 km² (17.5%) had protected area status, most commonly national forests (21.3%) (Table 4.1). Protected areas within PCAs were managed primarily by state (34.5%) and federal governments (33.6%).

We identified 242 least-cost paths (LCPs) 3.8–573.6-km long (Figure 4.5), and a total linkage area of 26,871 km² in the eastern USA, of which 3,887 km² (14.5%) was within protected areas. The most common land designation for linkage protection was conservation easement (21.9%), and protected areas within linkages were primarily state-managed (35.6%) (Table 4.1). The circuit connectivity map suggested highest connectivity within the Great Plains PCA, the Great Lakes PCA, and the Appalachian PCA, and in Canada north of Lake Superior (Figure 4.6). Direct linkages between the Great Plains and Great Lakes PCAs have medium connectivity, while areas south of the Great Lakes PCA have low connectivity (Figure 4.5). There is high connectivity between the Great Lakes PCA and currently occupied habitat in Canada, extending east to the St. Lawrence River.

Assuming wolves use the lowest-CWD linkage to cross from the Great Lakes PCA to a core area in central Wisconsin where wolves are present (Thiel et al. 2009; Wisconsin DNR,

2021), we consider this a baseline suitable linkage (Figure 4.5). The only direct linkages between PCAs with a CWD equal to or less than this linkage is the Straits of Mackinac which connects the Great Lakes PCA with the Lower Peninsula Michigan PCA, and a linkage between the New England and Adirondacks PCAs. Four smaller core areas between Montreal and Quebec City, Canada, connect large areas of wolf habitat between Manitoba and Ontario with a larger core area east of the St. Lawrence River which in turn connects to the New England PCA. This potential route contains four short linkages with individual CWDs less than the baseline linkage.

4.5 DISCUSSION

We estimated gray wolf habitat across former range in the eastern USA, supporting our prediction that wolves occupy areas with low human disturbance and high natural land cover (Mladenoff et al., 1998; Smith et al., 2016). We estimated 65.3% of former range in the eastern USA is currently unsuitable for wolves. Following USFWS criteria (USFWS, 1992), we identified 6 core areas in the eastern USA that could maintain viable wolf populations after natural recolonization or reintroduction, of which only the Great Lakes PCA (population-sized core area) is currently occupied. Overall, 17.5% of core areas have protected status, primarily under state and federal jurisdiction. Connectivity between current wolf range and other PCAs appears limited due to extensive agriculture, high human populations, and presence of the Great Lakes. Consequently, recolonization of the three easternmost PCAs appears most plausible via dispersal through or from current wolf range in southern Canada.

Gray wolves are habitat generalists, thus climatic, geological, or biological landscape features including snow cover, elevation, or vegetation types may not strongly limit their distribution (Fechter and Storch, 2014). Habitat generalism formerly allowed wolves to occupy most of North America (Nowak, 1995) and suggests the diversity of natural landscapes in the eastern USA would not limit recolonization. Our model suggests landscape suitability for wolves is primarily limited by high human population density and extensive agriculture, with wolves occupying areas with greater proportions of natural cover. Because large parts of the eastern USA have been altered by humans (Ellis et al., 2010), we estimate only 34.7% of former wolf range (Nowak, 1995) is currently suitable for wolves.

The Great Plains, Appalachian, and New England PCAs could likely support independent populations of wolves whereas the Adirondacks and Lower Peninsula Michigan PCAs appear dependent on connectivity with other populations. We acknowledge the criteria we used for areas

required to sustain populations (see USFWS, 1992) may be conservative. We estimated 3 840 km² of habitat for a previously disjunct wolf population in central Wisconsin established around 1993 (Theil et al., 2009) that was at least initially dependent on connectivity with the Great Lakes PCA. Wolf populations considered viable can occupy areas 1,500–3,000 km² within protected areas in North America (Fritts and Carbyn, 1995). However, protected areas cover only 21.6% of unoccupied PCAs, compared to 55.6% in the Great Lakes PCA (Table 4.2). Wolf territory size may be inversely related to habitat quality (Kittle et al., 2015), and habitat quality in protected areas may benefit from lesser human disturbance and greater natural cover (Bassi et al., 2015), so the minimum area requirement for maintaining a population may be greater with lower protection status and habitat quality. While human tolerance and conflict mitigation are important where humans and large carnivores co-exist, it may be particularly important for wolf recolonization and persistence in unprotected areas, which represented most unoccupied wolf habitat in our study (Smith et al. 2016; Gantchoff et al., 2020).

Wolves in the Great Lakes PCA can disperse > 800 km in straight line distance (Michigan DNR, unpublished data), considerably greater than the longest linkage (574 km) we identified, yet typical dispersals in the Great Lakes region range from 20 to 100 km (Treves et al., 2009). Based on least-cost paths and circuit theory, we suggest the low suitability of areas connecting current wolf range with other PCAs likely limits recolonization more than linkage length does. Considering the CWD of the linkage in central Wisconsin, we suggest human disturbance and associated land use limit connectivity of many linkages within the USA, particularly in agricultural areas west and south of the Great Lakes PCA. Consequently, most linkages between current range and other PCAs incorporate areas in southern Canada, where there is reduced human disturbance (Homer et al., 2017). An exception may be the Straits of Mackinac, which could connect the Great Lakes and Lower Peninsula Michigan PCAs. Wolves can cross these straits when ice-covered, though crossings thus far appear too infrequent for population establishment (Stricker et al., 2019). Despite higher connectivity in southern Canada, human development along the St. Lawrence River may limit connectivity with the New England and Adirondacks PCAs, while anthropogenic mortality in Canada could reduce the frequency of dispersal into the eastern USA (Wydeven et al., 1998). Most linkages between current and potential range span multiple states or countries, so maintaining or improving connectivity for wolves in the eastern USA will depend on interjurisdictional cooperation, particularly in the

absence of federal protection (USFWS, 2020b). Wolves were listed under the Endangered Species Act to conserve the species in "a significant portion of its range", yet controversy has arisen over the interpretation of this phrase, and whether this goal has been met (USFWS, 2020b; Defenders of Wildlife et al. v. USFWS et al., 2022). Our study provides a framework for interpreting current gray wolf range in the eastern USA in relation to potential for further recolonization and habitat loss throughout former range. Policy and management toward further recolonization of gray wolves should consider potential overlap with former range of the federally endangered red wolf (*C. rufus*) (Hinton et al., 2013).

Although further recolonization of former range by gray wolves in the eastern USA appears restricted due to limited connectivity, our estimates may be conservative because wolf populations exhibit behavioral plasticity and can select for areas previously considered unsuitable (Mladenoff et al., 2009). Species distribution and connectivity models assume species are in equilibrium with their environment, yet recolonizing species are not (Guisan and Thuiller, 2005). Our models therefore represent only the current state of wolf distribution and potential for recolonization, and future changes are difficult to predict due to variation in dispersal rates, distances, and directions (Mech and Boitani, 2003). Recolonization of current range in the Great Lakes PCA required over 30 years (Treves et al., 2009), and European countries with high habitat fragmentation and human population densities are documenting wolf re-establishment after 100-200 years of absence (Reinhardt et al., 2019; Van Der Veken et al., 2021). Further, our linkages are theoretical least-cost paths and wolves undoubtedly move through areas we have not identified. Finally, our analysis does not account for occasional long-distance dispersals over frozen lakes (e.g., Orning et al., 2020). Given the conservativeness of our analysis and unpredictability of wolf dispersal, natural recolonization beyond the Great Lakes PCA appears possible long term.

Complete prey density data for the eastern USA were unavailable, however, our model performed well in identifying suitable areas and provided output similar to previous gray wolf distribution models (Mladenoff and Sickley, 1998; Smith et al., 2016). Land cover variables, such as natural land cover used in our study, may serve as a coarse surrogate for prey density (Hanberry, 2021), on which large carnivores depend (Wolf and Ripple, 2016). Wolves are ungulate specialists and white-tailed deer (*Odocoileus virginianus*) is the primary prey of wolves in the Great Lakes PCA (DelGiudice et al., 2009). Conservative estimates suggest PCAs

generally support deer densities > 5.8/km² (Hanberry, 2021), except the Adirondacks PCA, with typical densities \leq 2 deer/km² (Hinton et al., in revision), parts of the Great Plains PCA (Hanberry, 2021), and possibly northern Maine (MDIFW, 2007). However, northern Maine has 2.7–4.0 moose (*Alces alces*)/km², also an important prey species for wolves (DelGiudice et al., 2009; Kantar and Cumberland, 2013). Finally, several wolf-occupied areas in the Great Lakes PCA have deer densities < 5.8/km² (Hanberry and Hanberry, 2020; Gable et al., 2017); low ungulate densities can result in increased use of alternative prey such as beaver (*Castor canadensis*) and smaller mammals (Newsome et al., 2016).

The suitability of areas for large carnivore recolonization depends not only on their environmental conditions, but also human willingness to co-exist with them (Treves and Karanth, 2003; Gompper et al, 2015), as recolonization can be limited by human persecution (Mech et al., 2019, Recio et al., 2020). Human tolerance depends on real and perceived risks and benefits associated with large carnivore presence (Bruskotter and Wilson, 2014). Science-based public education on wolves could aid in promoting co-existence with humans (Slagle et al., 2013; Treves and Bruskotter, 2014), while increased regulations and conflict mitigation programs may help when more direct action is required (Musiani and Paquet, 2004; Boudreau et al., 2021), particularly in rural areas where humans and wolves share landscapes and interact more frequently (Smith et al., 2014). Our results allow for prioritization of areas most likely to be reoccupied and consequently, where promoting wolf co-existence with humans is most relevant.

4.6 CONCLUSIONS

Despite continuing land use change, suitable areas for large carnivore recolonization remain available (Smith et al., 2016). Many of those species, such as gray wolves, cougars (*Puma concolor*), and American black bears, have recolonized former range, but only partially (Ripple et al., 2014). Nevertheless, we estimate 65% of former wolf range in the eastern USA is currently unsuitable, and limited connectivity between occupied and unoccupied habitat may limit further wolf recolonization. Moreover, linkages for large carnivores often cross jurisdictional borders, highlighting the need for interjurisdictional cooperation if recolonization or reintroduction is desired. Our results suggest that while several parts of the eastern USA may not be recolonized naturally, there is sufficient remaining wolf habitat for reintroduction. Beyond the availability of habitat and linkages for large carnivores, their recolonization and persistence

will require human willingness to share landscapes with them. Knowing where and how large carnivore recolonization may occur can aid in prioritizing areas for conservation and promoting successful co-existence with humans (Olson et al., 2021).

TABLES AND FIGURES

<u>Table 4.1</u> Management jurisdictions and land designations of protected areas within core areas (i.e. suitable areas > 100 km²) and linkages (i.e. 1 km buffer around least-cost paths connecting core area pairs) for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995).

Protected status of core areas			Protected status of linkage			
Management	Area	%	Management	Area	%	
jurisdiction	(km^2)		jurisdiction	(km ²)		
State	106,238	34.5	State	1,342	35.6	
Federal	104,589	34.0	Unknown	694	18.4	
Land designation	33,415	10.9	Federal	537	14.2	
Unknown	26,873	8.7	Private	451	12.0	
Private	17,367	5.6	Land designation	391	10.4	
Local government	10,824	3.5	Local government	188	5.0	
Non-governmental organization	5,644	1.8	Non-governmental organization	128	3.4	
Other	3,078	1.0	Other	42	1.1	
Land designation	Area (km ²)	%	Land designation	Area (km ²)	%	
National forest	65,574	21.3	Conservation easement	825	21.9	

Table 4.1 (cont'd)

State resource management area	55,329	18.0	State conservation area	521	13.8
State conservation area	44,808	14.6	State resource management area	502	13.3
Conservation easement	25,228	8.2	National forest	257	6.8
State wilderness	11,459	3.7	State park	222	5.9
National grassland	9,550	3.1	Recreation management area	198	5.3
Local conservation area	9,407	3.0	National Wildlife Refuge	180	4.8
Wilderness area	9,221	3.0	Military land	147	3.9
Unknown easement	9,007	2.9	Marine protected area	136	3.6
National park	7,301	2.4	Private conservation	109	2.9
State park	7,133	2.3	Local park	91	2.4
Other	51,256	16.6	Other	583	15.5

Table 4.2

Management jurisdictions and protected area land designations within gray wolf (*Canis lupus*) population-sized core areas (> 12 800 km², PCAs) in the eastern USA (Nowak, 1995).

PROTECTED STATUS OF P	OPULATIO	N-SI	ZED CORE AREAS (PCAs)		
MANAGEMENT JURISDICT	TION	LAND DESIGNATION			
	Area			Area	
Great Plains PCA	(km ²)	%	Great Plains PCA	(km ²)	%
			State resource management		
Federal	49,384	64.3	area	17,984	23.4
State	24,079	31.3	Conservation easement	17,335	22.6
Non-governmental					
organization	2,684	3.5	National grassland	9,278	12.1
Local government	547	0.7	National forest	5,959	7.8
Other	132	0.2	National park	4,630	6.0
Total area	76,826		Other	21,640	28.1
	Area			Area	
Great Lakes PCA	(km ²)	%	Great Lakes PCA	(km ²)	%
State	30,513	40.6	National forest	24,196	32.2
			State resource management		
Federal	25,965	34.6	area	16,541	22.0
Local government	7,976	10.6	State conservation area	13,057	17.4
Land designation	7,549	10.1	Local conservation area	7,745	10.3
Other	3,073	4.1	Wilderness area	4,208	5.6
Total area	75,076		Other	9,329	12.4
	Area			Area	
Appalachian PCA	(km ²)	%	Appalachian PCA	(km ²)	%

Table 4.2 (cont'd)

Federal	38,715	52.3	National forest	25,209	34.1
State	31,175	42.1	State conservation area	15,321	20.7
			State resource management		
Joint	2,351	3.2	area	13,538	18.3
Non-governmental					
organization	1,259	1.7	Inventoried roadless area	3,651	4.9
Other	506	0.7	Wilderness area	2,575	3.5
Total area	74,006		Other	13,712	18.5
	Area			Area	
New England PCA	(km ²)	%	New England PCA	(km ²)	%
Non-governmental					
organization	10,972	37.3	National forest	4,986	16.9
Federal	9,143	31.1	Unknown easement	4,435	15.1
State	8,682	29.5	Forest stewardship easement	3,973	13.5
			State resource management		
Local government	566	1.9	area	3,561	12.1
Other	64	0.2	Conservation easement	3,156	10.7
Total area	29,427		Other	9,316	31.7
	Area			Area	
Adirondacks PCA	(km ²)	%	Adirondacks PCA	(km ²)	%
State	13,968	93.5	State wilderness	9,492	63.5
Non-governmental					
organization	443	3.0	Unknown easement	2,768	18.5
Federal	374	2.5	State conservation area	1,147	7.7
Local government	138	0.9	Military land	369	2.5

Table 4.2 (cont'd)

			State resource management		
Other	16	0.1	area	350	2.3
Total area	<u>14,939</u>		Other	813	5.5
Lower Peninsula Michigan	Area		Lower Peninsula Michigan	Area	
РСА	(km ²)	%	PCA	(km ²)	%
Federal	7,781	50.0	State conservation area	7,370	47.3
State	7,493	48.1	National forest	6,920	44.5
Private	246	1.6	Military land	578	3.7
Non-governmental					
organization	40	0.2	Wild and scenic river	156	1.0
			Private recreation or		
Other	15	0.1	education	125	0.8
Total area	<u>15,574</u>		Other	425	2.7

<u>Figure 4.1</u> Land cover throughout former range of gray wolves (*Canis lupus*) in the eastern USA (Nowak, 1995) and southern Canada approximating the northern limit of forest management in Ontario.



<u>Figure 4.2</u> Binary landscape suitability for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, and presence and pseudo-absence points in Minnesota, Wisconsin, and Michigan, USA, used for modeling.



<u>Figure 4.3</u> Relationship between the three most important variables of an ensemble model to predict habitat suitability for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA. Submodels are listed in order of relative contribution to the ensemble model: generalized boosted model (GBM), maximum entropy (MaxEnt), artificial neural network (ANN), multivariate adaptive regression splines (MARS), generalized additive model (GAM), generalized linear model (GLM), random forest (RF), flexible discriminant analysis (FDA), classification tree analysis (CTA), and surface range envelope (SRE).



<u>Figure 4.4</u> Landscape resistance for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, and the top third linkages in terms of priority based on cost-weighted distance and qualities of core areas they connect. Landscape resistance is overlaid with core areas of habitat in the USA, including six population-sized core areas (PCAs) that could host viable wolf populations (> 12,800 km²) (USFWS, 1992).



Figure 4.5 Core habitat areas (i.e. suitable patch area > 100 km²) for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada. Core areas in dark green, intersection with protected areas in light yellow. Linkages between core areas are categorized using equal intervals of their cost-weighted distance (CWD).



<u>Figure 4.6</u> Circuit connectivity for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, representing habitat connectivity for a gray wolf moving randomly through the landscape.



LITERATURE CITED

- Abrahms, B., Sawyer, S.C., Jordan, N.R., McNutt, J.W., Wilson, A.M., Brashares, J.S., 2017. Does wildlife resource selection accurately inform corridor conservation? J. Appl. Ecol. 54, 412–422. https://doi.org/10.1111/1365-2664.12714
- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x
- Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x
- Avgar, T., Lele, S.R., Keim, J.L., Boyce, M.S., 2017. Relative selection strength: Quantifying effect size in habitat-and step-selection inference. Ecol. Evol. 7, 5322–5330. https://doi.org/10.1002/ece3.3122
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x
- Bassi, E., Willis, S.G., Passilongo, D., Mattioli, L., Apollonio, M., 2015. Predicting the spatial distribution of wolf (Canis lupus) breeding areas in a mountainous region of Central Italy. PloS one 10, e0124698. https://doi.org/10.1371/journal.pone.0124698
- Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 180214. https://doi.org/10.1038/sdata.2018.214
- Benz, R.A., Boyce, M.S., Thurfjell, H., Paton, D.G., Musiani, M., Dormann, C.F., Ciuti, S., 2016. Dispersal ecology informs design of large-scale wildlife corridors. PLoS One 11, e0162989. https://doi.org/10.1371/journal.pone.0162989
- Bergstrom, B. J., Vignieri, S., Sheffield, S. R., Sechrest, W., Carlson, A. A., 2009. The Northern Rocky mountain gray wolf is not yet recovered. BioSci. 59, 991–999. https://doi.org/10.1525/bio.2009.59.11.11
- Beyer, D.E., Peterson, R.O., Vucetich, J.A., Hammill, J.H, 2009. Wolf population changes in Michigan. In: In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 65–85. http://doi.org/10.1007/978-0-387-85952-1_5
- Biek, R., Akamine, N., Schwartz, M.K., Ruth, T.K., Murphy, K.M., Poss, M., 2006. Genetic consequences of sex-biased dispersal in a solitary carnivore: Yellowstone cougars. Biol. Lett. 2, 312–315. https://doi.org/10.1098/rsbl.2005.0437
- Boitani, L., 2003. Wolf conservation and recovery. In: Mech, M. and Boitani, L. (Eds.), Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, IL, pp. 317–341. https://doi.org/10.14430/arctic540
- Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G., Payán, E., 2016. Jaguar densities across human-dominated landscapes in Colombia: the contribution of

unprotected areas to long term conservation. PLoS One 11, e0153973. https://doi.org/10.1371/journal.pone.0153973

- Boudreau, M., Gantchoff, M., Ramirez-Reyes, C., Conlee, L., Belant, J., Iglay, R. 2022. Using habitat suitability and landscape connectivity in the spatial prioritization of public outreach and management during carnivore recolonization. J. App. Ecol., 59, 757–767. https://doi.org/10.1111/1365-2664.14090
- Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., ..., Wydeven, A.P., 2008. The effects of breeder loss on wolves. J. Wildl. Manag. 72, 89–98. https://doi.org/10.2193/2006-305
- Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., ..., Bolker, B. M., 2017. glmmTMB balances speed and flexibility among packages for zeroinflated generalized linear mixed modeling. R. J. 9, 378–400. https://doi.org/10.3929/ethzb-000240890
- Bruskotter, J.T., Wilson, R.S., 2014. Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. Conserv. Lett. 7, 158–165. https://doi.org/10.1111/conl.12072
- Buchholtz, E.K., Stronza, A., Songhurst, A., McCulloch, G., Fitzgerald, L.A., 2020. Using landscape connectivity to predict human-wildlife conflict. Biol. Conserv. 248, 108677. https://doi.org/10.1016/j.biocon.2020.108677
- Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J., Ericsson, G., 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. J. Anim. Ecol. 80, 466–476. https://doi.org/10.1111/j.1365-2656.2010.01776.x
- Burnham, K.P., Anderson, D.R., 2004. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY. https://doi.org/10.1007/b97636
- Calenge, C., 2011. Home range estimation in R: the adehabitatHR package. Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France.
- Carroll, C., Phillips, M.K., Schumaker, N.H., Smith, D.W., 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conserv. Biol. 17, 536–548. https://doi.org/10.1046/j.1523-1739.2003.01552.x
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Sci. Adv. 1, e1400253. https://doi.org/10.1126/sciadv.1400253.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., ..., D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553
- Chetkiewicz, C.B., St. Clair, C.C., Boyce, M.S., 2006. Corridors for conservation: integrating pattern and process. Annu. Rev. Ecol. Evol. Syst. 37, 317–342. https://doi.org/10.1146/annurev.ecolsys.37.091305.110050

- CIESIN (Center for International Earth Science Information Network), 2020. Gridded population of the world, version 4 (GPWv4.11): population density adjusted to match 2015 revision of UN WPP country totals, revision 11. https://doi.org/10.7927/H4F47M65.
- Clavero, M., García-berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20, 110–110. https://doi.org/10.1016/j.tree.2005.01.003
- Core Team, 2020. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at: https://www. R-project.org/.
- Correa Ayram, C.A., Mendoza, M.E., Etter, A., Salicrup, D.R.P., 2016. Habitat connectivity in biodiversity conservation: A review of recent studies and applications. Prog. Phys. Geogr. 40, 7–37. https://doi.org/10.1177/0309133315598713
- Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B Biol. Sci. 366, 2642–2651. https://doi.org/10.1098/rstb.2011.0120
- Darimont, C.T., Paquet, P.C., 2002. Gray wolves, Canis lupus, of British Columbia's central and north coast: distribution and conservation assessment. Can. Field-Nat. 116, 416–422.
- Defenders of Wildlife et al v. U.S. Fish and Wildlife Service et al., 2022. No. 21-CV-00344-JSW, 2022 WL 499838 (N.D. Cal. Feb. 10, 2022). United States District Court, Northern District of California. Available at: https://biologicaldiversity.org/species/mammals/pdfs/Wolf-Order-2022-02-10.pdf
- DelGiudice, G.D., McCaffery, K.R., Beyer, D.E., Nelson, M.E., 2009. Prey of wolves in the Great Lakes region. In: Wydeven, A. P., Van Deelen, T. R., Heske, E. (Eds.), Recovery of Gray wolves in the Great Lakes region of the United States. Springer, New York, pp. 155– 173. https://doi.org/10.1007/978-0-387-85952-1_10
- Dewitz, J., 2019, National Land Cover Database (NLCD) 2016 Products: U.S. geological survey data release. https://doi.org/10.5066/P96HHBIE.
- Dondina, O., Meriggi, A., Bani, L., Orioli, V., 2022. Decoupling residents and dispersers from detection data improve habitat selection modelling: the case study of the wolf in a natural corridor. Ethol. Ecol. Evol. 34(6), 617–635. https://doi.org/10.1080/03949370.2021.1988724
- 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. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x
- Elith, J., Ferrier, S., Huettmann, F., Leathwick, J., 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. Ecol. Modell. 186, 280–289. https://doi.org/10.1016/j.ecolmodel.2004.12.007
- Elith, J., Leathwick, J. R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159
- Elliot, N.B., Cushman, S.A., Macdonald, D.W., Loveridge, A.J., 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. J. Appl. Ecol. 51, 1169–1178. https://doi.org/10.1111/1365-2664.12282

- Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D., Ramankutty, N., 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Glob. Ecol. Biogeogr. 19, 589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x
- Environment Canada, 2020. Canadian protected and conserved areas database. Ottawa, Canada: Environment and climate change Canada. Available at: https://www.canada.ca/en/environment-climate-change/services/national-wildlifeareas/protected-conserved-areas-database.html
- Erb, J., DonCarlos, M.W., 2009. An overview of the legal history and population status of wolves in Minnesota. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 49–64. http://doi.org/10.1007/978-0-387-85952-1_4
- Erb, J.D., Humpal, C., 2020. Minnesota wolf population update 2019. Minnesota Department of Natural Resources, St. Paul.
- Erb, J., Sampson, B., 2013. Distribution and abundance of wolves in Minnesota, 2012-13. Minnesota Department of Natural Resources. Available at: http://files.dnr.state.mn.us/fish_wildlife/wildlife/wolves/2013/wolfsurvey_2013.pdf
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
- Fechter, D., Storch, I., 2014. How many wolves (Canis lupus) fit into Germany? The role of assumptions in predictive rule-based habitat models for habitat generalists. PloS one 9, e101798. https://doi.org/10.1371/journal.pone.0101798
- Fieberg, J.R., Forester, J.D., Street, G.M., Johnson, D.H., ArchMiller, A.A., Matthiopoulos, J., 2018. Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. Ecography 41, 737–752. https://doi.org/10.1111/ecog.03123
- Fritts, S.H., Carbyn, L.N., 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. Restor. Ecol. 3, 26–38. https://doi.org/10.1111/j.1526-100X.1995.tb00072.x
- Gable, T., Windels, S., Olson, B., 2017. Estimates of white-tailed deer density in Voyageurs National Park: 1989-2016. NPS/VOYA/NRR—2017/1427
- Gallo, J.A., Greene, R., 2018. Connectivity analysis software for estimating linkage priority. Available at: https://doi.org/10.6084/m9.figshare.5673715.v6
- Gantchoff, M. G., Beyer Jr, D. E., Erb, J. D., MacFarland, D. M., Norton, D. C., Roell, B. J., ..., Belant, J. L., 2022. Distribution model transferability for a wide-ranging species, the Gray Wolf. Sci. Rep. 12, 13556.
- Gantchoff, M.G., Erb, J.D., MacFarland, D.M., Norton, D.C., Price Tack, J.L., Roell, B.J., Belant, J.L., 2021. Potential distribution and connectivity for recolonizing cougars in the Great Lakes region, USA. Biol. Conserv. 257, 109144. https://doi.org/10.1016/j.biocon.2021.109144
- Gantchoff, M., Laura, C., Belant, J.L., 2020. Planning for carnivore recolonization by mapping sex-specific landscape connectivity. Glob. Ecol. Conserv. 21, e00869.

https://doi.org/10.1016/j.gecco.2019.e00869

- Gastón, A., Blázquez-Cabrera, S., Garrote, G., Mateo-Sánchez, M.C., Beier, P., Simón, M.A., Saura, S., 2016. Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing Iberian lynx. J. Appl. Ecol. 53, 814– 824. https://doi.org/10.1111/1365-2664.12629
- Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360, 1232–1235. https://doi.org/10.1126/science.aar7121
- Gompper, M.E., Belant, J.L., Kays, R., 2015. Carnivore coexistence: America's recovery. Science 347, 382–383. https://doi.org/10.1126/science.347.6220.382-b
- Guisan, A., Theurillat, J.-P., 2000. Equilibrium modeling of alpine plant distribution: how far can we go? Phytocoenologia 30, 353–384. https://doi.org/10.1127/phyto/30/2000/353
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x
- Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Environmental predictors: issues of processing and selection, in: habitat suitability and distribution models. Cambridge University Press, Cambridge, pp. 61–109. https://doi.org/10.1017/9781139028271.011
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I., Regan, T.J.,..., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9
- Hanberry, B.B., 2021. Addressing regional relationships between white-tailed deer densities and land classes. Ecol. Evol. 11, 13570–13578. https://doi.org/10.1002/ece3.8084
- Hanberry, B.B., Hanberry, P., 2020. Rapid digitization to reclaim thematic maps of white-tailed deer density from 1982 and 2003 in the conterminous US. PeerJ, 8, e8262. https://doi.org/10.7717/peerj.8262
- Hemmingmoore, H., Aronsson, M., Åkesson, M., Persson, J., Andrén, H., 2020. Evaluating habitat suitability and connectivity for a recolonizing large carnivore. Biol. Conserv. 242, 108352. https://doi.org/10.1016/j.biocon.2019.108352
- Hill, J.E., Boone, H.M., Gantchoff, M.G., Kautz, T.M., Kellner, K.F., Orning, E.K, Parchizadeh, J., Petroelje, T.R., Wehr, N.H., Finnegan, S.P., Fowler, ..., Belant, J.L., 2022. Quantifying anthropogenic wolf mortality in relation to hunting regulations and landscape attributes across North America. Ecol. Evol. 12, e8875. https://doi.org/10.1002/ece3.8875
- Hill, J.E., DeVault, T.L., Belant, J.L., 2021. A review of ecological factors promoting road use by mammals. Mamm. Rev. 51, 214–227. https://doi.org/10.1111/mam.12222
- Hinton, J.W., Chamberlain, M.J., Rabon Jr, D.R., 2013. Red wolf (Canis rufus) recovery: a review with suggestions for future research. Animals 3, 722–744. https://doi.org/10.3390/ani3030722
- Hinton, J.W., Proctor, C., Kelly, M.J., van Manen, F.T., Vaughan, M.R., Chamberlain, M.J.,

2016. Space use and habitat selection by resident and transient red wolves (Canis rufus). PLoS One 11, e0167603. https://doi.org/10.1371/journal.pone.0167603

- Homer, C., Colditz, R.R., Latifovic, R., Llamas, R.M., Pouliot, D., Danielson, P., ..., Vulpescu, M., 2017. Developing a new North American land cover product at 30m resolution: methods, results and future plans. AGU Fall Meeting Abstracts Vol. 2017, pp. GC52C-01.
- Hunt, L.M., Boxall, P., Englin, J., Haider, W., 2005. Remote tourism and forest management: a spatial hedonic analysis. Ecol. Econ. 53, 101–113. https://doi.org/10.1016/j.ecolecon.2004.06.025
- Imbert, C., Caniglia, R., Fabbri, E., Milanesi, P., Randi, E., Serafini, M., ... Meriggi, A., 2016. Why do wolves eat livestock? Factors influencing wolf diet in northern Italy. Biol. Conserv. 195, 156–168. https://doi.org/10.1016/j.biocon.2016.01.003
- Jędrzejewski, W., Jędrzejewska, B., Zawadzka, B., Borowik, T., Nowak, S., Mysłajek, R.W., 2008. Habitat suitability model for Polish wolves based on long-term national census. Anim. Conserv. 11, 377–390.
- Jimenez, M.D., Bangs, E.E., Boyd, D.K., Smith, D.W., Becker, S.A., Ausband, D.E., ..., Laudon, K. (2017). Wolf dispersal in the Rocky Mountains, Western United States: 1993–2008. J. Wildl. Manag. 81, 581–592. https://doi.org/10.1002/jwmg.21238
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. Biol. Invasions 13, 2785–2797. https://doi.org/10.1007/s10530-011-9963-4
- Kantar, L.E., Cumberland, R.E., 2013. Using a double-count aerial survey to estimate moose abundance in Maine. Alces 49, 29–37.
- Keeley, A.T.H., Beier, P., Gagnon, J.W., 2016. Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc. Ecol. 31, 2151–2162. https://doi.org/10.1007/s10980-016-0387-5
- Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Iwachewski, E., Mofatt, S., Mosser, A., Patterson, B.R., Douglas, E.B., ..., Fryxell, J.M., 2015. Wolves adapt territory size, not pack size to local habitat quality. J. Anim. Ecol. 84, 1177–1186. https://doi.org/10.1111/1365-2656.12366
- Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. Bioscience. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2
- Lamb, C.T., Mowat, G., Reid, A., Smit, L., Proctor, M., McLellan, B.N., ..., Boutin, S., 2018. Effects of habitat quality and access management on the density of a recovering grizzly bear population. J. Appl. Ecol. 55(3), 1406–1417. https://doi.org/10.1111/1365-2664.13056
- Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3, 1–7. https://doi.org/10.2174/1874213001003030001
- Licht, D.S., Fritts, S.H., 1994. Gray wolf (Canis lupus) occurrences in the Dakotas. Am. Midl. Nat. 132, 74–81. https://doi.org/10.2307/2426202
- Linnell, J.D.C., Swenson, J.E., Anderson, R., 2001. Predators and people: conservation of large

carnivores is possible at high human densities if management policy is favourable. Anim. Conserv. 4, 345–349. https://doi.org/10.1017/S1367943001001408

- Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2013. Invasion ecology. Wiley and Sons, New Jersey, NJ.
- Maiorano, A.L., Boitani, L., Chiaverini, L., Ciucci, P., 2017. Uncertainties in the identification of potential dispersal corridors: the importance of behaviour, sex, and algorithm. Basic Appl. Ecol. 21, 66–75 https://doi.org/10.1016/j.baae.2017.02.005
- Mancinelli, S., Falco, M., Boitani, L., Ciucci, P. (2019). Social, behavioural and temporal components of wolf (Canis lupus) responses to anthropogenic landscape features in the central Apennines, Italy. J. Zool. 309, 114–124. https://doi.org/10.1111/jzo.12708
- Manitoba Natural Resources and Northern Development (MNRND), 2022. Manitoba 2022 hunting guide. Available at: https://www.gov.mb.ca/nrnd/fishwildlife/pubs/fish_wildlife/huntingguide.pdf
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x
- Martínez-Meyer, E., González-Bernal, A., Velasco, J.A., Swetnam, T.L., González-Saucedo, Z.Y., Servín, J., ..., Heffelfinger, J.R., 2021. Rangewide habitat suitability analysis for the Mexican wolf (Canis lupus baileyi) to identify recovery areas in its historical distribution. Divers. Distrib. 27(4), 642–654. https://doi.org/10.1111/ddi.13222
- McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E., Contasti, A.L., 2010. Considering ecological dynamics in resource selection functions. J. Anim. Ecol. 79, 4–12. https://doi.org/10.1111/j.1365-2656.2009.01613.x
- McRae, B.H., Kavanagh, D.M., 2011. Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle, WA. Available at: https://linkagemapper.org/
- McRae, B. H., Shah, V. B., 2009. Circuitscape user's guide. The University of California, Santa Barbara, CA. Available at: http://www.circuitscape.org
- MDIFW (Maine Department of Inland Fisheries and Wildlife), 2007. Deer population management system and database. Augusta, ME: MDIFW. Available at: https://www.maine.gov/ifw/docs/deer-managementsystem2007.pdf
- Mech, L.D., 1989. Wolf population survival in an area of high road density. Am. Midl. Nat. 121, 387–389. https://doi.org/10.2307/2426043
- Mech, L.D., 2017. Where can wolves live and how can we live with them? Biol. Conserv. 210, 310–317. https://doi.org/10.1016/j.biocon.2017.04.029
- Mech, L.D., 2020. Unexplained patterns of grey wolf Canis lupus natal dispersal. Mamm. Rev. 50, 314–323. https://doi.org/10.1111/mam.12198
- Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, M. and Boitani, L. (Eds.), Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, IL, pp. 317– 341. https://doi.org/10.14430/arctic540
- Mech, L.D., Isbell, F., Krueger, J., Hart, J., 2019. Gray wolf (Canis lupus) recolonization failure:

a Minnesota case study. Can. Field-Nat. 133, 60–65. https://doi.org/10.22621/cfn.v133i1.2078

- Messier, F. (1985). Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology, 63(2), 239-245. https://doi.org/10.1139/z85-037
- Michigan Department of Natural Resources (2008). Estimating wolf abundance in Michigan. Available at: http://www.mich.gov/documents/dnr/Estimating_Wolf_Abundance_in_Michigan_060208_ 239125_7.pdf
- Mladenoff, D.J., Clayton, M.K., Pratt, S.D., Sickley, T.A., Wydeven, A.P., 2009. Change in occupied wolf habitat in the northern Great Lakes region. In: In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, pp. 119–138. https://doi.org/10.1007/978-0-387-85952-1_8
- Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conserv. Biol. 9, 279–294. https://doi.org/10.1046/j.1523-1739.1995.9020279.x
- Mladenoff, D., Sickley, T.A., 1998. Assessing potential gray wolf restoration in the northeastern United States : A spatial prediction of favorable habitat and potential population levels. J. Wildl. Manage. 62, 1–10. https://doi.org/10.2307/3802259
- MNRF (Ministry of Natural Resources and Forestry), 2020. Wolf and coyote hunting regulations. Available at: https://www.ontario.ca/document/ontario-hunting-regulations-summary/wolf-and-coyote
- Morales-González, A., Fernández-Gil, A., Quevedo, M., Revilla, E., 2022. Patterns and determinants of dispersal in grey wolves (Canis lupus). Biol. Rev. 97, 466–480. https://doi.org/10.1111/brv.12807
- Muff, S., Signer, J., Fieberg, J. (2020). Accounting for individual-specific variation in habitatselection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. J. Anim. Ecol. 89, 80–92. https://doi.org/10.1111/1365-2656.13087
- Musiani, M., Paquet, P.C., 2004. the practices of wolf persecution, protection, and restoration in Canada and the United States. Bioscience 54, 50–60. https://doi.org/10.1641/0006-3568(2004)054[0050:TPOWPP]2.0.CO;2
- Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., ..., Ripple, W.J., 2016. Food habits of the world's grey wolves. Mamm. Rev. 46, 255–269. https://doi.org/10.1111/mam.12067
- Nowak, R.M. 1995. Another look at wolf taxonomy. In: Carbyn, L.N., S.H. Fritts, and D.R. Seip (Eds.). Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Canada, pp. 375–397.
- O'Neil, S.T., Beyer, D.E., Bump, J.K., 2019. Territorial landscapes: incorporating densitydependence into wolf habitat selection studies. R. Soc. Open Sci. 6, 190282. https://doi.org/10.1098/rsos.190282

- Olson, E.R., Goethlich, J., Goudos-Weisbecker, B., 2021. Attitudes towards a transient carnivore prior to recolonization. Wildl. Soc. Bull. 45, 191–201. https://doi.org/10.1002/wsb.1166
- Olson, E.R., Stenglein, J.L., Shelley, V., Rissman, A.R., Browne-Nuñez, C., Voyles, Z., ..., Van Deelen, T., 2015. Pendulum swings in wolf management led to conflict, illegal kills, and a legislated wolf hunt. Conserv. Lett. 8, 351–360. https://doi.org/10.1111/conl.12141
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124, 1263–1273. https://doi.org/10.1111/oik.02224
- Orning, E.K., Romanski, M.C., Moore, S., Chenaux-Ibrahim, Y., Hart, J., Belant, J.L., 2020. Emigration and first-year movements of initial wolf translocations to Isle Royale. Northeast. Nat. 27, 701–708. https://doi.org/10.1656/045.027.0410
- Osipova, L., Okello, M.M., Njumbi, S.J., Ngene, S., Western, D., Hayward, M.W., Balkenhol, N., 2019. Using step-selection functions to model landscape connectivity for African elephants: Accounting for variability across individuals and seasons. Anim. Conserv. 22, 35–48. https://doi.org/10.1111/acv.12432
- Ouellette, M., Remmel, T.K., Perera, A.H., 2020. A spatial database of historical wildfire and timber harvesting in the boreal Area of the Undertaking of Ontario: the methodological framework. Ontario MNRF, TR 37.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197. https://doi.org/10.1890/07-2153.1
- Piper, W.H., 2011. Making habitat selection more "familiar": a review. Behav. Ecol. Sociobiol. 65, 1329–1351. https://doi.org/10.1007/s00265-011-1195-1
- Powell, R.A., Proulx, G., 2003. Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense. ILAR J. 44, 259– 276. https://doi.org/10.1093/ilar.44.4.259
- R Core Team, 2021. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at: https://www. R-project.org/.
- Recio, M.R., Singer, A., Wabakken, P., Sand, H., 2020. Agent-based models predict patterns and identify constraints of large carnivore recolonizations, a case study of wolves in Scandinavia. Biol. Conserv. 251, 108752. https://doi.org/10.1016/j.biocon.2020.108752
- Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C.A., Krone, O., Ansorge, H., Mueller, T., 2019. Military training areas facilitate the recolonization of wolves in Germany. Conserv. Lett. 12, e12635. https://doi.org/10.1111/conl.12635
- Rio-maior, H., Nakamura, M., Álvares, F., Beja, P., 2019. Designing the landscape of coexistence : integrating risk avoidance , habitat selection and functional connectivity to inform large carnivore conservation. Biol. Conserv. 235, 178–188. https://doi.org/10.1016/j.biocon.2019.04.021
- Ripari, L., Premier, J., Belotti, E., Bluhm, H., Breitenmoser-Würsten, C., Bufka, L.,..., Heurich, M, 2022. Human disturbance is the most limiting factor driving habitat selection of a large

carnivore throughout Continental Europe. Biol. Conserv. 266, 109446. https://doi.org/10.1016/j.biocon.2021.109446

- Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biol. Conserv. 145, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., ..., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 151–162. https://doi.org/10.1126/science.1241484
- Rodríguez, J.P., Brotons, L., Bustamante, J., Seoane, J., 2007. The application of predictive modelling of species distribution to biodiversity conservation. Divers. Distrib. 13, 243–251. https://doi.org/10.1111/j.1472-4642.2007.00356.x
- Ruid, D.B., Paul, W.J., Roell, B.J., Wydeven, A.P., Willging, R.C., Jurewicz, R.L., Lonsway, D.H., 2009. Wolf–human conflicts and management in Minnesota, Wisconsin, and Michigan. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, pp. 279–295. https://doi.org/10.1007/978-0-387-85952-1_18
- Scott, R.W., Huff, F.A., 1996. Impacts of the Great Lakes on regional climate conditions. J. Great Lakes Res. 22, 845–863. https://doi.org/10.1016/S0380-1330(96)71006-7
- Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier performance in R. Bioinformatics, 21, 3940–3941.
- Slagle, K., Zajac, R., Bruskotter, J., Wilson, R., Prange, S., 2013. Building tolerance for bears: a communications experiment. J. Wildl. Manag. 77, 863–869. https://doi.org/10.1002/jwmg.515
- Smith, J.A., Duane, T.P., Wilmers, C.C., 2019. Landscape and urban planning moving through the matrix: promoting permeability for large carnivores in a human-dominated landscape. Landsc. Urban Plan. 183, 50–58. https://doi.org/10.1016/j.landurbplan.2018.11.003
- Smith, J.B., Nielsen, C.K., Hellgren, E.C., 2014. Illinois resident attitudes toward recolonizing large carnivores. J. Wildl. Manag. 78, 930–943. https://doi.org/10.1002/jwmg.718
- Smith, J.B., Nielsen, C.K., Hellgren, E.C., 2016. Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx 50, 555–564. https://doi.org/10.1017/S0030605314001227
- Spitz, D.B., Hebblewhite, M., Stephenson, T.R., 2017. 'MigrateR': extending model-driven methods for classifying and quantifying animal movement behavior. Ecography, 40, 788– 799. https://doi.org/10.1111/ecog.02587
- Statistics Canada, 2020. Road Network File, Catalogue no. 92-500-X. Available at: https://www150.statcan.gc.ca/n1/en/catalogue/92-500-X
- Stauffer, G., Roberts, N.M., MacFarland, D., van Deelen, T.R., 2020. Evaluation of alternative methods for estimating wolf abundance in Wisconsin, USA. Wisconsin Department of Natural Resources, Wisconsin.
- Stricker, H.K., Gehring, T.M., Donner, D., Petroelje, T., 2019. Multi-scale habitat selection model assessing potential gray wolf den habitat and dispersal corridors in Michigan, USA.

Ecol. Modell. 397, 84–94. https://doi.org/10.1016/j.ecolmodel.2018.12.021

- Suraci, J.P., Clinchy, M., Zanette, L.Y., Wilmers, C.C., 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol. Lett., 22, 1578–1586. https://doi.org/10.1111/ele.13344
- Svenning, J.-C., Skov, F., 2004. Limited filling of the potential range in European tree species. Ecol. Lett. 7, 565–573. https://doi.org/10.1111/j.1461-0248.2004.00614.x
- Thiel, R.P., 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. Am. Midl. Nat. 113, 404. https://doi.org/10.2307/2425590
- Thiel, R.P., Hall, W., Heilhecker, E., Wydeven, A.P., 2009. An isolated wolf population in central Wisconsin. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, pp. 107– 117. http://dx.doi.org/10.1007/978-0-387-85952-1
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C, ..., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. https://doi.org/10.1038/nature02121
- Thorsen, N.H., Hansen, J.E., Støen, O.G., Kindberg, J., Zedrosser, A., Frank, S.C., 2022. Movement and habitat selection of a large carnivore in response to human infrastructure differs by life stage. Mov. Ecol. 10, 1–14. https://doi.org/10.1186/s40462-022-00349-y
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD a platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x
- Thurfjell, H., Ciuti, S., Boyce, M.S., 2014. Applications of step-selection functions in ecology and conservation. Mov. Ecol. 2, 4. https://doi.org/10.1186/2051-3933-2-4
- Treves, A., Bruskotter, J., 2014. Tolerance for predatory wildlife. Science 344, 476–477. https://doi.org/10.1126/science.1252690
- Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv. Biol. 17, 1491–1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x
- Treves, A., Martin, K.A., Wiedenhoeft, J.E., Wydeven, A.P., 2009. Dispersal of gray wolves in the Great Lakes region. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 191–204. http://doi.org/10.1007/978-0-387-85952-1_12
- Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A., Wydeven, A.P., 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conserv. Biol. 18, 114–125. https://doi.org/10.1111/j.1523-1739.2004.00189.x
- United States Census Bureau, 2010. Decennial census of population and housing. Available at: https://www.census.gov/programs-surveys/decennial-census/decade/decennial-publications.2010.html
- United States Census Bureau, 2020. TIGER/Line shapefiles 2020: roads. Available at:
https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html.

- United States Geological Survey, 1996. USGS EROS archive: digital elevation global 30 arcsecond elevation (GTOPO30). https://doi.org/10.5066/F7DF6PQS
- United States Geological Survey, 2016. National hydrography dataset. Available at: https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-nationalhydrography-products
- United States Geological Survey Gap Analysis Project, 2018. Protected Areas Database of the United States (PAD-US): U.S. Geological Survey Data Release. https://doi.org/ 10.5066/P955KPLE.
- USFWS (U.S. Fish and Wildlife Service), 1992. Recovery plan for the eastern timber wolf. Twin Cities, Minnesota.
- USFWS (U.S. Fish and Wildlife Service), 2008. Post-delisting monitoring plan for the western Great Lakes distinct population segment of the gray wolf. U.S. Fish and Wildlife Service, Twin Cities Field Office and Midwest Region, Bloomington, MN and Ft. Snelling, MN.
- USFWS (U.S. Fish and Wildlife Service), 2009. threatened and endangered species system: delisting report. US Government Printing Office, Washington, DC
- USFWS (U.S. Fish and Wildlife Service), 2020a. Gray wolf biological report: information on the species in the lower 48 United States. US Government Printing Office, Washington, DC.
- USFWS (U.S. Fish and Wildlife Service), 2020b. Endangered and threatened wildlife and plants; removing the gray wolf (Canis lupus) from the list of endangered and threatened wildlife. Federal Register, 85, 69778–69895.
- Václavík, T., Meentemeyer, R.K., 2012. Equilibrium or not? modelling potential distribution of invasive species in different stages of invasion. Divers. Distrib. 18, 73–83. https://doi.org/10.1111/j.1472-4642.2011.00854.x
- van den Bosch, M., Beyer Jr, D.E., Erb, J.D., Gantchoff, M.G., Kellner, K.F., MacFarland, D. M., Norton, D.C., ..., Belant, J.L., 2022. Identifying potential gray wolf habitat and connectivity in the eastern USA. Biol. Conserv. 273, 109708. https://doi.org/10.1016/j.biocon.2022.109708
- Van Der Veken, T., Van Den Berge, K., Gouwy, J., Berlengee, F., Schamp, K., 2021. Diet of the first settled wolves (Canis lupus) in Flanders, Belgium. Lutra 64, 45–56.
- Vasudev, D., Fletcher, R.J., Goswami, V.R., Krishnadas, M., 2015. From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography 38, 967– 978. https://doi.org/10.1111/ecog.01306
- Wielgus, R.B., 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biol. Conserv. 106, 381–388. https://doi.org/10.1016/S0006-3207(01)00265-8
- Wisconsin Department of Natural Resources, 2021. Wisconsin gray wolf monitoring report 15 april 2020 through 14 april 2021. Available at: https://widnr.widen.net/s/vlfpznrl2w/wisconsin_gray_wolf_2020_2021_final
- Wolf, C., Ripple, W.J., 2016. Prey depletion as a threat to the world's large carnivores. R. Soc.

Open Sci. 3, 160252. https://doi.org/10.1098/rsos.160252

- Wolf, C., Ripple, W.J., 2017. Range contractions of the world's large carnivores. R. Soc. Open Sci. 4, 170052. https://doi.org/10.1098/rsos.170052
- Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3, 165–173. https://doi.org/10.1017/S13679430000086X
- Wydeven, A.P., Fuller, T.K., Weber, W., MacDonald, K., 1998. The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. Wildl. Soc. Bull. 26, 776–784.
- Wydeven, A.P., Wiedenhoeft, J.E., Schultz, R.N., Thiel, R.P., Jurewicz, R.L., Kohn, B.E., Van Deelen, T.R., 2009. History, population growth, and management of wolves in Wisconsin. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 87– 105. http://doi.org/10.1007/978-0-387-85952-1_6
- Yang, L., Jin, S., Danielson, P., Homer, C., Gass, L., Bender, S.M., ..., Xian, G., 2018. A new generation of the United States national land cover database: requirements, research priorities, design, and implementation strategies. ISPRS J. Photogramm. Remote Sens. 146, 108–123. https://doi.org/10.1016/j.isprsjprs.2018.09.006
- Zeller, K.A., Jennings, M.K., Vickers, T.W., Ernest, H.B., Cushman, S.A., Boyce, W.M., 2018. Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers. Distrib. 24, 868–879. https://doi.org/10.1111/ddi.12742
- Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., Liberg, O., 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behav. Ecol. 25(6), 1353–1364. https://doi.org/10.1093/beheco/aru134

APPENDIX

<u>Figure A</u> DHARMa residual tests for a binomial general linearized model, used in Chapter 3 to predict the relationship between anthropogenic disturbances and gray wolf (*Canis lupus*) habitat suitability in Minnesota, Wisconsin, and Michigan, USA, 1989–2020. From left to right: Kolmogorov-Smirnov test, DHARMa nonparametric dispersion test, and outlier test.

