2017

# THE SPATIAL ECOLOGY OF GRAY WOLVES IN THE UPPER PENINSULA OF MICHIGAN, 1994–2013

Shawn O'Neil
*Michigan Technological University*, stoneil@mtu.edu

Recommended Citation
O'Neil, Shawn, "THE SPATIAL ECOLOGY OF GRAY WOLVES IN THE UPPER PENINSULA OF MICHIGAN, 1994–2013", Open Access Dissertation, Michigan Technological University, 2017.
https://doi.org/10.37099/mtu.dc.etdr/451

# THE SPATIAL ECOLOGY OF GRAY WOLVES IN THE UPPER PENINSULA OF MICHIGAN, 1994–2013

By

Shawn T. O’Neil

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In Forest Science

MICHIGAN TECHNOLOGICAL UNIVERSITY

2017

This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Forest Science.

School of Forest Resources and Environmental Science

| | |
|---|---|
| Dissertation Advisor: | *Dr. Joseph K. Bump* |
| Committee Member: | *Dr. John A. Vucetich* |
| Committee Member: | *Dr. Christopher R. Webster* |
| Committee Member: | *Dr. Dean E. Beyer, Jr.* |
| Committee Member: | *Dr. Min Wang* |
| School Dean: | *Dr. Terry Sharik* |

## Table of Contents

Preface....................................................................................................... iv

Acknowledgments....................................................................................... v

Abstract..................................................................................................... vii

1. Introduction............................................................................................. 1
    1.1. Spatiotemporal variation, habitat selection, and habitat fitness ..................... 1
    1.2. Study system........................................................................................ 3
    1.3. Research objectives ............................................................................. 5
2. Identifying habitat bottlenecks: Functional responses in winter distribution of white-tailed deer (*Odocoileus virginianus*)............................................................... 8
3. Empirical evidence of preemptive habitat selection by a top predator during 19 years of population recovery ............................................................................... 63
4. A simulation of conceptual used and available habitat distributions under assumptions of strong territoriality and population growth.................................. 104
5. Implications of territoriality and density dependence on long term comparisons of used to available habitat distributions.......................................................... 124
6. Spatially varying density dependence drives a shifting mosaic of survival in a recovering apex predator (*Canis lupus*)................................................................ 171
7. Competing risks and partial compensation for human-caused mortality in Upper Peninsula wolves............................................................................................ 201
8. Literature cited....................................................................................... 230

# PREFACE

This dissertation is a collaborative project involving long-term monitoring data collected by the Michigan Department of Natural Resources (DNR) over the last two decades. The material in these chapters includes analysis of data collected by the DNR during 1992 – 2014. The structure of this dissertation is that of a series of manuscripts, that are intended to be published. Dr. Dean Beyer, Jr. is a DNR lead research biologist. Dean shared the data and provided oversight for the overall project. Dr. Joseph Bump provided advising and guidance in terms of writing and analysis. Shawn O'Neil analyzed the data and wrote the chapters in this dissertation.

# Acknowledgments

First and foremost, I would like to thank my advisor, Dr. Joseph K. Bump, who has provided support at every step of the process. Joseph has gone out of his way to dedicate his time and energy to my work and has greatly exceeded my expectations for an academic advisor. Beyond the office and the classroom, Joseph has taken interest in providing professional mentorship and supporting my career aspirations, and has played a critical role in helping me secure an exciting new position in wildlife conservation. I couldn't ask for a better advisor, mentor, or friend. Thank you, Joseph, for being the selfless person that you are.

Thanks to my committee. Dr. John Vucetich, Dr. Chris Webster, and Dr. Min Wang have always responded to my requests for help and guidance and each has had a generous open door policy over the years. Dr. Vucetich in particular has helped me to expand my thinking and challenged me to improve my writing. In addition, his positive feedback has helped me build confidence in my work, and his advice has provided inspiration and direction. Last but not least, I'd like to give special thanks to Dr. Dean Beyer, Jr. None of this would have been possible without Dean, who was a strong advocate of our involvement in the project from the very beginning. Once we got things rolling, Dean was always available for questions, and could always help put things in context.

Research was made possible by funding from the Michigan Department of Natural Resources, MTU grant # 751B4300037. The project was also supported in part by Federal Aid in the Wildlife Restoration Act under Pittman-Robertson project W-147-R. Additional funding was provided by a National Science Foundation grant to JKB (NSF #1545611), the DeVlieg Foundation and the Ecosystem Science Center (within the School of Forest Resources and Environmental Science at Michigan Technological University, MI, USA). The Michigan Involvement Committee of Safari Club International provided funding for radio-collars and other equipment. We thank Erin Largent, Robert Doepker, Steve Carson, Brian Roell, and Chris Webster for assisting with data needs during the analysis. Mike Haen, Brad Johnson, Donald Lonsway, Jeff Lukowski and Kristie Sitar assisted with capturing and radio-collaring wolves. Pilots Neil Harri, Dean Minett, and Gordon Zuehlke collected collared wolf relocation data. Anna Nisi and Emily Fifelski assisted with data processing. Finally, we would like to thank G. Shankara, W. Perger, and other administrators of the Computational Research Center and the Superior supercomputer at Michigan Technological University for providing access to these powerful resources.

Thanks to my friends and family for seeing me through and giving me the time I needed.

Megan, thank you for your patience and your trust, and for believing in me.

# Abstract

All natural processes are dynamic in space and time. Establishing the links between spatiotemporal patterns and ecological processes is critical for improving our understanding of natural systems. Empirical data representing wildlife populations is accumulating and increasingly involves spatiotemporal components. Wildlife monitoring programs for threatened, endangered, or other species of interest often involve radio-tracking of a sample of individual animals combined with census data. Such data are valuable both for conservation and management of populations and for testing ecological theories about species distribution and what influences patterns over time. We used 20 years of radio telemetry and snow tracking data to evaluate spatiotemporal patterns in gray wolf (*Canis lupus*) distribution, habitat selection, survival, and mortality in the Upper Peninsula (UP) of Michigan, USA. Wolves recolonized the study area during the early 1990s and exceeded a population size of 600 individuals before the end of the study. In addition, wolves were on the Endangered Species List during the majority of the study. This work therefore explores the spatial ecology of endangered wolves during a period of population recovery. We analyzed winter prey distributions of wolves, evaluated theoretical and modern empirically-driven models of density dependent habitat selection, estimated annual survival, and explored cause-specific mortality. Our methods included isodar analysis, spatiotemporal generalized linear mixed models of habitat selection, proportional hazards models with time-dependent spatial covariates, and competing risks analysis. Winter prey distributions exhibited a habitat functional response depending on winter snow conditions, resulting in a geographic prey limitation that affected wolf territory occupancy within the study area. Density-dependence in habitat selection revealed that wolf selection patterns were more consistent with an ideal-preemptive habitat distribution, as opposed to the ideal-free distribution. Density-dependent habitat selection patterns revealed decreasing selection for prey availability at greater wolf densities, while selection for anthropogenic features such as road density increased. However, selection across time exhibited occupancy-dependence as opposed to density-dependence. Wolf annual was survival ~ 75% and was influenced by sex, age, transient status, agriculture, habitat edge, wolf density, and Julian day, as well as several individual factors. Survival declined as wolf density increased, resulting in a shifting mosaic of wolf survival. Human-caused mortality increased with wolf density and was the primary mortality source of UP wolves, comprising ~ 17% annually. Much of human-caused mortality was attributed to illegal killing. Human-caused mortality was partially compensated for by natural mortality, and negative impacts on population growth rate were most evident when human-caused and natural mortality were both high. The spatial ecology of wolves in this study describes patterns associated with a growing and shifting population. Density-dependent effects population dynamics occurred with expanding wolf range, where later colonizers were forced to utilize habitats closer to human populations. Theoretical tests revealed potential for source-sink population dynamics. Evidence suggested the population had stabilized by the end of the study, and that suitable habitat was saturated. Future conservation of the population will likely depend on preservation of high quality source habitats and managing human conflicts associated with high wolf density areas occurring near population centers.

# 1. Introduction

## 1.1 Spatiotemporal variation, habitat selection, and habitat fitness

Novel opportunities are increasing in the collection and analysis of ecological data that can reveal patterns that are dynamic in space and time. Access to spatiotemporal data has spurred methodological advancements and modern statistical approaches that allow ecologists to study animal movement (Lima and Zollner 1996, Rubenstein and Hobson 2004, Morales et al. 2010, McClintock et al. 2012), spatial structure in populations (Guisan and Thuiller 2005, Engelbrecht et al. 2007, Kery et al. 2011, Royle et al. 2013), and patterns in habitat that demonstrate fascinating interactions between animals and their environments (Bump et al. 2009, Wunder 2010, Murray et al. 2013, McLoughlin et al. 2016). Knowledge that is gained from such advancements has clear value in terms of basic science and our understanding of the natural world (Massol et al. 2011). In addition, opportunities in ecological conservation and management are increasingly vast. The ability to know where and when key events are occurring contributes to better integration of scientific knowledge and management of animal populations (Frantz et al. 2009, Richard and Armstrong 2010, Anderson and Gaston 2013, Cromsigt et al. 2013, Coates et al. 2016). One important area in wildlife management is the understanding of habitat selection (Rosenzweig 1981, Orians and Wittenberger 1991, McLoughlin et al. 2010, Morris 2011). While historically most studies of habitat selection offered a “snapshot” of linkages between animals, accumulation of spatiotemporal data associated with long-term monitoring programs have resulted in new opportunities to apply habitat use and selection concepts in ways that integrate temporal components of the process. Quantifying temporal variation within and alongside traditional habitat selection approaches can reveal the influences that important population processes (i.e. density dependence) and changes in resource availability have on wildlife-habitat relationships (Morris 2003b, McLoughlin et al. 2010, Matthiopoulos et al. 2011, Aarts et al. 2013, Matthiopoulos et al. 2015). In addition, these processes may interact with each other to influence habitat selection (van Beest et al. 2015). Evaluating spatiotemporal variation in habitat selection can reveal better understanding of "true" ecological niches, contributions of habitat types to species fitness, and trends in wildlife-human conflicts associated with dynamic trends in space use.

Long-term monitoring programs that provide spatiotemporal data also offer opportunities for ecologists to carry out empirical tests of ecological theory. Habitat selection as a field of study is typically viewed as an applied science. However, its study is deeply rooted in ecological niche and optimal foraging theory (Rosenzweig 1991, Brown et al. 1999, Pulliam 2000, Hirzel and Le Lay 2008). More recently, applications of density-dependent habitat selection can be traced to more recent theory involving density-fitness habitat relationships (Morris 1988, Morris 2003a, McLoughlin et al. 2010). While modern studies typically acknowledge density dependent habitat selection theory, direct tests of the theory can be performed with spatiotemporal data. Such tests improve our understanding of our species, and also can provide evidence for or against commonly made assumptions. For example, the assumption that density and/or occupancy is indicative of habitat 'quality' is based on the theoretical Ideal-Free distribution (Morris 1988, Morris 1989), which in itself assumes optimal foraging and near-perfect perception of habitat benefits at varying levels of competition. These assumptions can easily be violated in the real world, but ecologists generally expect that divergence from expected behaviors (i.e. violations of assumptions) don't dramatically skew inferences from traditional models. Nonetheless, tests of habitat selection theory are rare and should be performed whenever possible to validate expectations of population-level behaviors.

### 1.2 Study system

Our study area was the UP of Michigan, located in the northern Great Lakes region of the USA. The study area was predominantly characterized by long winters with heavy snowfall; > 100 cm of snowfall was common throughout the UP, with 350–500 cm typically falling within lake effect snow belts (Eichenlaub et al. 1990). Greatest snowfall totals generally occurred at local elevations > 300 m within ~ 30 km of the Lake Superior shoreline in the northern UP and Keweenaw Peninsula (National Operational Hydrologic Remote Sensing Center 2004). Coldest temperatures occurred in January, with average daily maxima of -7–0° C; average daily minimums were ~ -15° C in January and February across the study area (Eichenlaub et al. 1990). The UP was characterized by dense northern hardwood forests. Coniferous tree species included balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and tamarack (*Larix laricina*). Further details on forest and land cover types are available in O'Neil and Bump (2014).

The Michigan wolf population occurred solely in the UP during the time period of the study. Wolves were virtually non-existent in the UP from the 1950s–1970s, with sporadic occurrences documented in the 1980s and recovery likely beginning in 1988 (Beyer et al. 2009). From the early 1990s – 2014, the wolf population in Michigan transitioned from being locally extinct to exceeding 600 animals (Michigan Department of Natural Resources 2015), occupying virtually all available suitable habitat in the Upper Peninsula (UP). During this time period, the population went from being protected under the Endangered Species Act (ESA), to being hunted (2013), and to again being protected (Dec. 2014). Michigan's wolf monitoring program provided a unique and rare opportunity to assess these dynamics, as wolves' spatial distribution and population growth was tracked from early recovery through widespread recolonization. Capturing and collaring efforts began in 1992, with multiple packs monitored by 1995, the first year effectively included in this study. The population was counted during the years following, and steadily increased through the 1990s. Wolves in the UP were federally protected under the ESA from 1974 – 2007, 2008 – 2009, 2009 – 2011, and following the completion of this study (2014). A detailed chronology of wolves ESA status in the Western Great Lakes region can be found at http://www.fws.gov/midwest/wolf/.

White-tailed deer (*Odocoileus virginianus*) are the primary prey for wolves in the region, and deer populations are constrained by severe winters with heavy snowfall, especially in the higher latitudes of the study area (Potvin et al. 2005). Limiting factors for wolves included road density and deer density (Mladenoff and Sickley 1998, Potvin et al. 2005). Since road densities are low throughout the UP, deer densities likely have a strong influence on the upper limit of the wolf population (Potvin et al. 2005). Biological carrying capacity estimates have ranged from 600 to 1,350 wolves (Beyer et al. 2009). Deer are migratory throughout much of the UP due to harsh winter conditions. When snow depth exceeds ~ 30 cm, deer migrate south and congregate in dense stands of eastern hemlock and northern white cedar (Shi et al. 2006, Witt et al. 2012, Murray et al. 2013). Deer have used the same winter range consistently over time; this has likely been a result of learned behavior (passing of behavioral traits; Nelson 1998) combined with predictable patterns in snow depth and cover. Within these habitats, hemlock, cedar and other coniferous tree species provide cover and intercept snow while a northwest weather flow generates lake effect snow with greatest accumulation at higher elevations several km offshore of Lake Superior. Variability in winter severity determines whether deer will migrate to winter range in the southern regions of the study area (Van Deelen et al. 1998) while the northern regions receive much greater snowfall resulting in consistent annual migrations.

## 1.3 Research objectives

Our research objectives were centered on a long-term monitoring study of the gray wolf (*Canis lupus*) population in the Upper Peninsula (UP) of Michigan, USA. Michigan's wolf population has recolonized the UP naturally starting in the early 1990s following extirpation that had occurred by the 1960s (Beyer et al. 2009). The legal status of wolves in this sub-population and elsewhere has been controversial as occupied range has expanded (Bruskotter et al. 2014, Chapron et al. 2014, Vucetich and Nelson 2014, Olson et al. 2015, Chapron and Treves 2016). Details are described further in the next section. Management objectives of the Michigan wolf population have generally involved A) facilitating the recovery of the UP wolf population, and B) managing human conflicts associated with human coexistence with a top predator that was historically undesired (Mech 1995, Mech and Boitani 2010). Thus, my research objectives include providing information that will improve management of the population in addition to more general objectives aimed at answering intriguing ecological questions.

### *Conservation and management objectives*

Conservation and management objectives were focused on wolf survival, mortality, dispersal, and the impact that humans and habitat have had on these parameters over time. Specifically, these objectives were to:

- Evaluate changes in wolf distribution over time (Chapters 3, 5 & 6)
- Estimate monthly and annual survival rates of radio-collared wolves over fifteen years of monitoring (Chapter 6)
- Test for influences of seasonal, spatial, time-dependent, and management-based covariates on survival and mortality of wolves (Chapters 6 & 7)
- Develop spatial 'risk' maps that indicate hazardous areas for wolves and potential areas of human conflict (Chapter 6)
- Identify collared wolves that dispersed from their packs and test survival effects associated with season, age, and sex (Chapter 6)
- Test for difference between survival rates of dispersers vs. non-dispersers (Chapter 6)

- Estimate contributions of human vs. natural-caused mortality to overall mortality (Chapter 7)
- Estimate impacts of and natural compensation for human-caused mortality (Chapter 7)

*Ecological research objectives*

My ecological research objectives involved studying density dependence in wolf habitat selection, identifying habitat functional responses in white-tailed deer distributions and predicting winter habitat, linking spatiotemporal variation in wolf habitat selection to theoretical expectations, and evaluating the effect of density dependence on wolf survival and mortality over time. Specifically:

- Identify habitat functional responses in white-tailed deer winter distribution, where habitat use depends on scale-dependent interacting habitat types and variation in snow conditions (Chapter 2)
- Compare changes in wolf density over time in separate habitat types to evaluate the theoretical habitat distribution (Ideal-free vs. territorial alternatives such as Ideal-despotic or Ideal-preemptive; Chapter 3)
- Evaluate density-dependent habitat selection based on shifting occupancy and habitat availability (Chapters 4 & 5)
- Investigate density dependent mechanisms influencing wolf survival and mortality (Chapters 6 & 7)
- Investigate support for additive vs. compensatory human-caused mortality in wolves (Chapter 7)

# 2. Identifying habitat bottlenecks: Functional responses in winter distribution of white-tailed deer (*Odocoileus virginianus*)[1]

## Abstract

Functional responses in habitat selection recognize that selection is dynamic and varies as a function of one or more resource availabilities. Generalized functional response habitat models allow for the effects of environmental predictors to be measured in this context, which is useful for evaluating seasonal trade-off situations, density dependent habitat selection, and selection for habitat that may vary in availability depending on weather or climate. White-tailed deer (*Odocoileus virginianus*) exhibit migratory behavior when deep snow (> 30 cm) occurs in winter, moving from summer range into areas with dense conifer cover and reduced snow depth. While basic winter habitat needs are understood, questions remain about where and when deer use key habitat components such as eastern hemlock (*Tsuga Canadensis*). We hypothesized that incorporating functional responses into habitat selection models of white-tailed deer in winter would result in better predictions of deer wintering complexes. We fit generalized functional response (GFR) models to maps of deer winter occurrence across the Upper Peninsula of Michigan, USA. We updated the best fitting model structures with a conditional autoregressive spatial random effect using Integrated Nested Laplace Approximations in R package INLA. Models accounting for spatial autocorrelation and functional responses in habitat selection resulted in excellent fit to deer winter

---

[1] The material contained in this chapter is in preparation for submission to the *Journal of Wildlife Management*

occurrence data, indicating support for the GFR model and its specified interactions between food, cover, and conditions variables. Our results are useful for exploring the context of key drivers of seasonal habitats, and offer a framework for prediction under scenarios of climate and land cover change. To our knowledge this analysis is the first to explicitly model functional responses to availability of multiple environmental features representing conditions, forage, and cover based on long-term winter observations of deer winter range.

## Introduction

An enduring challenge for wildlife managers is making habitat selection analyses both analytically robust and ecologically realistic. The analytical capacity to easily examine functional responses in habitat selection studies has significantly improved the ecological realism and management relevance of habitat research. Functional responses in habitat selection do not assume constant resource selection across habitats, rather selection is dynamic and varies as a function of resource availability (Mysterud and Ims 1998). For example, consider an ungulate population studied in a snowy region with limited winter habitat. In years of heavy snow individuals would likely exhibit strong selection for winter cover, but such selection might be weak in years of low snow. Identifying functional responses in habitat selection is critical to understanding key habitat components and effective management, which is especially important for highly valued large ungulate populations.

Functional responses in habitat selection are common when trade-offs exist between resources that do not co-occur in space and time. Such is the case for white-tailed deer (*Odocoileus virginianus*) winter habitat in Michigan's Upper Peninsula (UP), where heavy snowfall limits forage availability and therefore the quality of cover habitat depends on both localized reductions in snow depth and accessibility of winter food such as regenerating aspen or maple forests. As a result, estimates of long-term deer winter distributions suggest that winter habitat extent may be < 25% of summer range on average (R. Doepker, Michigan Department of Natural Resources, unpublished data). Deer in the UP are mostly migratory due to deep snow cover throughout the region during winter months. When snow depth exceeds ~ 30 cm, deer begin their migration to wintering complexes, where dense coniferous trees (e.g. northern white cedar *Thuja occidentalis,* eastern hemlock *Tsuga canadensis*) intercept snowfall and provide refuge from deep snow throughout the winter. Deer wintering complexes (DWCs) have been recognized as essential for overwintering survival in northern regions of the UP, as lower snow depth in DWCs provide greater accessibility to forage and reduces the energetic costs of movement, presumably helping deer escape from predators (Witt et al. 2012). Despite recognition of the critical importance of hemlock and cedar in overwintering of deer in the UP, there is limited understanding of the combinations of environmental variables that drive persistence of these habitats on a broad scale (Witt et al. 2012). Improving deer winter range has been identified as a critical management priority in the Upper Great Lakes area (Michigan Department of Natural Resources 2015), as deer are considered a recreational attraction regionally and serve as the primary prey for a federally listed gray wolf (*Canis lupus*) population. Yet spatially explicit models that identify and describe key winter habitat predictors are currently lacking, in part likely due to limited knowledge about density, movement, and space use.

Predictive habitat modeling involves complicated species-environment relationships which vary spatially and temporally at multiple scales (Turner 2005). For example, seasonal variation in habitat selection may result from shifts in the distribution of available resources, changes in diet preference, or limitations associated with harsh weather conditions (Godvik et al. 2009, Beyer et al. 2013, van Beest et al. 2014b). Scale-dependent spatial responses have been widely observed and are often associated with behavioral patterns. At finer patch scales, foraging behavior might have a strong influence on habitat selection while cover requirements and other necessary conditions might drive selection patterns at broader scales (Anderson et al. 2005, O'Neil and Bump 2014). Spatial heterogeneity in distribution of resources, temporal variation on multiple scales, interspecific interactions, and density dependence all contribute to complex dynamics in habitat use (including habitat selection, e.g. Beyer et al. 2010, McLoughlin et al. 2010). Complex dynamics are often ignored in analysis; at best, habitat models approximate them. Consequently, residual spatial autocorrelation often arises from missing information in spatial studies, which can undermine results (Dormann 2007, Beale et al. 2010).

Predictions of wildlife species distributions that rely exclusively on simple correlations between GIS-based environmental characteristics and animal locations provide limited management value because links to relevant ecological dynamics are often missing (Guisan and Thuiller 2005, Elith and Leathwick 2009, McLoughlin et al.

2010). Methods that focus on ecological process are increasingly identified as analytically robust and realistic (Dormann et al. 2012, Matthiopoulos et al. 2015). Embracing the complexities in habitat use is likely to be more informative and should provide more accurate predictions even when data options are limited.

Our objective was to develop a predictive model to explain white-tailed deer winter occurrence based on interacting habitat predictors at local and regional scales. In doing so, we tested for functional responses in winter habitat use involving a large set of environmental predictors representing food, water and cover availability as well as regional conditions (e.g. topographic variation, human influences, and snow depth). We hypothesized that functional responses would improve predictions of deer winter habitat use in our study area, thereby providing an opportunity to explore deer habitat selection when availability/accessibility of limited habitat is dynamic. In particular, we expected variation in habitat use to depend on regional conditions such as snow depth that vary on a north-to-south gradient (Shi et al. 2006).

## Methods

### *Approach*

We developed a predictive model to explain deer occurrence in winter based on interacting habitat predictors (e.g. functional responses in habitat use) using multiple logistic regression as a base modeling framework and adding structure in the form of local-regional interacting variables and spatial random effects. We compared environmental attributes of areas occupied by deer in the UP during winter; environmental attributes were computed at local and regional spatial scales using GIS.

Starting with a “naïve” fixed-effects model as a baseline, we added fixed-effect interactions, second-order terms, and a spatial random effect to account for residual spatial autocorrelation. As a final step, we merged the local and regional scale models to test for a functional response in habitat selection (local variation in habitat selection conditional on regional habitat availability). We selected the best model based on several fit criteria, and used it to predict winter range. This approach allowed us to make valid comparisons of the relative effects included in the model, by plotting changes in model-predicted deer winter occurrence with associated changes in local-to-regional availability of environmental attributes. Our analytical approach balances complex model structure with available information while avoiding overfitting. The resulting high accuracy winter habitat suitability map can be used to prioritize critical habitat improvement projects.

*Environmental predictors*

We generated 18 environmental predictors using ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA), each expected to influence the probability of a cell on the landscape being deer winter range. Briefly, each predictor was included to represent habitat potential based on one or more of the following requirements: winter cover, browse availability, and conditions (e.g. ability to escape from predators, human influence, and food/cover accessibility). Predictors included hemlock and cedar basal area, hemlock and cedar patch area, and proportions of coniferous and mixed forest as dominant cover types (winter cover); proportion of area with maple or aspen as dominant cover type (browse availability); and average annual winter snow depth, interspersion (density of interface between forage and cover variables), elevation, slope, aspect, topographic roughness, topographic radiation aspect index, stream density, road density, and proportion of developed impervious surface (conditions). Full descriptions of these variables, *a priori* biological reasoning for their inclusion, and data sources are available in Appendix 2A.

To account for how selection of different habitat attributes may vary by spatial scale (Gaillard et al. 2010), we assessed each predictor at 4 spatial scales by specifying radial buffers of 0.5, 1, and 3 km to quantify local habitat (Witt et al. 2012), and 10 km to quantify regional availability of the same attributes. This considers local patch to regional and landscape-scale selection of potential winter habitat. For each variable, we applied a circular moving window that assigned either the neighborhood mean statistic for continuous variables or proportion of landscape statistic for discrete variables at each cell on the landscape (Appendix 2A). We used the ArcPy module for Python 2.7.2 to iterate through each predictor, generating a raster surface for each scale-specific metric. All predictor variables were median-centered prior to model-fitting.

### *Analysis*

The dependent variable in our models was presence/absence of deer during winter, which was generally defined as the time period with > 30 cm of snow depth in areas where deer migrate conditionally. This time period on average occurred from December – April throughout the majority of the study area, although length of season was variable. Deer winter range has been mapped by state biologists as early as the 1930s, with remapping surveys occurring every 10–20 years since. The most recent survey occurred in 2013 (http://www.michigan.gov/dnr/0,4570,7-153-

10363_10856_10905-339639--,00.html). Mapped winter range was largely the same in 2013 as it was during the previous survey (2005). We used these most recent surveys (2005 and 2013) to designate winter range, so that it represented the same time period as that of environmental predictors (i.e. independent variables).

We systematically sampled our study area, placing evenly spaced point locations 2 km apart. At each cell location a 1 or 0 was assigned to indicate whether or not deer were present during surveys in 2005 or 2013. Point locations were then updated with values corresponding to each environmental predictor at each scale of analysis. The binary winter range indicator was the dependent variable $Y_i$ in subsequent logistic regression models, where $Y \sim Bernoulli(p_i)$ and $p_i$ represents the probability of deer occurrence at each cell. We assumed the deer winter range maps represented true presence or absence during an average winter when snow depth exceeded 30 cm, so the predicted response was interpreted as the probability of occurrence during winter (i.e. in discrete geographical space; Aarts et al. 2012). We initially performed independent separate analyses for models with local scale predictors and models with regional scale predictors. Ultimately, we combined local and regional models to test for local effects conditional on regional availabilities. We describe the general model structure for local and regional models next, with more specific considerations and details of the combined model in the following sections. Our analytical approach is summarized in Fig 2.1.

In both local and regional models, we built the matrix of environmental covariates $\mathbf{X}$, with $\mathbf{x}' = x_1, \ldots, x_k$ indexing the list of predictors. We computed Pearson's correlation coefficient $r$ for each pair of predictors, checking for $|r| > 0.7$ (Dormann et al. 2013) and removed one of the two predictors if they were highly correlated. We then proceeded to build logistic regression models incrementally, starting with the simplest form of the model and adding structure (2nd order terms, pairwise interactions, random effects) until the number of parameters became unreasonably large (e.g. a ratio of *n* samples to *k* parameters < 20; Rue et al. 2009), at which point we reduced the model by removing redundant variables (described in following sections and in Fig. 2.1). Our baseline model (M1; Appendix 2B eq. 1) included only the main effects for each predictor, while a second model (M2) included main effects and 2nd order terms (Appendix 2B eq. 2). A third model (M3) included all pairwise interactions between predictors (Appendix 2B eq. 3). To select a best-fitting spatial scale (i.e. radial buffer) for local models, we compared model parsimony with and without each variable by adapting ΔAIC methods from LaForge et al. (2015; see Appendix 2B for details).

We fit each model using the INLA (Integrated Nested Laplace Approximation) package (Rue et al. 2009) in R 3.2.2 (R Core Team 2015). R-INLA provides a highly flexible environment for fitting a large variety of spatial and spatiotemporal models using a Bayesian hierarchical modeling framework (Rue et al. 2009, Blangiardo et al. 2013). This approach is particularly useful because it allows for fitting basic non-spatial models (GLMs or simple regression models) and then extending them with latent effects to model spatiotemporal dependence (Lindgren and Rue 2013, Bivand et al. 2015).

For each model, we measured fit by calculating Pearson's *r* between mean predicted values and observed values, and by computing Watanabe's AIC (WAIC; Watanabe 2013). To assess predictive accuracy, we performed cross-validation using the conditional predictive ordinate (CPO) statistic and reported mean log-CPO$_i$ (LCPO) where lower scores indicate greater predictive accuracy (Beguin et al. 2012). For comparison, we also provided the more broadly-applied Area-Under-Curve (AUC) statistic (Robin et al. 2011). We assessed residual spatial autocorrelation by computing Moran's I (Dale and Fortin 2014) based on observed vs. model-predicted values. We added a spatial random effect to the resulting local and regional models to adjust for spatial dependence that remained unexplained by the covariates. We applied an intrinsic conditional autoregressive (CAR; Besag et al. 1991) spatial model in R-INLA. To avoid overfitting, we fit a series of spatial models, increasing the value of the shape parameter in the logGamma prior until the ratio of observations to effective parameters was ~ 20 (Rue et al. 2009, Beguin et al. 2012; see Appendix 2B for details on R-INLA model structure).

Next, we ranked the effect size of model parameters (i.e. covariates) by computing the absolute value of $\hat{\beta}/SE(\hat{\beta})$ from the marginal posterior density estimates of each predictor. Marginal posterior densities from INLA are normally distributed, so computing the effect size using the mean and standard error results in a Z-value which is often used for hypothesis tests in frequentist statistics. To avoid final models with redundant parameters, we ranked effect sizes and eliminated variables with values < 1.96. Hence, we considered variables unnecessary if their 95% credible intervals contained 0. We refer to the final local and regional models as M4$_{\text{local}}$ and M4$_{\text{regional}}$.

*Combined GFR Model*

We combined predictors from M4$_{\text{local}}$ and M4$_{\text{regional}}$ to test for interactions between local and regional availabilities of forage and cover variables as well as variation in regional conditions. To accomplish this, we started with a CAR model that included all the individual effects and 2nd order terms, and local interactions retained in $M4_{local}$. To model the habitat use functional response, we added interactions between local forage and cover variables and regional availabilities of these variables. We also included interactions with regional conditions. Thus, deer winter occurrence was modeled as a function of all local variables, with the effects of forage and cover allowed to realistically vary depending on actual regional availabilities and conditions (i.e. the GFR, see Appendix 2B; Matthiopoulos et al. 2011, Aarts et al. 2013). Once fitted, we reduced this model using the same methods as previous models, where sets of variables with low effect sizes were sequentially dropped from the model until all remaining interactions and 2nd order terms had Z-values > 1.96.

The final model was referred to as $M4_{GFR}$ and was evaluated using the same goodness-of-fit and accuracy statistics as the local and regional models. We explored functional responses from $M4_{GFR}$ by generating a matrix of local-regional interactions and reporting positive or negative interactions between variables if the 95% credible interval of the effect's marginal posterior did not overlap 0. We present a graphical exploration of functional responses of deer winter habitat dependent on the effects of local hemlock basal area because this species is of particular management interest in the region due to its long-term decline and its importance for deer winter cover. We also predicted winter probability of occurrence based on the best-fitting model of $M4_{local}$, $M4_{regional,}$ and $M4_{GFR}$, with predictions for low, average, and high snow depth years. Median annual snow depth was calculated for 12 winters of daily snow depth data with 1 km spatial resolution (2003 – 2015; National Operational Hydrologic Remote Sensing Center); we computed the 12-year average (mean of medians) and standard deviation at each cell location. Low and high snow depth years were evaluated by subtracting or adding one cell-specific standard deviation from the cell's 12-year mean, thus capturing spatial and temporal variation in snow depth across the UP.

## Results

White-tailed deer winter occurrence was driven largely by reduced snow depth, lower elevations, and cedar forest availability, which reflects the north-to-south migration that occurs in the study area during most winters. However, our models revealed complex spatial dynamics including functional responses that indicate increases in winter habitat selection for many other predictors under certain conditions.

Table 2.1 includes all environmental covariates considered in local, regional, and combined GFR models of winter deer occurrence (further described in Appendix 2A). Covariates in the local model consistently predicted best when quantified using a 3-km radial buffer; the lone exception was average snow depth which produced best fit using the 0.5 km radial buffer. However, the best fit for local models was achieved when all variables were assessed at the same buffer size (Table 2.2). For both local and regional models, incorporating interactions between the availabilities of environmental variables (M3) substantially improved model fit and predictive accuracy when compared to simpler models (M1, M2; Table 2.2). In each case, models were further improved by fitting the CAR model (i.e. spatial random effects to model spatial autocorrelation) and subsequently removing redundant variables based on effect sizes ($M4_{\text{local}}$, $M4_{\text{regional}}$, $M4_{\text{GFR}}$). Results of $M4_{\text{local}}$ and $M4_{\text{regional}}$ thus allowed us to focus on the environmental covariates (measured at two separate scales) with the strongest influence on deer winter occurrence. Including functional response interactions further improved model fit ($M4_{GFR}$), indicating that local predictors varied with differences in their regional availabilities and other regional conditions.

*Local and regional model results*

Drivers of deer winter occurrence included environmental variables that represented winter browse availability, winter cover, and conditions such as elevation and snow depth. The influence of these multiple predictors varied when assessed at local vs. regional scales (Fig. 2.2). We report results from $M4_{local}$ and $M4_{regional}$ independently, allowing for scale-dependent comparisons. Model results for the main effects are reported in the context of all other predictors in the model occurring at their median value, and $\hat{\beta}$ denotes the mean of the marginal posterior density for each predictor (Fig. 2.2). In terms of effect size (change in Y with corresponding change in X; Fig. 2.3), the strongest predictors of winter occurrence at both regional and local scales indicated that probability increased with increasing cedar average basal area ($\hat{\beta}_{\text{Cedar, local model}} = 0.150$, SE = 0.013, Fig. 2.3M) and cedar average patch area ($\hat{\beta}_{\text{CedarPatch, regional model}} = 0.075$, SE = 0.010, Fig. 2.3M), and decreased with increasing snow depth ($\hat{\beta}_{\text{Snow, local model}} = -0.013$, SE = 0.002; $\hat{\beta}_{\text{Snow, regional model}} = -0.018$, SE = 0.003, Fig. 2.3A). Second order terms were supported in local models for average cedar basal area ($\hat{\beta}_{\text{Cedar}^2\text{, local model}} = -6.541e^{-4}$, SE = $2.010e^{-4}$) and average snow depth ($\hat{\beta}_{\text{Snow}^2\text{, local model}} = -3.024e^{-5}$, SE = $1.225e^{-5}$).

Winter occurrence was also negatively associated with greater elevation with a stronger effect at the local scale than regional scale ($\hat{\beta}_{\text{Elevation, local model}}$ = -0.034, SE = 0.003; $\hat{\beta}_{\text{Elevation, regional model}}$ = -0.007, SE = 0.003, Fig. 2.3B), as well as support for a second order term at the local scale ($\hat{\beta}_{\text{Elevation}^2\text{, local model}}$ = 7.159e$^{-5}$, SE = 1.246e$^{-5}$). At the local scale, deer occurrence in winter was also positively related to increasing proportions of the landscape with maple as the dominant forest cover type ($\hat{\beta}_{\text{Maple, local model}}$ = 3.069, SE = 0.568, Fig. 2.3H), proportion of mixed forest cover types ($\hat{\beta}_{\text{Mixed, local model}}$ = 3.442, SE = 1.491, Fig. 2.3I), greater interspersion ($\hat{\beta}_{\text{Interspersion, local model}}$ = 0.174, SE = 0.068, Fig. 2.3D), average percent impervious surface ($\hat{\beta}_{\text{Impervious, local model}}$ = 0.456, SE = 0.180, Fig. 2.3F), and proportion of coniferous forest as dominant cover type ($\hat{\beta}_{\text{Conifer, local model}}$ = 1.767, SE = 0.962, Fig. 2.3G). Notably, although the main effect of average hemlock basal area had a negative sign ($\hat{\beta}_{\text{Hemlock, local model}}$ = -0.050, SE = 0.024), its second order term had a strong positive sign ($\hat{\beta}_{\text{Hemlock}^2\text{, local model}}$ = 2.223e$^{-3}$, SE = 6.541e$^{-4}$). When extrapolated across its available range of values, it was evident that average hemlock basal area had a strong positive influence on deer winter occurrence at values above ~ 25% basal area (Fig. 2.3N). Second order terms were additionally supported at the local scale for maple as dominant cover type ($\hat{\beta}_{\text{Maple}^2\text{, local model}}$ = -8.483, SE = 1.998), interspersion ($\hat{\beta}_{\text{Edge}^2\text{, local model}}$ = -0.030, SE = 0.012), average percent impervious surface ($\hat{\beta}_{\text{Impervious}^2\text{, local model}}$ = -0.163, SE = 0.032), and proportion of coniferous forest as dominant cover type ($\hat{\beta}_{\text{Conifer}^2\text{, local model}}$ = -14.72, SE = 2.793). Posterior densities for other predictors measured at the local scale largely overlapped zero (Appendix 2C). At the regional scale, winter occurrence was positively associated with average stream density ($\hat{\beta}_{\text{Stream, regional model}}$ = 1.273, SE = 0.514; $\hat{\beta}_{\text{Stream}^2\text{, regional model}}$ = -1.317, SE = 0.476, Fig. 2.3E), and negatively associated with slope ($\hat{\beta}_{\text{Slope, regional model}}$ = -1.855, SE = 0.294; $\hat{\beta}_{\text{Slope}^2\text{, regional model}}$ = 0.766, SE = 0.135, Fig. 2.3C), hemlock average patch area ($\hat{\beta}_{\text{HemlockPatch, regional model}}$ = -0.139, SE = 0.021, Fig. 2.3N), average percent impervious surface ($\hat{\beta}_{\text{Impervious, regional model}}$ = -1.245, SE = 0.299, Fig. 2.3F), interspersion ($\hat{\beta}_{\text{Interspersion, regional model}}$ = -0.427, SE = 0.174, Fig. 2.3D), proportion of southern aspects ($\hat{\beta}_{\text{South, regional model}}$ = -4.220, SE = 1.793, Fig. 2.3J), and proportion of coniferous forest as dominant cover type ($\hat{\beta}_{\text{Conifer, regional model}}$ = -4.323, SE = 1.874, Fig. 2.3G). Main effects overlapped zero for average road density, proportion of landscape with aspen or maple as dominant cover types, topographic radiation aspect index, and landscape surface roughness (Fig. 2.2). However, 2nd order terms were supported for each of these predictors (Appendix 2D). Posterior marginal densities for all predictors and interactions included in $\text{M4}_{\text{local}}$ and $\text{M4}_{\text{regional}}$ are reported in the Appendices (2C-E).

*Combined GFR model results*

Functional response interactions were revealed by $\text{M4}_{\text{GFR}}$, which was also the best fit to the data given the models considered (Table 2.2). Once redundant variables were eliminated the final combined model ($\text{M4}_{\text{GFR}}$) included 24 parameters representing functional response interactions between local and regional variables (Table 2.2, Table 2.3). Table 2.3 shows the local-regional interactions considered in matrix form, with rows representing local effects and columns representing regional effects. The intersection in the matrix between the local and regional variable indicates the interaction effect. Positive and negative signs indicate interactions with Z-values > 1.96; otherwise, the effect was dropped from the model. Of 65 functional response interactions considered, 24 were retained. Most commonly, interactions involved regional conditions (Average Snow Depth, Slope, Topographic Radiation Aspect Index) and cover variables (Cedar and Hemlock local and regional availabilities), with evidence for changes in the effects of forage (% Mixed Forest, Aspen-Dominant Forest, Maple-Dominant Forest) and cover variables (local Hemlock and Cedar) depending on regional conditions and cover (regional Hemlock and Cedar).

Functional response interactions involving the effect of average percent hemlock basal area at the local scale conditional on regional availabilities of other predictors are shown graphically to demonstrate the functional response (Fig. 2.4). The effect of local hemlock basal area varied depending on regional availabilities of forage (Maple-Dominant Forest), regional availabilities of other quality cover (i.e. Area Cedar Forest), and regional conditions (Snow Depth, Interspersion, Topographic Radiation Aspect Index). These effects are plotted in log-odds of use for ease of interpretation (Fig. 2.4). We discuss this example and its implications below.

## Discussion

The strongest predictors of deer winter occurrence at both local and regional scales included cedar forest (i.e. average cedar basal area and average cedar patch area), as its effect resulted in a nearly 100% increase in probability of occurrence from lower availability percentiles for cedar forest to upper availability percentiles. Elevation (-), hemlock basal area (+), and snow depth (-) also had strong local effects while snow depth (-) and slope (-) had strong regional effects. Although the effects of other predictors were comparatively small in this context, their influences were conditionally dependent on other predictors. For example, consider that the median value for average snow depth within the study area was approximately 36 cm. Also, the median value for % basal area cedar was approximately 9% while the median average patch area of cedar was 17 km$^2$. Referring to Fig. 2.3 and locating the predicted probability value corresponding to these medians on the Y-axes (Figs. 2.3A, 2.3M), the probability of winter occurrence under such conditions was only ~ 10%. Thus, any additional effects would be limited by the strong influences of snow and cedar. Plotting predicted effects of environmental characteristics across their range of availability (Fig. 2.3) was key to this understanding (i.e. reporting main effects alone can be misleading). Under different conditions (e.g. lower snow depth and/or greater cedar basal area), other predictors could have greater influences. Understanding local effects in the context of regional conditions is a therefore a primary motivation for modeling the functional response in habitat selection.

We modeled environmental predictors of forage and cover conditional on their regional availabilities, as well as other regional conditions such as snow depth, elevation, slopes, and stream densities among others. Including functional response interactions improved model accuracy and fit when compared to models without functional responses ($M4_{local}$ and $M4_{regional;}$ Table 2.2), suggesting that local-regional interactions were relevant predictors of deer winter occurrence. For example, results from $M4_{GFR}$ indicated that the positive effect of high quality cover variables such as hemlock and cedar basal area increased as regional average snow depth increased, while the effect of lower quality cover or potential forage variables (% mixed forest dominant, % aspen dominant) decreased as snow depth increased (Table 2.3). Additional functional response interactions involved regional conditions such as elevation, slope, topographic radiation index, stream densities, proportion of impervious surfaces, and interspersion (Table 2.3).

We demonstrated functional response interactions graphically in Fig. 2.4. Local hemlock basal area varied from 0% to approximately 60% and had a positive influence on deer winter occurrence on average (e.g. bold line in the middle of each plot), with log-odds increasing from 0 to 4.25 across this range. Converting to odds ratios indicates that a location with 60% average local basal area is exp(4.25) ≈ 70 times more likely to support deer winter occurrence than a location without hemlock. Fig. 2.4 shows this effect is conditional on other predictors. The change in log-odds across the same range increases to +7.65 for areas with greater regional interspersion between deciduous and coniferous forests (~ 4 km/km$^2$; 75th percentile, Fig. 2.4A), and +6.17 for areas with greater regional snow depth (~ 42 cm; 75th percentile, Fig. 2.4B). Comparatively, the effect of local hemlock basal area declines with greater proportions of maple or cedar dominant forest (Fig. 2.4C, Fig. 2.4D), which suggests either conditional selection of these alternative features and/or a response to hemlock being less available under the same conditions (e.g. less likely for >50% basal area hemlock to occur where forest is dominated by other species). Interactions can be explored in similar fashion for any set of predictors, and have potential to provide valuable insight when wildlife habitat management projects require spatially explicit decision tools. In our example not all hemlock stands were frequently used by deer (Witt et al. 2012), but promoting hemlock regeneration may be needed to increase winter habitat potential. Consequently, our analysis can be used to determine the conditions under which deer select hemlock, and thus indicate where habitat modifications can be effective and optimized.

Including functional responses in habitat models also offers a framework for exploring the potential effects of dynamic conditions on predicted habitat suitability. For example, if winter habitat potential is arbitrarily defined as > 25% probability of winter occurrence, our model ($M4_{GFR}$) predicted approximately 11,326 $km^2$ of winter habitat, covering 30% of the study area considered (37,374 $km^2$; Fig. 2.5B). The remainder of the UP (i.e. southern regions) is generally considered annual deer winter range, as snow depth rarely exceeds 30 cm. During a mild winter with snow depth roughly one SD below average, the area of this predicted habitat increases to 18,228 $km^2$ (49% of study area, Fig. 2.5C). However, given a severe winter with snow depth one SD above average, predicted winter habitat decreases to 4,887 $km^2$, only 13% of the study area (Fig. 2.5A). Assuming the remainder of the UP (≈ 5,236 additional $km^2$) comprises winter habitat regardless of winter conditions, our model predicts that a severe winter would limit deer winter habitat potential to < 24% of the entire UP (Fig. 2.5A).

Large ungulates interact with their environment in complex ways. Ungulates are widely regarded as habitat generalists, meaning that habitat selection patterns can be variable and difficult to predict. For example, specialist behavior may be observed at low densities (e.g. stronger selection of high quality habitats) but habitat selection may be weaker at high densities, reflecting more generalist behavior (van Beest et al. 2015). Identifying functionally relevant predictors in any situation is key to fitting models that offer ecological insight and are subsequently more suitable for extrapolation (Elith and Leathwick 2009). We found evidence that including functional responses in habitat selection models is promising in this regard. Functional responses in habitat use recognize that the relationship between the environment and the animal depends on the relative availability of specific habitat attributes such as food and cover, implying a trade-off situation where high quality forage and cover habitats do not necessarily occur in the same geographic location (Mysterud and Ims 1998). In this situation, an animal might only select high quality forage *given* that cover habitat is also accessible nearby (Massé and Côté 2009). These responses have been increasingly observed in ungulates. Early findings indicated that lifetime reproductive success in red deer (*Cervus elaphus*) was not always maximized by selecting the highest quality grasslands; instead, when red deer were highly abundant they selected lower quality forage on average to avoid negative impacts of competition (McLoughlin et al. 2006). Similar findings have been reported for elk and moose (*Alces alces*) in other systems, especially when density-dependent habitat selection and competition between sympatric species is relevant (van Beest et al. 2014a, van Beest et al. 2015).

When managing a population, identifying predictors of species distribution may only be sufficient when stakeholders can address questions such as "which habitat components are most limiting under what conditions?" Consideration of functional responses in habitat selection is crucial for developing powerful habitat models and answering these questions. In our system, results confirm that winter habitat is driven largely by elevation, snow depth, and winter cover (cedar and hemlock forest) on the local scale. However, regional conditions play an important role in determining use of important forage and cover habitat indicators such as the local availability of maple, aspen, and mixed forest. Our predictive models help to reveal sets of conditions that vary in importance with spatial scale and also interact with each other to influence the realized ecological niche.

Despite a rigorous and robust modeling procedure, future advancements may be made by improving the spatial and temporal scales at which deer winter occurrence has historically been measured. Surveys of winter deer habitat use in the UP rely heavily on researchers' ability to detect deer sign while driving roads; this is an effective method because deer tracks and browse sign are easy to detect when snow cover exists. However, confidence in less accessible areas away from roads is lower, in some cases requiring assumptions based on contiguity of habitat type. Our observations are thus most relevant at a coarse scale, whereas inference about local patch/stand scale (i.e., < 0.5 km) habitat selection or diet preferences would require more detailed research (e.g., a GPS-collar project). Since surveys are not carried out each year, our predictions of habitat potential during years with lower or greater snow depth than average will benefit from continued evaluation. We also emphasize that habitat quality may be related to deer density or probability of use, but only when certain conditions are met (Van Horne 1983). We caution against conclusions that model-predicted probabilities of deer occurrence are highly correlated with fitness-based habitat quality, especially at fine scales. Key predictors in our model such as cedar basal area and snow depth represent major limiting factors for deer landscape use in winter, but without measuring doe overwintering survival and/or reproductive success (e.g. Gaillard et al. 2010) it is not possible to speculate on fitness benefits incurred at different deer winter habitat locations. Nonetheless, given known limitations about the spatial extent of winter range along with winter's potential constraint on variation in annual growth rates in ungulates, gathering fitness-based data would conceivably require less effort since it could be focused on smaller areas which support the majority of the population.

## Management Implications

In the UP of Michigan, heavy snowfall during winter is the primary condition limiting winter habitat to < 25% of summer range for white-tailed deer. Functional responses in habitat use revealed a landscape where habitat potential became progressively patchy as snow depth increased (Fig. 2.5). Deer increasingly rely on the availability of dense conifer (cedar and hemlock) when snow depth is greatest, but utilize areas with greater browse availability (aspen, maple, and mixed forest types) when snow depth is less limiting or when high quality cover is available (Table 2.3, Appendix 2C-E). Limitations associated with winter severity may contribute to boom-bust population cycles associated with the UP deer herd; harsh winters such as those of 2012-2013 and 2013-2014 contribute to die-offs that may reduce the population by as much as 50%. In contrast, these populations are often able to rebound quickly when winters are short and mild and high quality forage is abundant. Our results are consistent with previous findings that have acknowledged a trade-off in habitat use depending on variation in winter severity as well as configuration of surrounding habitat (Morrison et al. 2003, Jensen et al. 2011, Witt et al. 2012). However, to our knowledge this analysis is the first to explicitly model functional responses to availability of multiple environmental features representing conditions, forage, and cover based on long-term winter observations of deer winter range. Overall, “naïve” winter habitat use models that only represented simple relationships between environmental predictors and deer occurrence were not accurate or realistic for assessment of winter distribution of deer in Michigan’s UP. Modeling functional responses in habitat use and fitting models with spatial effects resulted in models that were better fits to the occurrence data and predicted distribution with greater accuracy and ecological realism. Modeling functional responses in habitat selection can help to reveal the context for selection of important attributes. These models are useful decision tools because they can make predictions under a wider and dynamic range of conditions, thus informing spatial prioritization of habitat improvement projects.

Table 2.1. Variables considered in local, regional, and functional response habitat selection models of deer winter occurrence in the Upper Peninsula of Michigan, USA.

| Variable | Description | Source Data | Source |
|---|---|---|---|
| Snow Depth | Average snow depth (mm) during winters of 2003–2014 | Continuous | Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center 2004) |
| Hemlock Basal | Average % basal area hemlock within moving window | Continuous | USFS National Risk Map (Ellenwood and Krist 2007) |
| Cedar Basal | Average % basal area cedar within moving window | Continuous | USFS National Risk Map (Ellenwood and Krist 2007) |
| Hemlock Patch Area | Area (km$^2$) of hemlock-dominated cover types within moving window | Continuous | USFS National Risk Map (Ellenwood and Krist 2007) |
| Cedar Patch Area | Area (km$^2$) of cedar-dominated cover types within moving window | Continuous | USFS National Risk Map (Ellenwood and Krist 2007) |
| Coniferous | % of coniferous-dominant forest land cover types within moving window | Discrete | USFS National Risk Map (Ellenwood and Krist 2007) |
| Elevation | Average elevation (m) within moving window | Continuous | USGS 30m Digital Elevation Model (DEM; http://nationalmap.gov/index.html) |
| Slope | Average degrees | Continuous | USGS 30m DEM |

| | | | |
|---|---|---|---|
| | slope within moving window | | |
| Roughness | Average terrain ruggedness index within moving window | Continuous | USGS 30m DEM; ArcGIS Geomorphometry and Gradient Metrics (Evans et al. 2014) |
| Southern Aspect | % of landscape with south-facing slopes (1/0) | Discrete | USGS 30m DEM |
| Topographic Radiation Aspect Index | Average TRAI value within moving window | Continuous | USGS 30m DEM; ArcGIS Geomorphometry and Gradient Metrics (Evans et al. 2014) |
| Maple | % of Maple dominant vegetation within moving window | Discrete | USFS National Risk Map (Ellenwood and Krist 2007) |
| Aspen | % of Aspen dominant vegetation within moving window | Discrete | USFS National Risk Map (Ellenwood and Krist 2007) |
| Mixed Forest | % of mixed forest land cover types within moving window | Discrete | Michigan Gap Analysis Project (Donovan et al. 2004) |
| Interspersion | Average density (km/km$^2$) of hard edge between coniferous and deciduous land cover types | Continuous | Michigan Gap Analysis Project (Donovan et al. 2004) |
| Road Density | % of mixed forest land cover | Discrete | US Census Bureau TIGER/Line (https://www.census.gov/geo/maps |

| | | | |
|---|---|---|---|
| | types within moving window | | -data/data/tiger-line.html) |
| Developed | Average % impervious surfaces within moving window | Continuous | National Land Cover Database (Xian et al. 2011) |
| Stream Density | Average density (km/km$^2$) of streams or rivers within moving window | Continuous | US Census Bureau TIGER/Line (https://www.census.gov/geo/maps-data/data/tiger-line.html) |

Table 2.2. Summary of fit statistics (Pearson's *r* of fitted vs. model-predicted values [*r*], Watanabe's AIC [WAIC], Log- conditional predictive ordinate statistic [LCPO], Area-Under-Curve statistic [AUC]) from models of winter deer occurrence in Michigan's Upper Peninsula, USA. Model formulations included at minimum "naïve" main effects (M1), main effects and 2nd order terms for non-linear response curves associated with predictors (M2), main effects, 2nd order terms, and all pairwise interactions between main effects (M3), and main effects, 2nd order terms, and all pairwise interactions between main effects plus a spatial random effect (Conditional Autoregressive [CAR]; M4). Local models were fitted at multiple spatial scales and $\mathrm{M4}_{\mathrm{GFR}}$ included interactions between local forage and cover variables and regional forage, cover, and conditions variables.

| Model | Buffer (km) | *r* | WAIC | LCPO | AUC | *k* predictors |
|---|---|---|---|---|---|---|
| $\mathrm{M1}_{\text{local 1}}$ | 0.5 | 0.451 | 8251 | 0.441 | 0.781 | 17 |
| $\mathrm{M1}_{\text{local 2}}$ | 1.0 | 0.469 | 8092 | 0.432 | 0.791 | 17 |
| $\mathrm{M1}_{\text{local 3}}$ | 3.0 | 0.483 | 7946 | 0.424 | 0.800 | 17 |
| $\mathrm{M1}_{\text{multiscale}}$ | 0.5, 1.0, 3.0 | 0.474 | 8037 | 0.429 | 0.793 | 17 |
| $\mathrm{M2}_{\text{local 1}}$ | 0.5 | 0.470 | 8105 | 0.433 | 0.796 | 33 |
| $\mathrm{M2}_{\text{local 2}}$ | 1.0 | 0.491 | 7908 | 0.425 | 0.808 | 33 |
| $\mathrm{M2}_{\text{local 3}}$ | 3.0 | 0.514 | 7686 | 0.411 | 0.820 | 33 |
| $\mathrm{M2}_{\text{multiscale}}$ | 0.5, 1.0, 3.0 | 0.508 | 7752 | 0.415 | 0.816 | 33 |
| $\mathrm{M3}_{\text{scale 1}}$ | 0.5 | 0.522 | 7850 | 0.424 | 0.829 | 153 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $M3_{\text{scale 2}}$ | 1.0 | 0.551 | 7537 | 0.408 | 0.847 | 153 |
| $M3_{\text{scale 3}}$ | 3.0 | 0.621 | 6675 | 0.357 | 0.886 | 153 |
| $M3_{\text{multiscale}}$ | 0.5, 1.0, 3.0 | 0.616 | 6735 | 0.360 | 0.884 | 153 |
| **$M4_{\text{local (CAR)}}$** | **3.0** | **0.861** | **4253** | **0.228** | **0.985** | **45** |
| $M1_{\text{regional}}$ | 10.0 | 0.449 | 8227 | 0.439 | 0.775 | 17 |
| $M2_{\text{regional}}$ | 10.0 | 0.516 | 7600 | 0.406 | 0.831 | 33 |
| $M3_{\text{regional}}$ | 10.0 | 0.691 | 5728 | 0.306 | 0.921 | 153 |
| **$M4_{\text{regional (CAR)}}$** | **10.0** | **0.838** | **4551** | **0.244** | **0.979** | **47** |
| **$M4_{\text{GFR (CAR)}}$** | **3.0, 10.0** | **0.870** | **3982** | **0.214** | **0.986** | **63** |

Table 2.3. Matrix of local-regional interactions retained in a generalized functional response (GFR) deer winter habitat model ($M4_{GFR}$), where indicators of forage and cover availability measured at the local scale (3 km radial buffer; rows) were modeled conditional on regional predictors of forage, cover, and other conditions (10 km radial buffer, columns). Signs indicate whether or not each local-regional interaction was retained in the final model fit and whether the local predictor's influence increased (+), decreased (-), or stayed the same when values of regional predictors increased; regional effects of % Mixed Forest and Road Density are omitted from the table because 95% credible intervals for their interactions and main effects overlapped zero.

Regional Scale Effect

| | | | Maple | Aspen | Mixed | Cedar | Hemlock |
|---|---|---|---|---|---|---|---|
| | | | + | | + | + | + |
| Local Scale Effect | Maple | + | - | + | | | + |
| | Aspen | | + | | | | |
| | Cedar | + | | - | | - | - |
| | Hemlock | - | + | + | | | |
| | Snow | - | | - | - | + | + |
| | Elevation | + | + | | | | |
| | Slope | - | - | - | + | - | |
| | TRAI | + | - | | | - | - |
| | Stream | | - | | | + | |
| | Impervious | - | | | - | | |
| | Interspersion | - | | | | | + |

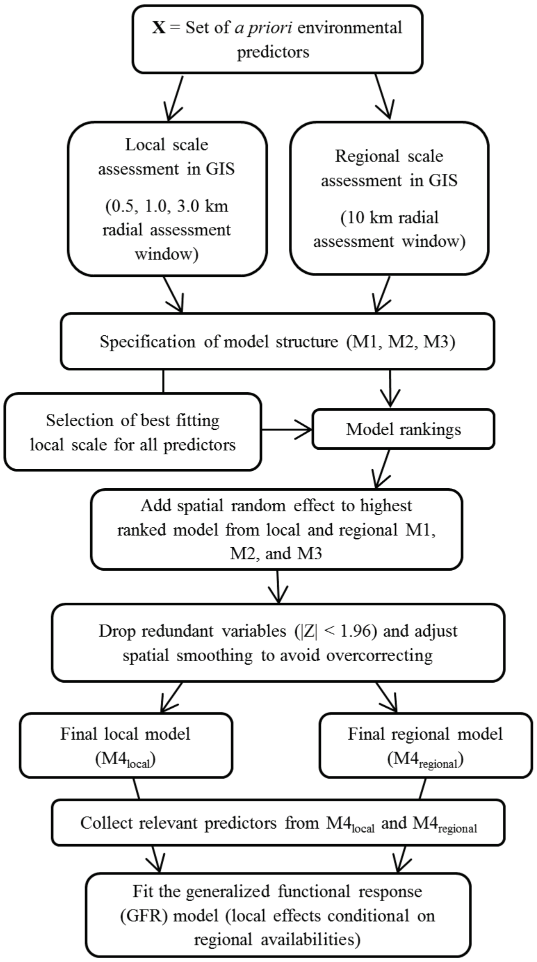

Figure 2.1. Flow diagram describing the model building process for fitting habitat use functional response models to white-tailed deer winter occurrence data in the Upper Peninsula of Michigan, USA. This process included fitting models at local and regional scales separately, with model structures for main effects only (M1), main effects and 2nd order terms (M2), and all pairwise interactions (M3); the generalized functional response ($M4_{GFR}$) involved fitting models with local effects conditional on regional availabilities.

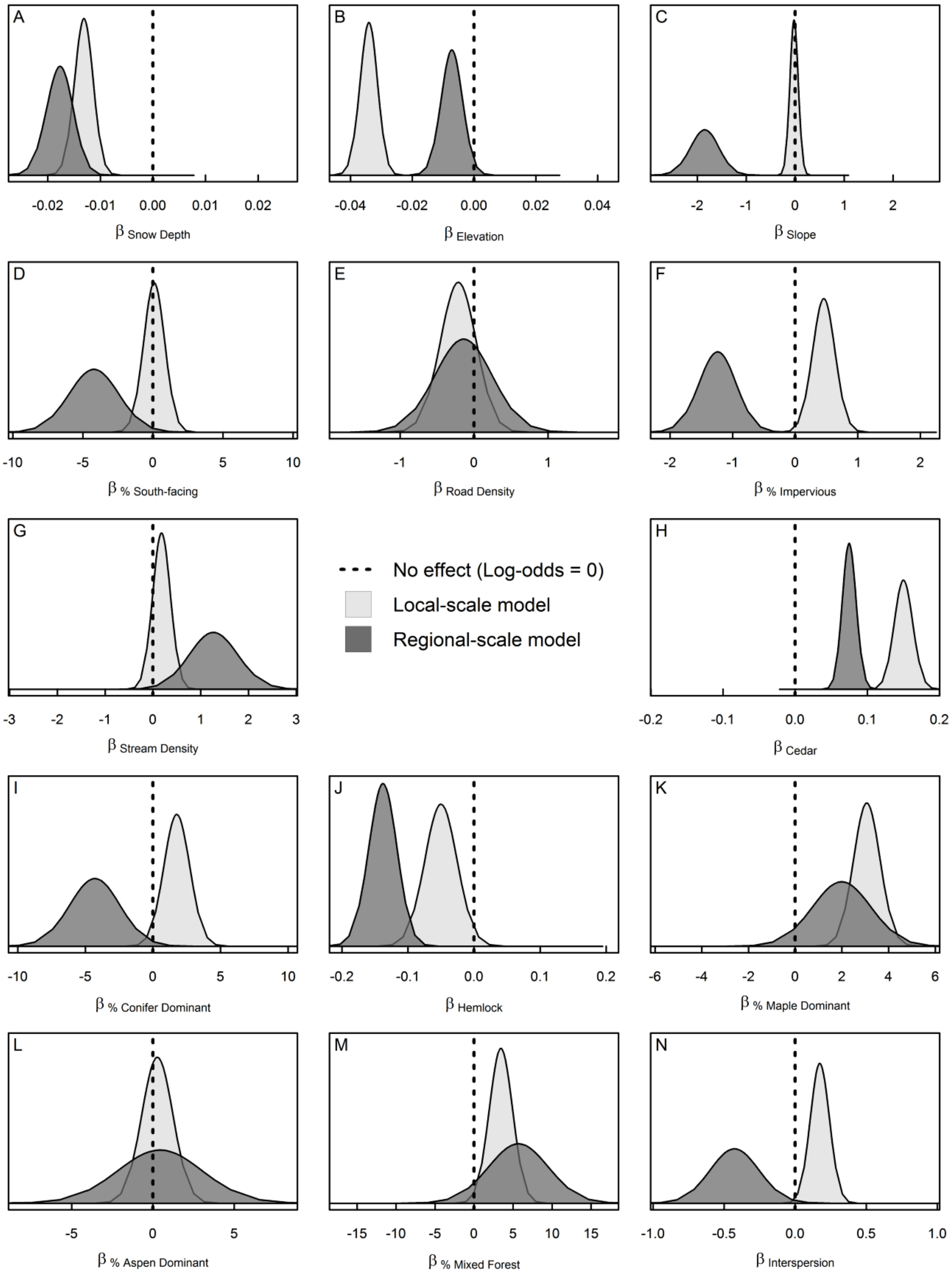
A
-0.02
-0.01
0.00
0.01
0.02
β Snow Depth
B
-0.04
-0.02
0.00
0.02
0.04
β Elevation
C
-2
-1
0
1
2
β Slope
D
-10
-5
0
5
10
β % South-facing
E
-1
0
1
β Road Density
F
-2
-1
0
1
2
β % Impervious
G
-3
-2
-1
0
1
2
3
β Stream Density
No effect (Log-odds = 0)
Local-scale model
Regional-scale model
H
-0.2
-0.1
0.0
0.1
0.2
β Cedar
I
-10
-5
0
5
10
β % Conifer Dominant
J
-0.2
-0.1
0.0
0.1
0.2
β Hemlock
K
-6
-4
-2
0
2
4
6
β % Maple Dominant
L
-5
0
5
β % Aspen Dominant
M
-15
-10
-5
0
5
10
15
β % Mixed Forest
N
-1.0
-0.5
0.0
0.5
1.0
β Interspersion

Figure 2.2. Posterior marginal density distributions of environmental predictors from the best local and regional models (predictors measured using 3 and 10 km radial buffers, respectively) of white-tailed deer winter occurrence in the Upper Peninsula, Michigan, USA. Effects of the topographic Roughness and Radiation Aspect Index are not shown because their main effects were not relevant predictors at either model scale.

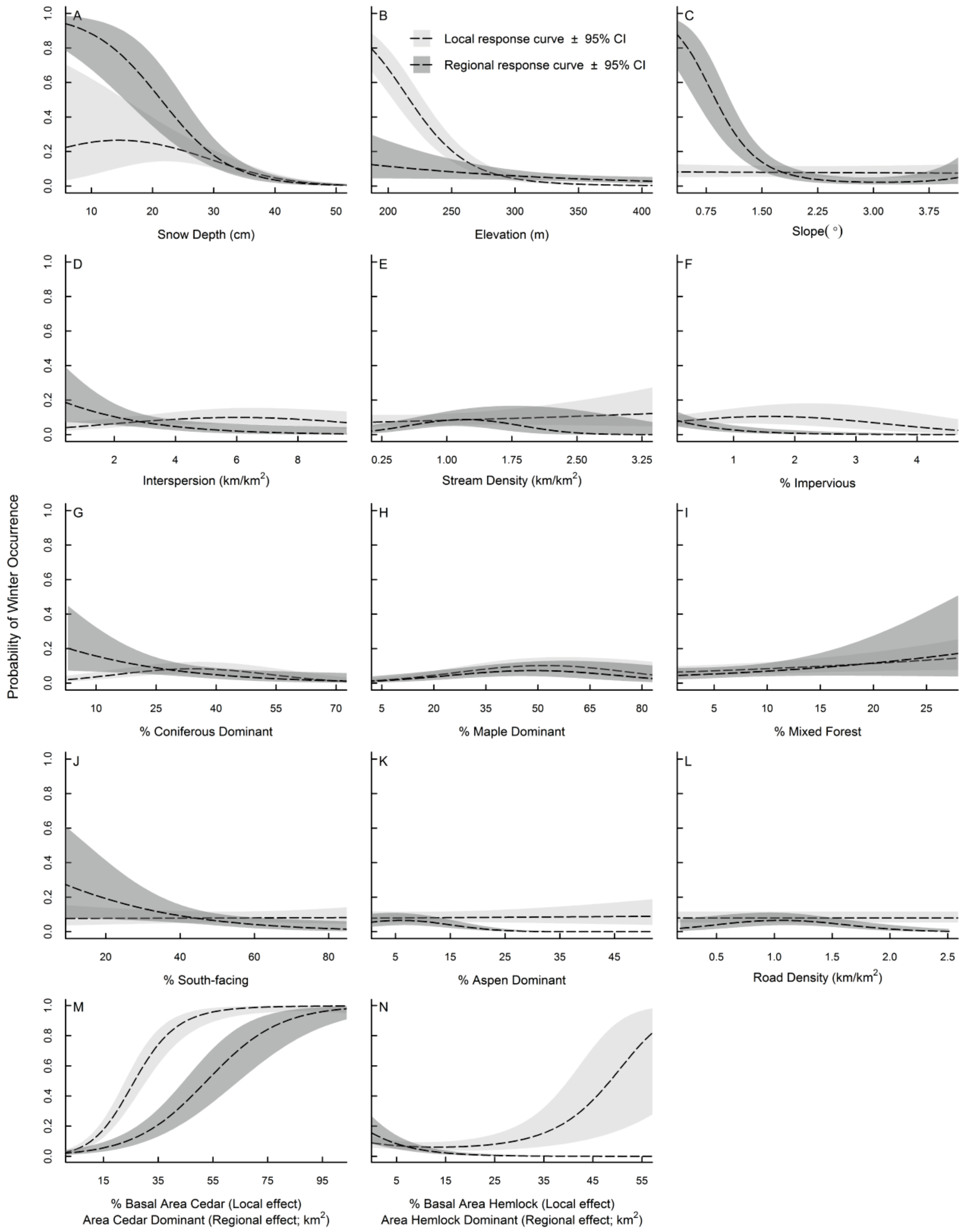
Probability of Winter Occurrence
0.0
0.2
0.4
0.6
0.8
1.0
A
B
C
D
E
F
G
H
I
J
K
L
M
N
Local response curve ± 95% CI
Regional response curve ± 95% CI
10 20 30 40 50
Snow Depth (cm)
200 250 300 350 400
Elevation (m)
0.75 1.50 2.25 3.00 3.75
Slope( °)
2 4 6 8
Interspersion (km/km$^2$)
0.25 1.00 1.75 2.50 3.25
Stream Density (km/km$^2$)
1 2 3 4
% Impervious
10 25 40 55 70
% Coniferous Dominant
5 20 35 50 65 80
% Maple Dominant
5 10 15 20 25
% Mixed Forest
20 40 60 80
% South-facing
5 15 25 35 45
% Aspen Dominant
0.5 1.0 1.5 2.0 2.5
Road Density (km/km$^2$)
15 35 55 75 95
% Basal Area Cedar (Local effect)
Area Cedar Dominant (Regional effect; km$^2$)
5 15 25 35 45 55
% Basal Area Hemlock (Local effect)
Area Hemlock Dominant (Regional effect; km$^2$)

Figure 2.3. Predicted change in the probability of deer winter occurrence with corresponding changes in local and regional availabilities of environmental predictors (measured using 3 and 10 km radial buffers, respectively). Response curves ± 95% credible intervals for each predictor are based on setting all other variables equal to their median values and allowing one predictor to vary across its range of values on the study site, the Upper Peninsula of Michigan, USA. Effects of the topographic Roughness and Radiation Aspect Index are not shown because their main effects were not relevant predictors in either model.

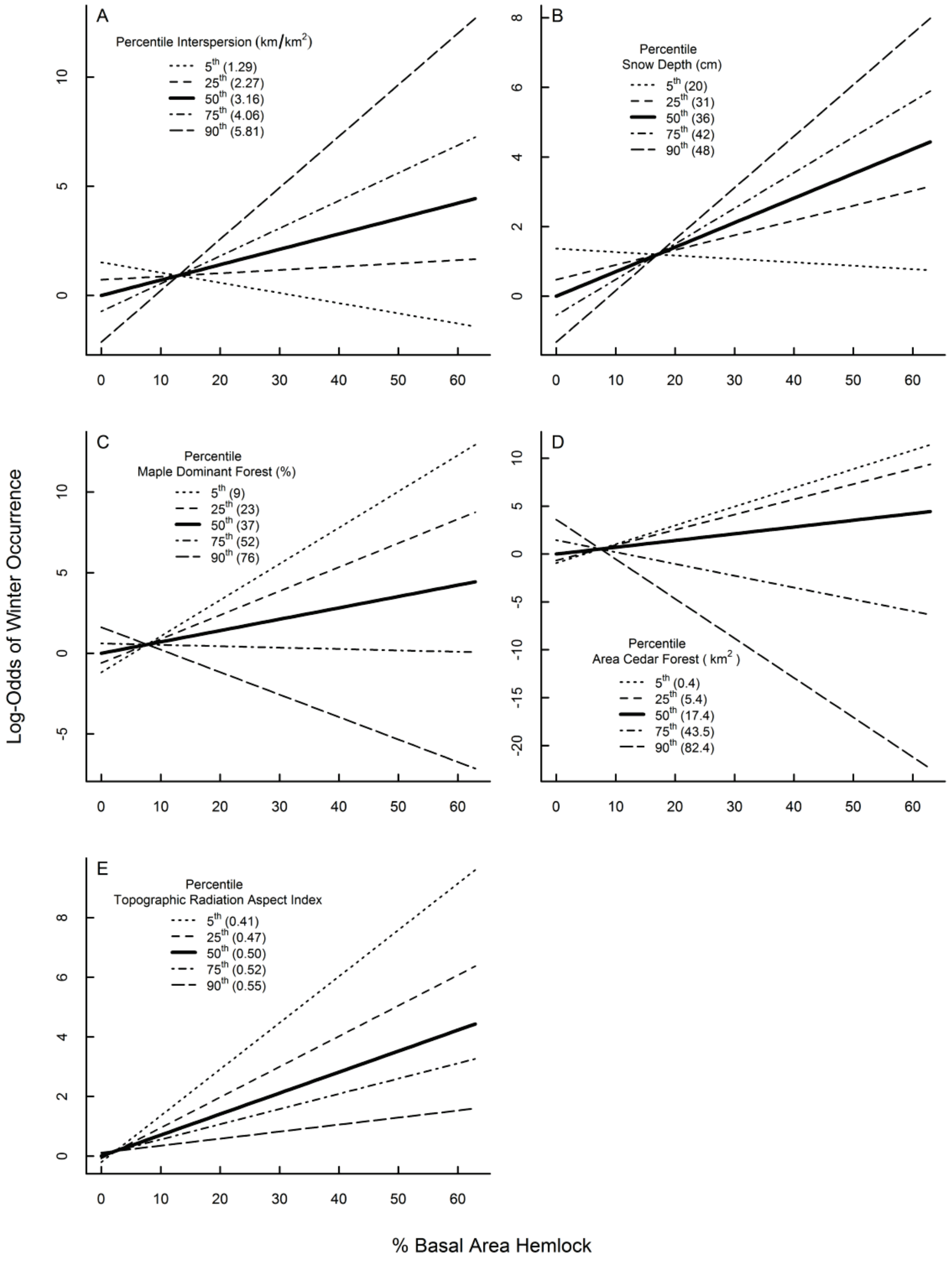

Figure 2.4. Example of the functional response in habitat selection during winter, where deer selection of greater % hemlock basal area (e.g. log-odds of winter occurrence) varies depending on regional availabilities of density of deciduous-coniferous forest

edge (i.e. interspersion), average snow depth, % maple dominant forest, patch area of cedar-dominant forest, and topographic radiation index.

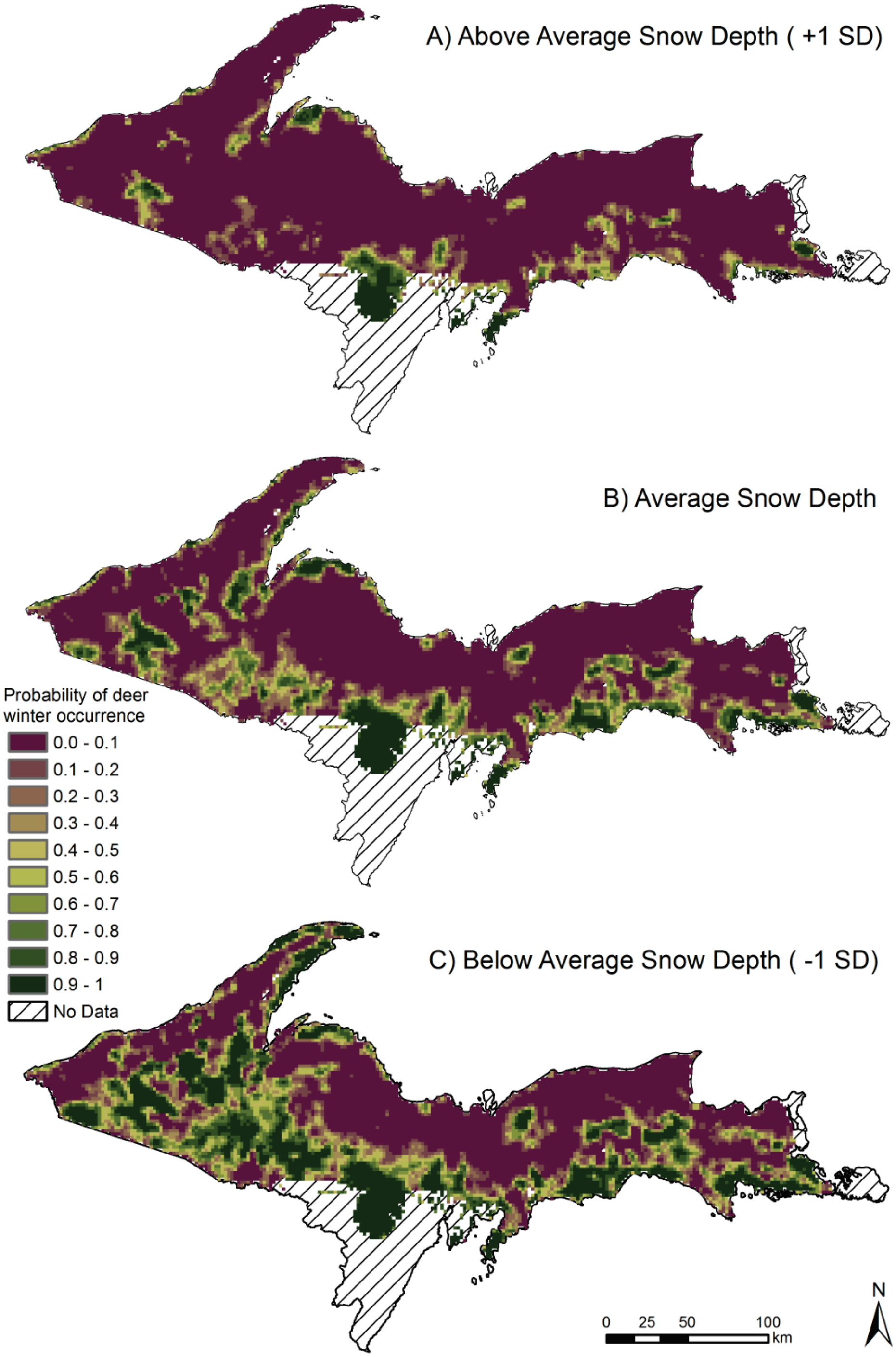

Figure 2.5. Predicted probability of deer winter occurrence in the Upper Peninsula of Michigan, USA based on A) above-average snow depth conditions, B) average snow depth conditions, and C) below-average snow depth conditions.

## Appendix 2A. Environmental predictors of winter deer occurrence

Environmental predictors were chosen to represent habitat potential based on food (browse availability), cover, and regional conditions. We summarize these below and include a reference table for quick access.

***Food variables representing winter browse potential***

1. Proportion of **maple forest** as dominant cover type: Early successional maple species (primarily *Acer saccharum, Acer rubrum)* are a major food source for deer in winter. Understory maple buds and stems are often heavily browsed but offer a consistent food source due to the species' ability to tolerate herbivory (Witt and Webster 2010, Jensen et al. 2011). Quantifying maple forest at the landscape level serves as an index for the availability of these food items, as understory measurements were not possible.
2. Proportion of **aspen forest** (*Populus grandidentata, Populus tremula*) as dominant cover type: Aspen forest, especially early successional vegetation, offers a year-round food source for deer which may be particularly important at the end of the winter season (McCaffery et al. 1974, Doepker et al. 1994, Van Deelen et al. 1996).

***Cover variables representing snow depth reduction potential and associated access to understory vegetation for foraging***

3. **Hemlock** basal and patch area: Hemlock is a known key component of winter habitat for deer, especially in the northern regions of Michigan's UP where snowfall commonly exceeds 400 cm (Witt and Webster 2010, Jensen et al. 2011, Witt et al. 2012). Hemlock provides high quality cover and potential browse, although hemlock regeneration may be suppressed by high deer use (Murray et al. 2013). We measured hemlock basal area at the local scale and the total patch area of hemlock dominant forest at the regional scale (see Table 2A.1).

4-5. **Cedar** basal and patch area: Northern white cedar swamps are heavily favored by deer in winter; cedar availability is more broadly distributed in the more southern regions of our study area. Cedar provides cover and food availability. Deer often migrate large distances (north-to south) to cedar swamp complexes during winter (Doepker et al. 1994, Van Deelen et al. 1998, Shi et al. 2006).

6-7. Proportion of **coniferous forest** as dominant cover type: Deer will use other coniferous forest types for winter cover to some extent; other cover types are generally less favored than hemlock and cedar but species such as white pine (*Pinus strobus*) may be a preferred food source when available (Doepker et al. 1994, Van Deelen et al. 1998, Shi et al. 2006). This variable includes all coniferous species present in the UP of Michigan: balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), eastern hemlock (*Tsuga canadensis*), tamarack (*Larix laricina*), white pine, and red pine (*Pinus resinosa*).

8. Proportion of **mixed forest** as dominant cover type: This cover type includes components of quality cover and quality winter browse mentioned above, and thus may be an important winter habitat type under moderate conditions. Mixed forest may occur near transition zones, may be important corridor features (for movement between dense conifer stands), and may represent finer-scale interspersion than could be measured at our scales of analysis.

***Conditions variables representing factors that either limit or promote access to winter habitat components***

9. Average **snow depth**: Snow depth is perhaps the primary limiting factor for deer winter habitat (Doepker et al. 1994, Shi et al. 2006, Witt et al. 2012); duration of snow depth > 30 cm also may influence the ability of deer to survive winter. Deep snow reduces mobility, increases energetic costs associated with movement, and limits access to important food resources.
10. **Elevation**: Greater snowfall occurs at higher elevations and important winter cover tree species are more common at lower elevations and along river bottoms. Lower elevation has previously been linked to deer use of hemlock stands (Witt et al. 2012).
11. **Slope**: Greater slopes impede movement and often occur at higher elevations which are presumed to be a limiting condition. However, slopes are sometimes associated with river valleys characterized by greater cedar and hemlock abundance and the availability of water sources; areas with greater slopes may be

avoided by deer under some circumstances but selected under other circumstances.

12. **Roughness**: This predictor represents the ruggedness of terrain. More rugged terrain may be avoided by deer, especially in areas with greater snow depths. Rugged terrain may impede movement; deer may be more vulnerable to predation in these “terrain traps.”
13. **Southern aspects**: South-facing slopes may represent a shorter winter season and/or lower snow depths. See explanation of the Topographic Radiation Aspect Index.
14. **Topographic Radiation Aspect Index** (TRASP): This variable combines slope and aspect to indicate the amount of solar radiation received at a location on the landscape (Roberts and Cooper 1989). Areas with greater TRASP values may provide greater access to food resources and may result in lower snow depths; alternatively, greater TRASP values may contribute to greater incidence of crust layers in deep snow, which may increase deer vulnerability to predators such as wolves (*Canis lupus*; Telfer and Kelsall 1984, Nelson and Mech 1986, Vucetich et al. 2012).
15. **Interspersion** (density of coniferous-deciduous forest edge): Similar to the mixed cover variable, interspersion represents juxtaposition of high quality winter cover and high quality winter forage. Low values of interspersion indicate a more homogeneous landscape, whereas high values represent structure and

complexity that is likely to provide more of the necessary components of winter habitat (Witt et al. 2012).

16. **Stream density**: Streams can be an important water source in winter. When many other water bodies are frozen, sections and pockets of faster moving water stay open year round. Stream networks often coincide with cedar swamp habitat, thus providing corridors between habitat patches. Deer can also browse on cedar branches that overhang stream and creek banks.
17. **Road density**: Plowed roads allow deer to move between habitat patches more easily; intermediate road densities may also indicate additional food sources associated with small residential or rural communities, including supplemental feeding sites (legal by permit in the UP, https://www.michigan.gov/dnr/0,4570,7-153-10366_37141_37705-250066--,00.html) and food plots (i.e. standing crops). Many of the roads in the UP are forest roads, which are associated with logging; road densities thus may also indicate to some extent the potential for food stemming from recent cuts.
18. Percent developed **impervious surface**: Human population density is relatively low throughout the UP. Impervious surfaces are an index for human development; deer likely avoid the highest values but there are very few cities in the study area. Thus, similar to road densities, intermediate proportions of impervious surface may indicate potential for supplemental food and temporary cover. These areas might also serve as refuge from predators, because wolves

generally avoid greater road densities and impervious surfaces in our study area (Potvin et al. 2005, Stenglein 2014).

## Appendix 2B. Detailed methods and formulas

### ***Models M1, M2, and M3 for local-scale models (0.5, 1, or 3 km radial buffer) and regional-scale models (10 km radial buffer)***

In generalized linear model notation, our baseline model (M1) took the form:

$$Logit(p) = \ln\left(\frac{p}{1-p}\right) = \mathbf{X\beta} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \varepsilon \quad (1)$$

where $k$ indicates the number of predictors in the model formula. M1 was then extended with 2nd order terms (M2), resulting in:

$$Logit(p) = \ln\left(\frac{p}{1-p}\right) = \mathbf{X\beta} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \beta_{k+1} x_i^2 + \ldots + \beta_{k+j} x_j^2 + \varepsilon \quad (2)$$

where $x_i, \ldots, x_j \subseteq x_1, \ldots, x_k$ with length $j$, with specific elements representing non-linear functional forms for the relationship between $\text{logit}(Y)$ and $x$. Models M1 and M2 were considered “naïve” because potential interactions between different habitat features were not specified. Thus, the third model (M3) included all pairwise interactions as fixed effects:

$$
\begin{aligned}
&Logit(p) = \ln\left(\frac{p}{1-p}\right) = \mathbf{X\beta} = \\
&\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k \text{ (1st order terms)} \\
&+\beta_3 x_1 x_2 + \ldots + \beta_{k+\binom{k}{2}} x_{k-1} x_k \text{ (interactions between 1st order terms)} \\
&+\beta_{k+\binom{k}{2}+1} x_i^2 + \ldots + \beta_{k+\binom{k}{2}+j} x_j^2 \text{ (2nd order terms)} + \varepsilon
\end{aligned}
\tag{3}
$$

where coefficients $(\beta)$ and fixed terms are indexed as in Eq. (2). Including all pairwise interactions between $k$ predictors results in $k + \left(\frac{k!}{(k-2)!2!}\right)$ or equivalently $k + \binom{k}{2}$ coefficient estimates, representing the estimated effect of each individual predictor $x_1, \ldots, x_k$ in addition to the pairwise interactions $x_1 x_2,\ x_1 x_3, \ldots, x_{k-1} x_k$ and 2nd order terms.

### *Selection of best-fitting radial buffer for local-scale models*

An additional step was to select the best-fitting spatial scale for predictors (i.e. 500, 1000, or 3000 m radial buffer) in the local model (i.e. $M_{\text{local}}$). First, for each scale we fit a separate model for M1, M2, and M3, and compared goodness-of-fit and predictive accuracy metrics (Pearson's *r*, WAIC, LCPO, AUC) to select the best fit of the three. Next, we compared model parsimony with and without each variable by calculating WAIC, and comparing it to a reduced model without variable *x*: for each scale we calculated a specific ΔWAIC corresponding to the effects of variable *x* (and its associated 2nd order and interaction terms for models M2 and M3), where $\Delta\text{WAIC}_{\text{variable }(x)} = \text{WAIC}_{\text{full model - variable }(x)} - \text{WAIC}_{\text{full model}}$ (adapted from Laforge et al. 2015). The "best" spatial scale for each predictor was that with the lowest ΔWAIC. If

$\Delta\text{WAIC}_{\text{variable }(x)}$ was > 0 for any $x$, we did not consider that predictor in the final local model. The final local model was fit using the best-fitting spatial scale for each predictor and fit statistics were compared to models from previous steps which considered predictors independently at scales 1 (500 m radial buffer), 2 (1000 m radial buffer), and 3 (3000 m radial buffer).

***Conditional autoregressive model formulation***

The intrinsic conditional autoregressive (CAR) model takes the form

$$Logit(p) = \ln\left(\frac{p}{1-p}\right) = \mathbf{X\beta} + f(s) + \varepsilon \tag{4}$$

where $f(s)$ represents the spatial random effect in a latent Gaussian model (Beguin et al. 2012). Following notation in Beguin et al. (2012), in the CAR model, $f(s)$ models spatial dependence based on the following conditional distribution:

$$f_s(s) \mid f_s(s'), s \neq s', \lambda_s \sim N\left(\frac{1}{n_s}\sum_{s\sim s'} f_s(s'), \frac{1}{n_s\lambda_s}\right) \tag{5}$$

In (6), $s \sim s'$ tells us that the two cells are neighbors (i.e. next to each other or sharing a single boundary point), $n_s$ indicates the number of neighbors for cell $s$, and $\lambda_s$ is a precision hyperparameter, which is assigned a logGamma prior by default (Besag et al. 1991, Beguin et al. 2012, Bivand et al. 2015). An uninformative prior for $\lambda_s$ generally results in lower spatial smoothing, resulting in a large number of effective parameters which can lead to overfitting. Alternatively, specifying an informative prior for $\lambda_s$ can increase spatial smoothing which reduces potential for overfitting to local observations.

### *Functional response habitat use models*

In studies where habitat covariates are quantified in continuous environmental space (e.g. most species distribution models), it is possible to incorporate the GFR into habitat models by letting habitat selection coefficients vary as a function of region-specific availabilities (Matthiopoulos et al. 2011, Aarts et al. 2013). For example, in a generalized linear mixed model the effect of a single predictor represented by the coefficient $\beta_i$, can be quantified at regional location $l$ by including pairwise interactions between $x_i$, its regional expectation, and the regional expectations of all other covariates in $\mathbf{x}$:

$$\beta_{i,l} = \gamma_{i,0} + \sum_{j=1}^{I} \delta_{i,j} E[\mathbf{x}_j]_l + \varepsilon_{i,l} \tag{6}$$

where $E[\mathbf{x}_j]_l$ is the average value of the $j$th environmental predictor in the $l$th region, $\delta_{i,j}$ is the fixed effect slope coefficient, and $\gamma_{i,0}$ is the intercept coefficient (formula adapted from Aarts et al. 2013). Notably, this formulation implies the use of random intercepts for each region, fixed and random effects for all covariates, and fixed effects for all pairwise interactions between each covariate and its regional expectation (Aarts et al. 2013). Thus, as the number of regions and the length of $\mathbf{x}'$ increase, the number of parameters required to fit a habitat selection model will quickly become large. In many cases, observed ecological data will not be sufficient to support such complex models, so a simpler model may be necessary. Considerations of scale can direct efforts to simplify the GFR while respecting the limitations of observed data.

To assess functional responses in habitat use, we fit simplified versions of the GFR by first assuming that our environmental predictors as measured represented local-to-regional scale availability (i.e. 0.5 km – 10 km radial buffer area). That is, region-specific availabilities at different scales were accounted for in the moving window approach (10 km radial buffer) to quantifying habitat predictors, and we modelled local probability of occurrence as a function of regional availabilities of forage, cover, and conditions.

## Appendix 2C. Coefficient estimates from local-scale habitat models

Posterior marginal density estimates for local scale ($M4_{local}$) models of deer winter occurrence, with $\hat{\beta}$ notation indicating the mean of the posterior distribution and $Z$ indicating effect size ($\hat{\beta}/SE[\hat{\beta}]$). Environmental predictors were summarized using a circular assessment window with a 3000 m radial buffer. Model structure included main effects, 2nd order (squared terms), and local interactions; parameters were dropped from the model if $|Z| < 1.96$ and all of its associated interactions and 2nd order terms also had $|Z| < 1.96$.

| Parameter | $\hat{\beta}$ | $SE(\hat{\beta})$ | Lower 95% CI | Upper 95% CI | Z |
|---|---|---|---|---|---|
| (Intercept) | -2.4505 | 0.2182 | -2.8800 | -2.0300 | -11.230 |
| Snow Depth | -0.0131 | 0.0018 | -0.0167 | -0.0097 | -7.418 |
| Hemlock Basal Area | -0.0502 | 0.0245 | -0.0983 | -0.0021 | -2.051 |
| Cedar Basal Area | 0.1503 | 0.0129 | 0.1250 | 0.1760 | 11.631 |

| | | | | | |
|---|---|---|---|---|---|
| % Impervious | 0.4564 | 0.1795 | 0.1040 | 0.8090 | 2.542 |
| Stream Density | 0.1796 | 0.1865 | -0.1860 | 0.5460 | 0.963 |
| Road Density | -0.2157 | 0.2433 | -0.6970 | 0.2590 | -0.887 |
| Interspersion | 0.1737 | 0.0675 | 0.0417 | 0.3070 | 2.573 |
| Slope | -0.0237 | 0.0860 | -0.1930 | 0.1450 | -0.276 |
| % Mixed Forest | 3.4420 | 1.4905 | 0.5150 | 6.3700 | 2.309 |
| % Aspen Dominant | 0.2681 | 0.9616 | -1.6200 | 2.1500 | 0.279 |
| % Maple Dominant | 3.0692 | 0.5681 | 1.9600 | 4.1900 | 5.402 |
| % Conifer Dominant | 1.7668 | 0.9616 | -0.1150 | 3.6600 | 1.837 |
| % South-facing | 0.0870 | 0.7529 | -1.3900 | 1.5600 | 0.116 |
| Elevation | -0.0341 | 0.0028 | -0.0398 | -0.0287 | -11.985 |
| Topo. Radiation Aspect | -0.5049 | 1.1260 | -2.7200 | 1.7000 | -0.448 |
| Snow Depth$^2$ | -0.0001 | 0.0001 | -0.0001 | -0.0001 | -2.468 |
| Hemlock Basal$^2$ | 0.0022 | 0.0006 | 0.0009 | 0.0035 | 3.403 |
| Cedar Basal$^2$ | -0.0006 | 0.0002 | -0.0010 | -0.0002 | -3.258 |
| % Impervious$^2$ | -0.1629 | 0.0321 | -0.2280 | -0.1010 | -5.064 |
| Interspersion$^2$ | -0.0304 | 0.0118 | -0.0537 | -0.0074 | -2.581 |
| % Maple$^2$ | -8.4833 | 1.9980 | -12.4000 | -4.5900 | -4.246 |
| % Conifer$^2$ | -14.7164 | 2.7931 | -20.3000 | -9.2900 | -5.269 |
| Elevation$^2$ | 0.0001 | 0.0001 | 0.0001 | 0.0001 | 5.745 |
| Snow Depth: Cedar Basal | 0.0003 | 0.0001 | 0.0002 | 0.0006 | 4.492 |
| Snow Depth: % Impervious | -0.0030 | 0.0013 | -0.0056 | -0.0006 | -2.384 |

| | | | | | |
|---|---|---|---|---|---|
| Snow Depth: Stream Density | 0.0085 | 0.0023 | 0.0041 | 0.0130 | 3.777 |
| Snow Depth: Road Density | 0.0100 | 0.0023 | 0.0055 | 0.0146 | 4.358 |
| Snow Depth: Slope | -0.0027 | 0.0011 | -0.0049 | -0.0007 | -2.646 |
| Snow Depth: Conifer | -0.0432 | 0.0076 | -0.0583 | -0.0285 | -5.716 |
| Snow Depth: South-facing | -0.0145 | 0.0067 | -0.0277 | -0.0014 | -2.165 |
| Hemlock Basal: Road Density | 0.0668 | 0.0256 | 0.0169 | 0.1170 | 2.616 |
| Cedar Basal: Road Density | -0.0425 | 0.0131 | -0.0684 | -0.0168 | -3.237 |
| Cedar Basal: Slope | 0.0260 | 0.0086 | 0.0092 | 0.0431 | 3.023 |
| Cedar Basal: Roughness | -0.0001 | 0.0001 | -0.0001 | -0.0001 | -2.849 |
| % Impervious: % Mixed | -9.8137 | 2.0786 | -14.0000 | -5.8200 | -4.721 |
| Stream Density: Road Density | 0.9498 | 0.3358 | 0.2940 | 1.6100 | 2.828 |
| Stream Density: Slope | 0.3158 | 0.0776 | 0.1650 | 0.4690 | 4.068 |
| Road Density: % Mixed | -6.1573 | 2.4648 | -11.0000 | -1.3500 | -2.498 |
| Road Density: % Aspen | -4.2698 | 1.7221 | -7.6800 | -0.9160 | -2.479 |
| Road Density: % Maple | -2.9045 | 0.7978 | -4.4700 | -1.3400 | -3.641 |
| Road Density: Elevation | 0.0051 | 0.0017 | 0.0018 | 0.0084 | 3.065 |
| % Mixed: South-facing | -16.6982 | 6.1029 | -28.7000 | -4.7400 | -2.736 |
| % Maple: % Conifer | -14.8530 | 4.0777 | -23.0000 | -6.9400 | -3.642 |
| % Maple: % South-facing | 8.3362 | 2.7547 | 2.9400 | 13.8000 | 3.026 |
| % Maple: Topo. Rad. Aspect | -17.8917 | 4.5646 | -26.9000 | -8.9700 | -3.920 |

## Appendix 2D. Coefficient estimates from regional-scale habitat models

Posterior marginal density estimates for regional scale ($M4_{regional}$) models of deer winter occurrence, with $\hat{\beta}$ notation indicating the mean of the posterior distribution and $Z$ indicating effect size ($\hat{\beta}/SE[\hat{\beta}]$). Environmental predictors were summarized using a circular assessment window with a 10,000 m radial buffer. Model structure included main effects, 2nd order (squared terms), and regional interactions; parameters were dropped from the model if $|Z| < 1.96$ and all of its associated interactions and 2nd order terms also had $|Z| < 1.96$.

| Parameter | $\hat{\beta}$ | $SE(\hat{\beta})$ | Lower 95% CI | Upper 95% CI | $Z$ |
|---|---|---|---|---|---|
| (Intercept) | -2.6543 | 0.2866 | -3.2300 | -2.1000 | -9.260 |
| Snow Depth | -0.0178 | 0.0026 | -0.0229 | -0.0129 | -6.957 |
| % Impervious | -1.2447 | 0.2991 | -1.8400 | -0.6630 | -4.162 |
| Stream Density | 1.2731 | 0.5135 | 0.2720 | 2.2900 | 2.479 |
| Road Density | -0.1444 | 0.3923 | -0.9180 | 0.6230 | -0.368 |
| Interspersion | -0.4271 | 0.1735 | -0.7680 | -0.0863 | -2.461 |
| Slope | -1.8551 | 0.2944 | -2.4400 | -1.2800 | -6.300 |
| % Mixed Forest | 5.6686 | 3.8865 | -2.0000 | 13.3000 | 1.459 |
| % Aspen Dominant | 0.4283 | 2.6390 | -4.7600 | 5.6000 | 0.162 |
| % Maple Dominant | 1.9867 | 1.2629 | -0.4980 | 4.4600 | 1.573 |
| % Conifer Dominant | -4.3232 | 1.8743 | -8.0300 | -0.6670 | -2.307 |
| % South-facing | -4.2200 | 1.7926 | -7.7500 | -0.7120 | -2.354 |

| | | | | | |
|---|---|---|---|---|---|
| Elevation | -0.0072 | 0.0035 | -0.0141 | -0.0004 | -2.067 |
| Topo. Radiation Aspect | 4.9955 | 2.8441 | -0.5620 | 10.6000 | 1.756 |
| Roughness Index | 0.0003 | 0.0002 | -0.0002 | 0.0007 | 1.145 |
| Cedar Patch | 0.0751 | 0.0097 | 0.0563 | 0.0943 | 7.753 |
| Hemlock Patch | -0.1385 | 0.0214 | -0.1810 | -0.0970 | -6.471 |
| Stream Density$^2$ | -1.3174 | 0.4762 | -2.2600 | -0.3870 | -2.766 |
| Road Density$^2$ | -1.6601 | 0.5244 | -2.7000 | -0.6430 | -3.166 |
| Slope$^2$ | 0.7655 | 0.1345 | 0.5050 | 1.0300 | 5.690 |
| % Aspen$^2$ | -63.9681 | 11.3704 | -86.6000 | -41.9000 | -5.626 |
| % Maple$^2$ | -8.8576 | 2.7636 | -14.3000 | -3.4700 | -3.205 |
| Topo. Rad. Aspect$^2$ | 136.8405 | 21.6507 | 94.2000 | 179.0000 | 6.320 |
| Roughness$^2$ | 0.0000 | 0.0000 | 0.0000 | 0.0000 | -2.920 |
| Snow Depth: Stream Density | 0.0203 | 0.0055 | 0.0097 | 0.0312 | 3.720 |
| Snow Depth: Slope | -0.0082 | 0.0025 | -0.0132 | -0.0034 | -3.301 |
| Snow Depth: % Mixed | -0.2588 | 0.0445 | -0.3470 | -0.1720 | -5.810 |
| Snow Depth: % Maple | 0.0262 | 0.0100 | 0.0066 | 0.0460 | 2.616 |
| Snow Depth: % South | -0.0500 | 0.0111 | -0.0719 | -0.0283 | -4.503 |
| % Impervious: % Mixed | -28.4230 | 4.5823 | -37.5000 | -19.5000 | -6.203 |
| Stream Density: Interspersion | 1.0333 | 0.2996 | 0.4470 | 1.6200 | 3.449 |
| Stream Density: % Aspen | 19.7844 | 3.3340 | 13.3000 | 26.4000 | 5.934 |
| Stream Density: Roughness | -0.0006 | 0.0002 | -0.0010 | -0.0001 | -2.518 |
| Stream Density: Hem. Patch | 0.1626 | 0.0300 | 0.1050 | 0.2220 | 5.416 |

| | | | | | |
|---|---|---|---|---|---|
| Road Density: % Conifer | 14.3347 | 2.0970 | 10.3000 | 18.5000 | 6.836 |
| Road Density: Roughness | 0.0012 | 0.0002 | 0.0009 | 0.0015 | 7.203 |
| Interspersion: % Mixed | -10.9112 | 2.1833 | -15.2000 | -6.6400 | -4.997 |
| Interspersion: % South | -4.2376 | 0.6647 | -5.5600 | -2.9500 | -6.375 |
| Interspersion: Hem. Patch | 0.0075 | 0.0029 | 0.0018 | 0.0133 | 2.542 |
| Slope: Roughness | -0.0003 | 0.0001 | -0.0005 | -0.0001 | -3.266 |
| % Aspen: % Maple | 17.0465 | 8.0656 | 1.3300 | 33.0000 | 2.113 |
| % Aspen: % South | 53.3873 | 11.5375 | 30.8000 | 76.1000 | 4.627 |
| % Maple: % South | 20.9941 | 4.7219 | 11.8000 | 30.3000 | 4.446 |
| % Maple: Hem. Patch | -0.2673 | 0.0568 | -0.3800 | -0.1570 | -4.704 |
| % South-facing: Elevation | 0.0413 | 0.0118 | 0.0184 | 0.0647 | 3.502 |
| % South-facing: Roughness | -0.0055 | 0.0007 | -0.0070 | -0.0041 | -7.406 |
| Elevation: Hem. Patch | -0.0002 | 0.0001 | -0.0004 | 0.0000 | -2.530 |
| Roughness: Hem. Patch | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 4.016 |

## Appendix 2E. Coefficient estimates from generalized functional response habitat models

Posterior marginal density estimates for generalized functional response ($M4_{GFR}$) models of deer winter occurrence, with $\hat{\beta}$ notation indicating the mean of the posterior distribution and $Z$ indicating effect size ($\hat{\beta}/SE[\hat{\beta}]$). Environmental predictors representing local (3000 m radial buffer) food and cover habitat were fit conditional on the availabilities of regional (10,000 m radial buffer) food, cover, and other conditions. Model structure included main effects, 2nd order (squared terms), and local-regional interactions; parameters were dropped from the model if $|Z| < 1.96$ and all of its associated interactions and 2nd order terms also had $|Z| < 1.96$.

| Parameter | $\hat{\beta}$ | $SE(\hat{\beta})$ | Lower 95% CI | Upper 95% CI | $Z$ |
|---|---|---|---|---|---|
| (Intercept) | -3.2213 | 0.2551 | -3.7304 | -2.7284 | -12.626 |
| **Local Effects** | | | | | |
| Snow Depth | -0.0090 | 0.0030 | -0.0150 | -0.0030 | -2.945 |
| Hemlock Basal | 0.0704 | 0.0256 | 0.0203 | 0.1210 | 2.747 |
| Cedar Basal | 0.1438 | 0.0144 | 0.1158 | 0.1724 | 9.970 |
| % Impervious | 0.4810 | 0.1909 | 0.1071 | 0.8563 | 2.520 |
| Stream Density | 0.3077 | 0.2854 | -0.2518 | 0.8686 | 1.078 |
| Road Density | 0.6968 | 0.2459 | 0.2118 | 1.1775 | 2.834 |

| | | | | | |
|---|---|---|---|---|---|
| Interspersion | 0.1700 | 0.0548 | 0.0627 | 0.2779 | 3.102 |
| Slope | 0.2127 | 0.1032 | 0.0102 | 0.4152 | 2.062 |
| % Mixed Forest | 7.1705 | 1.7550 | 3.7324 | 10.6219 | 4.086 |
| % Aspen Dominant | -0.8114 | 1.3132 | -3.4009 | 1.7559 | -0.618 |
| % Maple Dominant | 3.1814 | 0.6782 | 1.8581 | 4.5198 | 4.691 |
| % Conifer Dominant | 2.5119 | 0.9813 | 0.5942 | 4.4457 | 2.560 |
| Elevation | -0.0793 | 0.0059 | -0.0911 | -0.0678 | -13.322 |
| Snow Depth$^2$ | -0.0001 | 0.0001 | -0.0001 | -0.0001 | -2.518 |
| % Impervious$^2$ | -0.1374 | 0.0335 | -0.2047 | -0.0732 | -4.106 |
| % Conifer$^2$ | -5.8002 | 2.0467 | -9.8453 | -1.8071 | -2.834 |
| Snow Depth: % Impervious | -0.0026 | 0.0013 | -0.0053 | -0.0001 | -2.014 |
| Snow Depth: Stream Dens. | 0.0140 | 0.0026 | 0.0089 | 0.0191 | 5.410 |
| Snow Depth: Road Density | 0.0130 | 0.0025 | 0.0081 | 0.0179 | 5.217 |
| Snow Depth: % Conifer | -0.0477 | 0.0076 | -0.0628 | -0.0329 | -6.254 |
| Cedar Basal: Road Density | -0.0431 | 0.0134 | -0.0696 | -0.0168 | -3.212 |
| Cedar Basal: Slope | 0.0492 | 0.0107 | 0.0283 | 0.0703 | 4.594 |
| Cedar Basal: Roughness | -0.0001 | 0.0001 | -0.0001 | -0.0001 | -3.818 |
| % Impervious: % Mixed | -6.0191 | 2.0857 | -10.1994 | -2.0021 | -2.886 |
| Stream Density: Slope | 0.2533 | 0.0881 | 0.0817 | 0.4274 | 2.876 |
| Road Density:% Aspen | -8.1676 | 1.8361 | -11.7975 | -4.5867 | -4.448 |
| Road Density:% Maple | -4.0313 | 0.8574 | -5.7125 | -2.3459 | -4.702 |
| Road Density: Elevation | 0.0051 | 0.0017 | 0.0018 | 0.0083 | 3.065 |

**Regional Effects**

| | | | | | |
|---|---|---|---|---|---|
| % Maple | 4.1733 | 0.9398 | 2.3305 | 6.0206 | 4.440 |
| % Aspen | 3.5582 | 1.9157 | -0.2028 | 7.3194 | 1.857 |
| Cedar Patch | 0.0553 | 0.0089 | 0.0380 | 0.0729 | 6.216 |
| Hemlock Patch | -0.1010 | 0.0181 | -0.1369 | -0.0659 | -5.587 |
| Snow Depth | -0.0097 | 0.0042 | -0.0180 | -0.0016 | -2.326 |
| Elevation | 0.0689 | 0.0072 | 0.0549 | 0.0832 | 9.552 |
| Slope | -1.3755 | 0.2476 | -1.8645 | -0.8918 | -5.554 |
| Topo. Radiation Aspect | 2.2669 | 3.3471 | -4.2874 | 8.8539 | 0.677 |
| Stream Density | -0.0556 | 0.5315 | -1.1007 | 0.9867 | -0.105 |
| % Impervious | -0.7723 | 0.2539 | -1.2778 | -0.2800 | -3.041 |
| Interspersion | -0.8077 | 0.1329 | -1.0706 | -0.5484 | -6.075 |
| % Maple | 4.1733 | 0.9398 | 2.3305 | 6.0206 | 4.440 |
| Local:Regional Interactions | | | | | |
| Cedar Basal: Cedar_Patch | -0.0007 | 0.0002 | -0.0012 | -0.0003 | -3.330 |
| Cedar Basal: Snow Depth | 0.0004 | 0.0001 | 0.0002 | 0.0006 | 3.910 |
| Cedar Basal: Slope | -0.0470 | 0.0156 | -0.0778 | -0.0164 | -3.009 |
| Ced. Basal: Top. Rad. Asp. | -0.3819 | 0.1432 | -0.6669 | -0.1043 | -2.667 |
| Ced. Basal: Stream Density | 0.0685 | 0.0238 | 0.0220 | 0.1154 | 2.878 |
| Hemlock Basal: % Maple | -0.5414 | 0.0884 | -0.7167 | -0.3695 | -6.127 |
| Hem. Basal: Cedar Patch | -0.0074 | 0.0012 | -0.0098 | -0.0051 | -6.157 |
| Hem. Basal: Snow Depth | 0.0006 | 0.0003 | 0.0001 | 0.0011 | 2.117 |
| Hem. Basal: Top. Rad. Asp | -0.9445 | 0.3032 | -1.5421 | -0.3514 | -3.115 |
| Hem. Basal: Interspersion | 0.0624 | 0.0163 | 0.0306 | 0.0946 | 3.830 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| % Mixed: Snow Depth | -0.1185 | 0.0244 | -0.1668 | -0.0709 | -4.851 |
| % Mixed: Slope | 5.5986 | 1.3966 | 2.8532 | 8.3369 | 4.009 |
| % Mixed: % Impervious | -18.9514 | 3.5226 | -25.9677 | -12.1271 | -5.380 |
| % Maple: % Maple | -8.9429 | 2.7166 | -14.2882 | -3.6206 | -3.292 |
| % Maple: % Aspen | 17.9839 | 5.8327 | 6.5912 | 29.4828 | 3.083 |
| % Maple: Hemlock Patch | 0.1424 | 0.0425 | 0.0596 | 0.2263 | 3.353 |
| % Maple: Elevation | 0.0250 | 0.0047 | 0.0159 | 0.0342 | 5.390 |
| % Maple: Slope | -3.1747 | 0.5813 | -4.3217 | -2.0390 | -5.461 |
| % Maple: Top. Rad. Asp. | -74.8021 | 10.1357 | -94.8287 | -55.0233 | -7.380 |
| % Maple: Stream Density | -4.3102 | 1.1361 | -6.5518 | -2.0904 | -3.794 |
| % Aspen: Cedar Patch | -0.0983 | 0.0415 | -0.1799 | -0.0169 | -2.368 |
| % Aspen: Hemlock Patch | 0.5256 | 0.1156 | 0.2994 | 0.7532 | 4.546 |
| % Aspen: Snow Depth | -0.0441 | 0.0154 | -0.0744 | -0.0140 | -2.867 |
| % Aspen: Slope | -4.9721 | 1.0433 | -7.0265 | -2.9298 | -4.766 |

# 3. Empirical evidence of preemptive habitat selection by a top predator during 19 years of population recovery[2]

## Abstract

Habitat selection studies commonly work under assumptions of an Ideal-Free habitat distribution (IFD), where relationships between animal density and habitat imply differences in relative habitat quality. The IFD is the basis for inference in modern habitat modeling approaches which include resource selection functions (RSFs) and species distribution models (SDMs). Theoretical habitat distributions are rarely tested empirically, and alternatives to the IFD may have greater support if an animal exhibits territorial behavior at a spatial scale that matches analyses. We used 19 years of monitoring data from gray wolves (*Canis lupus*) in the Upper Peninsula of Michigan, USA, to test assumptions of IFD to alternative distributions including the Ideal-Despotic distribution (IDD), and Ideal-Preemptive distribution (IPD) using isodar analyses. The latter habitat distributions occur when dominant groups or individuals depress the fitness of those that are less-experienced or inferior (IDD), or pre-emptively colonize the best habitats thereby excluding later arrivals (IPD). In either alternative, the density-habitat suitability relationship becomes unreliable, and habitat suitability is better determined via measures of fitness such as survival, reproduction, or growth rate. The Michigan wolf population increased from ~ 50 to > 600 individuals during our study, and habitat selection patterns were most consistent with the IPD; to our knowledge, this constitutes the first formal test of theoretical density dependent habitat selection in large carnivores.

---

[2] The material contained in this chapter is in preparation for submission to *Ecology*

An IPD suggests potential mismatches between animal density and habitat quality and can lead to source-sink population dynamics.

## Introduction

Habitat selection is fundamental to animal ecology. Although rarely stated, most habitat selection studies work under the assumption of an Ideal-Free Distribution (IFD), where a population's fitness is maximized across habitats through differences in density (density-dependent habitat selection; Fretwell and Lucas 1969, Morris 1988). Assumptions of IFD are often untested, which can lead to false conclusions about relative habitat quality (Van Horne 1983). Species presence or density may not be correlated with other components of fitness such as reproductive success and/or survival (Van Horne 1983, Gaillard et al. 2010), especially when intraspecific competition and territoriality influence habitat selection processes (Pulliam 1988, Pulliam and Danielson 1991). In such cases, predictions from the theoretical IFD are inappropriate and alternative theories of species distribution should be explored.

Animals should distribute themselves in a way that maximizes fitness and minimizes competition for resources. Thus, habitat selection should be functionally dependent on conspecific density, due to its relationship with resource availability and competition (e.g. McLoughlin et al. 2010). The IFD is based on habitat matching rules stating that, if animals are approximately optimal foragers, then a given habitat's suitability (e.g. habitat A) decreases as a function of conspecific density (Fretwell and Lucas 1969, Morris 1988). As density increases, individuals should begin to select an alternative habitat (e.g. habitat B) to achieve the same average fitness benefits as those in the first habitat (Morris 1988, Pulliam and Danielson 1991). In general, habitat B may be qualitatively or quantitatively inferior to habitat A (Morris 2003a), but will provide equivalent fitness benefits (such as reproductive success) at densities lower than that of habitat A (Morris 1988, Morris 2003b). Under IFD, fitness will be approximately equal between habitats while density varies, suggesting differences in available resources between the two. Evidence for IFD has accumulated from several systems involving primarily non-territorial species (Mobaek et al. 2009, van Beest et al. 2014a). However, less attention has been given to theoretical distributions where animals either compete directly for territory (Ideal-despotic or Ideal-dominant distribution [IDD]; Fretwell and Lucas 1969, Oro 2008, Mosser et al. 2009) or preemptively occupy the "best" habitat sites (Ideal preemptive distribution [IPD; Pulliam and Danielson 1991]). In the latter situation, habitat matching becomes more complex and the prediction of equal fitness between habitats breaks down (Morris 1994).

Direct tests of theoretical habitat models for territorial species are lacking. Although we might assume IDD or IPD for many territorial species, it is unclear whether current data match theoretical expectations (Morris 1994, Morris 2003a, b, McLoughlin et al. 2006, Haché et al. 2013). Isodar theory is a framework for testing theoretical habitat distributions, and can reveal the effect of density dependence on habitat selection patterns(Morris 2003a). A habitat isodar is generated by separating a population's geographic distribution into distinguishable classes (e.g., habitat A vs. habitat B), where the animal's density can be estimated in each class (Morris 1987, 1988). Repeated estimation of density in each class (i.e. over time) and plotting paired densities in habitat

A vs. habitat B produces the isodar, which can take a variety of shapes (Morris 1994). Regression analysis of the paired densities frequently takes a linear functional form, where the intercept can reveal differences in resources between habitats (quantitative differences) and the slope reveals differences in habitat structure (qualitative differences; Morris 1988, Morris 2003a). The linear isodar often suggests an IFD, but observation of unequal fitness between habitats and/or despotic behavior can alternatively reveal the IDD (Morris 1994, Mosser et al. 2009). Other patterns may emerge; non-linear isodars can indicate preemptive habitat selection (Pulliam and Danielson 1991, Morris 1994) and gaps in the isodar are associated with Allee effects (Morris 2002). The specific shape of a non-linear isodar can imply remarkable patterns that might otherwise go undetected. For example, saturation of a limited number of high quality sites can result in niche-shifts or switching of preferred habitats (an asymptotic isodar; Morris 1994), and differences in the variance of site quality between the habitats is predicted by a sigmoidal isodar (Morris 1994). Testing hypotheses related to theoretical habitat selection distributions is important for many reasons, including 1) detecting fundamental differences in how density dependence might operate within a population (Rodenhouse et al. 1997), 2) understanding potential for realized vs. fundamental niche mismatches and source-sink habitat dynamics under IDD or IPD (Pulliam 1988, Pulliam 2000), 3) implications of differences in genetic flow through a population (Gaggiotti 1996, Falcy 2015), and 4) scale-dependent spatial variation in perceived habitat fitness across a landscape. Testing hypotheses related to theoretical habitat selection distributions is important for many reasons, including 1) fundamental differences in how density dependence might operate within a population (Rodenhouse et al. 1997), 2) potential for realized vs. fundamental niche mismatches and source-sink habitat dynamics under IDD or IPD (Pulliam 1988, Pulliam 2000), 3) implications of differences in genetic flow through a population (Gaggiotti 1996, Falcy 2015), and 4) scale-dependent spatial variation in perceived habitat fitness across a landscape.

Our objectives were to explore competing hypotheses about the theoretical habitat distribution of a large, territorial and iconic predator (gray wolves, *Canis lupus*) and compare observations of density-dependent habitat selection to those expected under IFD, IDD or IPD. To accomplish this, we evaluated fitness-density relationships (Fretwell and Lucas 1969) and applied isodar analysis (Morris 1988, 1994) to a 19-year time series of wolf observational data gathered during a period of recolonization to the Upper Great Lakes region.

We predicted that wolf isodars and fitness-density relationships would be more consistent with IDD (Fig. 3.1D & 3.1C) or IPD (Fig. 3.1E & 3.1F) than IFD (Fig. 3.1A & 3.1B). Under IFD, if two habitats differ in suitability, then fitness declines as a function of density in both habitats but the average density in one habitat is consistently higher than the other. In this model, the inferior habitat should be unoccupied when density is low in the superior habitat (Fig. 3.1A & 3.1B; Morris 1988, 1994, McLoughlin et al. 2010). Territorial species might achieve an IFD under the density assessment hypothesis, where new arrivals respond to cues about density from existing occupants and establish alternative sites rather than challenge existing competitors (Fretwell and Lucas 1969). This scenario is plausible for wolves, which advertise their presence and communicate vocally as well as intensively marking territory boundaries via scent-marking (Mech and Boitani 2010). Direct competition may be uncommon at relatively low densities because if existing habitat is relatively suitable and unoccupied, the risk of challenging current occupants might outweigh the cost of selecting less suitable habitat (e.g., Cubaynes et al. 2014, Cassidy et al. 2015). Evidence of IFD is a linear isodar with equal fitness and varying densities among habitats (Morris 1994). Under IDD, interference from existing competitors reduces potential habitat quality, such that the alternative (but inferior) unoccupied habitat might appear to have equivalent benefits (Morris 1994). Since a linear isodar may still be observed, other evidence may be needed to conclude an IDD. In general, the key signature of IDD would be unequal average fitness between habitats (Morris 1994). The IPD model (Fig. 3.1E & 3.1F) offers an interesting alternative hypothesis to IDD. The IPD was inspired by the process of breeding site selection by migrants (Pulliam 1988, Pulliam and Danielson 1991) but could conceivably be applicable to any recolonizing territorial species. Under IPD, access to a site is determined by first arrival and selection of the best available site. The preemptive distribution results in a non-linear isodar (Morris 1994, Fig. 3.1F) which distinguishes it from the IFD or IDD alternatives.

## Methods

### *Overview*

We explored variation in wolf densities and growth rate among habitat types over 19 years of population recovery using non-parametric distribution tests and isodar analysis. Isodar analysis involves data which reflect spatial and temporal variation in density across a heterogeneous landscape (≥ 2 habitat types), such that habitat selection influences species distribution and fitness and/or density conceivably vary between habitats. For wolves, these data can be gathered by repeatedly documenting pack territory locations (i.e. through aerial surveys and ground tracking) and estimating pack sizes over time. Spatial structure of the wolf territories combined with pack sizes can be used to generate smoothed estimates of wolf density which is subsequently used in isodar analysis. We implemented a Principal Components Analysis (PCA) of correlated landscape predictors based on prey availability, potential for human influence, and land cover attributes. PCA results were used in generalized linear models of wolf occurrence to establish the most important predictors of wolf habitat, and the top three predictors were evaluated with isodar plots. We performed linear and non-linear regression analysis of isodar plots and used cross-validation to select a best-fitting functional form. The shape of the best-fitting isodar

Wolves in the UP were federally protected under the ESA from 1974 - 2007, 2008 – 2009, 2009 – 2011, and again following the completion of this study (2014). A detailed chronology of wolves ESA status in the Western Great Lakes region can be found at http://www.fws.gov/midwest/wolf/.

### *Data collection*

Wolves were live-captured using foot-hold traps during spring and summer 1992–2013 as part of a larger Michigan Department of Natural Resources (DNR) wolf monitoring program (Beyer et al. 2009). Individuals were chemically immobilized (ketamine hydrochloride and xylazine, 100 mg/ml) using 0.11 mg/kg ketamine hydrochloride and 2 mg/kg xylazine and fitted with VHF radiocollars (Telonics, Inc., Mesa, Arizona, USA; Potvin et al. 2005). Wolves were located by fixed-wing single-engine aircraft approximately 1–2 times per week, and coordinates were uploaded to a database for use in GIS. The telemetry study is further described in Potvin et al. (2005), Vucetich et al. (2012), and Beyer et al. (2009).

We used data from Michigan DNR wolf track counts to estimate wolf abundance and variation in wolf density over space and time. The track counts began in 1992 and continued throughout the duration of the study. The study site was divided into 21 units, each counted every year from 1992–2006. During winter, all passable roads were surveyed from trucks and snowmobiles. Pack sizes and territory boundaries were established by intensive tracking efforts, with trackers using information from radio-collared wolves as well as recording all sign, such as territory markings, scat, and all individual sets of tracks (Potvin et al. 2005). An accuracy assessment of the ground tracking efforts was conducted during a 4-year independent study (Vucetich et al. 2012), which revealed a 4% average difference between the separate counts (Beyer et al. 2009). In 2007, the state adopted a geographically stratified sampling plan to reduce the cost and effort of the survey. A panel design was implemented to increase the precision of abundance estimates (Schreuder 1993), which also ensured that some sampled units were counted during successive years.

### *Estimation of Territory Boundaries*

Each wolf territory was established by a combination of radio-collar locations and track surveys. Following detection of a pack, territories were monitored either by aerial telemetry relocations from ≥ resident wolves or by repeatedly visiting the site via the annual tracking survey. This allowed us to document pack presence and territory persistence over the course of the study. We delineated annual territory boundaries using the following framework: first, if ≥ 30 telemetry locations were available for a pack during a year (e.g. year = time *t*), we generated a unique territory home range for year *t*. If there were < 30 locations for year *t*, but ≥ 30 locations were available over the course of a 2- or 3-year time period (*t-1, t, t+1*), we generated the territory home range using a 3-year moving window. For all other years that packs were known to be present at their site, we generated long-term average territories using either A) locations from previous years, i.e. territories from previous steps, B) a combination of telemetry locations and tracks from surveys, or C) a minimum convex polygon based on track locations across years.

When telemetry locations were available (*n* ≥ 30), we used a fixed kernel density estimator to create a utilization distribution (UD) for each pack territory during either year *t* or the 3-year moving window. The kernel bandwidth was estimated using the "plug-in" method (Uboni et al. 2015b) , after first removing outlying locations (≥ 5 km from pack territory; Fuller 1989) and any individual wolves that did not consistently occupy a territory. We defined the territory home range as the 95% volume isopleth from the UD. Home ranges and bandwidth estimators were analyzed using packages 'adehabitatHR' and 'ks' in R 3.2.2 (Calenge 2006, Duong 2007, R Core Team 2015).

### *Wolf Density*

Packs were counted during track survey efforts. The entire study area was counted from 1995–2006. For survey units that were not surveyed every year starting in 2007, we assumed that packs persisted if they were detected the years directly before and after the year for which the count did not occur. We used the midpoint to extrapolate pack size in these cases. The last year included in the study was 2013 but surveys continued the following year, allowing us to use data from 2014 to make extrapolations. We created a longitudinal matrix with pack territory as the subject unit (rows) and year as the time unit (columns). For each year in the study, each pack was either detected, assumed present, or not detected, and pack size estimates were recorded in a related table. We summed rows of the matrix to estimate total wolves and compared results to the Michigan DNR's abundance estimates (Michigan Department of Natural Resources 2015) to verify that our assumptions of occupancy and pack size were reasonable. The matrix was linked to a geodatabase with polygons for all territory home ranges estimated each year; all packs with counts $\geq 2$ were included in subsequent steps while lone individuals were assigned to remaining geographic space (i.e. area not occupied by an existing pack during year $t$). We converted pack sizes to density (wolves / 1000 km$^2$) for each territory, and ultimately generated a smoothed surface for each year using a circular moving window with radius equal to that of an average wolf territory size during the study. The final result of this analysis was a set of raster surfaces representing spatiotemporal variation in wolf density during the study, demonstrated by an animation in the Supplementary files (Appendix 3A). Geoprocessing steps were completed in

ArcMap 10.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) using ArcPy for Python 2.7.2.

### *Habitat Suitability Model*

We used a generalized linear mixed model (GLMM) with a binary response to identify habitat types likely to be used by wolves within the study area. The GLMM was fitted to Principal Components Analysis (PCA) predictors of correlated landscape covariates associated with prey densities (e.g. buck harvest index and deer wintering complex habitat), human influences (e.g. road density, distance to highways, % impervious surface, % protected land), and landscape features (elevation, slope, forest-open edge, stream density). Further details about the development of the model and corresponding PCA are available in (Appendix 3B). Using the results, we ranked habitat covariates by their effect size (Z-score) and delta score (predicted change in probability of occurrence corresponding to a change in predictor $x$). We selected the top three covariates to represent key differences in habitat perceived by wolves and used them in subsequent isodar assessments.

### *Isodar Analysis*

We developed isodars for the three most important habitat covariates $(x_{1,}x_2, x_3)$ using methods similar to Falcy (2015), which are appropriate for continuous data. Continuous habitat data were represented by raster surfaces corresponding to principal components identified as strong predictors of habitat selection. While isodar analyses typically consider discrete habitat types, RSFs or SDMs predominantly rely on continuous data to make predictions about habitat quality. A solution for using these data in isodar analysis is to reclassify relevant habitat variables into paired bins representing values above and below the mean for a given variable (Falcy 2015). Based on the results of the habitat suitability model, we separated the top-ranked PCA predictors into 6 classes using a quantile (equal area) reclassification of the relevant principal components in ArcMap. We dropped the middle two classes (i.e. values nearest to the median) and combined the 1st and 2nd (low values) and 5th and 6th (high values) to represent the paired habitat types. We sampled 20 random point locations from each paired bin for each year in the study. To represent regional wolf density at the sampled point locations, we specified a radial buffer twice the size of an average wolf home range and computed the mean wolf density at time *t* within the buffer.

We plotted habitat pairs for each habitat predictor $(x_{1,} x_2, x_3)$ corresponding to the mean annual wolf density in each binned habitat type. We fitted linear and non-linear candidate models to each isodar (Table 3.1), where the response variable (density in habitat A) represented the preferred habitat type based on RSF results. We used leave-one-out cross validation to evaluate the models based on root-mean squared prediction error (RMSPE), with lowest scores indicating best predictive fit to the data.

### *Comparison of fitness in separate habitats*

We estimated spatial variation in local growth rates among habitat types by pooling estimates of wolf density each year and evaluating the change in density over time. Since wolf density trends can be highly stochastic at the local scale, we evaluated changes at the 5th, 25th, 50th, 75th, and 95th percentile of the sampled densities, and estimated the “growth rate,” e.g. $r = \log(\frac{density_{t+1}}{density_t})$. We assumed that differences in growth rate trends between habitats indicated differences in fitness (Morris 1994). Due to differences in site quality, growth rate could vary between habitat types, potentially operating on different time scales. To account for this, we compared growth rates in different habitats for early (1995 – 2001), mid (2002 – 2007), and late (2008 – 2013) recovery time periods. For each time period, we conducted a two-sample non-parametric Mann-Whitney test (Hollander et al. 2013) of the hypothesis that the distribution of growth rates sampled from habitat A (superior habitat) was shifted to the right of those sampled from habitat B (inferior habitat).

## Results

Wolf abundance estimates in the UP increased from 80–658 during the time period of the study (1995–2013), and corresponding estimates of wolf density were spatially variable, ranging from 0 – 70 wolves / $km^2$, with the maximum value occurring in the far western UP in 2011 where several large packs were observed utilizing overlapping territories. Mean wolf density for the overall study area was approximately 1.7 wolves / $km^2$ in 1995 and increased to 11.1 wolves / $km^2$ in 2011 before apparently stabilizing (10.5 wolves / $km^2$ in 2013; Appendix 3A).

The habitat suitability model revealed that the top three predictors of wolf occupancy were indices of prey availability (PC1-prey, $\hat{\beta}=0.417$, $P<0.001$), human influence (PC1-human, $\hat{\beta}= -0.244$, $P<0.001$), and favorable land cover with high stream densities (PC2-land, $\hat{\beta}=0.379$, $P<0.001$; Table 3.2). Prey availability was generated from a PCA of distance to and proportion of deer wintering complexes and annual buck kill reported from surveys (Tables 3.3 & 3.4). Human influence was positively associated with proportions of impervious surface, road density, and distance to highway and negatively associated with proportion of public lands (e.g. National or State Forest; Tables 3.3 & 3.4). The principal component index for land cover was largely driven by stream densities, with greater stream densities associated with greater PC2-land values (Tables 3.3 & 3.4). Further details about the habitat model are available in Appendix 3B.

Regression of wolf density in contrasting habitat types showed differences in density in different habitats, as expected from the results of our habitat suitability model (Table 3.2, Fig. 3.2). Wolf density was greatest when prey availability was high and human influence was low (Fig. 3.2). Although relative probability of wolf occurrence increased in landscapes with greater stream densities (Table 3.2), it appeared that wolf densities were greater overall when stream densities were lower. Regression models fit to densities in separate habitats indicated that non-linear relationships between densities in paired habitat types were the best fit for all three habitat predictors. Cross-validation statistics are summarized in Table 3.5. This suggests evidence that wolves used a pre-emptive site selection strategy while colonizing the study area. The best fitting curve was sigmoidal for isodars representing habitat differences in prey availability and favorable land cover, and asymptotic for habitat differences in human influence (Table 3.1, Table 3.5, Fig. 3.3).

We observed a difference in growth rates between habitats with contrasting prey availabilities during the early and late time periods. Median growth rate ($r$) was 0.15 in habitats with greater prey availability (habitat A) and 0.05 with lower prey availability (habitat B) during 1995 – 2001, and the Mann-Whitney test revealed a location shift in the distribution ($W$ = 1.08e05, $n_A$ = 518, $n_B$ = 386, $p$ =0.018). We did not observe a difference in the distributions during 2002 – 2007 (median $r_{\mathrm{A}}$ = 0.10, $r_B$ = 0.12; $W$ = 1.3e05, $n_A$ = 503, $n_B$ = 529, $p$=0.691). Interestingly, growth rates were higher in habitat B than in habitat A during 2008 – 2013 (median $r_{\mathrm{A}}$ = 0.00, $r_B$ = 0.06; $W$ = 1.2e05, $n_A$ = 449, $n_B$ = 592, $p$=0.691, $p$ = 0.002 [$r_A < r_{\mathrm{B}}$]). We did not observe differences in growth rates between paired habitats with differences in human influence or land cover characteristics for any of the three time periods (Appendix 3C). Changes in local density over time (i.e. estimates of local growth rate) revealed surprisingly similar distributions for the latter habitat types given expectations of IPD or IDD. Details on the comparisons across the distribution are available in Appendix 3C.

## Discussion

Territorial species are often assumed to distribute themselves according to IDD or IPD theory. IDD is difficult to demonstrate empirically, as it requires snapshots of species density in contrasting habitat types combined with relevant information about habitat fitness. Reproductive rates (McLoughlin et al. 2006) and estimates of survival (Franklin et al. 2000, Aldridge and Boyce 2007) are often related to habitat in order to check assumptions about habitat selection and its relationship with fitness. However, growth rate is often the best overall indicator of a habitat's productivity (Morris 1994, Matthiopoulos et al. 2015). If measures of productivity differ substantially between habitat types, this may be seen as evidence for IDD or IPD; if animals follow habitat matching rules then fitness should be equal on average while density is optimized (Morris 1988). Mosser et al. (2009) showed differences in reproductive rates between habitats and documented despotism in Serengeti lions, and Falcy (2015) modeled spawning site selection in Chinook salmon and concluded results that were more consistent with IPD given non-linearity in resulting isodars. In contrast, territorial Ovenbirds (*Seiurus aurocapilla*) appeared more consistent with an IFD, defying theoretical expectations (Haché et al. 2013).

We hypothesized that wolf habitat selection over a 19 year recovery period would reveal an IDD. Alternatively, wolf recolonization could be consistent with IPD due to pre-emptive site selection strategies and territorial cues such as howling and scent-marking that could limit intraspecific conflict at low densities (Fretwell and Lucas 1969). An IPD is often viewed as a certain type of IDD (Pulliam and Danielson 1991, Haché et al. 2013) and does not necessarily exclude dominant-subordinate behavior. A key signature of IPD is a non-linear isodar (Morris 1994, Falcy 2015). Non-linear regression fits to isodars of wolf densities indeed suggested IPD in our study. However, IPD should reveal differences in productivity between habitat types similar to IDD because high quality habitat sites are typically limited and provide greater fitness benefits (Morris 1994, Haché et al. 2013). Evidence for IPD/IDD based on assessment of spatially varying growth rates (i.e. changes in local density across time) varied in our study, which is likely due to complexities in local demographic rates, immigration vs.

emigration, and landscape patterns that may promote or suppress local source-sink dynamics (Heinrichs et al. 2016).

While isodars were non-linear for all three paired habitat types, growth rates only varied for prey availability. Further, the contrast in growth rates in high vs. low prey availability habitats switched direction over time, suggesting that density dependence may complicate comparisons of productivity between habitats depending on time scale. For example, in our study growth rates were significantly higher with greater prey availability early in the study (Appendix 3C). However, by the middle of the study there was no evident difference in growth rates between habitats and during the late time period growth rates were actually higher in the lower quality sites (Appendix 3C). This result is consistent with a pre-emptive site selection process but may also indicate density-dependent regulation which at times may promote a system that appears to follow an IFD through adaptive habitat selection (Morris and MacEachern 2010), adjustment of territory size (Ridley et al. 2004), and other mechanisms. It is important to note situations where the IFD might appear to be a better fit to empirical data for territorial species.

When disparities exist in an environment with varying habitat quality, density dependence may become a strong regulating force in areas where habitat quality promotes rapid growth. Under the IPD model, animals that arrive early establish territories in the highest quality habitat and preempt the use of these habitats by individuals arriving later (Pulliam and Danielson 1991). This would seemingly result in site-dependent as opposed to density-dependent regulation (Rodenhouse et al. 1997).

However, IDD or IPD models do not account for adjustments to territory size (Ridley et al. 2004, Haché et al. 2013). Territory size is likely habitat and density dependent in wolves (Rich et al. 2012 and Kittle et al. 2015, but see Mattisson et al. 2013), and this could result in a system that appears to be more consistent with the IFD (Haché et al. 2013). In high quality habitat with abundant prey, wolves can achieve high densities by reducing territory size and tolerating some degree of territory overlap between packs (Rich et al. 2012) without necessarily losing fitness benefits, resulting in an apparent IFD. These highest quality habitats may reach an equilibrium where mortality and emigration balance out reproduction; if dispersal increases at high densities (Matthysen 2005), these habitats likely contribute a surplus of individuals that diffuse into lower quality habitats. Importantly, this situation could appear to be consistent with either IFD or IDD/IPD, and is also likely to contribute to source-sink population dynamics (Haché et al. 2013, Heinrichs et al. 2016). We observed variation in wolf density and productivity in habitats with contrasting prey availability. Isodars suggested an IPD, but differences in productivity switched directions over the course of the study. With respect to prey availability as a habitat indicator, we documented highest growth rates in the better habitat early in the study, no difference in growth rates between habitats in the middle of the study, and higher growth rates in the lower quality habitats later in the study. We view this as further evidence that populations may occur anywhere on the continuum between IFD and IDD (e.g. Ridley et al. 2004, Haché et al. 2013). In fact, it is not inconceivable that a population could transition from IPD to IFD to IDD during a recolonization event. This could occur because density dependence can locally influence multiple vital rates, promote adjustments in territory size and movement between habitats of varying quality, and contribute to despotic behavior (i.e. Cubaynes et al. 2014)

While non-linear isodars were the case for all three habitat predictors, we did not detect differences in local growth rates for habitat types contrasting human influence and land cover characteristics. Wolf densities were greater where human influence was lower (Fig. 3.2), but this did not translate to a difference in productivity between habitats during any time period (Appendix 3A). Wolves may occur at lower densities in areas prone to human conflict due to an avoidance strategy, lower survival rates, or a combination of both. In some cases, areas prone to human conflict may represent habitat sinks with increased mortality risk. For example, increased mortality risk was associated with greater proportions of agricultural land cover in our study area (Chapter 6). Lower survival rates could suppress local densities without impacting growth rate if increased mortality was compensated for by greater reproduction locally or by immigration from nearby ‘source’ populations (Pulliam 2000, Heinrichs et al. 2016). Interestingly, wolves colonizing the study area did not initially demonstrate strong selection for areas with lower human influence, and paired mean densities in the contrasting habitat types stayed relatively similar across the time series (e.g. Fig. 3.3A). This may reflect the relatively low levels of human influence throughout the study area, where only the most developed areas (< 1% of the study area) were avoided as a response to perceived risk.

A sigmoidal isodar was the best fit to paired densities in contrasting habitats with differences in prey availability and land cover characteristics (primarily stream densities). This result may indicate that variance of site quality is greater in the lower quality habitat (Morris 1994). Furthermore, the best sites may actually occur in the overall lower quality habitat than in the higher quality habitat despite being fewer in number (see Fig. 9 in Morris 1994). Theoretical fitness-density curves cross each other in this case, and density may occasionally be greater in the lower quality habitat than in the higher quality habitat (Morris 1994). This is not unreasonable for our study area. First, prey availability is not evenly distributed in the winter due to deep snow. White-tailed deer winter habitat can be severely constrained during severe winters which could lead to very high prey densities. In areas with less deer winter habitat, prey availability would be lower overall, but deer would become more concentrated in small areas during winter which would presumably make hunting easier. Thus, a few of the best territory sites could occur where prey availability is relatively low overall, and wolves may have colonized these areas first leading to a pre-emptive distribution and a sigmoidal isodar shape. Similarly, stream densities may represent high quality hunting grounds (e.g. Kauffman et al. 2007), but the highest stream densities were relatively limited. Wolves appeared to initially prefer greater stream densities when occupying the landscape (Table 3.2, Table 3.3, Fig. 3.3C), but ultimately this characteristic was not a major constraint on density (Fig. 3.2, Fig. 3.3C).

Evidence for preemptive habitat distributions is rare (Sergio and Newton 2003, Zając et al. 2006, Petty and Grossman 2010). Our study is the first (to our knowledge) to document non-linear isodars for a large carnivore species, and the first to show shifts in fitness benefits (i.e. shifting from IPD to IFD) corresponding to spatiotemporal variation in density dependence. Even more uncommon is a sigmoidal isodar based on empirical evidence. Sigmoidal isodars indicate complex fitness-density relationships between habitats, and suggest that the best overall sites may occur in areas that are not considered high quality habitat. This scenario may be more common than previously realized, as large variance in site quality is likely in habitats that are disturbed or fragmented. The IPD is generally considered to be a precondition for source-sink population dynamics (Pulliam 1988, Pulliam and Danielson 1991, Morris 2003a). Source-sink dynamics are also more likely where species exhibit rapid growth and occupy interspersed habitats of contrasting quality (Heinrichs et al. 2016). These conditions evidently occur within our study system, and are probably not uncommon for large carnivores in other systems. Understanding preemptive habitat selection and its potential to occur in a source-sink system is important for conserving species of concern such as wolves, because source habitats likely contribute disproportionately to population dynamics and are often difficult to identify (Heinrichs et al. 2016).

Table 3.1. Linear, curvilinear, and non-linear candidate regression models for fitting theoretical isodars to annual snapshots of wolf density occurring in separate habitat types. Candidate models include linear isodars representing Ideal-free (IFD) or Ideal-despotic (IDD) habitat distributions and non-linear isodars representing ideal-preemptive distributions (Morris 1994).

| Model | Formula | Theoretical Model |
|---|---|---|
| Linear (LM1) | $Y=\beta_0+\beta_1 X+\varepsilon$ | IFD/IDD; consumer-resource or additive interference |
| Log-Log (LM2) | $\log(Y)=\beta_0+\beta_1\log(X)+\varepsilon$ | IFD/IDD; continuous input or multiplicative interference |
| LogX (LM3) | $Y=\beta_0+\beta_1\log(X)+\varepsilon$ | IPD; fewer sites in higher quality habitat |
| Asymptotic (NLS1) | $Y=\phi_1+(\phi_2-\phi_1)\exp[-\exp(\phi_3)X]$ | IPD; large differences in site quality between habitats |
| Logistic (NLS2) | $Y=\dfrac{\phi_1}{1+\exp[-(X-\phi_2)/\phi_3]}+\varepsilon$ | IPD; unequal variances in site qualities between habitats |

Table 3.2. Results from a resource selection probability function (RSPF) indicating the relative influence of predictors of wolf occupancy in the Upper Peninsula of Michigan, USA. Predictor strength is indicated by effect size (Z) and the change in predicted probability of occurrence corresponding to changes in the predictor across its range of values in the study area (*dY/dX*); the three strongest predictors (in bold) were used for isodar analyses.

| Predictor | $\hat{\beta}$ | $SE(\hat{\beta})$ | *Z* | *P* | *dY/dX* |
|---|---|---|---|---|---|
| Intercept | 0.005 | 0.018 | 0.30 | 0.767 | NA |
| **PC-Prey 1** | **0.417** | **0.013** | **32.89** | **< 0.001** | **0.606** |
| PC-Prey 2 | -0.073 | 0.020 | -3.63 | < 0.001 | -0.114 |
| PC-Topo 1 | -0.173 | 0.017 | -10.35 | < 0.001 | -0.372 |
| PC-Topo 2 | 0.299 | 0.017 | 18.00 | < 0.001 | 0.497 |
| PC-Land Cover 1 | 0.048 | 0.017 | 2.85 | 0.004 | 0.144 |
| **PC-Land Cover 2** | **0.379** | **0.019** | **19.66** | **< 0.001** | **0.707** |
| **PC-Human 1** | **-0.244** | **0.013** | **-18.34** | **< 0.001** | **-0.618** |
| Protected Land | 0.159 | 0.018 | 8.77 | < 0.001 | 0.104 |
| Snow | -0.045 | 0.019 | -2.35 | 0.019 | -0.157 |

Table 3.3. Component loadings from four separate Principal Components Analyses of geographic variation in prey availability, human impacts, topographic features, and land cover in the Upper Peninsula of Michigan, USA. Principal components were used as predictors in wolf habitat selection models.

| Loadings | | | | | | |
|---|---|---|---|---|---|---|
| PCA | Predictors | PC1 | PC2 | PC3 | PC4 | PC5 |
| Prey availability | % Deer wintering complex | 0.67 | -0.228 | 0.706 | | |
| | Distance to deer wintering complex | -0.671 | 0.22 | 0.708 | | |
| | Buck kill index | 0.317 | 0.948 | | | |
| Human influence | Distance to highway | 0.430 | 0.398 | -0.540 | 0.500 | -0.339 |
| | Road Density | -0.449 | -0.265 | -0.684 | 0.182 | 0.478 |
| | % Developed Impervious | -0.571 | -0.181 | -0.116 | | -0.792 |
| | % Agriculture | -0.436 | 0.334 | 0.445 | 0.691 | 0.150 |
| | Protected Land | 0.312 | -0.792 | 0.171 | 0.488 | |
| Topographic | Elevation | -0.440 | 0.548 | -0.662 | -0.261 | |
| | Slope | -0.615 | 0.126 | 0.220 | 0.747 | |
| | Topographic | -0.578 | -0.118 | 0.527 | -0.611 | |

| | | | | | |
|---|---|---|---|---|---|
| | Roughness Index | | | | |
| | Radiation Aspect Index | 0.306 | 0.819 | 0.485 | |
| Land Cover | Stream Density | 0.190 | 0.908 | 0.372 | |
| | Forest-Open Edge Density | -0.636 | 0.191 | -0.215 | -0.717 |
| | % Open | -0.62 | 0.262 | -0.251 | 0.695 |
| | % Water & wetlands | -0.418 | -0.266 | 0.868 | |

Table 3.4. Landscape variables from Principal Components Analysis (PCA) used in a Resource Selection Probability Function for wolves in the Upper Peninsula of Michigan, USA. Four separate PCAs were applied to summarize geographic variation in prey availability, human impacts, topographic features, and land cover in the study area; The first and second components (PC1 and PC2) explained ≥ 50% of the variance in each PCA.

| Variable | Description | Prop. Variance explained |
|---|---|---|
| Prey - PC1 | Positive association with prey winter habitat and prey densities | 0.67 |
| Prey - PC2 | Positive association with buck kill index | 0.30 |
| Human - PC1 | Human impact - positive association with road density, developed areas, and % agriculture, negatively associated with greater distance to highway and proportion of public land (e.g. national forest) | 0.52 |
| Topographic - PC1 | Lower elevation and slope, less rugged | 0.25 |
| Topographic - PC2 | Positive association with south-facing slopes | 0.25 |
| Land Cover - PC1 | Generally forest-dominated, negative association with greater edge densities, open habitats, water, and wetlands | 0.56 |
| Land Cover - PC2 | Positive association with greater stream | 0.25 |

| | |
|---|---|
| | densities |
| Snow depth | Greater average snow depths in winter |
| Protected Land | Greater proportions of national and state forest |

Table 3.5. Cross-validation rankings for isodar regression models comparing wolf densities in habitats with high vs. low prey availability, human influence, and favorable land cover. LM3, NLS1, and NLS2 indicate non-linear regression model fits, while LM1 and LM2 indicate linearity (see Morris 1994). Non-linear isodars are indicative of pre-emptive habitat distributions (Morris 1994).

| Habitat Predictor | Ranking | Model | RMSE |
|---|---|---|---|
| Prey Availability | 1 | NLS2 | 1.965 |
| | 2 | NLS1 | 2.044 |
| | 3 | LM3 | 2.164 |
| | 4 | LM1 | 2.171 |
| | 5 | LM2 | 3.850 |
| Human Influence | 1 | LM3 | 2.103 |
| | 2 | NLS1 | 2.158 |
| | 3 | NLS2 | 2.185 |
| | 4 | LM1 | 2.326 |
| | 5 | LM2 | 2.443 |
| Land Cover | 1 | NLS2 | 1.889 |
| | 2 | NLS1 | 2.094 |
| | 3 | LM3 | 2.108 |
| | 4 | LM1 | 2.187 |
| | 5 | LM2 | 2.312 |

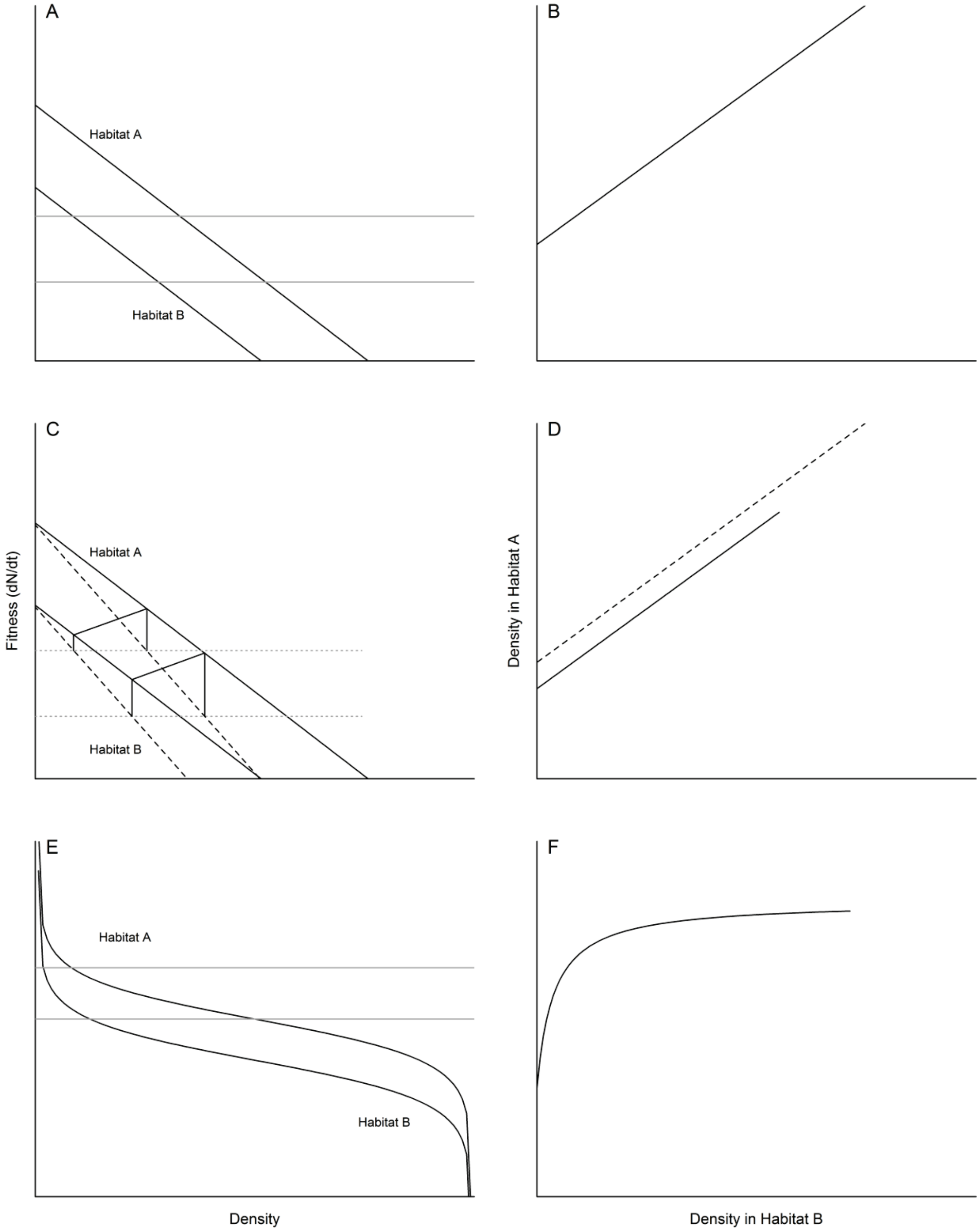

Figure 3.1. Theoretical fitness-density relationships and resulting isodars under the

Ideal-Free Distribution (IFD; A, B), the Ideal-Despotic Distribution (IDD; C, D), and the Ideal-Preemptive Distribution (IPD; E, F). Figures adapted from Morris (1994).

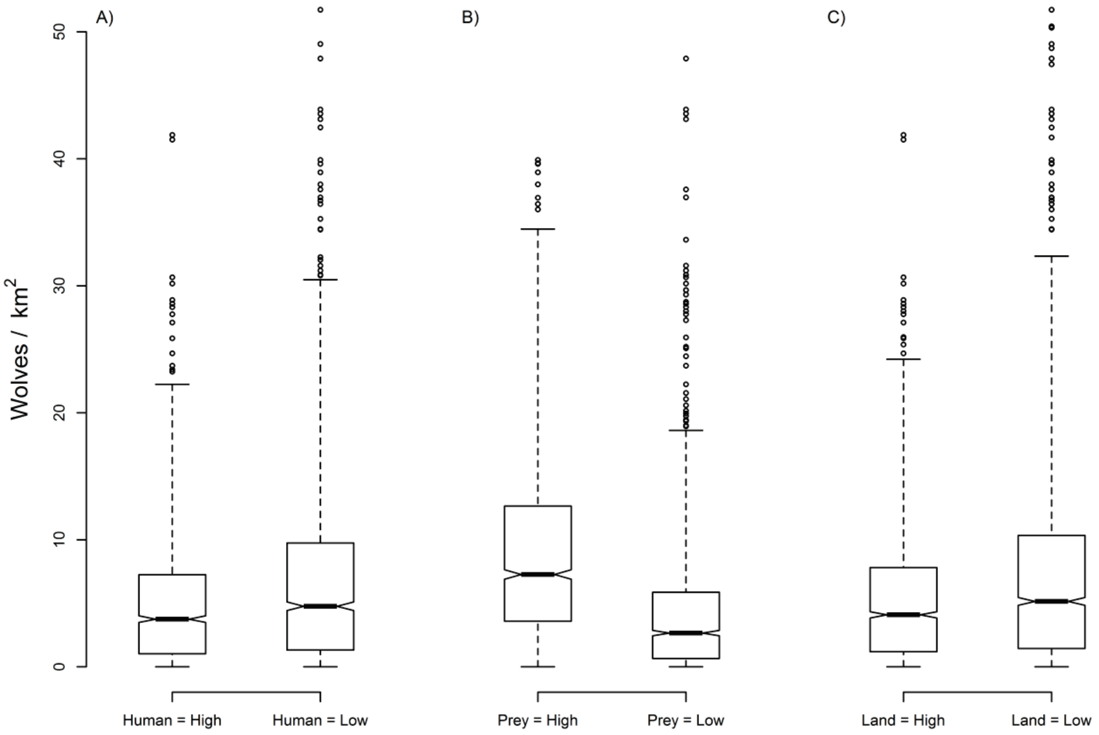

Figure 3.2. Distributions of estimated wolf density at randomly selected locations within contrasting habitat types representing low vs. high human influence (A), prey availability (B), and favorable land cover (C) in Upper Michigan, USA, 1995 – 2013.

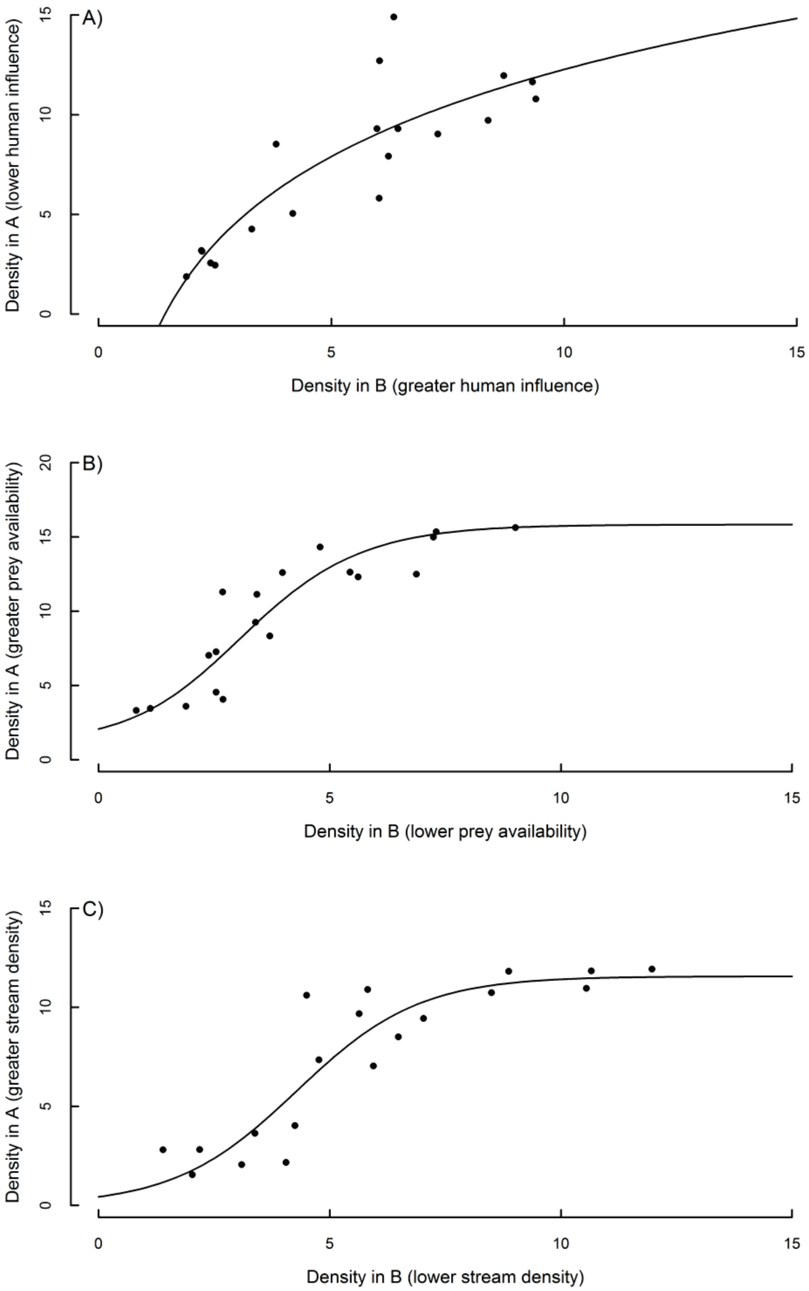

Figure 3.3. Empirical isodars fit to a time series of mean wolf densities occurring within contrasting habitat types representing low vs. high human influence (A), prey availability (B), and favorable land cover (C) in Upper Michigan, USA, 1995 – 2013. Non-linear isodars indicate preemptive, density dependent habitat selection.

## Appendix 3A. (Video Animation) Spatiotemporal change in wolf density in the Upper Peninsula, MI, USA, 1995-2013.

A time-lapse animation is available in the online supplementary files for this document.

## Appendix 3B. Probability of occurrence models of wolf habitat use in the Upper Peninsula, MI, USA, 1995 – 2013.

We modeled wolf occurrence in our study area by repeatedly drawing 500 random locations from occupied habitat (used habitat) and 500 random locations from unoccupied habitat (unused habitat) each year of the study. The response variable for analysis was thus a Bernoulli distributed variable indicating habitat use at a random coordinate; $P(used) \sim Bernoulli(n, p)$.

*Landscape variables*

Landscape predictors were developed to model habitat suitability in the study area, with continuous random variables chosen to represent prey availability, human influence, topographic variation, and land cover characteristics. Each variable is described in detail below.

A. **Indices of Prey Availability**

*Variable:* Buck Harvest

*Source:* Michigan Department of Natural Resources (MDNR)

*Unit:* Antlered bucks killed / km$^2$

*Description & Measurement:* Buck harvest data were collected from mail surveys during white-tailed deer hunting season across the Upper Peninsula (UP) by the MDNR (e.g. Frawley 2010). Harvest numbers were summarized by area (km$^2$) at the county level, and a circular moving window ($r$ = 4.02 km) was used to smooth the results at the same scale as other predictors. A continuous raster surface of 30 m cell size was thus generated for each year in the study, representing mean bucks harvested / km$^2$. This was done using focal statistics in ArcGIS 10.1 (hereafter, ArcGIS; Environmental Systems Research Institute, Redlands, CA, USA).

---

*Variable*: % Deer Wintering Complex

*Source*: MDNR (e.g. http://www.michigan.gov/dnr/0,4570,7-153-10363_10856_10905-339639--.html)

*Unit*: Percent of area mapped as deer wintering complex (%)

*Description & Measurement*: White-tailed deer (*Odocoileus virginianus*) are migratory throughout much of the UP due to harsh winter conditions, and congregate in dense stands of primarily eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*) when snow depth exceeds approximately 30 cm (Shi *et al.* 2006; Witt *et al.* 2012; Murray, Webster & Bump 2013). Deer winter range was been mapped by state biologists as early as the 1930s, with surveys occurring every 10 – 20 years since. The most recent surveys occurred in 2005 and 2013. We used the maps from 2005 and 2013 to classify the study area as winter habitat (deer wintering complex, or DWC), or non-winter habitat. We generated the percent of landscape variable using a circular moving window ($r = 4.02$ km) to summarize the area mapped as DWC at each location. A continuous raster (30 m cell) was generated for the study area to represent this metric. We assumed no significant change in DWC habitat throughout the study. Seasonal migration is a learned behavior and results in high fidelity to winter ranges, such that the same DWCs are repeatedly utilized year after year (Nelson 1998, Nelson et al. 2004).

--

*Variable*: Distance to Deer Wintering Complex

*Source*: MDNR (see PDWC)

*Unit*: Distance to nearest DWC (km)

*Description & Measurement*: See description for '% Deer Wintering Complex.' We generated distance to DWC (km) by creating a Euclidean distance raster surface in ArcGIS and subsequently calculating the average distance within the circular moving window across the study site. No significant change in DWC habitat was assumed over the course of the study (see '% Deer Wintering Complex').

--

*Variable*: Annual Snow Depth

*Source*: National Climate Data Center (http://www.ncdc.noaa.gov/)

*Unit*: Average Daily Snow Depth (cm), 1 Nov – 30 Mar

*Description & Measurement*: We downloaded daily snow depth data from the National Climatic Data Center (NCDC) for all weather stations on the study site. We calculated the mean winter snow depth at each station (1 Nov – 30 Mar) for each year in the study. We used Empirical Bayesian Kriging in ArcGIS (EBK; http://www.esri.com/news/arcuser/1012/empirical-byesian-kriging.html) to interpolate a raster surface for each year based on the weather station point data. Parameters for the EBK analysis included an output cell of 500 m, maximum number of points = 50, local model overlap = 2, simulated semivariograms = 50, and a standard circular neighborhood with radius = 150,000 m, maximum neighbors = 12, and minimum neighbors = 3. The resulting raster surface represented interannual and spatial variation in snow depths during the study.

## B. **Human Influence and Infrastructure**

*Variable:* % Agriculture

*Source*: National Land Cover Database (NLCD; http://www.mrlc.gov/)

*Unit*: Percentage of landscape comprising agricultural cover types (%)

*Description & Measurement*: Agricultural cover types were reclassified from NLCD products for years 1992, 2001, 2006, and 2011. The early years of the study were linked to results from the 1992 product (wolf biological years 1995-1997), and 2001 product (wolf biological years 1998-2003), while later years corresponded to the 2006 (wolf years 2004-2008) and 2011 products (wolf years 2009-2013). Agricultural cover types included pasture/hay, row crops, small grains, and fallow ground, and were assigned a value of 1, with all other cover types reclassified to Null values. The moving window was applied to calculate the percentage of landscape comprising agriculture at each location (30 m cell) in the study area.

--

*Variable*: Distance to Major Road

*Source*: U.S. Census Bureau (http://www.census.gov/geo/maps-data/data/tiger.html)

*Unit*: Distance to nearest major road (km)

*Description & Measurement*: TIGER\Line roads were downloaded from the U.S. Census Bureau for the years 1990 and 2000-2014. We queried primary and secondary roads from the database for each year that the data were available. In the Upper Peninsula, these were almost entirely major highway routes. 1990 was removed from consideration because the classification scheme did not match the later years. Road coverages were similar in the 2000 data, however, so we used the 2000 file for the early study years. We calculated Euclidean distance to primary and secondary roads and applied the circular moving window to the resulting raster surface. For study years 2000-2013 we recalculated this metric every two years (i.e. 2002, 2004, … , 2012) to represent temporal changes in extent of roads.

--

*Variable*: Minor Road Density

*Source*: U.S. Census Bureau (see HWY)

*Unit*: Distance of Minor Roads / Unit Area (km / km$^2$)

*Description & Measurement*: TIGER\Line roads were described in 'Distance to Major Road.' For minor road densities, we queried local roads and trails from the TIGER\Line database. We then calculated minor road density within the moving window using the Line Density tool in ArcGIS. The temporal representation of these features was the same as in 'Distance to Major Road.'

--

*Variable*: % Impervious Surface

*Source*: NLCD (http://www.mrlc.gov/index.php)

*Unit*: Percent of landscape comprising impervious surfaces (%)

*Description & Measurement*: In addition to the NLCD products, we also acquired the 2001, 2006, and 2011 Percent Developed Imperviousness product. In order to capture the best available temporal resolution for this feature, early study years were assigned to the 2001 product while later years (post-2002) were assigned to the 2006 and 2011 products (see description for '% Agriculture'). We summarized % impervious (focal mean) within the moving window described previously to create the index for human population density and infrastructure.

--

*Variable*: % Protected Land

*Source*: USGS Protected Areas Database (http://gapanalysis.usgs.gov/padus/ )

*Unit*: Percentage of landscape comprising public/protected land ownership

*Description & Measurement*: Protected areas in the UP of Michigan included National and State Forests, National Park Service land ownership, U.S. Fish and Wildlife Service, and various small tracts of land belonging to state or non-profit based conservancy projects or land trusts. We summarized the % landscape (focal mean) within the moving window to create an index of protected land where higher values represented lower potential for human development and disturbance.

--

**C. Natural Features**

*Variable*: % Open

*Source*: NLCD

*Unit*: Percent of landscape comprising open cover types (%)

*Description & Measurement*: We used NLCD products to calculate the percentage of open cover types occurring on the landscape. Open cover types and forested land were reclassified to a binary raster (1 = open), which was used to assess the proportion of open cover occurring within the moving window. Open cover types included grassland/herbaceous, pasture/hay, row crops, small grains, fallow ground, herbaceous/emergent wetlands, bare ground, and quarries, mines, or pits. The analysis was repeated for 1992, 2001, 2006, and 2011 NLCD products to represent land cover change during the study.

--

*Variable*: Open:Forested Edge Density

*Source*: NLCD

*Unit*: Distance of the open:forested linear feature / Unit Area (km / $km^2$)

*Description & Measurement*: We used NLDC products to create two binary rasters: one representing open cover types (see '% Open'), and one which included all forested cover types vs. other features. We defined the boundary between these two features as an edge, converted the boundary to line features in ArcGIS, and calculated the line density within the moving window described previously. The analysis was repeated for 1992, 2001, 2006, and 2011 NLCD products.

--

*Variable*: % Open Water & Wetlands

*Source*: NLCD

*Unit*: Percent of landscape comprising open water and wetlands

*Description & Measurement*: We used NLCD products to reclassify emergent/herbaceous wetlands and open water cover types. A binary raster was created for these cover types using methods described in '% Open.' We evaluated the percentage of landscape comprising open water and wetlands within the moving window. The analysis was repeated for the 1992, 2001, 2006, and 2011 NLCD products.

--

*Variable*: Stream Density

*Source*: Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/?rel=thext&action=thmname&cid=3&cat=MI+Geographic+Framework+Hydrography+%28v14a%29)

*Unit*: Distance of stream per unit area (km / km$^2$)

*Description & Measurement*: Hydrography files were downloaded from the Michigan Geographic Data Library. All streams and linear water features were selected from these data and clipped to the study area (FCC codes H3*– H4*). Linear stream features were converted to a 30 m density raster using the line density tool with 4.02 km radius.

--

*Variable*: Elevation

*Source*: USGS National Map (http://nationalmap.gov/)

*Unit*: Meters above sea level (m)

*Description & Measurement*: We downloaded a 30 m DEM from the National Map and calculated mean elevation within the moving window described previously.

--

*Variable*: Slope

*Source*: USGS DEM (see Elevation)

*Unit*: Degrees of slope (°)

*Description & Measurement*: We used the DEM described in 'Elevation' to compute degrees slope using ArcGIS, and calculated the mean slope within the moving window.

--

*Variable*: Terrain ruggedness

*Source*: USGS DEM (see Elevation)

*Unit*: Index of terrain ruggedness

*Description & Measurement*: We used the DEM to compute the average terrain ruggedness index value within the moving window. The analysis was performed using the ArcGIS Geomorphometry and Gradient Metrics toolbox (Evans et al 2014). The index measures topographic heterogeneity and is fully described in Evans et al. (2014).

--

*Variable*: Topographic radiation aspect index

*Source*: USGS DEM (see Elevation)

*Unit*: Index of heat load

*Description & Measurement*: We used the DEM to compute the average heat load index value within the moving window. The analysis was performed using the ArcGIS Geomorphometry and Gradient Metrics toolbox (Evans et al 2014). The index measures potential for direct solar radiation and warmer temperatures based on a slope-aspect transformation; the method is fully described and referenced in Evans et al. (2014).

--

*Principal Components Analyses of landscape predictors*

We separated landscape predictors into four separate classes (prey availability, human influence, topographic variation, land cover characteristics) and performed Principal Components Analyses (PCA) to reduce from many correlated landscape predictors to fewer uncorrelated predictors (e.g., see Panzacchi et al. 2015). The PCA was performed in R 3.2.2 (R Core Team 2015) on the correlation matrix of the predictors in each category (Venables and Ripley 2002). We selected the first and second principal components from each analysis to use as predictors in wolf habitat models. The first and second components explained ≥ 50% of the variance in each case, and served as landscape variables that were relevant to wolf life history, fitness, and habitat requirements on the landscape. For human influence, we replaced the 2nd component with the ‘Protected Land’ variable in habitat models due to its ability to predict habitat use and ease of interpretation. We also added the ‘Snow’ predictor to models independently because of its potential to influence habitat and because it did not fall under any particular category. Tables 3 and 4 in the main text show the results of the PCAs and the resulting indices considered in wolf habitat models.

*Habitat Analysis*

We were interested primarily in the ability of landscape predictors to influence wolf habitat use at the population level within the study area. As a baseline, we used a generalized linear model for a binary response variable

$$Logit(p) = \ln\left(\frac{p}{1-p}\right) = \mathbf{X\beta} = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \varepsilon \tag{7}$$

where $k$ indicates the number of predictors in the model formula and $(x_1,...,x_k)$ indicates the vector of habitat predictors with $\beta_1,...,\beta_k$ regression coefficients. We added a random intercept (Year) to the model to account for repeatedly sampling from the study area over time (Hebblewhite and Merrill 2008). The logit link was used to transform the linear response into a probability; we interpreted this as relative probability of occurrence due to the strong assumptions associated with modeling habitat selection processes (e.g. Lele et al. 2013).

Our model included predictors for prey (Prey-PC1, Prey-PC2), human influence (Human-PC1, Protected Land), topographic variation (Topo-PC1, Topo-PC2), land cover characteristics (Land-PC1, Land-PC1), and snow. Each of these predictors was relevant to habitat use (Table 2, main text) so we did not implement model reduction or model selection. The resulting model discriminated reasonably between predicted used and unused locations according to the Receiving Operator Characteristic (AUC = 0.803; Robin et al. 2011). We selected the top three predictors for isodar analyses based on rankings of predicted influence on probability of selection (change in predicted Y with change in X) and effect size (|Z-value|). The top predictors were Prey-PC1 with greater values indicating greater prey availability, Human-PC1 with greater values indicating more human impacts, and Land-PC2 with greater values strongly associated with greater stream densities. These results are summarized in Tables 2 and 3, main text.

## Appendix 3C. Growth rate differences in separate habitats

| Time Period | Habitat Predictor | Percentile | *rA* | *rB* | Mann-Whitney test (rA > rB) |
|---|---|---|---|---|---|
| 1995 - 2001 | Prey Availability | 5th | -1.68 | -3.02 | |
| | | 25th | -0.32 | -0.88 | |
| | | median | 0.15 | 0.05 | **W = 9.2e04, p = 0.018** |
| | | 75th | 0.79 | 0.98 | |
| | | 95th | 2.82 | 4.05 | |
| | Human Influence | 5th | -2.48 | -2.37 | |
| | | 25th | -0.54 | -0.61 | |
| | | median | 0.13 | 0.13 | W = 1.3e05, p = 0.555 |
| | | 75th | 0.77 | 1.01 | |
| | | 95th | 4.41 | 3.16 | |
| | Land Cover | 5th | -2.22 | -2.40 | |
| | | 25th | -0.57 | -0.52 | |

| | | | | | |
|---|---|---|---|---|---|
| | | median | 0.16 | 0.13 | W = 2.2e05, p=0.203 |
| | | 75th | 1.03 | 0.79 | |
| | | 95th | 3.36 | 3.51 | |
| 2002 - 2007 | Prey Availability | 5th | -0.98 | -1.09 | |
| | | 25th | -0.21 | -0.24 | |
| | | median | 0.10 | 0.12 | W = 1.3e05, p = 0.691 |
| | | 75th | 0.43 | 0.54 | |
| | | 95th | 1.55 | 1.69 | |
| | Human Influence | 5th | -0.86 | -1.43 | |
| | | 25th | -0.23 | -0.21 | |
| | | median | 0.14 | 0.15 | W = 1.2e05, p = 0.535 |
| | | 75th | 0.51 | 0.54 | |
| | | 95th | 1.67 | 1.54 | |
| | Land Cover | 5th | -1.27 | -0.89 | |
| | | 25th | -0.19 | -0.22 | |
| | | median | 0.12 | 0.12 | W = 2.1e05, p = 0.541 |
| | | 75th | 0.51 | 0.48 | |
| | | 95th | 1.62 | 1.59 | |
| 2008 - 2013 | Prey Availability | 5th | -0.67 | -0.72 | |
| | | 25th | -0.12 | -0.13 | |
| | | median | 0.00 | 0.06 | W = 1.1e05, p = 0.998* |
| | | 75th | 0.15 | 0.24 | |
| | | 95th | 0.51 | 1.04 | |
| | Human Influence | 5th | -0.59 | -0.66 | |

|  |  |  |  |  |
|---|---|---|---|---|
|  | 25th | -0.10 | -0.13 |  |
|  | median | 0.04 | 0.05 | W = 1.2e05, p = 0.658 |
|  | 75th | 0.22 | 0.27 |  |
|  | 95th | 0.82 | 0.82 |  |
| Land Cover | 5th | -0.7 | -0.58 |  |
|  | 25th | -0.14 | -0.1 |  |
|  | median | 0.03 | 0.05 | W = 2.1e05, 9 = 0.705 |
|  | 75th | 0.25 | 0.22 |  |
|  | 95th | 0.77 | 0.81 |  |

* Indicates the null hypothesis of the opposite test (rB > rA) would be true

# 4. A simulation of conceptual used and available habitat distributions under assumptions of strong territoriality and population growth[3]

## Abstract

Habitat selection is a dynamic behavioral process which can be influenced by many variables, including species territoriality. The effect of territoriality on temporally-varying, density dependent habitat selection trends has received little attention at the landscape scale. Specifically, the availability distribution is a key component of modern habitat selection models and can be constrained substantially at the population level when animals employ a preemptive site occupancy strategy. The implication is that the geographic availability of all habitat types shrinks in size as populations increase and vice versa. Depending on the degree of preference or avoidance of a particular habitat and the relative abundance of the habitat, the selection ratio can vary in ways that may be unanticipated. We simulated 4 scenarios of density (or occupancy) dependent habitat selection under the assumption that increases in occupancy led to constricted geographic availability of habitats. Depending on the initial habitat distribution and the nature of habitat use, the selection ratio increased, decreased, or remained constant over time. The change in the selection ratio is akin to a density dependent change in the (β) coefficients from modern habitat selection models and depends on the convergence or divergence of habitat use and availability distributions. For example, if the central tendencies of used and available habitat distributions diverge, the strength of habitat selection increases.

---

[3] The material contained in this chapter is being prepared for submission to an undetermined journal

Alternatively, the used and available distributions may converge, resulting in weaker selection, or move in parallel, resulting in constant selection.

## Introduction

Modeling and understanding animal habitat selection occurring within dynamic systems is an ongoing challenge for ecologists. Distributions of used and available habitat can be highly variable, especially when populations fluctuate and the distributions of available resources or habitat are not stationary (McLoughlin et al. 2010, Aarts et al. 2013, Matthiopoulos et al. 2015). A question that often motivates researchers is whether or not habitat *selection* patterns are sensitive to these changes (van Beest et al. 2014a, van Beest et al. 2015). Answering this question relies heavily on assumptions about accessibility of important habitat types or resources (Beyer et al. 2010, Lele et al. 2013). Radio telemetry studies may track a population over the course of a time series, making targeted inference about the spatiotemporal process challenging.

Territoriality and associated changes in occupancy as a population increases can pose problems for traditional analytic approaches to the question of habitat selection. Habitat selection may be much different at low population densities than it is at high densities (Matthiopoulos et al. 2015, Yackulic et al. 2015). In Upper Michigan, USA, for example, gray wolves (*Canis lupus*) began to repopulate the region in the early 1990s and the population continued to grow from < 50 individuals (pre-1995) to > 600 (post-2010; Michigan Department of Natural Resources 2015). During this time, wolves established territories throughout the Upper Peninsula (UP) in areas where prey were abundant and human development was minimal. By the end of the time series, available suitable habitat for new colonizing packs was likely limited. From a habitat selection perspective, the available habitat distribution at the end of the study likely bore little resemblance to its distribution during early recolonization. Although this alone has consequences for habitat selection, the change in availability could also influence the used habitat distribution. For example, animals may adapt and become tolerant of lower quality habitat if choosing to do so poses less risk and thus offers potentially equal fitness benefits as competing for the best habitat (e.g. see ideal-despotic habitat distribution theory; Fretwell & Lucas 1969, Morris 1988). Alternatively, new arrivals can be “preempted” from existing habitats (Pulliam 1988, Pulliam and Danielson 1991, Morris 1994). Such site-dependent regulation (Rodenhouse et al. 1997) may have a strong influence on habitat selection.

Habitat selection is often perceived as a behavioral process. Understanding the influence that preemptive or despotic habitat distributions might have on traditional habitat selection models (Boyce and McDonald 1999, Manly et al. 2002, Johnson et al. 2006) is crucial to correctly interpreting an animal’s behavior. For example, an animal may exhibit preference for a specific limited habitat requirement (e.g. preferred food source). As population increases, habitats with more of the preferred food source become less available. At this point, individuals may adjust to changing conditions, thus changing their behavior (i.e. becoming more tolerant of lower quality habitat, or choosing to use an alternative food source). In this case, both the used and availability distributions shift. Habitat *selection* might remain constant if the rate of change in both distributions is balanced, but the strength of selection could appear to increase or decrease if the rate of change in used and available distributions is not equal. In fact, any combination of density- or time-dependent habitat selection scenarios is conceivable, and the observed dynamics would depend on strength of preference, relative availability, and substitutability of a given resource or habitat type. Thus, we suggest that understanding the nature of habitat selection requires tracking shifts in both habitat distributions (used *and* available), in order to correctly interpret any change (or lack thereof) in the habitat selection ratio (e.g. selection of a discrete habitat type, or a coefficient shift for a continuous habitat metric; see Aarts et al. 2013 and McDonald 2013 for explanation of selection ratios for discrete vs. continuous habitat representations).

Our objective was to provide a conceptual framework for understanding and graphically plotting used and available habitat distributions for theoretical habitat metrics under varying scenarios of preference, availability, and substitutability. Changes in the corresponding selection ratio (increase vs. decrease in strength of selection) depend on divergence or convergence of the central tendencies of used and habitat distributions; we demonstrated this by generating arbitrary habitat distributions on a spatial grid, simulating an increasing population where more and more units become occupied over the course of the time series, and plotting subsequent used and available habitat distributions along with their corresponding selection ratios. Conceptual results are informative and the method can easily be applied empirically.

## Methods

We explored the effect of changing habitat availability (aka, a functional response in habitat selection; Aarts et al. 2013) on continuous habitat coefficients for four scenarios of increasing population growth: S1 = a finite habitat type with strong selection and limited availability, S2 = an abundant habitat type which is selected for but not limited, S3 = a limited habitat type that is initially selected for but is increasingly substituted for by another habitat type as its availability declines, and S4 = an abundant habitat type with no initial selection, but becomes increasingly selected for as a substitute for another limited habitat type (e.g. the habitat in S3).

For each scenario, we simulated occupancy on a 10 × 10 grid and specified 15 time steps.  To model increases in occupancy, we specified a sigmoidal logistic growth function to represent an increase of proportion occupied from approximately 0.05 to 0.75 across the 15 unit time series. We used the 'scurve' function in R 3.2.2 package 'LS2Wstat' (Nunes et al. 2014, R Core Team 2015) to extrapolate the values between 0.05 and 0.75 at time $t = (1, 2, \ldots, 15)$. For each scenario, we specified a probability distribution function (PDF) for a continuous random variable representing an arbitrary habitat metric of interest, where the shape of the PDF was chosen depending on the scenario. For all cases, low values represented low quality habitat and vice versa. For example, a habitat with limited resources would have greatest density at values near or below 0, with greater values (i.e. upper tail of distribution) representing a limited supply of high quality habitat. Alternatively, a habitat with abundant resources would have greatest density at values above zero. We assumed constant territory size and occupancy in each example (e.g. Ridley et al. 2013, Haché et al. 2013) such that occupied territories could not overlap or change in size and once geographical units were occupied they remained so for all subsequent time steps.

*Scenario 1 (S1)*

In S1, we simulated dynamic habitat selection of a relatively limited, finite habitat type. Each geographical unit was assigned a habitat value $X_1 = (x_1, x_2, ..., x_{100})$ based on a normally distributed random variable with mean 0 and variance 1, i.e. $X_1 \sim N(0,1)$ (Fig. 4.1A). We specified the probability of an animal occupying a geographical unit *i* to be a sigmoidal function of $X_1$, with probability increasing as $X_1$ increased (Fig. 4.1B):

$$P(i=1) = \frac{1}{1+e^{-0.15x_1}} \tag{8}$$

where *i* = 1 indicates selection of unit *i*. The proportion occupied at each time unit similarly followed a sigmoidal function with a slope coefficient of 0.33: $N(t) = \frac{1}{1+e^{-0.33t}}$, where *N(t)* represented the number of units occupied at time *t*. We simulated occupancy by randomly sampling *n* units from the grid at each time step without replacement, where

$$n = \begin{cases} n(t) & \text{if } t = 1 \\ n(t) - n(t-1) & \text{otherwise (t > 1)} \end{cases} \tag{9}$$

and probability of occupying unit *i* followed (1). At each time step we estimated the used ($f_u[X_1]$) and available ($f_a[X_1]$) distributions of the habitat $X_1$ by computing its mean in the occupied (used) and remaining unoccupied (available) units. We repeated the procedure 100 times to generate a sample of independent time series. We then graphically plotted the used and available habitats as a function of time, and computed the ratio of used to available habitat at each time step: $\beta(X_1, t) = \frac{\exp(f_{u,t}[X_1])}{\exp(f_{a,t}[X_1])}$. As a final step, we used a local polynomial regression smoother to fit a trend line to the simulated used and available distribution time series and selection ratios.

*Scenario 2 (S2)*

In S2, we simulated dynamic habitat selection of an abundant but used habitat type. Each geographical unit was assigned a habitat value $X_2 = (x_1, x_2, ..., x_{100})$, which was based on a Beta distribution, i.e. $X_2 \sim Beta(\alpha = 5, \beta = 1)$ (Fig. 4.2A). The probability of occupancy for unit *i* in this case was specified similar to (1), with a slope parameter of 0.5 (instead of 0.15) and the range defined by $X_2$'s range. Selection of $X_2$ was thus slightly weaker than that of $X_1$, with an increase in probability of ~ 0.9 across the range of $X_2$ (Fig. 4.2B). Occupancy was otherwise simulated as in (2), and the used and available distributions along with corresponding selection ratios were estimated similar to S1.

*Scenario 3 (S3)*

In S3, we simulated dynamic habitat selection of a limited habitat type, this time defining rules for a declining probability of occupancy as occupancy increased. A motivating example would be an animal that switches from a preferred food item to an alternative source, thereby substituting one habitat type for another. Geographical units were assigned habitat values $X_3 = (x_1, x_2, ..., x_{100})$, which were based on a Beta distribution with highest density at low values, i.e. $X_3 \sim Beta(\alpha = 1, \beta = 5)$ (Fig. 4.3A). To model declining habitat use, we defined an initial probability of occupancy similar to S1 and S2, defining a slope parameter of 0.75 and range defined by $X_3$'s range, which corresponded to an initial probability of use increase of 100% across the full range of possible values (Fig. 4.3B). In this case, probability of use was a declining function of occupancy, modeled through the **β** coefficients of a generalized linear model (GLM) with a binomial response and logit link function. For example, the curve defining the initial relationship between $X_3$ and probability of use can be expressed as the linear model $\text{logit}(Y) = -7.5 + 15x + \varepsilon$, where $x$ is the habitat value (in this case, $X_3$). We specified use of $X_3$ to decline to near zero at occupancy > 0.75, using a logistic function for $\beta_0$ and $\beta_1$ in the GLM

$$\beta_0 = \frac{-7.5}{1 + \exp\{(0.5 - x) / -0.06\}} \tag{10}$$

$$\beta_1 = \frac{15}{1 + \exp\{(0.5 - x) / -0.06\}} \tag{11}$$

where $x$ was the proportion of units occupied. We used the 'SSlogis' function in R (Pinheiro et al. 2011) to estimate the scale and point of inflection parameters. Simulations proceeded as in S1 and S2, with estimation of used and available distributions along with the corresponding selection ratio.

*Scenario 4 (S3)*

S4 represents the substitute habitat type for S3, with initial selection near zero but increasing as occupancy increases. Geographical units were assigned habitat values $X_4 = (x_1, x_2, ..., x_{100})$, which were based on a Beta distribution with highest density at greater values, i.e. $X_4 \sim Beta(\alpha = 4, \beta = 2)$ (Fig. 4.4A). We defined an initial probability of use as in previous scenarios, this time with a slope parameter of 0.01 indicating very weak initial selection (Fig. 4.4B). In contrast to $X_3$, selection of $X_4$ was an increasing function of occupancy. Similar to S3, we specified an increase in $\beta_0$ and $\beta_1$ using logistic functions:

$$\beta_0 = \frac{-7.5}{1 + \exp\{(0.5 - x) / 0.06\}} \tag{12}$$

$$\beta_1 = \frac{7.5}{1 + \exp\{(0.5 - x) / 0.06\}} \tag{13}$$

where $x$ was the proportion of units occupied. Contrary to the previous example, the scale parameter is positive, resulting in a decreasing effect on $\beta$. Simulations proceeded as in the other scenarios.

## Results

*Scenario 1 (S1)*

Fig. 4.5 illustrates the simulated change in occupancy for one iteration of the 15-step time series, using S1 as an example. In S1, the animal exhibits strong selection for the habitat (greater habitat suitability in darker green), such that by the end of the time series the majority of remaining unoccupied units have unsuitable habitat values (Fig. 4.5, Fig. 4.6A). The results of all simulations are shown in Fig. 4.6. In S1, the strong selection for habitat $X_1$ resulted in a decline in both the used ($f_u[X_1]$) and available ($f_a[X_1]$) distributions (Fig. 4.6A). However, in this example, the depletion of remaining available habitat was evident by the end of the time series, resulting in a decline in the value of available habitat that was steeper than that of the used habitat (Fig. 4.6A). As a result, the selection ratio (use proportional to availability) increased with increasing occupancy over time (Fig. 4.6B).

### *Scenario 2 (S2)*

In S2, the animal used habitat at a rate that was nearly proportional to its availability (Figs. 4.2A, 4.2B, 4.6C). In this case, the used or available habitat distributions were both relatively static. As a result, the selection ratio also remained constant as occupancy increased (Fig. 4.6D).

### *Scenario 3 (S3)*

S3 demonstrates declining selection over time, as the animal's probability of using an initially preferred habitat type decreases as that habitat type becomes less available. The distribution of used habitat decreases more rapidly than that of the available habitat distribution (Fig. 4.6E), resulting in a declining selection ratio with increasing occupancy (Fig. 4.6F).

### *Scenario 4 (S4)*

In S4, the animal does not exhibit initial use of the habitat, but increases its use as occupancy increases. The result is an increasing used habitat distribution and a decreasing available habitat distribution (Fig. 4.4G), leading to an increasing selection ratio (Fig. 4.4H).

## Discussion

Habitat suitability modeling is necessary for understanding species requirements, but the effect of territoriality on modern habitat selection models has received little attention. Quantifying habitat selection often relies on a comparison between habitats used by an animal and habitats deemed to be available (Johnson 1980, Manly et al. 2002, Johnson et al. 2006). A disproportionate ratio between use and availability is the basis for inference in the broadly applied resource selection function (RSF; Boyce et al. 2002, Johnson et al. 2006). In addition, other habitat modeling tools such as species distribution models (SDMs; Phillips et al. 2006, Austin 2007) also rely on these comparisons, although it is not always explicitly stated (McDonald et al. 2013). Habitat selection can be dynamic, with multiple processes influencing an animal's space use as well as its perception of habitat or resource availability (McLoughlin et al. 2010, Aarts et al. 2013). We've demonstrated the effect that territoriality can have on the habitat selection ratio through competitive exclusion. Our framework is useful for investigating the behavioral mechanisms or ecological processes that cause changes in habitat selection when territorial behavior imposes constraints on habitat availability.

Density dependence has been identified as a major driver of spatiotemporal variation in habitat selection (McLoughlin et al. 2006, van Beest et al. 2014a, van Beest et al. 2015). Density dependent habitat selection has been primarily studied under the assumption of an ideal-free distribution (Morris 1988), which precludes geographic constraints on space use. Density dependent habitat selection is expected for territorial species, but space use patterns such as territory colonization and occupancy can have a profoundly different effect on the habitat selection process. Specifically, if competitive exclusion imposes ‘invisible barriers’ on geographic habitat availability at the landscape level (e.g. Pulliam and Danielson 1991, Rodenhouse et al. 1997), then habitat use, availability, and selection will be heavily dependent on the proportion of habitat occupied overall. Temporal variation in habitat selection can then be attributed to the importance and relative abundance of a given habitat type. We’ve shown that if a habitat is essential and limited in availability, then the habitat selection ratio is likely to increase with increasing density or occupancy, even while animals shift their utilization to lower quality habitat characteristics. However, abundant habitats that are used proportional to their availabilities (as in S2) may be interpreted as unimportant by researchers (e.g. no statistical effect in the habitat model) even if they receive high utilization (Aarts et al. 2013); this lends itself to the importance of an informed understanding of the specific rates of habitat utilization by individuals or populations (Millspaugh et al. 2006, Hooten et al. 2013) as well as estimates of relative habitat availability. A comprehensive analysis accounting for temporal change will also help to reveal habitats that are being substituted for (as in S3) or being used as a substitute (as in S4; van Beest et al. 2014b).

In our simulations, we assumed that landscape-level increases in density and occupancy did not result in changes in territory size and degree of overlap between territories. In reality, territorial individuals or groups may adjust shape, size, and boundaries of their home ranges to accommodate an increasing population (Ridley et al.

2004, Haché et al. 2013). If this is the case, then later arrivals or new colonizers may have access to some habitat and resources that were assumed to be unavailable in our simulation framework. Thus, habitat availability would be underestimated for the population, especially near the end of the time series. However, overlap in territories would have to be largely significant in order to marginalize the landscape occupancy-dependent effects that we observed. Moreover, overlap or crowding effects typically indicate that density dependent habitat selection is more consistent with that expected from an ideal-free distribution, as opposed to the ideal-preemptive or ideal-despotic alternatives (Morris 1994, Haché et al. 2013). Habitat selection and space use patterns are inescapably complex, and thus expectations or assumptions of territoriality should be qualified and tested whenever possible.

Simulated scenarios of habitat use, availability, and selection under strong assumptions of territoriality indicate that habitat selection can be temporally dynamic in ways that may be unexpected. Selection for a particular habitat can increase even when the habitat used by the individual or group declines over time due to density dependent saturation of high suitability habitat. In addition to providing ecologically relevant information that can often be overlooked, exploring temporal trends in habitat use and availability distributions will likely result in a more broadly informed analysis overall, and can reveal explanations for unexpected patterns in habitat selection. While this conclusion can also be applied to gregarious and social species, its significance is especially relevant to territorial species with population fluctuations resulting in range expansion or contraction over time. Modern evaluations of habitat suitability should recognize the potential for territoriality to constrain distributions of habitat availability, which are crucial for accurately assessing habitat selection.

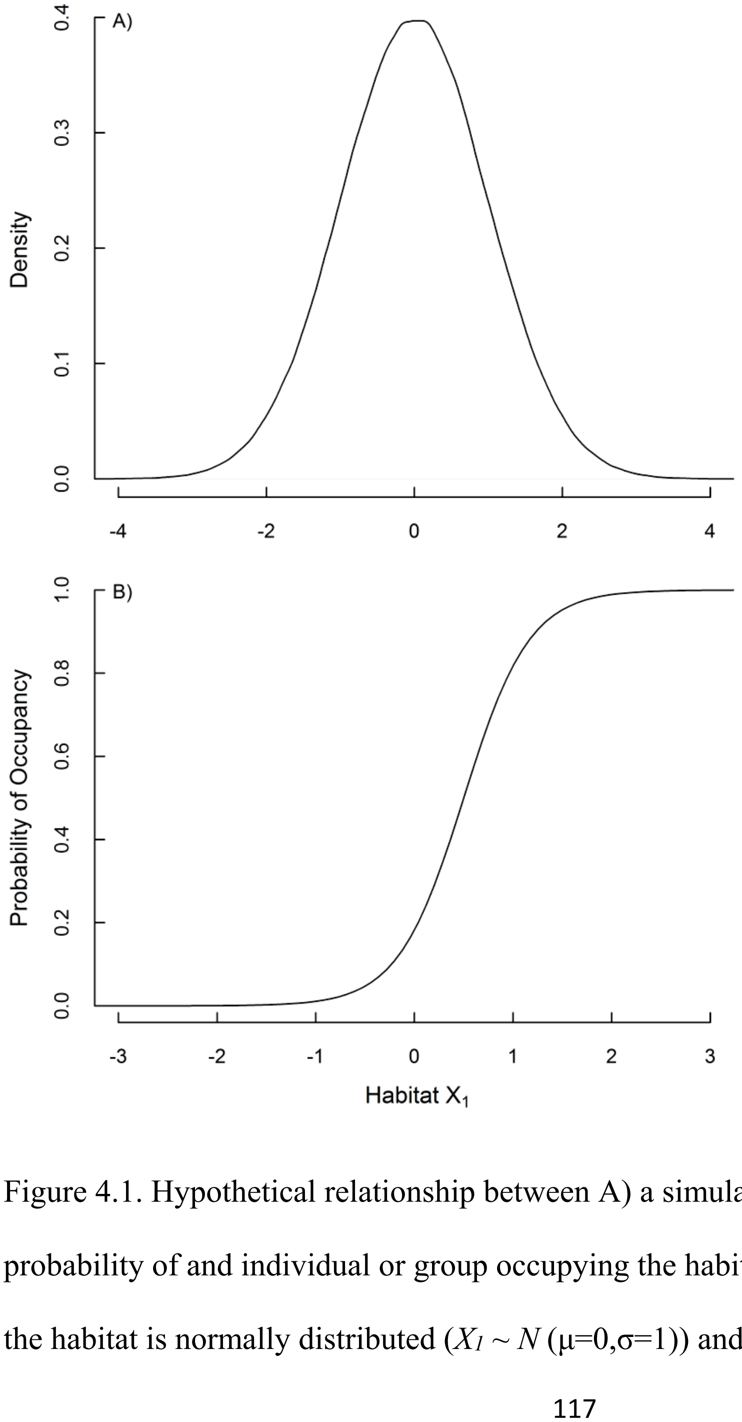

Figure 4.1. Hypothetical relationship between A) a simulated habitat and B) the probability of and individual or group occupying the habitat for Scenario 1 (S1). In S1, if the habitat is normally distributed ($X_1 \sim N$ (μ=0,σ=1)) and occupancy is related to larger

habitat values, then suitable habitat is limited such that selection will deplete available habitat over time.

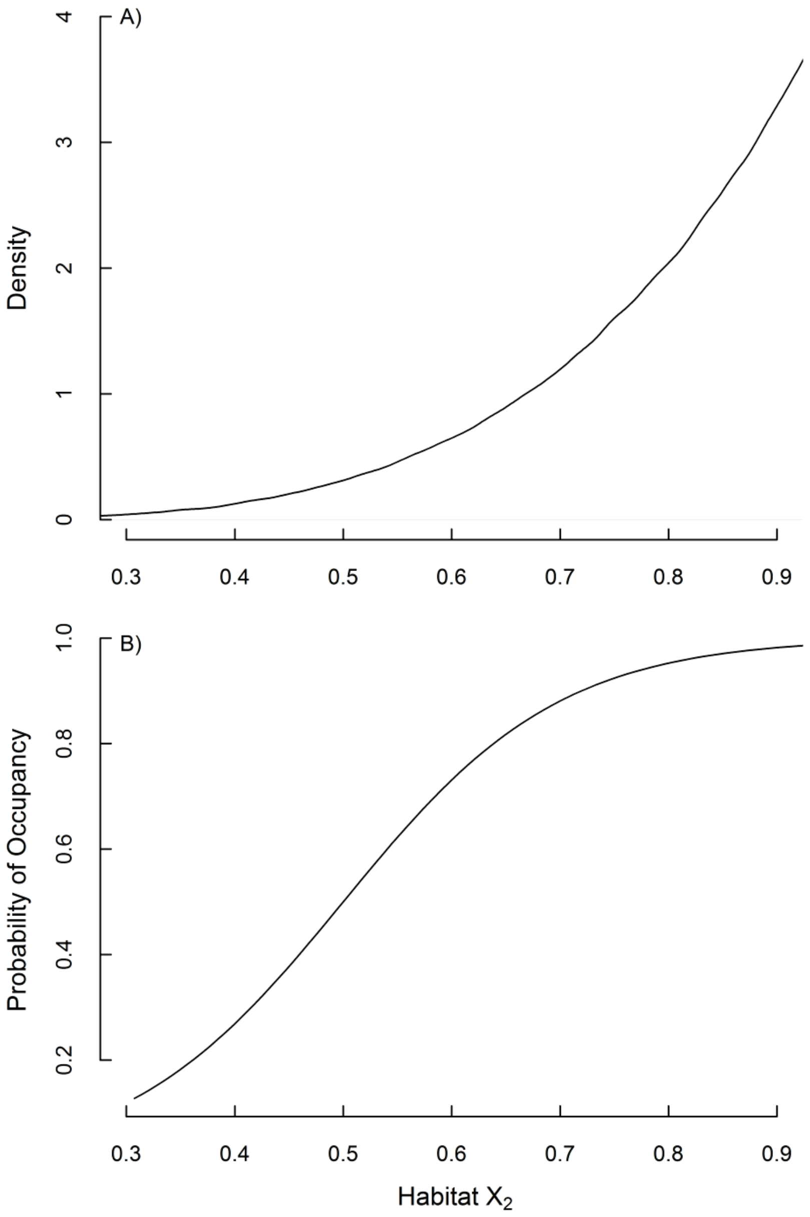

Figure 4.2. Hypothetical relationship between A) a simulated habitat and B) the probability of and individual or group occupying the habitat for Scenario 2 (S2). In S2, the habitat is Beta distributed ( $X_2 \sim Beta(\alpha = 5, \beta = 1)$ ); although occupancy increases with increasing habitat values, the habitat type is more abundant and thus is less likely to be depleted.

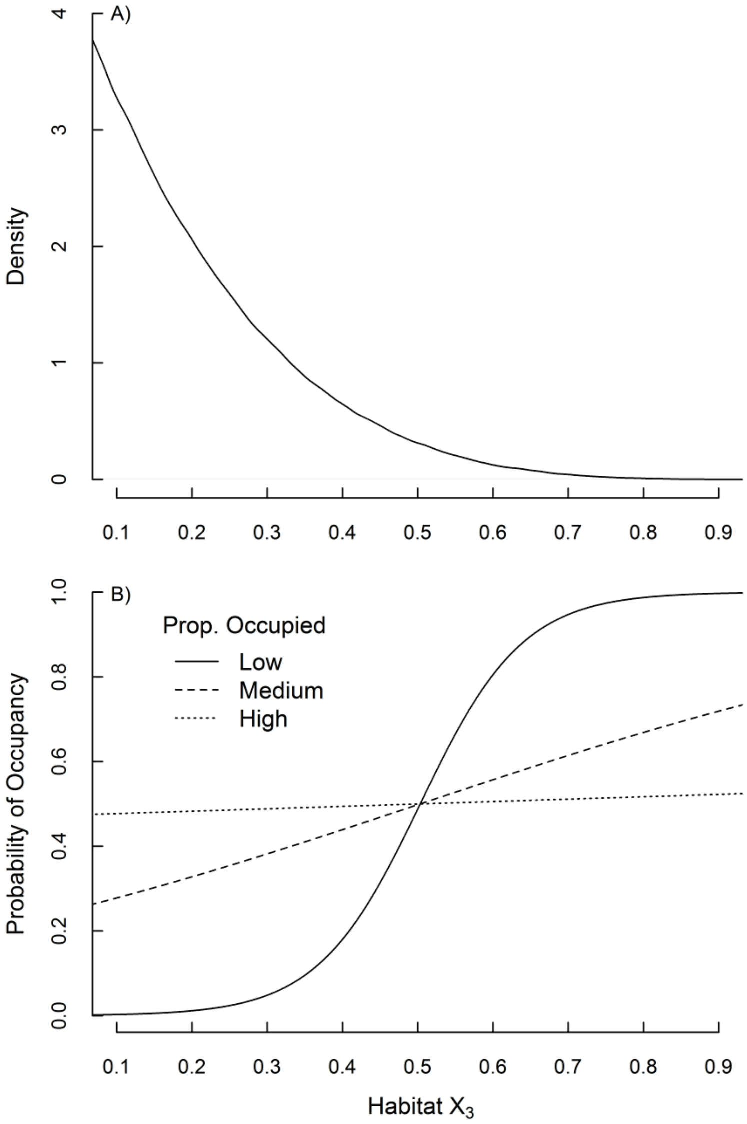

Figure 4.3. Hypothetical relationship between A) a simulated habitat and B) the probability of an individual or group occupying the habitat for Scenario 3 (S3). In S3, the habitat is Beta distributed ( $X_3 \sim Beta(\alpha = 1, \beta = 5)$ ) and probability of occupancy depends initially on $X_3$ but declines as the proportion of the landscape occupied increases. This scenario may occur when an animal switches to an alternative habitat type as the initial habitat becomes less available.

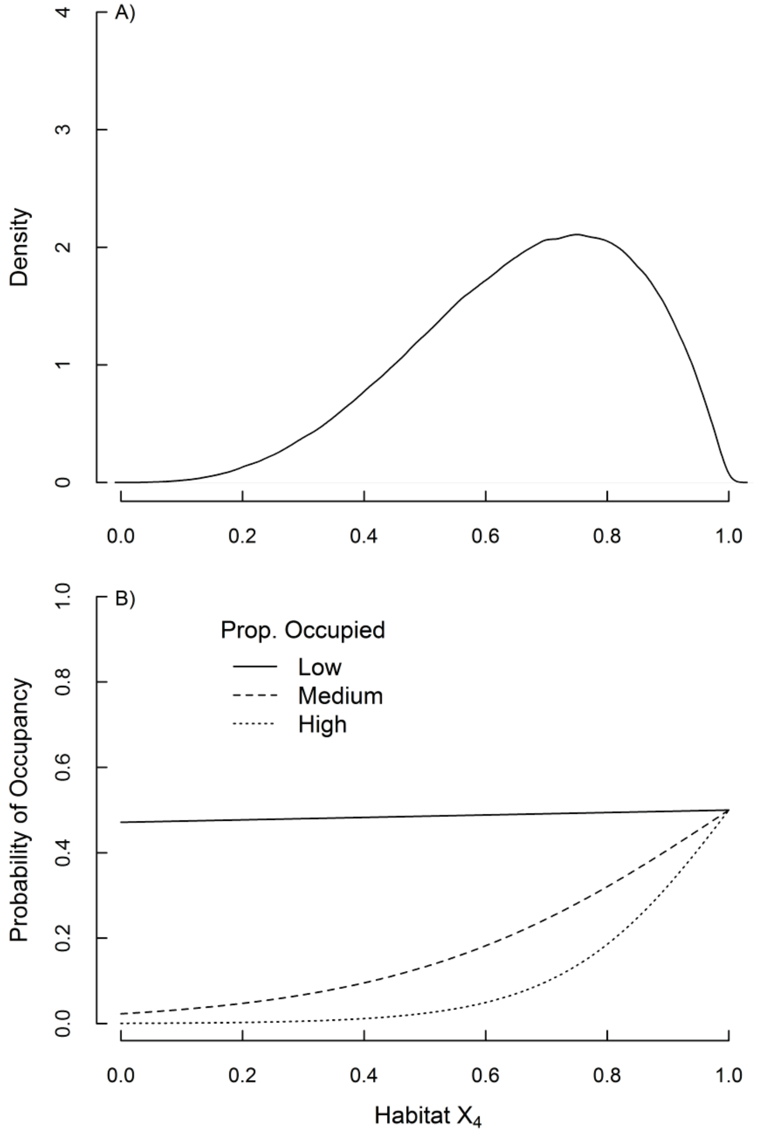

Figure 4.4. Hypothetical relationship between A) a simulated habitat and B) the probability of an individual or group occupying the habitat for Scenario 4 (S4). In S4, the habitat is Beta distributed ( $X_4 \sim Beta(\alpha = 4, \beta = 2)$ ) with no initial relationship between $X_4$ and occupancy. However, as occupancy increases, habitat $X_4$ becomes increasingly important. This scenario may occur when an animal switches from an alternative habitat type.

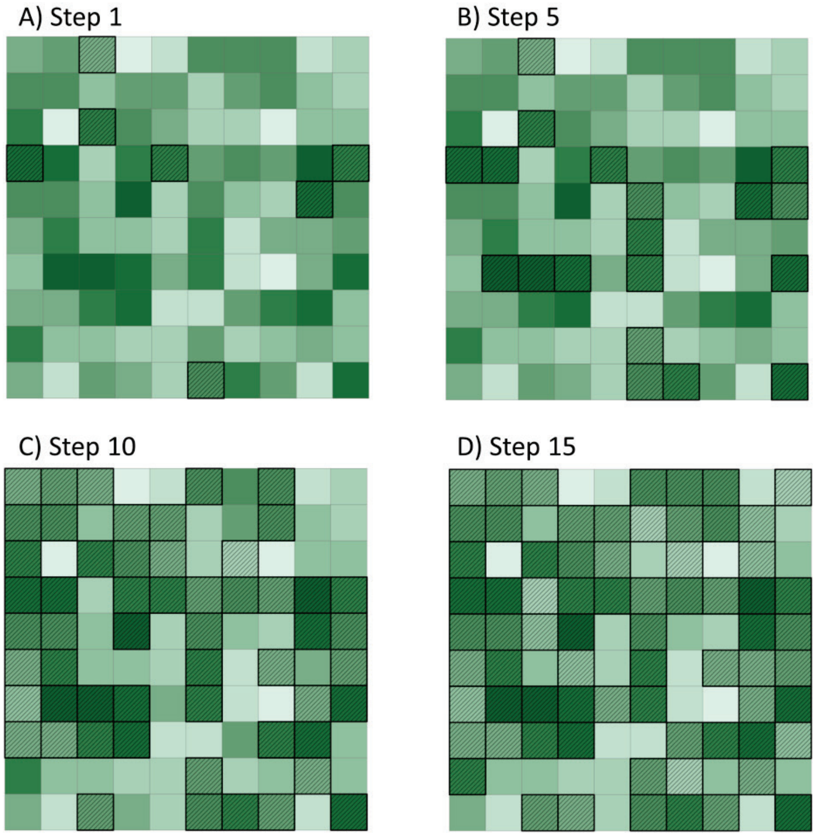

Figure 4.5. Demonstration of one simulation iteration of increasing occupancy over time from ~ 5% of units occupied to ~ 75% occupied for a limited but preferred habitat type. Bolded grid units with hash marks represent units that have become occupied at, e.g.

time steps 1 (A), 5 (B), 10 (C), 15 (D), while darker shades indicate greater habitat suitability.

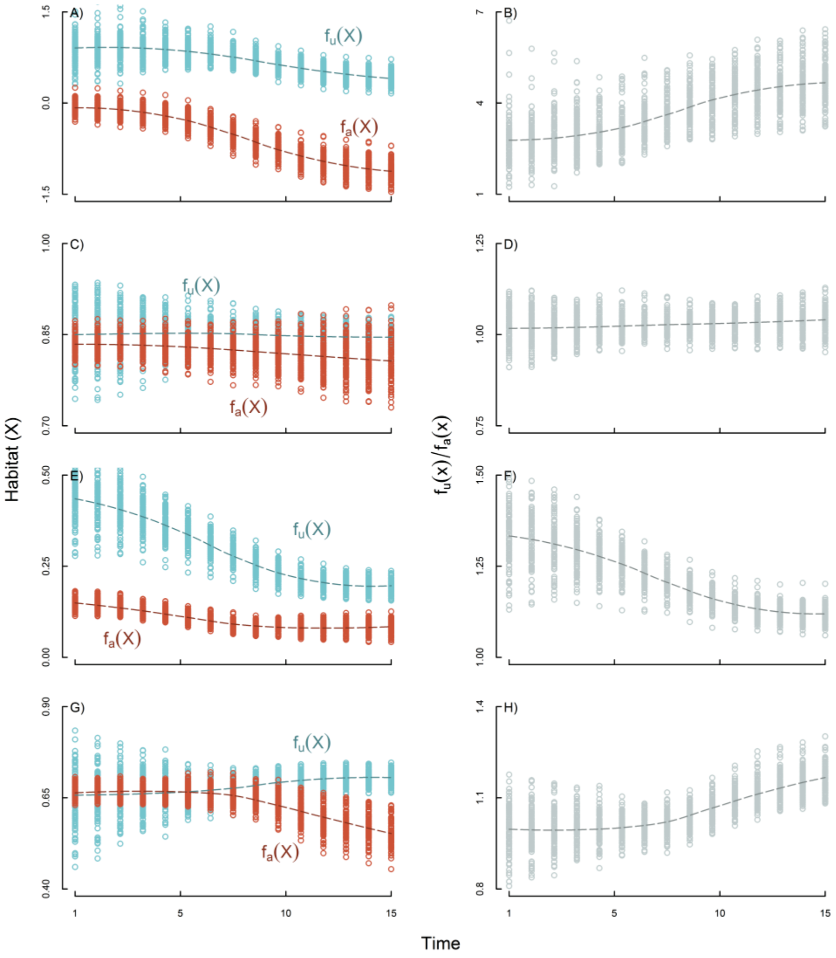

Figure 4.6. Results from simulations of used and available habitat (1st panel column; A,C,E,F) and corresponding selection ratios (2nd panel column; B,D,F,H) under assumptions of strong territoriality and increasing occupancy over time. Four hypothetical scenarios were evaluated in simulations, including an important, limited

habitat (A,B), abundant but important habitat (C,D), limited substitutable habitat (E,F), and more abundant substitute habitat (G,H). Results show that the change in the selection ratio is dependent on convergence or divergence between used and available habitat distributions as occupancy increases over time.

# 5. Implications of territoriality and density dependence on long term comparisons of used to available habitat distributions[4]

## Abstract

Habitat selection is a process that spans space, time, and individual life histories. Ecological analyses of animal distributions and preferences are most accurate when they account for inherent dynamics of the habitat selection process. Since habitat selection is a function of habitat availability, strong territoriality can constrain the habitat perceived to be available to individual animals or groups attempting to colonize or establish new territory. When considering a population change over time, broad-scale changes in habitat availability can drive density dependent variation in habitat selection. We investigated density dependent habitat selection over a 19-year period of gray wolf (*Canis lupus*) recovery in Michigan, USA using a generalized linear mixed model (GLMM) framework with habitat selection coefficients conditioned on random effects for wolf packs and random year intercepts (e.g. crossed random effects). In addition, we allowed habitat selection coefficients to vary as interactions with increasing wolf density over space and time. Results indicated that the probability of pack occupancy was driven largely by winter prey availability and human impact indices, but that selection coefficients for multiple predictors were density dependent. Density dependent habitat selection models had good fit to pack occupancy data, but changes in occupancy at the landscape level tracked changes in used and availability distributions more explicitly across time. Spatiotemporal dynamics and population changes can cause considerable

---

[4] The material contained in this chapter is in preparation for submission to the *Journal of Applied Ecology*

variation in wildlife-habitat relationships; we encourage modelers to adopt flexible approaches to account for potential influences of territoriality when applying traditional habitat selection procedures.

## Introduction

Investigating an organism's habitat preference and quantifying its realized niche is fundamental for ecologists (*sensu* Hutchinson 1957; Boyce and McDonald 1999; Pulliam 2000; Hirzel and Le Lay 2008). Population ecology and conservation biology in particular rely on habitat selection studies because identifying the factors influencing distributions, densities, gene flow, and fitness characteristics in species is necessary to manage populations and conserve habitat. Resource or habitat selection functions (RSFs or HSFs; Aarts et al. 2013) and species distribution models (SDMs) are broadly used to explore biotic elements that drive habitat use and species range (Warton and Aarts 2013). HSFs and SDMs have contributed greatly to our understanding of animal-habitat relationships, but applications are often limited in terms of predictive and explanatory capacity (Zurell et al. 2009, Yackulic et al. 2013).

Habitat selection is a process that spans multiple dimensions (3D space, time, life history; Morris 2003, Keating and Cherry 2009; Uboni et al. 2015a). The most accurate ecological analyses of animal distributions and preferences are those that recognize the inherent dynamics of the habitat selection process (McLoughlin et al. 2010, van Beest et al. 2015). Habitat selection is a function of habitat availability (a habitat selection functional response; Mysterud and Ims 1998, Matthiopoulos et al. 2011), and changes in availability may coincide with variation in the local population density of inter- or intraspecifics (density dependent functional responses; Tardy et al. 2014, van Beest et al. 2015). Changes in habitat availability can also occur as a result of environmental stochasticity (e.g. drought), or human impacts (e.g. land cover change). The degree to which functional responses are linked to density likely depends on the nature of competitive behavior between or among species. Evidence suggests that ideal-free consumers generalize their habitat selection with increases in conspecific density (Blix et al. 2014, van Beest et al. 2014a, van Beest et al. 2014b). In this case, the distribution of available habitat may change in composition but geographic availability can remain constant. However, territorial species are not as well understood and the implication of increasing density on corresponding availability distributions has not been addressed in a habitat selection framework.

Theory on pre-emptive or ideal-dominant habitat distributions suggests that territorial species should increase their use of sub-optimal habitat types as density increases (Fretwell and Lucas 1969, Pulliam and Danielson 1991, Morris 1994). Habitat matching under either of these scenarios is likely to be more complex than that of the ideal-free case, where variation in density theoretically reflects the quality of underlying habitats (Morris 1994). When assessing temporal variation in habitat selection by territorial species, treatment of the available habitat distribution (i.e. the probability density function of all locations available to be selected over an area of interest; Northrup *et al.* 2013) becomes complicated by the potential for exclusion (Pulliam and Danielson 1991, Rodenhouse et al. 1997) and/or despotism (Fretwell and Lucas 1969, Mosser et al. 2009). More specifically, the habitat distribution that is available to early arrivals will be different than that available to later arrivals. Assuming early arrivals recognize and occupy the best available sites (Pulliam and Danielson 1991), the available habitat distribution for later arrivals will not include these sites until they are again vacated.

By definition, evaluation of habitat selection in RSFs or HSFs depends on the ratio of used habitat to available habitat; if this ratio is ≠ 1, we conclude selection for (ratio >1) or against (ratio <1) a defined habitat type (Johnson 1980, Manly et al. 2002). The selection ratio is often assumed constant for relatively short-term studies, with inference occurring at the local population level. However, when temporal variation imposes changes in the used habitat distribution, the available habitat distribution, or both distributions, the resulting output can be difficult to interpret. When shifts in resource availability occur concurrently with changes in species density, attributing temporally-varying habitat selection coefficients to the appropriate process can be challenging (density-dependence, functional response, or both; McLoughlin et al. 2010, Matthiopoulos et al. 2015). This is especially true when territoriality influences the habitat available to colonizing animals.

In this paper, we introduce a methodological workflow to evaluate habitat selection by territorial animals in the presence of changing population density and environmental variation. To demonstrate our approach, we used a combination of long-term radio collar and snow tracking data on gray wolves (*Canis lupus*) during a period 20-year period of recolonization to the Upper Peninsula of Michigan. Our objectives were to 1) identify important predictors of wolf habitat selection occurring within our study area, 2) test for temporal variation in habitat selection, and 3) explore density dependent trends in habitat selection corresponding to the most important habitat predictors. In (3), we focus on density dependent habitat selection (hereafter, DDHS) by explicitly accounting for functional responses that occurred due to long-term changes in habitat predictors, such as a gradual decline in prey density. We also highlight the importance of modeling spatially varying density within a study area in addition to long-term population trends, as DDHS can occur at multiple scales (van Beest et al. 2014b, Laforge et al. 2016). We employ a site-occupancy approach (Rodenhouse et al. 1997) to account for changes in the habitat availability distributions for multiple habitat predictors. Under the assumption of competitive exclusion, we apply habitat selection models to each annual snapshot of wolf locations, but constrain the availability distribution to areas not already occupied by existing wolf packs.

Understanding DDHS for territorial species is valuable for multiple reasons. Changes in density or abundance may alter the response curves of predictors in a model, particularly if the population has undergone long-term growth or decline during the study. Furthermore, predictions of the ecological niche based on current conditions may be unreliable because populations are not likely to be at equilibrium with their environmental surroundings at any given time (though often assumed to be; Yackulic et al. 2015). In such cases, habitat quality may be reflected by habitat selection patterns only at low population densities (e.g., van Beest et al. 2014a), especially under assumptions of theoretical ideal-despotic or pre-emptive habitat distributions. Inferences from models that include density data while accounting for corresponding changes in habitat availability are also more likely to reflect population dynamics that are of interest. Variation in the population growth rate is likely to be partially dependent on habitat selection (Morris 1994, Matthiopoulos et al. 2015), with positive average growth rates typically associated with higher quality habitat (Pulliam 2000, Hirzel and Le Lay 2008). Furthermore, detecting behavioral changes associated with DDHS can reveal much about the limiting nature of a given habitat predictor (Fig. 5.1; Appendix 5A). For example, the distribution of used habitat typically will shift toward lower quality habitat as population density increases and quality sites become saturated; however, the available distribution (i.e. what remains and is not used) may also shift if quality habitat is limited (Fig. 5.1A). If the decline in the available distribution is steeper than that of the used distribution, than habitat selection *actually gets stronger* (Fig. 5.1B), indicating the finite nature of the given habitat predictor while also demonstrating its importance to the species. Understanding the influence of density-dependent mechanisms on habitat selection is especially critical for territorial and social carnivores such as wolves, particularly in areas where recolonization or range expansion is occurring.

## Methods

### *Overview*

We used radio-collar data from gray wolves in Michigan, USA to assess the effect of increasing wolf density on wolf habitat selection at the territory scale during a period of recolonization, 1995 – 2013. We expected wolves to recolonize based on the ideal despotic (IDD; Fretwell & Lucas 1969) or ideal preemptive distribution (IPD; Pulliam & Danielson 1991), where individuals either pre-emptively occupy highest quality sites (Rodenhouse et al. 1997), or claim territories based on competitive superiority (Mosser et al. 2009). By this expectation, highest quality sites would be selected first while abundance increased, until all of the best habitats were occupied. Packs would then compete for habitat and increasingly occupy marginal territories, potentially leading to source-sink dynamics and declines in vital rates and/or population growth rates (Pulliam 2000, Mosser et al. 2009, Cubaynes et al. 2014). We assumed that the distribution of habitat availability from an individual wolf pack's perspective varied depending on population abundance and local densities, such that areas occupied by existing packs became unavailable to new colonizers.

From a resource selection standpoint, this process would result in location and scale shifts in both the used and available habitat distributions, potentially leading to density-dependent habitat selection (McLoughlin et al. 2010) as the used habitat distribution becomes increasingly dependent on the *per capita* available habitat distribution. Importantly, we note that density-dependent habitat selection in territorial species can take any form if the available habitat distribution is allowed to vary with occupancy. For example, preference or avoidance of a given habitat suitability predictor could increase if the rate of change in the available distribution exceeds the rate of change in the used distribution. Alternatively, preference or avoidance could become weaker or remain constant (Fig. 5.1).

*Methodological framework*

Assessment of density-dependent habitat selection requires spatially explicit information on species distribution and abundance that also captures temporal variation at relevant scales (Matthiopoulos et al. 2015). These data are often gathered from long-term monitoring studies that include a population census or estimate of density that is repeated at a regular interval. Radio and GPS telemetry are perhaps the most broadly applied method for monitoring species distribution across time (Northrup et al. 2013). The Resource Selection Function (RSF; Manly et al. 2002, Johnson et al. 2006), its equivalent habitat selection function (HSF; Aarts et al. 2013, Matthiopoulos et al. 2015), and the Resource Selection Probability Function (RSPF; Lele and Keim 2006, Lele et al. 2013) are widely established tools for analyzing these data. These methods become increasingly powerful when combined with population information and/or indices of abundance (Matthiopoulos et al. 2015, Coates et al. 2016). In particular, the effect of density on habitat selection can reveal important insights about the realized vs. fundamental niche (Hirzel and Le Lay 2008, McLoughlin et al. 2010, van Beest et al. 2014b). Density-dependent habitat selection has not yet received thorough exploration for territorial species. This may be partly due to the difficulty in accurately defining habitat availability (Beyer et al. 2010, Aarts et al. 2013, Lele et al. 2013).

We approached this problem by assuming that site occupancy and territoriality were the primary mechanisms imposing constraints on habitat availability as the wolf population increased. Following derivations of the use-availability likelihood in McDonald (2013) and Aarts et al. (2013), we define relative habitat use as the probability density function $f_u X$:

$$f_u\left(X\right)=\frac{w(X)f_a(X)}{\int_E w(X)f_a(X)dX} \tag{14}$$

where the available distribution $f_a X$ within the study area comprises environmental covariates $X$ in multi-dimensional environmental space $E$, and $w(X)$ is the RSF or RSPF (Aarts et al. 2013, Lele et al. 2013). Equation 1 can be rearranged to show that $w(X)$ is proportional to the ratio of use to availability for the set of covariates $X$ (Aarts et al. 2013). Specifying habitat use as a weighted distribution (Lele and Keim 2006, Aarts et al. 2013) reveals the important implication that changes in relative use depend on changes in availability, unless otherwise adjusted for in $w(X)$ (e.g., McLoughlin et al. 2010, Matthiopoulos et al. 2011). To obtain the desired information about habitat selection (e.g. estimate $w(X)$ and the set of effects $\beta$), McDonald (2013) showed that a logistic regression approach can be used to obtain $\hat{\beta}$ by sampling used and available locations from the distribution of geographically available habitat (typically coded as 1's for used and 0's for pseudo-availability; Northrup *et al*. 2013) under the following conditions: the availability sample $S_a$ is $iid$ and represents all areas in $f_a X$ equally, the sampling domain *D* is the same for the used sample $S_u$, $S_a$ and $S_u$ do not depend on each other, and the exponential link is used to obtain the predicted values for $\hat{w}(X)$. Taking these constraints into account, it becomes apparent that a density-dependent habitat selection model for territorial animals is only valid when the availability distribution is realistically constrained to the unoccupied landscape for a given individual or group. Achieving this involves repetitively updating *D* to match the conditions being observed by a given individual or group *i* at a particular time *t*. In other words, traditional habitat selecting modeling can be used, but care must be taken to appropriately model the dynamic boundaries of the available habitat distribution and subsequent used and available sampling domains. To meet these criteria, we redefined the area available to each collared wolf pack in our study on an annual timestep. Our approach combined long-term occupancy patterns with radio-telemetry data to generate annual snapshots of area occupied, area available, and regionally varying wolf density. Thus, we were able to draw pack- and year-specific use and available samples from a dynamic sampling domain accounting for changes in wolf distribution and density over time.

### *Data collection*

Wolves were live-captured using foot-hold traps during spring and summer 1992 – 2013 as part of a larger Michigan Department of Natural Resources (DNR) wolf monitoring program (Beyer et al. 2009). Individuals were chemically immobilized (ketamine hydrochloride and xylazine, 100 mg/ml) using 0·11 mg/kg ketamine hydrochloride and 2 mg/kg xylazine and fitted with VHF radiocollars (Telonics, Inc., Mesa, Arizona, USA; Potvin et al. 2005). Wolves were located by fixed-wing single-engine aircraft approximately 1-2 times per week. Further details on the telemetry study can be found in Potvin et al. (2005), Vucetich et al. (2012), and Beyer et al. (2009).

We used data from Michigan DNR wolf track counts to estimate variation in wolf density over space and time. Track counts began in 1992 and continued throughout the duration of the study. The study site was divided into 21 units and all passable roads were surveyed during winter from trucks and snowmobiles (Potvin et al. 2005). Pack sizes and territory boundaries were established by intensive tracking efforts, with trackers using information from radio-collared wolves as well as recording all sign, such as territory markings, scat, and individual sets of tracks (Potvin et al. 2005). An accuracy assessment of the ground tracking efforts was conducted during an independent study (Vucetich et al. 2012), which revealed a 4% average difference between the separate counts (Beyer et al. 2009). In 2007, the state adopted a geographically stratified sampling plan to reduce the cost and effort of the survey. A panel design was implemented to increase the precision of abundance estimates which ensured that some sampled units were counted during successive years. Further description of the survey is provided online (http://www.wolfandwildlifestudies.com/downloads/Estimating_Wolf_Abundance_in_Michigan_060208_239125_7.pdf) with details about its development available in Potvin et al. (2005) and Beyer et al. (2009).

### *Estimation of territory boundaries*

Each wolf territory was established by a combination of radio-collar locations and track surveys. Following detection of a pack, territories were monitored either by aerial telemetry relocations from ≥ 1 resident individual wolves or by repeatedly visiting the site via the annual tracking survey. This allowed us to document pack presence and territory persistence over the course of the study. We delineated annual territory boundaries using the following framework: first, if ≥ 30 telemetry locations were available for a pack during a year (e.g. year = time $t$), we generated a unique territory home range for year $t$. If there were < 30 locations for year $t$, but ≥ 30 locations were available over the course of a 2- or 3-year time period ($t-1$, $t$, $t+1$), we generated the territory home range using a 3-year moving window. For all other years that packs were known to be present at their site, we generated long-term average territories using either A) locations from previous years, i.e. territories from previous steps, B) a combination of telemetry locations and tracks from surveys, or C) a minimum convex polygon based on track locations occurring over the full time series.

When telemetry locations were available ($n \geq 30$), we used a fixed kernel density estimator to create a utilization distribution (UD) for each pack territory during either year *t* or the 3-year moving window. The kernel bandwidth was estimated using the "plug-in" bandwidth estimator (Duong 2007) after first removing outlying locations (≥ 5 km from pack territory; Fuller 1989) and any individual wolves that did not consistently occupy a territory. We defined the territory home range as the 95% volume isopleth from the UD. Home ranges and bandwidth estimators were analyzed using packages 'adehabitatHR' and 'ks' in R 3.2.2 (Calenge 2006, Duong 2007, R Core Team 2015).

### *Annual Wolf Density*

Packs were counted during track survey efforts. The entire study area was counted from 1995–2006. For survey units that were not surveyed every year starting in 2007, we assumed that packs persisted if they were detected the years directly before and after the year for which the count did not occur. We used the midpoint to extrapolate pack size in these cases. The last year included in the study was 2013 but surveys continued the following year, allowing us to use data from 2014 to make extrapolations. We created a longitudinal matrix with pack territory as the subject unit (rows) and year as the time unit (columns). For each year in the study, each pack was either detected, assumed present, or not detected, and pack size estimates were recorded in a related table. We summed rows of the matrix to estimate total wolves and compared results to the Michigan Department of Natural Resources [DNR]'s abundance estimates (Michigan Department of Natural Resources 2008, 2015) to verify that our assumptions of occupancy and pack size were reasonable. The matrix was linked to a geodatabase with polygons for all territory home ranges estimated each year; all packs with counts $\geq 2$ were included in subsequent steps while lone individuals were assigned to remaining geographic space (i.e. area not occupied by an existing pack during year $t$). We converted pack sizes to density (wolves / 1000 $km^2$) for each territory, and ultimately generated a smoothed surface for each year using a circular moving window with radius approximately equal to median wolf dispersal distance (km), which was based on an exponential distribution with $\lambda = 1/55$ (from Treves et al. 2009). Geoprocessing steps were completed in ArcMap 10.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) using ArcPy for Python 2.7.2.

### *Landscape variables*

To characterize habitat in the study area, we considered land cover and topographic characteristics (i.e. natural features), indices of prey availability, and measures of human infrastructure and density (Fuller et al. 2003, Oakleaf et al. 2006, Mladenoff et al. 2009). For natural features, we used 30 m Digital Elevation Models (DEMs) to quantify topography, including measures of elevation, slope, and aspect. We used National Land Cover Data (NLCD) to quantify land cover characteristics, such as open areas (i.e. inverse of forested land), water/wetlands, and edge habitat (interface between forested and open areas). Stream densities were also derived from Michigan's hydrography framework. Land cover characteristics were evaluated using the 1992, 2001, 2006, and 2011 products to represent any land cover change occurring during the time series. We considered several predictors assumed to be representative of prey availability on the landscape. Wolves primarily prey on white-tailed deer (*Odocoileus virginianus*) in the UP; although population estimates were unavailable for deer over the entire course of the study, buck harvest data estimated by hunter surveys (e.g. Frawley 2010) provided a consistent index for overall deer density at the county level. However, most deer in the UP are obligate seasonal migrators due to heavy winter snowfall. Consequently, high concentrations of deer in winter are found in dense coniferous canopy cover, often consisting of eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*), which intercept large amounts of snowfall and provide important cover (Witt et al. 2012). These deer wintering complexes (hereafter, DWCs) have been mapped by state biologists since the 1930s (see Appendix 5B for details). Distance to DWC and proportion of DWC within a moving window were combined in a principal components analysis to create an index of winter prey availability (see Appendix 5B). Measures of human infrastructure, indices of human population density, and proportion of public land were generated from NLCD, TIGER/Line roads files, and the U.S. Protected Areas Database (GAP Analysis program; see Appendix 5B). The percent developed impervious data product was used as an index for human activity, agricultural land was extracted from NLCD land cover products, and minor roads, and major highways were separated from each TIGER/Line file. Protected areas were extracted from GAP products and comprised mainly land under state and federal ownership. We used moving window analyses to develop spatially-explicit surfaces for each landscape feature considered. The size of the circular assessment window was set to 50.75 km$^2$, which was ¼ of the mean wolf home range estimated during the study. Spatial variables were evaluated in ArcGIS 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We standardized each variable for each year in the analysis to remove temporal trends in covariate values prior to model-fitting. Hence, each covariate's value was relative to its availability on the study site for any given year. Full details on the data sources, development and representation of spatial landscape variables are provided in Appendix 5B. Spatial analysis of environmental features often produces many correlated predictors, which can interfere with model-fitting and interpretation of results (Dormann et al. 2013). To reduce the number of variables considered and avoid redundant predictors, we initially fit generalized linear models using penalized maximum likelihood to select a subset of predictors from the original set (Friedman et al. 2010, Tibshirani et al. 2012). Details on preliminary model reduction are in Appendix 5C.

### *Use/Availability Sampling Design and Resource Selection Probability Functions*

To characterize the used ( $f_u X$ ) and available distributions ( $f_a X$ ) necessary for estimating an RSF, we used a random sampling design (Northrup et al. 2013), where habitat used by wolves was compared to available habitat (i.e. not occupied by other packs) at the territory level (2nd order selection; Johnson 1980). At the wolf pack level, each year-specific pack territory boundary represented the sampling domain for used locations for individual *i* and time *t* ( $S_u^{ti}$ ). The availability sampling domain ( $S_a^{ti}$ ) was specific to each individual and year as well, and was based on the boundaries described in *Estimation of Territory Boundaries*. We assumed that wolf dispersal follows an exponential distribution with a mean distance of 55 km ( $\lambda = 1/55$ ; Treves et al. 2009). In this case, 95% of dispersal distances are less than 165 km, so we buffered 165 km from the center of the individual's home range to set a maximum geographic range for $S_a^{ti}$ . We restricted geographic availability for each individual by removing all areas known to be occupied at time *t* from the buffered home range. $S_a^{ti}$ was the union of individual *i*'s home range and unoccupied habitat within its range at time *t*. This analysis was repeated for all individuals and all years in the study. We drew 5 random locations from each $S_u^{ti}$ and 25 random locations from each $S_a^{ti}$ to characterize annual used and available distributions. All random locations were updated with values from landscape variables, standardized estimates of wolf density, and factors representing pack territory and biological year. We automated use-availability sampling using the ArcPy module in Python 2.7.2 and ArcMap 10.3 (Environmental Systems Research Institute, Inc., Redlands CA, USA).

We used a Generalized Linear Mixed Model (GLMM) framework to accommodate unbalanced subpopulations, repeated sampling of the same packs over multiple years, and correlations that may otherwise exist among packs (Hebblewhite and Merrill 2008, Bolker et al. 2009). We used the binomial family of distributions to approximate the use-availability likelihood (McDonald 2013), where used locations are coded 1 and availability locations coded 0. To represent our time- and pack-specific sampling design, we modelled pack and year as random (crossed random intercepts for pack and year + random pack coefficients; Hebblewhite and Merrill 2008; Bolker et al. 2009). This allowed estimates of $\beta$ to be conditioned on used and available sampling distributions for each pack-year.

We obtained estimates of $\beta$ by fitting models with Integrated Nested Laplace Approximation in R-INLA (Rue et al. 2009), which provides a highly flexible environment for fitting a large variety of spatial and spatiotemporal models using a Bayesian hierarchical modeling framework (Rue et al. 2009, Blangiardo et al. 2013). We fit a latent Gaussian model akin to $Y \sim \mathbf{X\beta} + f(t) + f(\mathbf{x}, i)$, where $Y$ represents used vs. available observations, $\mathbf{X}$ is the matrix of landscape variables with associated regression parameters $\boldsymbol{\beta}$, $f(t)$ is a random *iid* intercept for year, and $f(\mathbf{x}, i)$ represents random *iid* effects for pack. For all landscape variables, we included a density-dependent interaction effect where the main effect of the variable was modeled as a function of wolf density (McLoughlin et al. 2010). By default, all regression parameters were assigned uninformative Gaussian priors. To estimate the RSPF from the model, we included the mean of the marginal posterior density estimate for each $\beta$ in the RSPF (Logistic) model formula (Johnson et al. 2006, Lele and Keim 2006):

$$\hat{w}^*(\mathbf{X}) = \frac{\exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_k x_k)}{1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_k x_k)} \qquad (15)$$

Note that (2) refers to the population-level estimate, which is not specific to any pack or year. We reported population-level effects for model covariates, which corresponded to the average  across the full time series, including all packs and years (e.g. Hebblewhite & Merrill 2008). To demonstrate braod-scale spatial heterogeneity, density-dependence in probability of use, and temporal change, we also extrapolated fitted model values for the early (1995 – 2000), middle (2001 – 2006), and late (2007 – 2013) time periods of the study. These results were obtained by extracting pack- and year-specific fitted values from the model at each used/available sample point, and generating a spatially smoothed probability surfacesusing Empirical Bayesian Kriging in ArcGIS 10.3. We evaluated the model fit by computing Pearson's correlation (*r*) between mean predicted and observed values and assessing the model's ability to discriminate between occupied and unoccupied locations using the Receiving Operator Characteristic and Area Under Curve (AUC) statistic (Robin et al. 2011). Finally, we performed leave-one-out cross-validation via the log-conditional predictive ordinate statistic (LCPO; Held et al. 2010, Beguin et al. 2012).

## Results

### *Data Attributes*

During the course of the study, 371 individual wolves were captured and relocated by aerial surveys, and 30,091 locations were recorded. Track surveys identified 229 unique pack territories overall, with annual territory counts ranging from 33 (1995) to 102 (2006). Mean pack size during the study was approximately 4 wolves and increased over time, with annual means ranging from 2.74 (SE = 0.86) to 5.18 (SE = 3.40; Table 5.1). The wolf population increased from an estimated 80 individuals (1995) to 687 (2011) before evidently stabilizing (recent estimates 618 – 658; Michigan DNR

2015, Michigan DNR unpublished data). The overall population growth rate during this time declined from $r = 0.16$ (1995 – 1996) to $r = -0.01$ (2009 – 2010, 2011 – 2013), and appeared consistent with density-dependent logistic growth (Mills 2012). Mean wolf density increased from approximately 1.86 / 1000 km$^2$ in 1995 to > 15 / 1000 km$^2$ in 2011 – 2013 (Table 5.1) and was geographically variable (Fig. 5.2). Wolves recolonized the majority of suitable habitat during the study. Tracking and radio telemetry revealed 135 packs occupying ~ 63% of the UP by 2011 (Table 5.1). Sampling from used and available (unused) distributions over time resulted in 48,480 locations for the entire study period.

### *Variable selection*

Penalized maximum likelihood model reduction procedures resulted in dropping 5 of the initial 15 predictors of wolf habitat: % open cover types, % water/wetlands, distance to highway, topographic radiation aspect index, and average snow depth. Dropping predictors indicated that they did not contribute substantially to predictions of wolf habitat selection. Predictors retained in the subsequent modeling included buck kill index, winter prey index, stream density, slope, elevation, forested-open edge density, road density, % impervious developed, % agricultural land, and % public land (Table 5.2). Marginal posterior distributions for main effects in the final model (conditional on average wolf density) indicated that wolf habitat selection was driven by prey availability (buck kill and winter prey indices), human influence (% impervious surface), and topography (elevation and slope). The effects of elevation and slope were parabola-shaped (e.g. quadratic function; Table 5.2), indicating selection for intermediate topography. Credible intervals (95% CI) overlapped zero for all other effects at the population level. However, posterior CIs for density-dependent interactions were relevant (i.e. 95% CI did not include zero) for many effects even when the main effect was not a strong predictor of habitat selection (Table 5.2).

*Model fit & parameter estimates*

Diagnostics from our final model indicated good model fit ($r = 0.82$, AUC = 0.98, LCPO = 0.25), suggesting that density dependence was an important component of habitat selection in our study area. Specifically, the effect of winter prey decreased with increasing density ($\hat{\beta}_{w\text{int er prey} \times \text{density}} = -0.151,\ 95\%\ \text{CI} = [\text{-}0.194, \text{-}0.109]$), as did the effects of elevation ( $\hat{\beta}_{\text{elevation} \times \text{density}} = -0.384,\ [\text{-}0.484, \text{-}0.285]$ ; $\hat{\beta}_{\text{elevation}^2 \times \text{density}} = 0.158,\ [0.084, 0.232]$) and stream density ($\hat{\beta}_{\text{stream} \times \text{density}} = -0.151,\ [\text{-}0.202, \text{-}0.099]$ ). In contrast, effects increased significantly with density for road density ($\hat{\beta}_{\text{road} \times \text{density}} = 0.129,\ [0.052, 0.206]$ ), slope $\hat{\beta}_{\text{slope} \times \text{density}} = 0.134,\ [0.040, 0.227]$ ; $\hat{\beta}_{\text{slope}^2 \times \text{density}} = -0.008,\ [\text{-}0.062,\ 0.046]$, and % public land ($\hat{\beta}_{\text{public land} \times \text{density}} = 0.058,\ [0.009, 0.108]$ ). All other density-dependent terms had effects overlapping zero (Table 5.2), although the interaction with forested-open edge could be considered nearly significant ($\hat{\beta}_{\text{edge} \times \text{density}} = -0.066,\ [\text{-}0.133, 0.000]$ ). Relative effect sizes for interaction terms are more easily interpreted graphically (Fig. 5.3). For example, the change in the slope for winter prey (with respect to log-odds of wolf pack occurrence) is evident in Fig. 5.3A, but the overall effect of winter prey remains positive even at the highest wolf density. In contrast, the sign of the main effect for stream density was positive at low wolf density and negative at high wolf density (and ~ 0 at median wolf density), indicating density-dependent switching of preference (Fig. 5.3B). A similar transition was observed for the road density effect, although the change in selection was less dramatic (Fig. 5.3C). Density dependent changes are less evident for % public land (Fig. 5.3D), elevation (Fig. 5.3E), and slope (Fig. 5.3F), despite the statistical evidence of the interaction effect.

### *Mapping habitat selection*

Density dependent habitat selection predicted changes over time, as wolf pack occupancy expanded from the beginning of the study (1995) to the end (2013). Modelled probability of pack occurrences captured this dynamic (Fig. 5.4).

## Discussion

Territorial species should increase their use of sub-optimal habitat types as density increases (Fretwell and Lucas 1969, Pulliam and Danielson 1991, Morris 1994). Applied habitat selection models typically do not capture the spatiotemporal dynamics associated with density dependent changes in used and available habitat distributions. Understanding the potential for a functional response in habitat selection (Matthiopoulos et al. 2011, Aarts et al. 2013) associated with increases in density is critical for accurate habitat modeling in territorial species. Density dependent habitat selection dynamics in ideal-free consumers have received wide recognition (McLoughlin et al. 2010, van Beest et al. 2014a). However, little attention has been given to the case where changes in site occupancy influence the used and available habitat distributions for species that exhibit strong territoriality, and thus theoretically follow an ideal despotic or ideal preemptive habitat distribution (Morris 1994, Falcy 2015). We found that habitat selection was density dependent with respect to multiple habitat predictors for social and territorial gray wolves. However, changes in density (e.g. localized growth rates) varied temporally *and* spatially, which complicated interpretation of the habitat selection functional response.

Wolves' preference for areas with greater prey availability decreased as density increased (Table 5.2, Fig. 5.3). Similarly, weak preference for greater stream densities switched to avoidance as density increased (Table 5.2, Fig. 5.3). Selection of areas with greater road density, greater slopes, and greater proportion of public land increased with increasing wolf densities (Table 5.2, Fig. 5.3). We assumed that density dependence was primarily responsible for functional responses in habitat selection. However, a post-hoc assessment of interannual variation in used and available habitat distributions and associated selection ratios revealed that density did not fully explain changes over time (Fig. 5.3). While spatial heterogeneity in wolf density was clearly an important component of habitat selection, changes in overall landscape occupancy (see Table 5.1) appeared to be a better indicator of long-term change. For example, important predictors of wolf habitat selection included indices of prey availability and human impact (Table 2). Our density dependent habitat selection model suggested that preference for greater prey availability decreased with increasing wolf density. Used and available distributions of prey availability both declined over time (Fig. 5.5a, b), but increased with increasing wolf density (Fig. 5.5c). Since the rate of change in the prey availability distribution exceeded that of the used distribution, the selection ratio of prey availability evidently *increased* over time (Fig. 5.5d, e) which was not captured by changes in wolf density (Fig. 5.5f). This result matched expectations for a limited, preferred resource or habitat type (Fig. 5.1a, b) where availability becomes 'depleted' with increasing population size and occupancy. With respect to human impact, wolves avoided more developed areas but the modelled effect was not significantly density dependent (Table 5.2). Used and available distributions of human impact both increased over time. Similar to prey availability, the rate of change in the availability distribution exceeded that of the used distribution, leading to apparent increased avoidance over time (Fig. 5.6a, b, d). Again, this result was not reflected by changes in density, but was represented by changes in landscape occupancy over time.

Site-dependence, rather than density dependence, may be a more natural regulating mechanism for population abundance when species exhibit territoriality (Rodenhouse et al. 1997). Under preemptive habitat selection, sites with greatest suitability are selected above those of lesser suitability until the greatest suitability sites are all occupied (Pulliam and Danielson 1991, Morris 1994, Rodenhouse et al. 1997). Negative feedback in demographic rates occurs when lower quality sites are increasingly selected for (i.e. indicating the best sites have become saturated; Rodenhouse et al. 1997). In other work, we showed that the ideal preemptive habitat distribution is likely for wolves, and that localized increases in density occurred more rapidly in certain areas with greater prey availability and lower human influence (Chapter 3, this dissertation).

Furthermore, density dependence appeared to operate on a shorter time scale in these areas, and was lagged in areas with fewer high suitability sites. Under site-dependent regulation, density may be a poor predictor of large-scale changes in geographic availability of resources or suitable habitat sites. For example, wolf packs consistently occupy territories regardless of whether pack size is small (e.g. 3 wolves) or large (e.g. 10 wolves). In addition, density can increase rapidly in an area of high suitability and crowding can occur while landscape-level occupancy stays relatively constant. As a result, functional responses in habitat selection may be better explained by landscape-level occupancy as opposed to density when considering models that compare used to available habitat metrics for territorial species.

Proportion of landscape occupied is more directly related to the used vs. available habitat framework implemented in RSFs or RSPFs. If density information is available, it may be more appropriate to use it as the response variable (rather than presence/absence) in habitat models or population growth models as opposed to using RSFs or RSPFs (Matthiopoulos et al. 2015). Landscape occupancy is also simpler to interpret when modeling the effect that change over time has on the RSPF. In our study system, changes in density varied spatially and on multiple time scales which complicated interpretation (Chapter 3, this dissertation). In contrast, changes in occupancy over time were more intuitive when explaining long-term change in habitat preferences.

Spatiotemporal change in habitat model effects is expected when data are collected over a time series (Aarts et al. 2013, Matthiopoulos et al. 2015). Modeling density- or occupancy-specific selection functions can help to account for change. However, accurately modeling a dynamic availability distribution is critical, especially in territorial species' undergoing population change. We used random effects within our model framework to assess selection conditional on year and pack specific variation. Assuming territories were no longer available to new colonizers, we were able to redefine geographic habitat availability on an annual time step. As such, temporal changes in habitat selection associated with changing occupancy were accounted for. Random effects have an additional benefit which is rarely addressed in modern habitat modeling efforts, namely the opportunity to explore individual or group level heterogeneity (e.g. Hebblewhite and Merrill 2008). Random coefficients (also referred to as random slopes) defined on the individual or group with respect to one or more covariates allow one to explore deviations from the overall population-level mean, which can then be linked to performance-based metrics such as survival or reproduction (Gaillard et al. 2010, Coates et al. 2017). Although this was not our primary objective in this paper, our modelling framework presented the opportunity to explore differences in selection among wolf packs so we briefly present an example. In a post-hoc analysis, we compared average annual pack sizes for packs that exhibited greater selection for the prey availability index ($\beta$ coefficient > 75th percentile value) to those with weaker selection ($\beta$ coefficient < 25th percentile value). In a non-parametric Mann-Whitney distribution test, packs with weaker selection had lower pack sizes (2 – 7 wolves, $\bar{x} = 2.97$ wolves) than those with stronger selection (2 – 12 wolves, $\bar{x} = 4.01$ wolves; $W = 1079$, $p = 0.016$). This result would appear to indicate a fitness consequence associated with habitat selection by individual wolf packs, where packs that recognize and select habitats with greater prey availability may be able to achieve greater productivity (i.e. through reproduction and recruitment) than those with weaker habitat selection. However, it is again important to recognize that selection under the constraints of territorial behavior may be driven more by local or regional conditions (e.g. availability of prey in unoccupied areas) than an individual or group choice. The latter result is supported by our modelled evidence of a decline in selection of greater prey availability with increases in wolf density.

### *Conclusions*

Territorial animals should exhibit habitat selection patterns that are fundamentally different than those of more gregarious species. The effect of increasing occupancy and density over time means that what is perceived to be available to early colonizers is likely vastly different than later occupants. Accounting for density or occupancy dependent habitat selection at the landscape scale is critical for identifying and understanding key limiting habitat factors and their relative availabilities. In Michigan wolves, the limiting nature of prey availabilities was demonstrated by increasing wolf habitat selection over time, which was driven by rapidly declining geographic availability of areas that typically support overwintering white-tailed deer. This is an important example of a habitat selection functional response driven by colonization, density dependence, and changes in occupancy.

Table 5.1. Estimation of gray wolf minimum population, pack size, and occupancy during a 19 year period of recovery in Michigan, USA.

| Year | N | N /1000 km$^2$ | N (Packs) | Pack size (mean) | Pack size (SE) | Area occupied (km$^2$) | Proportion of study area occupied |
|---|---|---|---|---|---|---|---|
| 1995 | 80 | 1.86 | 27 | 2.74 | 0.86 | 5753 | 0.14 |
| 1996 | 116 | 2.70 | 23 | 3.33 | 1.81 | 6719 | 0.17 |
| 1997 | 112 | 2.61 | 31 | 2.89 | 1.08 | 9002 | 0.22 |
| 1998 | 140 | 3.26 | 39 | 3.14 | 1.39 | 9869 | 0.24 |
| 1999 | 174 | 4.05 | 55 | 3.02 | 1.32 | 13292 | 0.33 |
| 2000 | 216 | 5.02 | 65 | 3.21 | 1.46 | 16063 | 0.40 |
| 2001 | 249 | 5.79 | 73 | 3.49 | 2.06 | 15677 | 0.39 |
| 2002 | 278 | 6.47 | 70 | 4.29 | 2.34 | 15868 | 0.39 |
| 2003 | 321 | 7.47 | 79 | 4.56 | 2.54 | 15373 | 0.38 |
| 2004 | 360 | 8.37 | 89 | 4.60 | 2.76 | 17993 | 0.44 |
| 2005 | 405 | 9.42 | 98 | 4.59 | 2.54 | 20326 | 0.50 |
| 2006 | 434 | 10.10 | 99 | 4.65 | 2.71 | 19719 | 0.49 |
| 2007 | 509 | 11.84 | 111 | 4.91 | 2.50 | 22696 | 0.56 |
| 2008 | 520 | 12.10 | 122 | 4.40 | 2.66 | 23659 | 0.58 |
| 2009 | 577 | 13.42 | 120 | 5.18 | 3.40 | 22642 | 0.56 |
| 2010 | 557 | 12.96 | 128 | 5.06 | 3.16 | 23703 | 0.58 |
| 2011 | 687 | 15.98 | 135 | 5.07 | 2.81 | 25533 | 0.63 |
| 2012 | NA |  | 123 | NA | NA | 23335 | 0.57 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 2013 | 658 | 15.31 | 129 | 5.15 | 2.67 | 23967 | 0.59 |

Table 5.2. Posterior marginal distributions for predictors of wolf pack occurrence in the Michigan, USA, 1995-2013. Predictors were modeled as a function of wolf density, which varied both spatially and temporally. Models were fit using random effects for time and pack territory, thus accounting for repeated sampling of occurrence over time. Posterior distributions for each parameter were estimated using Integrated Nested Laplace Approximation in R (R-INLA), and reported effects correspond to the population-level effect while accounting for pack-level variation.

| Parameter | Mean | SD | 2.5th Percentile | 97.5th Percentile | Mode | mean/se |
|---|---|---|---|---|---|---|
| **Intercept** | **-9.776** | **0.552** | **-10.924** | **-8.750** | **-9.704** | **-17.711** |
| **Buck kill index** | **-0.802** | **0.169** | **-1.143** | **-0.478** | **-0.794** | **-4.741** |
| **Winter prey index** | **0.563** | **0.067** | **0.433** | **0.695** | **0.561** | **8.434** |
| Stream density | 0.088 | 0.078 | -0.066 | 0.239 | 0.090 | 1.137 |
| Elevation | 1.105 | 0.968 | -0.799 | 3.009 | 1.103 | 1.141 |
| **Elevation$^2$** | **-6.550** | **0.598** | **-7.784** | **-5.430** | **-6.481** | **-10.948** |
| Slope | -0.237 | 0.212 | -0.658 | 0.177 | -0.234 | -1.118 |
| **Slope$^2$** | **-1.393** | **0.136** | **-1.674** | **-1.140** | **-1.379** | **-10.263** |
| Forested-open edge density | 0.128 | 0.117 | -0.105 | 0.356 | 0.131 | 1.091 |
| Road density | -0.034 | 0.086 | -0.206 | 0.134 | -0.032 | -0.393 |

| | | | | | | |
|---|---|---|---|---|---|---|
| % Public land | -0.118 | 0.142 | -0.398 | 0.159 | -0.116 | -0.832 |
| **% Impervious** | **-1.542** | **0.199** | **-1.953** | **-1.173** | **-1.518** | **-7.748** |
| **Wolf density** | **0.817** | **0.057** | **0.706** | **0.928** | **0.817** | **14.401** |
| **Posterior distribution of interaction (x * wolf density)** | | | | | | |
| Buck kill index | 0.028 | 0.043 | -0.055 | 0.112 | 0.028 | 0.664 |
| **Winter prey index** | **-0.151** | **0.022** | **-0.194** | **-0.108** | **-0.151** | **-6.871** |
| **Stream density** | **-0.151** | **0.026** | **-0.202** | **-0.099** | **-0.151** | **-5.750** |
| **Elevation** | **-0.384** | **0.051** | **-0.484** | **-0.285** | **-0.384** | **-7.583** |
| **Elevation$^2$** | **0.158** | **0.038** | **0.084** | **0.232** | **0.158** | **4.196** |
| **Slope** | **0.134** | **0.047** | **0.040** | **0.227** | **0.134** | **2.817** |
| Slope$^2$ | -0.008 | 0.028 | -0.062 | 0.046 | -0.009 | -0.306 |
| Edge density | -0.066 | 0.034 | -0.133 | 0.000 | -0.066 | -1.950 |
| **Road density** | **0.129** | **0.039** | **0.052** | **0.206** | **0.129** | **3.301** |
| **% Public land** | **0.058** | **0.025** | **0.009** | **0.108** | **0.058** | **2.305** |
| % Impervious | -0.083 | 0.066 | -0.211 | 0.049 | -0.085 | -1.250 |

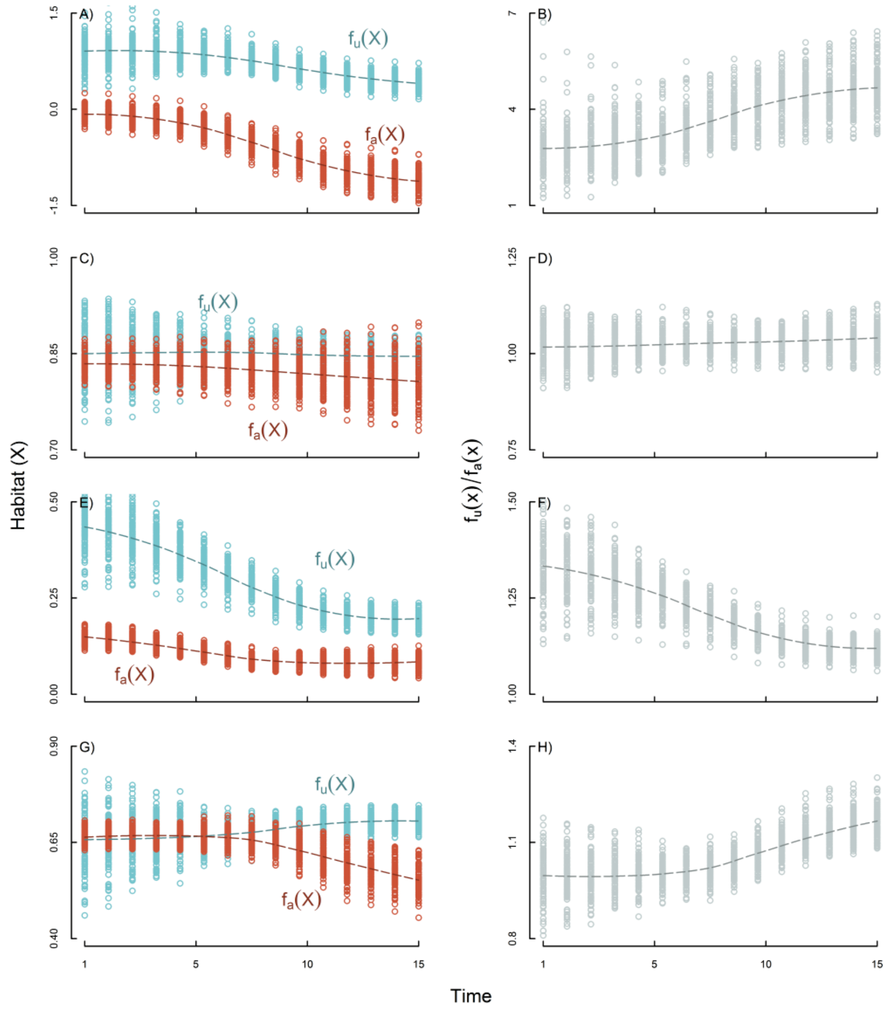

Figure 5.1. Results from simulations of used and available habitat (1st panel column; A,C,E,F) and corresponding selection ratios (2nd panel column; B,D,F,H) under assumptions of strong territoriality and increasing occupancy over time. Four hypothetical scenarios were evaluated in simulations, including an important, limited habitat (A,B), abundant but important habitat (C,D), limited substitutable habitat (E,F), and more abundant substitute habitat (G,H). Results show that the change in the

selection ratio is dependent on convergence or divergence between used and available habitat distributions as occupancy increases over time.

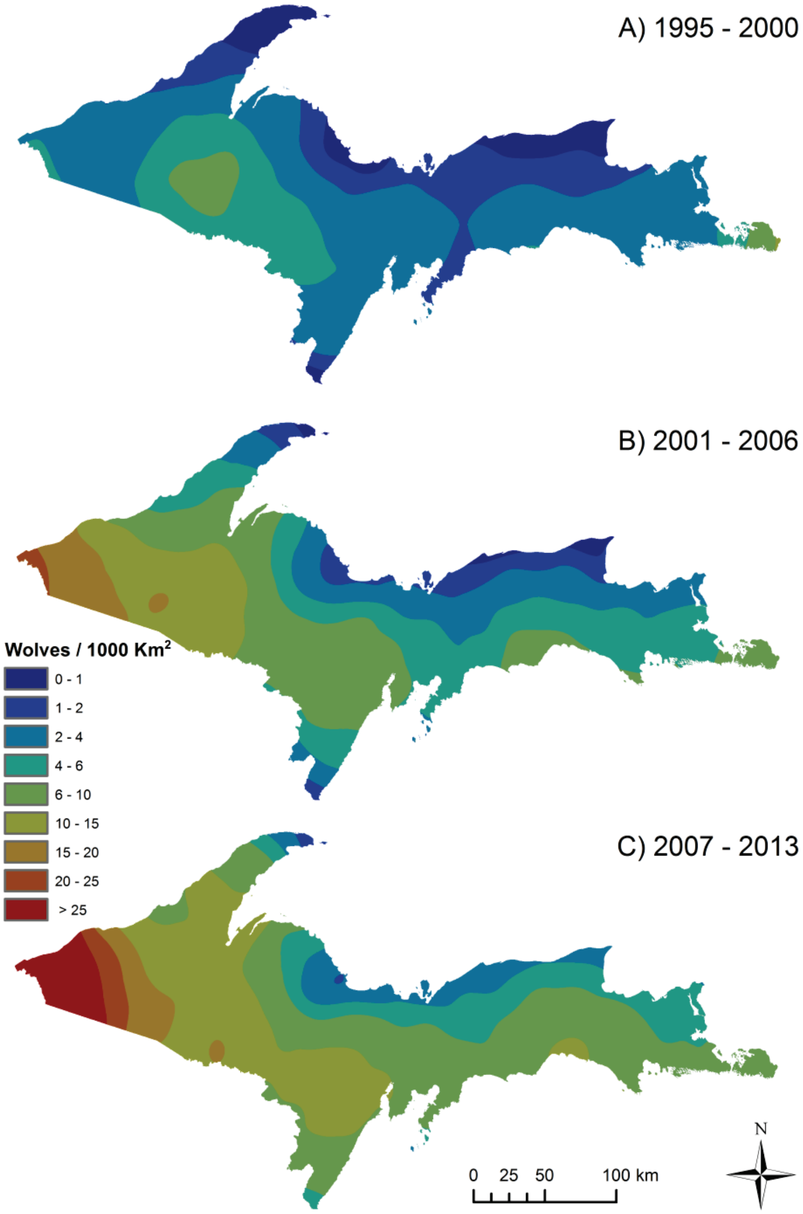

Figure 5.2. Spatially explicit smoothed estimates of wolf density from early recovery (1995 – 2000; A) to late (2007 – 2013; C) in Michigan, USA. Wolf density estimates were generated from winter tracking data and radio telemetry, with pack territories and

sizes being monitored annually during the study. Pack sizes and territory locations were converted to density (wolves / 1000 km$^2$) for each territory and smoothed using a circular moving window with radius approximately equal to median wolf dispersal distance (km), which was based on an exponential distribution with $\lambda = 1/55$. Smoothed surfaces were averaged across time periods to create snapshots for 1995 – 2000 (A), 2001 – 2006 (B), and 2007 – 2013 (C).

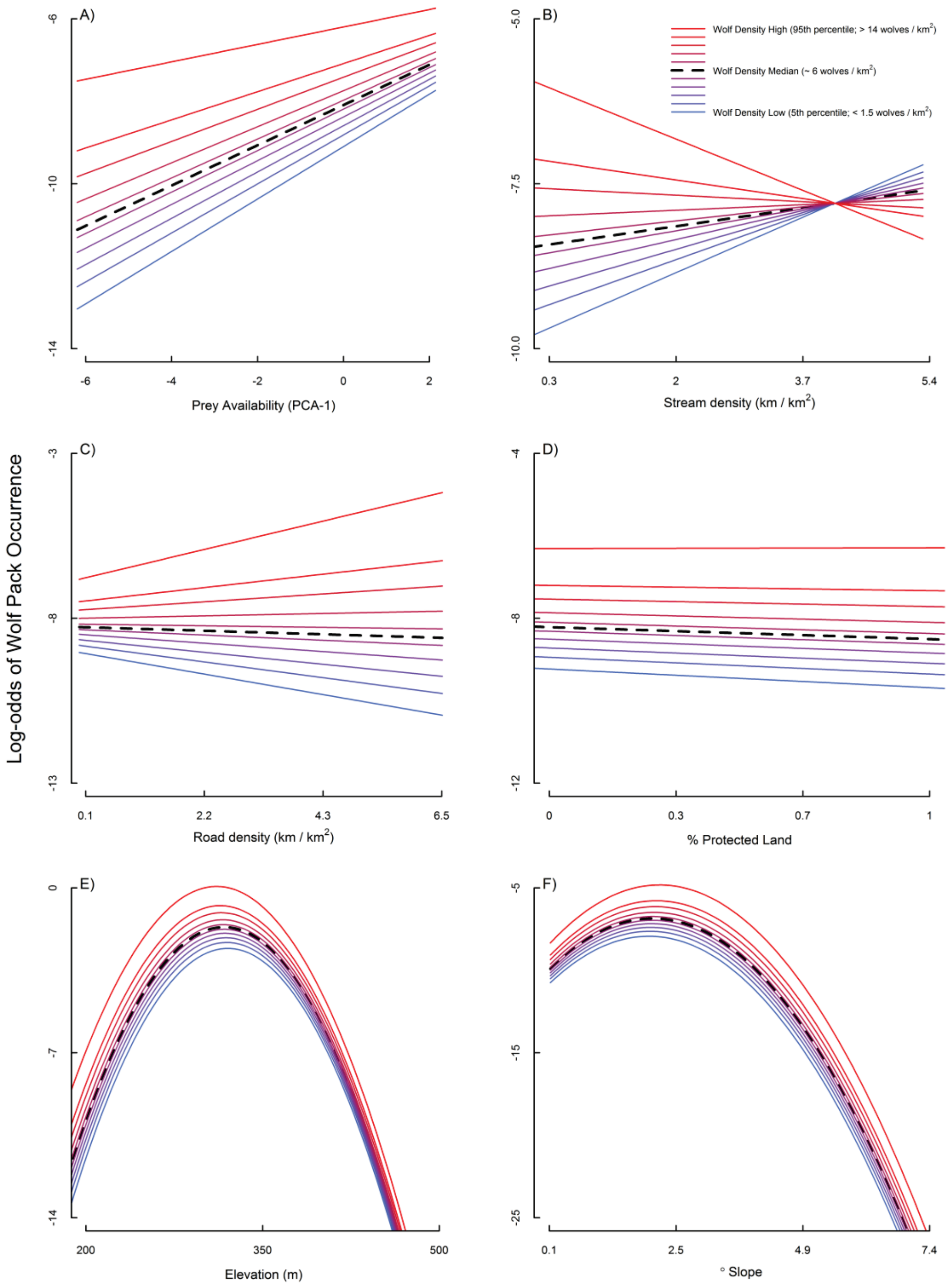

Figure 5.3. Log-odds of wolf pack occurrence from a resource selection probability function (RSPF) for wolves in Michigan, USA. Predictors of wolf pack occurrence were

fit as interactions with wolf density, which varied spatially and temporally over time. The RSPF was generated based on a Generalized Linear Mixed Model framework using the R package ‘INLA’ with coefficient estimates generated conditional on specific wolf packs and years. Density dependence was observed with respect to the effects of prey availability (A), stream density (B), road density (C), protected land (D), elevation (E), and Slope (F); in some cases, selection coefficients switched from positive to negative (stream density; B) or negative to positive (road density; C) as wolf density increased over time.

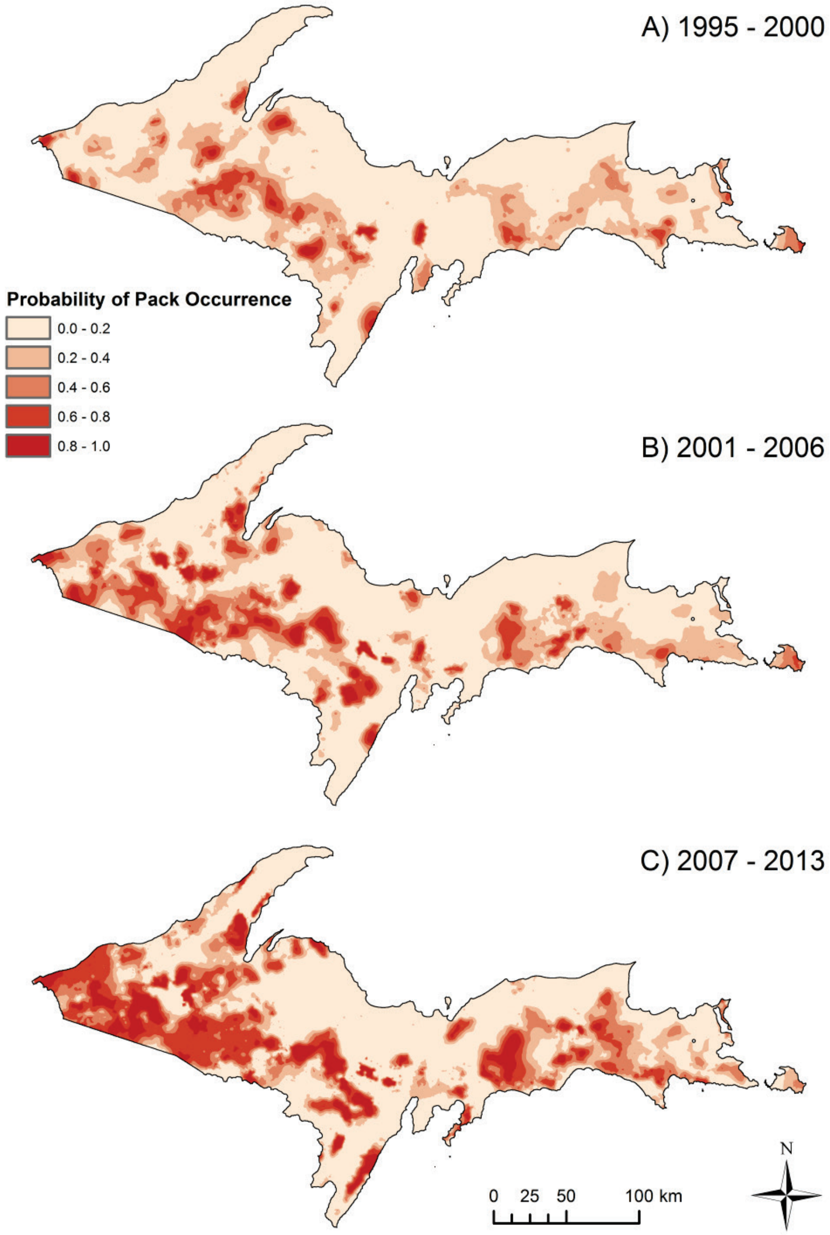

Figure 5.4. Model-fitted probability of wolf pack occurrence for three time periods (1995 – 2000; A, 2001 – 2006; B, and 2007 – 2013; C) during wolf recovery in Michigan, USA. Fitted probabilities were generated from a resource selection probability function (RSPF) which was generated based on a Generalized Linear Mixed Model framework using the R package 'INLA' with coefficient estimates generated

conditional on specific wolf packs and years and density dependent coefficient interactions.

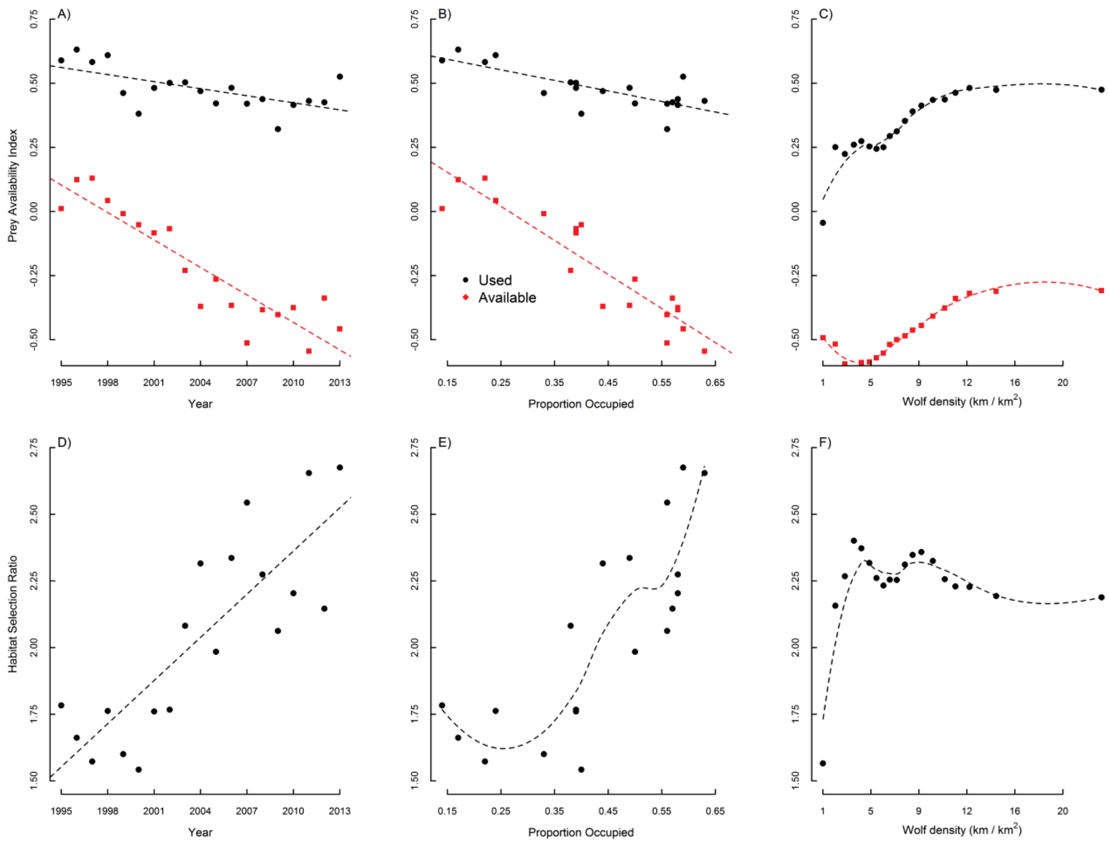

Figure 5.5. Comparisons of means for distributions of used and available winter prey availability (A, B, C) and habitat selection ratios (D, E, F) corresponding to changes in time (A, D), proportion of landscape occupied (B, E), and wolf density (C, F) for wolves in Michigan, USA, 1995 – 2013. Trends in habitat selection over time tracked changes in occupancy at the landscape level more closely than changes in wolf density, likely in part due to regional variation in wolf density across years.

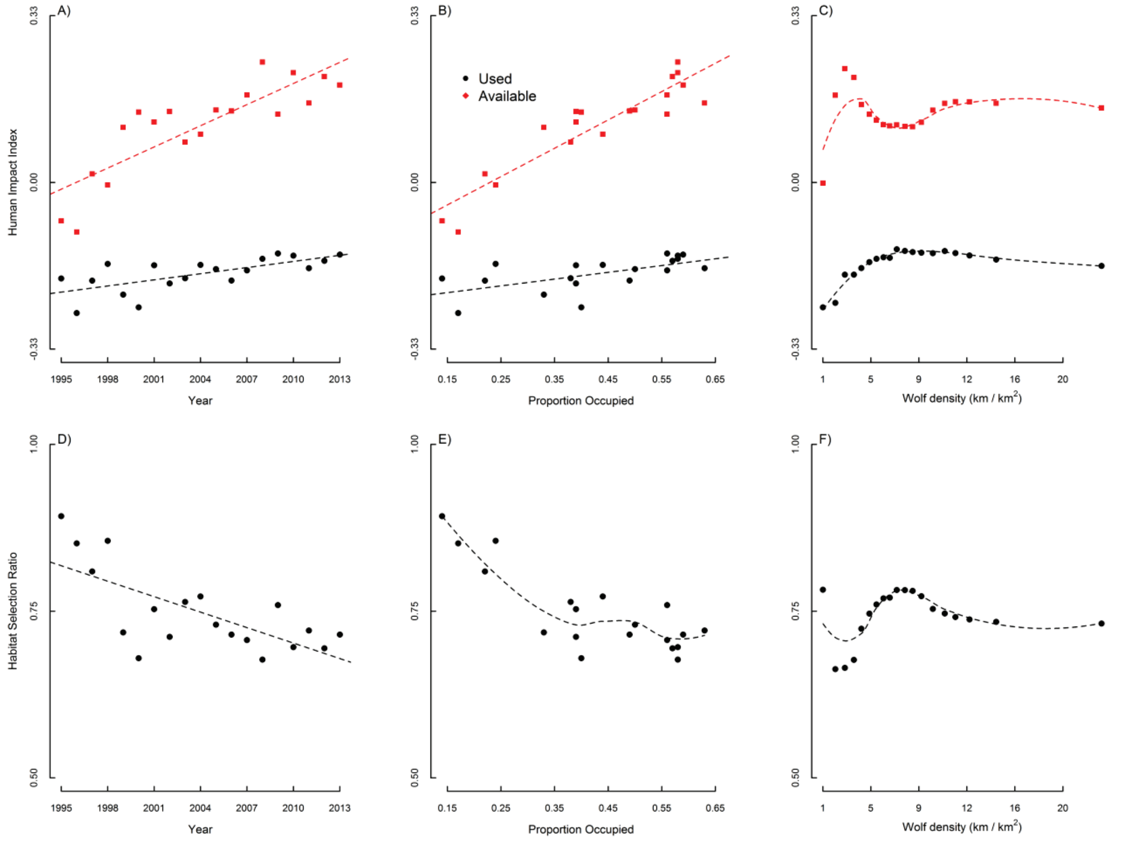

Figure 5.6. Comparisons of means for distributions of used and available human impact (A, B, C) and habitat selection ratios (D, E, F) corresponding to changes in time (A, D), proportion of landscape occupied (B, E), and wolf density (C, F) for wolves in Michigan, USA, 1995 – 2013.

# Appendix 5A.

## Candidate landscape variables in spatiotemporal habitat selection function (HSF) models, Michigan wolves 1994 – 2013.

### C. Indices of Prey Availability (Resources)

*Variable:* Buck Harvest

*Source:* Michigan Department of Natural Resources (MDNR)

*Original Unit:* Antlered bucks killed / km$^2$

*Description & Measurement:* Buck harvest data were collected from mail surveys during white-tailed deer hunting season across the Upper Peninsula (UP) by the MDNR (e.g. Frawley 2010). Harvest numbers were summarized by area (km$^2$) at the county level, and a circular moving window ($r$ = 4.02 km) was used to smooth the results at the same scale as other predictors. A continuous raster surface of 30 m cell size was thus generated for each year in the study, representing mean bucks harvested / km$^2$. This was done using focal statistics in ArcGIS 10.1 (hereafter, ArcGIS; Environmental Systems Research Institute, Redlands, CA, USA). Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf space use:* Positive (+). White-tailed deer are the primary prey source for wolves in Michigan, and MDNR has indicated that buck harvest numbers track the deer population consistently across time. Buck harvest was a consistent index for deer densities (i.e. prey availability) across the study area and was also measured each year. We expected wolf use to generally increase with increasing densities of bucks harvested, but suspected that density dependent habitat selection would regulate this relationship due to limitations in deer density, particularly in the northern regions of the study site (Potvin *et al.* 2005).

\---

*Variable*: PCA of % Deer Wintering Complex and Distance to Deer Wintering Complex

*Source*: MDNR (e.g. http://www.michigan.gov/dnr/0,4570,7-153-10363_10856_10905-339639--.html)

*Abbreviation*: PPC1

*Original Unit*: % of area within moving window, Distance to nearest DWC (km)

*Description & Measurement*: White-tailed deer (*Odocoileus virginianus*) are migratory throughout much of the UP due to harsh winter conditions, and congregate (i.e. “yard”) in dense stands of primarily eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*) when snow depth exceeds approximately 30 cm (Shi *et al.* 2006; Witt *et al.* 2012; Murray, Webster & Bump 2013). Deer winter range was been mapped by state biologists as early as the 1930s, with surveys occurring every 10 – 20 years since. The most recent surveys occurred in 2005 and 2013. We used the maps from 2005 and 2013 to classify the study area as winter habitat (deer wintering complex, or DWC), or non-winter habitat. We generated the percent of landscape variable using a circular moving window (*r* = 4.02 km) to summarize the area mapped as DWC at each location. We generated distance to DWC (km) by creating a Euclidean distance raster surface in ArcGIS and subsequently calculating the average distance within the circular moving window across the study site. A continuous raster (30 m cell) was generated for the study area to represent these metrics. We assumed no significant change in DWC habitat throughout the study. Seasonal migration is a learned behavior and results in high fidelity to winter ranges, such that the same DWCs are repeatedly utilized year after year (Nelson 1998; Nelson, Mech & Frame 2004). Since % DWC and distance to DWC contained similar information, we combined the variables using a principal components analysis, and extracted the first component for use in subsequent modeling. Increasing values of Prey-PC1 (i.e. PPC1) thus indicated increasing winter prey availability.

*Expected relationship with wolf space use:* Positive (+). Deer wintering range is only about 15% of annual range in higher snowfall zones of the UP (Doepker *et al.* unpublished report ). This represents a prey limitation that wolves must consider when establishing and defending territories. We expected wolf use to increase with increasing area of the landscape comprising DWC habitat and decreasing distance to DWC. This would correspond to a positive relationship with PPC1.

--

*Variable*: Annual Snow Depth

*Source*: National Climate Data Center (http://www.ncdc.noaa.gov/)

*Abbreviation*: SNOW

*Unit*: Average Daily Snow Depth (cm), 1 Nov – 30 Mar

*Description & Measurement*: We downloaded daily snow depth data from the National Climatic Data Center (NCDC) for all weather stations on the study site. We calculated the mean winter snow depth at each station (1 Nov – 30 Mar) for each year in the study. We used Empirical Bayesian Kriging in ArcGIS (EBK; http://www.esri.com/news/arcuser/1012/empirical-byesian-kriging.html) to interpolate a raster surface for each year based on the weather station point data. Parameters for the EBK analysis included an output cell of 500 m, maximum number of points = 50, local model overlap = 2, simulated semivariograms = 50, and a standard circular neighborhood with radius = 150,000 m, maximum neighbors = 12, and minimum neighbors = 3. The resulting raster surface represented interannual and spatial variation in snow depths during the study. Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf space use*: Conditional (+/-). In general, we expected habitat use to decrease with increasing snow depths (Houle et al. 2010, Uboni 2012), as habitat for prey became more limited (Potvin et al. 2005). However, greater snow depths may give wolves a hunting advantage, particularly during late winter when deer become more vulnerable and snow conditions become difficult to navigate (Vucetich et al. 2012). The use of DWCs may complicate this relationship; we expected greater selection of DWCs in areas (and winters) with deeper snow, as a response to more densely congregated prey.

## D. Human Influence and Infrastructure (Risks)

*Variable:* % Agriculture

*Source*: National Land Cover Database (NLCD; http://www.mrlc.gov/)

*Abbreviation*: AG

*Unit*: Percentage of landscape comprising agricultural cover types (%)

*Description & Measurement*: Agricultural cover types were reclassified from NLCD products for years 1992, 2001, 2006, and 2011. The early years of the study were linked to results from the 1992 product (wolf biological years 1995-1997), and 2001 product (wolf biological years 1998-2003), while later years corresponded to the 2006 (wolf years 2004-2008) and 2011 products (wolf years 2009-2013). Agricultural cover types included pasture/hay, row crops, small grains, and fallow ground, and were assigned a value of 1, with all other cover types reclassified to Null values. The moving window was applied to calculate the percentage of landscape comprising agriculture at each location (30 m cell) in the study area. Final values were standardized around their mean prior to being fit in models.

*Expected relationship with wolf space use*: Negative (-). Agriculture typically represents mortality risk for wolves, and is negatively associated with pack persistence (Oakleaf et al. 2006, Mladenoff et al. 2009, Stenglein 2014). Consequently, wolves are unlikely to select and maintain territories with a significant agricultural component, particularly when better habitat is available. We expected a negative relationship between wolf use and % agriculture, while recognizing that as wolf densities increased the relationship might change.

--

*Variable*: Distance to Major Road

*Source*: U.S. Census Bureau (http://www.census.gov/geo/maps-data/data/tiger.html)

*Abbreviation*: HWY

*Unit*: Distance to nearest major road (km)

*Description & Measurement*: TIGER\Line roads were downloaded from the U.S. Census Bureau for the years 1990 and 2000-2014. We queried primary and secondary roads from the database for each year that the data were available. In the Upper Peninsula, these were almost entirely major highway routes. 1990 was removed from consideration because the classification scheme did not match the later years. Road coverages were similar in the 2000 data, however, so we used the 2000 file for the early study years. We calculated Euclidean distance to primary and secondary roads and applied the circular moving window to the resulting raster surface. For study years 2000-2013 we recalculated this metric every two years (i.e. 2002, 2004, … , 2012) to represent temporal changes in extent of roads. Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf space use*: Positive (+). Many previous modeling efforts have indicated that wolf habitat is primarily limited by human activity and road densities. Some attention has been given to the type of road considered (Mladenoff et al. 1995, Oakleaf et al. 2006, Benson et al. 2014). While major roads are almost always avoided, lesser used roads can be utilized by wolves for traveling and territory marking (Lesmerises et al. 2012, Zimmermann et al. 2014). We split major and minor roads into separate classes to consider these possibilities. We expected wolf use to increase with increasing distance from major roads, because major roads are generally associated with higher levels of human activity and represent mortality risk.

--

*Variable*: Minor Road Density

*Source*: U.S. Census Bureau (see HWY)

*Abbreviation*: ROAD

*Unit*: Distance of Minor Roads / Unit Area (km / km$^2$)

*Description & Measurement*: TIGER\Line roads were described in 'Distance to Major Road.' For minor road densities, we queried local roads and trails from the TIGER\Line database. We then calculated minor road density within the moving window using the Line Density tool in ArcGIS. The temporal representation of these features was the same as in 'Distance to Major Road.'  Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf use*: Negative (-). Traditionally, road densities have been considered a strong negative driver of wolf habitat quality (Mladenoff et al. 1995; Mladenoff and Sickley 1998; Potvin et al. 2005). In general, wolf occurrence decreases with increases in human presence and disturbance, which often correlates with road density. However, in areas with relatively low human population density, wolves may select for areas with greater road densities than expected. This effect is context-specific, and depends on the level of disturbance, such as current or recent logging activity (Houle et al. 2010, Lesmerises et al. 2012, 2013) Wolf use of these features tends to increase as human activity decreases (Hebblewhite and Merrill 2008). Logging occurs year-round in the UP and minor road densities are correlated with hunting camps and recreational activity, thus on average we expected a negative relationship between wolf use and minor road densities.

--

*Variable*: % Impervious Surface

*Source*: NLCD (http://www.mrlc.gov/index.php)

*Abbreviation*: IMP

*Unit*: Percent of landscape comprising impervious surfaces (%)

*Description & Measurement*: In addition to the NLCD products, we also acquired the 2001, 2006, and 2011 Percent Developed Imperviousness product. In order to capture the best available temporal resolution for this feature, early study years were assigned to the 2001 product while later years (post-2002) were assigned to the 2006 and 2011 products (see description for '% Agriculture'). We summarized % impervious (focal mean) within the moving window described previously to create the index for human population density and infrastructure. Final values were standardized around their mean prior to being fit in models.

*Expected relationship with wolf use*: Negative (-). Imperviousness is used as an index of human activity and infrastructure, which wolves avoid if they can. We expected wolf use to decline rapidly as imperviousness increased.

--

*Variable*: % Protected Land

*Source*: USGS Protected Areas Database (http://gapanalysis.usgs.gov/padus/ )

*Unit*: Percentage of landscape comprising public/protected land ownership

*Description & Measurement*: Protected areas in the UP of Michigan included National and State Forests, National Park Service land ownership, U.S. Fish and Wildlife Service, and various small tracts of land belonging to state or non-profit based conservancy projects or land trusts. We summarized the % landscape (focal mean) within the moving window to create an index of protected land where higher values represented lower potential for human development and disturbance. Final values were standardized around their mean prior to being fit in models.

## C. Natural Features

*Variable*: % Open

*Source*: NLCD

*Abbreviation*: OPEN

*Unit*: Percent of landscape comprising open cover types (%)

*Description & Measurement*: We used NLCD products to calculate the percentage of open cover types occurring on the landscape. Open cover types and forested land were reclassified to a binary raster (1 = open), which was used to assess the proportion of open cover occurring within the moving window. Open cover types included grassland/herbaceous, pasture/hay, row crops, small grains, fallow ground, herbaceous/emergent wetlands, bare ground, and quarries, mines, or pits. The analysis was repeated for 1992, 2001, 2006, and 2011 NLCD products to represent land cover change during the study. Final values were standardized around their mean prior to being fit in models.

*Expected relationship with wolf use*: Negative (-). Wolves in northern forests often select cover types that are associated with prey access and ease of travel, and are negatively associated with human disturbances (Houle et al. 2010, Lesmerises et al. 2012, Kittle et al. 2015). In the UP, much of the open habitat is either associated with human disturbance such as logging and recreation, or agricultural land which represents risk to wolves. Wetlands are another open cover type, which may represent prey availability in the form of moose and beaver (Houle et al. 2010, Lesmerises et al. 2012), but moose are not abundant in the UP and beaver are, at best, a seasonal food source. We largely expected wolves in the UP to avoid open cover types, although the selection of this cover type is likely contextual. Alternatively, open areas may be used as hunting grounds, although this probably depends on the particular predator/prey system being studied (Kauffman et al. 2007). We considered seasonal and density dependent interactions to account for this possibility, as deep snow covers open areas in the winter, such that prey would likely only occur in these areas in the summer.

--

*Variable*: Open:Forested Edge Density

*Source*: NLCD

*Abbreviation*: EDGE

*Unit*: Distance of the open:forested linear feature / Unit Area (km / km$^2$)

*Description & Measurement*: We used NLDC products to create two binary rasters: one representing open cover types (see '% Open'), and one which included all forested cover types vs. other features. We defined the boundary between these two features as an edge, converted the boundary to line features in ArcGIS, and calculated the line density within the moving window described previously. The analysis was repeated for 1992, 2001, 2006, and 2011 NLCD products. Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf use*: Positive (+). There are several reasons that wolf habitat use should be positively associated with edgy habitat. First, these features likely represent high quality foraging habitat for deer, particularly in summer, while also providing access to cover. In addition, linear features such as the transition zone between cover types may increase prey encounter rates and represent escape obstacles (Kauffman et al. 2007, Houle et al. 2010, Lesmerises et al. 2012). Such features may also be useful as travel corridors and for marking territory boundaries. We expected habitat use to increase with increasing open:forested edge densities on our study site.

--

*Variable*: % Open Water & Wetlands

*Source*: NLCD

*Abbreviation*: WET

*Unit*: Percent of landscape comprising open water and wetlands

*Description & Measurement*: We used NLCD products to reclassify emergent/herbaceous wetlands and open water cover types. A binary raster was created for these cover types using methods described in '% Open.' We evaluated the percentage of landscape comprising open water and wetlands within the moving window. The analysis was repeated for the 1992, 2001, 2006, and 2011 NLCD products. Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf use*: Negative (-). Water and wetlands may be indicative of potential alternative prey sources (beaver, moose), but wolves prey primarily on deer throughout the UP. Wolves selected against open water features, although shorelines were a preferred cover type (Kittle et al. 2015). In general, we expected wolf use to decline as the proportion of open water and wetlands increased.

--

*Variable*: Stream Density

*Source*: Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/?rel=thext&action=thmname&cid=3&cat=MI+Geographic+Framework+Hydrography+%28v14a%29)

*Abbreviation*: STREAM

*Unit*: Distance of stream per unit area (km / km$^2$)

*Description & Measurement*: Hydrography files were downloaded from the Michigan Geographic Data Library. All streams and linear water features were selected from these data and clipped to the study area (FCC codes H3*– H4*). Linear stream features were converted to a 30 m density raster using the line density tool with 4.02 km radius. Final values were standardized around their mean for each study year prior to being fit in models.

*Expected relationship with wolf use*: Positive (+). Streams may represent higher prey availability, either via correlation with greater beaver densities (i.e. a seasonal/alternate prey source) or as preferred hunting territory (Kauffman et al. 2007, Lesmerises et al. 2012). We expected wolves to increase utilization with greater stream densities.

--

*Variable*: Elevation

*Source*: USGS National Map (http://nationalmap.gov/)

*Abbreviation*: ELEV

*Unit*: Meters above sea level (m)

*Description & Measurement*: We downloaded a 30 m DEM from the National Map and calculated mean elevation within the moving window described previously. Final values were standardized around their mean prior to being fit in models.

*Expected relationship with wolf use*: Negative (-), Quadratic (i.e. selection for intermediate elevation). Numerous studies have found a relationship between wolf territory use and elevation. While results are mixed, a common finding is that wolves do not utilize the highest elevations on the landscape, but also tend to select against lowlands on average (Lesmerises et al. 2012, Uboni 2012, Kittle et al. 2015). Thus, we expected selection for intermediate elevation on our study site (Milakovic et al. 2011). Although elevation does not exceed ~ 600 m in the UP, snowfall in winter tends to be greatest at higher elevations, and deer vacate these areas when snow exceeds ~ 30 cm.

--

*Variable*: Slope

*Source*: USGS DEM (see ELEV)

*Abbreviation*: SLO

*Unit*: Degrees of slope (°)

*Description & Measurement*: We used the DEM described in 'Elevation' to compute degrees slope using ArcGIS, and calculated the mean slope within the moving window. Final values were standardized around their mean prior to being fit in models.

*Expected relationship with wolf use*: Negative (-), Quadratic (i.e. selection for intermediate elevation). We anticipated a similar response to slopes as that of elevation. The range of elevation on our study site was not large, but the topography in many areas was rugged, resulting in significant slopes and changes in elevation. We expected wolves to use areas with shallow or intermediate slopes on our study site. Steeper areas are more difficult for wolves to navigate and may be risky, while flatter terrain has been associated with wolf hunting behavior (Kauffman et al. 2007). Most studies find a negative relationship between wolf use and slope (Houle et al. 2010, Milakovic et al. 2011, Lesmerises et al. 2012).

--

*Variable*: Terrain ruggedness

*Source*: USGS DEM (see Elevation)

*Unit*: Index of terrain ruggedness

*Description & Measurement*: We used the DEM to compute the average terrain ruggedness index value within the moving window. The analysis was performed using the ArcGIS Geomorphometry and Gradient Metrics toolbox (Evans et al. 2014). The index measures topographic heterogeneity and is fully described in Evans et al. (2014).

--

*Variable*: Topographic radiation aspect index

*Source*: USGS DEM (see Elevation)

*Unit*: Index of heat load

*Description & Measurement*: We used the DEM to compute the average heat load index value within the moving window. The analysis was performed using the ArcGIS Geomorphometry and Gradient Metrics toolbox (Evans et al. 2014). The index measures potential for direct solar radiation and warmer temperatures based on a slope-aspect transformation; the method is fully described and referenced in Evans et al. (2014).

# Appendix 5B.

## Preliminary model reduction to remove correlated and unnecessary predictor variables.

Our model included a large number of correlated variables so we fit generalized linear models using penalized maximum likelihood to select a subset of predictors from the original set. We used the elastic net regularization penalty in R package ‘glmnet,’ which combines lasso and ridge regression methods to discard irrelevant predictors and shrink coefficients of correlated predictors toward each other (Friedman et al. 2010, Tibshirani et al. 2012). We set the parameter $\alpha$ to 0.9, which causes performance similar to the lasso but also manages erratic model behavior resulting from highly correlated variables (Friedman et al. 2010). To determine which effects to keep, we used cross-validation to estimate best fit for the tuning parameter $\lambda$, where the method for $\lambda$ was set to choose the most regularized model with errors within one SE of the minimum mean cross-validated error (Friedman et al. 2010). To ensure consistency across the dataset, we ran a Monte Carlo simulation with 1000 iterations, randomly selecting 5000 records from our dataset, refitting the model with ‘glmnet’, and estimating $\lambda$ via the cross-validation routine. Each time we recorded which variables had not been discarded, and calculated the overall proportion ($p$) of model fits that included each variable $x$. We dropped variables with $p < 0.5$, and included the rest in subsequent models.

# 6. Spatially varying density dependence drives a shifting mosaic of survival in a recovering apex predator (*Canis lupus*)[5]

## Abstract

Understanding landscape patterns in mortality risk is crucial for promoting recovery of threatened and endangered species. Humans affect mortality risk in large carnivores, such as wolves (*Canis lupus*), but spatiotemporally-varying density dependence can significantly influence the 'landscape of survival.' This potentially occurs when density varies spatially and risk is unevenly distributed. We quantified spatiotemporal sources of variation in survival rates of gray wolves (*Canis lupus*) during a 21-year period of population recovery in Upper Michigan, USA. We focused on mapping risk across time using Cox Proportional Hazards (CPH) models with time-dependent covariates, thus exploring a shifting mosaic of survival. Extended CPH models and time-dependent covariates revealed influences of seasonality, density dependence and movement patterns, as well as individual-level factors and landscape predictors of risk. We used results to predict the shifting landscape of risk at the beginning, middle, and end of the wolf recovery time series. Survival rates varied spatially and declined over time. Long-term change was density-dependent, with landscape predictors such as agricultural land cover contributing negatively to survival. Survival also varied seasonally and depended on individual experience, sex, and movement within vs. outside territories. The shifting landscape of survival suggested that increasing density contributed to greater potential for human conflict and wolf mortality risk. Long-term spatial variation in key population

---

[5] The material contained in this chapter has been submitted to *Ecology and Evolution*

vital rates is largely unquantified in many threatened, endangered, and recovering species. Variation in risk may indicate potential for source-sink population dynamics, especially where individuals preemptively occupy suitable territories, which forces new individuals into riskier habitat types as density increases. We encourage managers to explore relationships between adult survival and localized changes in population density. Density-dependent risk maps can identify increasing conflict areas or potential habitat sinks which may persist due to high productivity in adjacent habitats.

## Introduction

Accurate estimates of key vital rates are crucial in promoting restoration and recovery of threatened and endangered species, especially where humans contribute to changes in population demographics. Anthropogenic impacts have driven many species to the brink of extinction (Vié et al. 2009); however, changes in conservation policy can in some cases allow for recovery. For example, changing perceptions and increased protections have contributed to increases in large carnivore populations over the past several decades (Chapron et al. 2014, Ripple et al. 2014, Smith et al. 2015). Gray wolves (*Canis lupus*) are arguably one of the most iconic examples of successful conservation policy (Beschta and Ripple 2009, Wydeven et al. 2009a, Mech and Boitani 2010). Nonetheless, some population segments remain endangered, in part due to the potential for human actions to reverse positive growth rates or inhibit continued range expansion (Liberg et al. 2012, Bruskotter et al. 2014, Olson et al. 2015).

Survival is an important driver of wolf populations, especially when humans contribute substantially to wolf mortality. Wolves in the U.S. are frequently subject to legal (e.g. hunting, lethal control), illegal (poaching), and incidental killing (e.g. vehicle strike) (Murray et al. 2010, Gude et al. 2012, Stenglein et al. 2015a). The relative influence of human-caused mortality is debated (Creel and Rotella 2010, Murray et al. 2010, Gude et al. 2012), with some subpopulations apparently sustaining high mortality rates (Adams et al. 2008, Creel and Rotella 2010, Mech and Boitani 2010). Monitoring and precise estimation of adult survival in the presence of human-caused mortality is a key input for effective management.

While survival estimation on its own is useful and informative for management, understanding driving mechanisms is necessary to guide decision-making. Annual survival in wolves is frequently related to the ‘riskiness’ of their environment. Greater mortality risk is often associated with variables that indicate potential for human impact. Wolves inhabiting areas with greater road densities, greater proportions of agricultural land cover, and more private land generally have lower survival rates than those that occupy more remote, protected areas (Fuller et al. 2003, Smith et al. 2010, Stenglein 2014). Survival can also be density dependent, especially in protected areas where populations saturate habitat. In these cases, survival may be regulated by intraspecific aggression as wolves compete for territory and prey (Cubaynes et al. 2014), or by reduced prey availability (Fuller et al. 2003, Marucco et al. 2012). Analyses that characterize habitat quality in terms of fitness metrics rather than density or distribution are ecologically informative and are a valuable tool for resource managers (Mosser et al. 2009, Gaillard et al. 2010).

Relating adult survival to environmental characteristics can identify habitat-limiting factors and potential sink habitats (habitats that are occupied frequently but contribute to negative average growth rates; (Aldridge and Boyce 2007, Hirzel and Le Lay 2008)). A habitat's fitness potential generally cannot be inferred from studies of habitat selection alone due to density-fitness relationships (Morris 1988) and/or complications associated with measuring the 'true' ecological niche (Pulliam 2000). Survival modeling with environmental covariates can provide one solution to this problem.

We evaluated spatiotemporal variation in wolf survival rates in Michigan, USA, from 1995 – 2013. In particular, we were interested in obtaining a reliable estimate for adult survival of the population (hereafter, $S(t)$ ), testing for density-dependent and/or temporal variation in $S(t)$ , and evaluating the relative influences on $S(t)$ within the study area. Hypothesized influences on $S(t)$ included individual-level factors (age, sex, body condition at capture, capture type, vaccination status, pack membership status) and continuous spatial covariates (distance from pack territory, habitat suitability metrics, and movement information). Testing for such effects contributes to 1) understanding of how management may influence the population, 2) evaluation of the factors that increase mortality risk, and 3) knowledge about habitat fitness and potential sink habitats being used by wolves.

## Methods

### *Field methods*

Wolves were captured using foot-hold traps during spring and summer, 1992 – 2013. Capturing efforts were part of an ongoing wolf monitoring and radio telemetry program with the Michigan Department of Natural Resources (Michigan Department of Natural Resources 2008, Beyer et al. 2009, Michigan Department of Natural Resources 2015). Some captures also occurred opportunistically in the fall, when wolves were incidentally caught by coyote (*Canis latrans*) trappers. After being collared, wolves were located by fixed-wing single-engine aircraft 1 – 2 times per week during the study. Field crews attempted to physically locate collars shortly after a mortality signal (< 1 week); fate was initially determined via field necropsy and cause of death was later updated as needed via lab necropsies at the Michigan Department of Natural Resources Wildlife Disease Laboratory. Detailed field methods are available in Beyer et al. (2009), Potvin, et al. (2005), and Vucetich et al. (2012).

### *Wolf packs, territories, and density*

The Michigan DNR tracked wolves in winter to complete an annual census of the wolf population and estimate spatial variation in wolf density. All passable roads were surveyed from trucks and snowmobiles (Potvin et al. 2005). Once tracks were detected, trackers recorded all signs (territory markings, scat, individual sets of tracks) to estimate pack sizes and establish pack boundaries. Further details on tracking methods and wolf abundance estimation are available in the references cited in the previous section and online at http://www.wolfandwildlifestudies.com/downloads/Estimating_Wolf_Abundance_in_Michigan_060208_239125_7.pdf.

We used a combination of radio-collar locations and track survey data to generate annual estimates of wolf density. Once detected, pack territories were monitored by aerial telemetry relocations or by repeatedly visiting known territory sites each winter to establish annual occupancy. Territory boundaries from radio telemetry data were generated using fixed kernel density estimation to create a 3D utilization distribution (UD), where the territory home range was defined as the 95% volume isopleth boundary. For years and/or packs with inadequate locations for estimation of the UD, we approximated territory boundaries by combining long-term telemetry locations associated with known packs and locations of tracks from the winter tracking survey. In cases where telemetry locations did not exist, we used a minimum convex polygon from long-term track locations.

We approximated spatiotemporal variation in wolf density by generating a longitudinal matrix representing pack persistence and changes in pack size over time. These data were linked to the pack territory boundaries in ArcMap 10.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Annual pack counts were converted to wolves / 1000 km$^2$. We generated a smoothed surface for annual wolf density each year using a circular moving window with radius equal to approximate median wolf dispersal in the Great Lakes region (≈ 38 km; Treves et al. 2009).

### *Landscape covariates*

We developed habitat metrics representing variability in land cover, topography, prey availability, and potential human influence using publicly available GIS data (Table

6.1). We used moving window analyses to develop spatially-explicit surfaces for each landscape feature considered. The circular assessment window was set to 50.75 km$^2$ (¼ of the mean wolf home range size), chosen to represent within-territory level variation. Each wolf observation was updated with habitat metrics corresponding to its location at the time, thus representing the effect of 'third-order' or location-based habitat selection (Johnson 1980, DeCesare et al. 2012).

*Survival Analysis*

We used extended Cox Proportional Hazards (CPH) models (Therneau and Grambsch 2000, Smith et al. 2010, Benson et al. 2014) to estimate wolf annual survival and test for effects of individual-level variation, monitoring and management, habitat, and movement (distance from pack home range and transience) on the hazard rate (i.e. risk of mortality). Specifically, we were interested in the survival function $S(t) = P(T \geq t)$, where $T$ is the random variable representing survival time (Murray 2006). To accommodate covariates in our model, we estimated the hazard function:

$$h(t, x, \beta) = h_0(t) r(x, \beta), \tag{16}$$

where the overall hazard is modeled as a function of the non-parametric baseline hazard $h_0(t)$ and the regression risk function $r(x, \beta) = \exp(\mathbf{X\beta}) = \exp(x_1\beta_1 + x_2\beta_2 + ... + x_k\beta_k)$ (Hosmer Jr and Lemeshow 1999, Murray 2006, DeCesare et al. 2014). Modeling the hazard according to this formulation allows for convenient and familiar interpretation of covariate effects, where the coefficients $\mathbf{\beta}$ indicate relative effects on the resulting hazard ratio. Subsequently, $S(t)$ can be determined provided the hazard function is known

(Murray 2006). The CPH model is flexible in that there is no parametric assumption on the hazard, only that the hazard ratio is constant over time (the proportional hazards assumption; Klein J. P. and Moeschberger, M.L. 2005, Therneau, T.M. and Grambsch, P.M. 2000). However, the CPH model can easily be extended to cases where predictors vary with time (Fox 2002, Fieberg and DelGiudice 2009).

We specified CPH models where the hazard was modeled according to a combination of individual, at-capture factors and time-varying age, habitat, movement and time of year covariates (Table 6.1). The event of interest in our models was the known death of the individual wolf, and the time to event interval began after the first capture. When fate was undetermined, we right-censored individuals at their last known location and time. Individuals that left the study area and were recovered dead elsewhere were also right-censored. Wolves were sexed, weighed, and aged at capture. We specified a time-dependent age covariate, where age was modelled as a smoothed function of time after capture (Therneau and Grambsch 2000, Fieberg and DelGiudice 2009, Moore 2016). During the early recovery phase (prior to 2004), most wolves received vaccinations for leptospirosis, canine distemper, and parvovirus and if necessary treatment for sarcoptic mange. In addition, wolves involved in depredation incidents were translocated during 1998 – 2002. A dummy indicator variable (0/1) was included for ‘Vaccine’ and ‘Ivomec.’ Similar indicator variables were considered for ‘Translocation,’ ‘Depredation,’ ‘Recaptured’ (i.e. trapped on > 1 occasion), and ‘Capture Type’ (researcher vs. incidentally trapped; Table 6.1).

We allowed habitat variables to change over time, with each covariate representing surrounding habitat according to each individual time-specific location. In addition, we quantified pack membership vs transience. Pack membership was assigned based on consistent observation within known pack territory boundaries. Alternatively, transient status was assigned when individuals left a known territory and did not return (e.g. Smith et al. 2010), or were never observed consistently occupying a territory. We referred to these individuals as ‘transients’ rather than dispersers, because dispersal implies permanently leaving a natal territory (Boyd and Pletscher 1999) which was not always known. For pack status, we quantified risk associated with exploratory movements by calculating the distance from each observation to the center of the pack’s home range. We also computed a variable indicating movement rate (distance/time) corresponding to the log-transformed distance between the current and last location, corrected for the time interval between observations. In the CPH model, we specified log-transformed distance from home range center as an interaction conditional on pack membership; for transients, the distance was calculated based on the geographic center of all observations for the individual.

To model potential long- and short-term trends and density dependent annual survival, we included variables for wolf density, day of year (DOY), and biological year. Each of these predictors was specified to have a non-linear functional relationship with the hazard, which we accommodated using cubic smoothing splines with an initial 5 degrees of freedom (Therneau and Grambsch 2000, Harrell 2015, Moore 2016).

We specified a full model by initially including all parameters (Table 6.1) and used a forward-backward search algorithm to identify the optimal reduced version of the model based on improvement in AIC associated with iteratively adding and removing parameters from the model (Moore 2016). To check the assumption of proportional hazards for the final reduced model, we plotted scaled Schoenfeld residuals over time for each covariate and tested for a statistically significant trend (i.e., $\beta(t) \neq 0$ ; DeCesare et al. 2014, Moore 2016). We fit all models using the 'survival' and 'rms' packages in R 3.2.2 (Therneau and Grambsch 2000, Harrell 2015, R Core Team 2015), with smoothing splines specified using 'pspline' and 'rcs' and model selection implemented using the 'step' function (Therneau and Grambsch 2000, Venables and Ripley 2002, Moore 2016).

*Risk maps*

We used our final model to predict spatial representations of annual survival rate at three time periods during the study: early recovery (1995 – 2000; < 250 wolves), mid recovery (2001 – 2006; 250 – 450 wolves), and late recovery (2007 – 2013; 450 – 700 wolves). To obtain estimates, we conditioned on the average or most common case for non-spatial variables, and projected cumulative annual survival estimates onto a map of the study area using the local estimates for relevant landscape predictors in the model formula:

$$\hat{S}_i(t) = \hat{S}_0(t)^{\exp(x_i'\hat{\beta})} \tag{17}$$

where $\hat{S}_i(t)$ represents expected survival probability for an 'average' individual at location *i* and time *t* (365 days in this case), and $\hat{S}_0(t) = \exp(-\hat{\Lambda}_0(t)) = \exp(\sum_{j:t_j \le t} \hat{h}_0(t_j))$ (Therneau and Grambsch 2000, Fieberg and DelGiudice 2009, DeCesare et al. 2014). For each time period, we estimated $S(t)$ separately for males and females with initial age set to 3 years, and specified relevant time-varying covariates such that their paths could be mapped through time for each prediction (Thomas and Reyes 2014). For the final risk maps, we averaged all survival probabilities for males and females to represent the population-level estimate.

## Results

We included 365 individual wolf encounter histories, with 176 known deaths occurring during the study. The remaining individuals were right-censored, either because fate was not determined or because they were retrieved dead later outside of the study area. A baseline CPH model fit without covariates estimated the overall annual survival rate for collared wolves during our study: $S(t)$ = 0.75 (95% CI = 0.70 – 0.80). CPH models fit with covariates revealed that multiple factors influenced the hazard (risk of mortality) and subsequent survival estimates. The best reduced model included capture-level covariates for sex, weight at capture, translocation status, and vaccine (Table 6.2). In addition, time-dependent covariates were supported for pack membership vs. transience, ageing (initial age + time after capture), day of year, distance from territory center, wolf density, forested-open edge density, percent agriculture, and elevation (Table 6.2). Schoenfeld residual tests indicated that the proportional hazards assumption was satisfied for all predictors (Table 6.3).

Mortality risk was greater for males ( $\hat{\beta} = 0.428,\ p = 0.016$ ) and increased with distance from the individual's territory when individuals were associated with a pack ( $\hat{\beta} = 0.217,\ p = 0.001$ ). In contrast, the distance effect reduced the hazard for transients ( $\hat{\beta} = -0.216,\ p = 0.001$ ). Pack membership reduced mortality risk ( $\hat{\beta} = -5.272,\ p < 0.001$ ), as did ageing (see Table 6.2 for effects of non-linear terms) and greater body weight at capture ( $\hat{\beta} = -0.013,\ p = 0.119$ ) although the ageing and weight effects were not statistically significant at the conventional $\alpha = 0.05$ threshold. Twenty-four wolves were translocated following a depredation event; our model indicated that this action may have reduced mortality risk following translocation ( $\hat{\beta} = -0.541,\ p = 0.124$ ). Vaccinations may have similarly reduced mortality risk ( $\hat{\beta} = -0.320,\ p = 0.121$ ). Relatively low sample sizes for the latter effects may have limited our ability to detect a statistically significant effect.

Landscape covariates representing prey availability, land cover, topography, and human influence had relatively little effect on mortality risk, with only three of the original 12 landscape predictors retained in the final model (forested-open edge density, % agriculture, elevation; Table 6.2). Mortality risk increased with greater proportions of agriculture ($\hat{\beta} = 0.159,\ p = 0.037$) and also with increasing edge densities and elevation, although the latter two effects were not statistically significant at $\alpha = 0.05$ (Table 6.2).

We detected seasonal (day of year) and density-dependent effects on mortality risk, which had non-linear effects on the hazard (Table 6.2; Figs. 6.1 and 6.2). In particular, mortality risk was greatest in winter and lowest in summer (Fig. 6.2C), resulting in lower cumulative survival probabilities during the winter (Fig. 6.1). Survival was density-dependent, with the estimated hazard increasing with greater wolf densities; the increase was sharp initially before apparently stabilizing at moderate densities (Fig. 6.2E). Density-dependence associated with spatiotemporal variation in wolf density was reflected by our risk maps, as estimated survival rates declined the most in the highest wolf density areas over time (Fig. 6.3).

## Discussion

Adult survival is a key driver of wolf population dynamics (Fuller et al. 2003) and provides important information about how preferred habitats influence relative fitness. Linking habitat to population vital rates such as survival is likely to be more valuable for long-term management and conservation of populations than focusing solely on habitat selection or species distribution (Franklin et al. 2000, Gaillard et al. 2010), especially when a species likely deviates from the theoretical ideal-free habitat distribution (Mosser et al. 2009). Our CPH models related patterns in wolf movement and territory use to variation in space and time, suggesting that the spatial ecology of the species is a key component of understanding long-term fitness and population trends. By identifying the most relevant predictors of wolf survival and mortality risk, we could extrapolate predictions of a key fitness indicator spatially and temporally, providing a valuable tool for effective management of a controversial but ecologically fundamental top predator.

Wolves in our study area had survival rates similar to other U.S. populations. Recent estimates have ranged from 0.75 (Wydeven et al. 2009b, Smith et al. 2010) to 0.79 (Adams et al. 2008, Wydeven et al. 2009a, Cubaynes et al. 2014). However, the spatiotemporal landscape of survival has not been explored with the detail provided here. From the results of our analysis, we identified four areas of focus that are broadly relevant under the context of spatiotemporal variation in wolf survival and mortality risk: 1) long-term temporal variation and density dependence in estimates of wolf survival, 2) short-term seasonal variation and its ecological relevance and potential management implications, 3) human impacts and the importance of wolves ability to navigate the anthropogenic ‘landscape of risk’ (e.g. Stenglein, J.L. et al. 2015a) and 4) the importance of identifying habitat quality based on fitness for despotic or pre-emptive habitat selectors (Van Horne 1983, Pulliam and Danielson 1991, Mosser et al. 2009).

### *Long-term variation and density dependence*

Density dependence was a driving force of long-term temporal variation in survival rates during our study. We included smoothed terms for time (biological year) in addition to wolf density, but the smooth time variable was not retained in the final model while spatiotemporal density was highly significant (Table 6.2). The effect was evident in spatial predictions of annual survival during early (1995 – 2000), mid (2001 – 2006), and late (2007 – 2013) recovery time periods (Fig. 6.3). When holding all other variables except density constant in our model, estimated UP-wide adult survival rates declined across the time series (Fig. 6.4). By the late time period, modeled survival was lowered throughout the majority of the study area (Fig. 6.4C), which we attributed mainly to broad-scale increases in wolf density because proportions of agriculture and forested-open edge densities were relatively constant at the scale of our analysis while wolf density varied over time (Fig. 6.4). Density-dependent regulation of survival rates in wolves can occur through increased intraspecific aggression when wolves are protected from human-caused mortality (Cubaynes et al. 2014). While we documented a few cases of wolves being killed by other wolves (MDNR, *unpublished data),* we observed more evidence that the declines in survival in our study area corresponded with increased potential for human conflict (e.g., see Murray et al. 2010). As wolves expanded their range, shifts in habitat use and selection resulted in greater exposure to sub-optimal habitat with greater proportions of agriculture and human development, subsequently increasing the risk of human-caused mortality.

### *Seasonal variation in survival rates*

We detected seasonal variation in the hazard rate for wolves in our study. Risk of mortality increased during fall and winter and appeared to peak in January (Fig. 6.2C). Several factors could contribute to increased mortality risk during fall and winter. Wolves may be more vulnerable to illegal human-caused mortality during this time period. Deer hunting with firearms in our study area typically began in mid-November, with a muzzleloader season concluding in mid-December. Illegal killing tends to occur opportunistically in heavily forested regions; wolves are probably most vulnerable to being killed illegally during hunting seasons. Seasonality in mortality risk also coincides with the heaviest snowfall time periods in the UP, and recreational trails receive heavy snowmobile use. Wolves are known to use forest roads and trails as travel routes and territory boundaries (Barja et al. 2004, Whittington et al. 2005, Kohn et al. 2009), which likely makes them more vulnerable to detection (Zimmermann et al. 2014). Alternatively, dispersal sometimes varies seasonally in wolf populations (Boyd and Pletscher 1999, Kojola et al. 2006) and transience was also associated with increased mortality risk in our study, indicating that dispersal could contribute to seasonal variation in mortality risk.

*Navigation of a risky landscape*

Drivers of mortality risk suggested that human impacts were the predominant hazard facing wolves, even in a population that was legally protected during the majority of the study (Beyer et al. 2009, Olson et al. 2015). Wolf mortality was primarily human-caused, with the majority of deaths occurring due to poaching, vehicle strikes, and other human causes such as legal euthanization or incidental trapping (MDNR, *unpublished data*). Records of known mortality sources indicated human mortality causes outnumbered other causes by > 2:1. In addition, illegal killing may be underestimated due to potential censoring bias (Liberg et al. 2012, Stenglein et al. 2015c), although estimates of informative censoring were relatively low in a similar neighboring population (Stenglein 2014, Stenglein et al. 2015c).

Our final CPH model included effects such as proportion of agriculture, open-forest edge density, elevation, territory vs. transient, distance from territory, translocation, and experience, which suggests that occupying high quality ‘real estate’

(Mosser et al. 2009), developing knowledge of territory, and learning to navigate a risky landscape (i.e. for transients) are keys to long-term survival for wolves. Evidence for this includes the following: First, experience mattered, as risk generally decreased as wolves got older and transients were more likely to survive as they aged and established new territories. Second, density-dependence in survival rates combined with habitat predictors indicative of risk may indicate potential for a source-sink process consistent with ideal-despotic or ideal-preemptive habitat distributions (Pulliam and Danielson 1991, Morris 2003a, Mosser et al. 2009). In this scenario, early colonizers would occupy the safest habitat and later colonizers would have to choose from riskier sites. This hypothesis is corroborated by higher survival rates predicted for wolves that consistently occupy territories as opposed to increased hazards for those that exhibit exploratory movements (greater distances from pack territory) and transience (unknown pack territory or transient movements). Source-sink dynamics are complex, and demonstration of source vs. sink habitat would require additional information on recruitment and immigration/emigration which would allow estimation of a net growth rate for specific habitats. Thus, spatial predictions of annual survival should be interpreted as mortality risk, which in this case is associated with potential human conflicts.

### *Conclusion*

Animals may not always select the highest quality habitat (Battin 2004). When territoriality is significant, site dependent regulation (Rodenhouse et al. 1997) likely results in uneven fitness across a landscape when the highest quality habitats become saturated (Mosser et al. 2009). Declining survival rates in wolves were related to spatiotemporal variation in wolf density during recolonization, indicating that mortality risk is density-dependent when safe habitats are limited. In this case, a mismatch between habitat suitability and occupancy may exist, and traditional habitat suitability analyses may not be adequate indicators of quality. Source-sink population dynamics may occur in this scenario; resource managers should seek to identify source habitats and preserve them to promote and sustain long-term, regional species recovery.

Table 6.1. List of codes and descriptions for all variables considered in a Cox Proportional Hazards model of wolf survival times in Michigan, USA, 1992 – 2013.

| Parameter | Variable Type | Description and coding |
|---|---|---|
| **Measured at capture** | | |
| Age | continuous (estimated) | age in years, estimate at trap or updated later via necropsy info |
| Sex | categorical factor (2 levels) | male, female |
| Capture Type | categorical factor (2 levels) | research, incidental |
| Vaccine | indicator | 1 = received vaccination, 0 otherwise |
| Ivomec | indicator | 1 = received ivomec, 0 otherwise |
| Weight | continuous | weight at capture (lbs) |
| **Time-dependent** | | |
| Capture Effects | | |
| Translocation[a] | indicator | 1 = translocated, 0 otherwise |
| Depredation[a] | indicator | 1 = depredation event, 0 otherwise |
| Recaptured[a] | indicator | 1 = trapped on > 1 occasion, 0 otherwise |
| Movement & Transience | | |
| Pack membership[a,c] | categorical factor (2 levels) | 0 = resident pack, 1 = transient |
| Distance (transient) | continuous | distance from center of all observations |
| Distance (resident pack) | continuous | distance from center of territory home range |

| | | |
|---|---|---|
| Movement rate | continuous | distance between current and last observation / time between observations |
| Habitat | | |
| Buck Kill index | continuous | Bucks killed per km2, measured within moving window |
| % Deer wintering complex (DWC) | continuous | Proportion of deer winter habitat within moving window |
| Distance to DWC | continuous | Distance to nearest deer winter habitat complex within moving window |
| Road Density | continuous | Road density (km / km2) within moving window |
| % Impervious Surface | continuous | Developed impervious surface % of landscape within moving window |
| % Agriculture | continuous | Agriculture % of landscape within moving window |
| % Protected Land | continuous | Public/protected % of landscape within moving window |
| Snow Depth | continuous | Long-term average of snow depth, 1 km spatial resolution[d] |
| Elevation | continuous | Average elevation (m) within moving window |
| Slope | continuous | Average degrees slope within moving window |
| Forested:Open Edge Density | continuous | Density of forested vs. open habitat edge (km / km2) within moving window |
| Stream Density | continuous | Stream density (km/km2) within moving window |
| Density Dependence and Time | | |
| Wolf Density[b] | continuous | Average annual wolf density within moving window (38 km buffer[e]) |

| | | |
|---|---|---|
| Biological Year[b] | continuous | non-linear effect of biological year |
| Day of Year[b] | continuous | non-linear effect of julian date (day of year) |
| Ageing[b] | continuous | non-linear effect of age over time, starting with estimated age at capture |

[a] indicator switches from 0 to 1 at the time of the event and remains 1 afterward

[b] non-linear effect; modeled using cubic spline function

[c] pack membership determined by association with known pack territory and homing movement behavior

[d] Snow Data Assimilation System (SNODAS; https://nsidc.org/data/g02158)

[e] approximate median wolf dispersal distance based on distances reported in Treves et al. (2009)

Table 6.2. Relative effects (log-hazard) of relevant predictors in a Cox Proportional Hazards model of wolf survival times in Michigan, USA, 1992 – 2013. Predictors in bold indicate *p* values < 0.05. Negative values correspond to reduced mortality risk.

| Parameter | $\hat{\beta}$ | $SE(\hat{\beta})$ | $Wald\ Z$ | $p$ |
|---|---|---|---|---|
| Sex | | | | |
| **Male** | **0.428** | **0.178** | **2.410** | **0.016** |
| Capture effects | | | | |
| Weight at capture | -0.013 | 0.008 | -1.560 | 0.119 |
| Translocation | -0.541 | 0.349 | -1.550 | 0.121 |
| Depredation | | | | |
| Recaptured | | | | |
| Researcher (vs. Incidental) | | | | |
| Vaccine | -0.320 | 0.208 | -1.540 | 0.124 |
| Ivomec | | | | |
| Movement and transience | | | | |
| **Territory membership** | **-5.272** | **1.139** | **-4.630** | **< 0.001** |
| **Distance from center of observations (transient)** | **-0.216** | **0.064** | **-3.390** | **0.001** |
| **Distance from territory (territory occupant)** | **0.433** | **0.132** | **3.290** | **0.001** |
| Movement rate | | | | |
| Habitat | | | | |

| | | | | |
|---|---|---|---|---|
| Buck kill index | | | | |
| % Deer Wintering Complex | | | | |
| Distance to Deer Wintering Complex | | | | |
| Road Density | | | | |
| % Impervious Surface | | | | |
| % Agriculture | **0.159** | **0.076** | **2.080** | **0.037** |
| % Protected Land | | | | |
| Snow Depth | | | | |
| Elevation | 0.199 | 0.125 | 1.590 | 0.112 |
| Slope | | | | |
| Forested:Open Edge Density (Edge), linear term | 1.895 | 0.975 | 1.940 | 0.052 |
| Edge$_1$ | -18.344 | 10.808 | -1.700 | 0.090 |
| Edge$_2$ | 31.693 | 18.897 | 1.680 | 0.094 |
| Stream Density | | | | |
| Density Dependence and Time | | | | |
| Age (cumulative) | 0.046 | 0.174 | 0.260 | 0.793 |
| Age$_1$ | -0.963 | 0.630 | -1.530 | 0.126 |
| Age$_2$ | 3.900 | 2.138 | 1.820 | 0.068 |
| **Day of Year (DOY), linear term** | **-0.012** | **0.004** | **-3.410** | **0.001** |
| **DOY$_1$** | **0.024** | **0.010** | **2.410** | **0.016** |
| **DOY$_2$** | **-0.068** | **0.039** | **-1.710** | **0.086** |
| Biological Year, linear term | | | | |

| | | | | |
|---|---|---|---|---|
| Biological Year, non-linear terms | | | | |
| **Wolf Density, linear term** | **1.619** | **0.627** | **2.580** | **0.010** |
| **Wolf Density$_1$** | **-15.358** | **6.112** | **-2.510** | **0.012** |
| **Wolf Density$_2$** | **33.694** | **13.567** | **2.480** | **0.013** |

Table 6.3. Results of the assumption of proportional hazards test using scaled Schoenfeld residuals for each individual predictor separately and for the full (global) model, where $p < 0.05$ indicates a statistically significant relationship between a predictor's effect and time.

| Parameter | $\rho$ | $\chi^2$ | $p$ |
|---|---|---|---|
| Age | -0.034 | 0.241 | 0.623 |
| Sex | 0.009 | 0.015 | 0.904 |
| Weight | 0.041 | 0.435 | 0.510 |
| Vaccine | -0.064 | 0.673 | 0.412 |
| Translocation | 0.027 | 0.144 | 0.705 |
| Agriculture | -0.024 | 0.129 | 0.720 |
| Elevation | -0.059 | 0.698 | 0.403 |
| Distance from Territory | -0.125 | 2.068 | 0.150 |
| Territory membership | -0.107 | 3.127 | 0.077 |
| Distance*Territory | -0.107 | 3.088 | 0.079 |
| Wolf density | -0.092 | 1.716 | 0.190 |
| Day of Year | -0.021 | 0.074 | 0.786 |
| Edge | -0.035 | 0.240 | 0.625 |
| GLOBAL | NA | 6.26 | 0.936 |

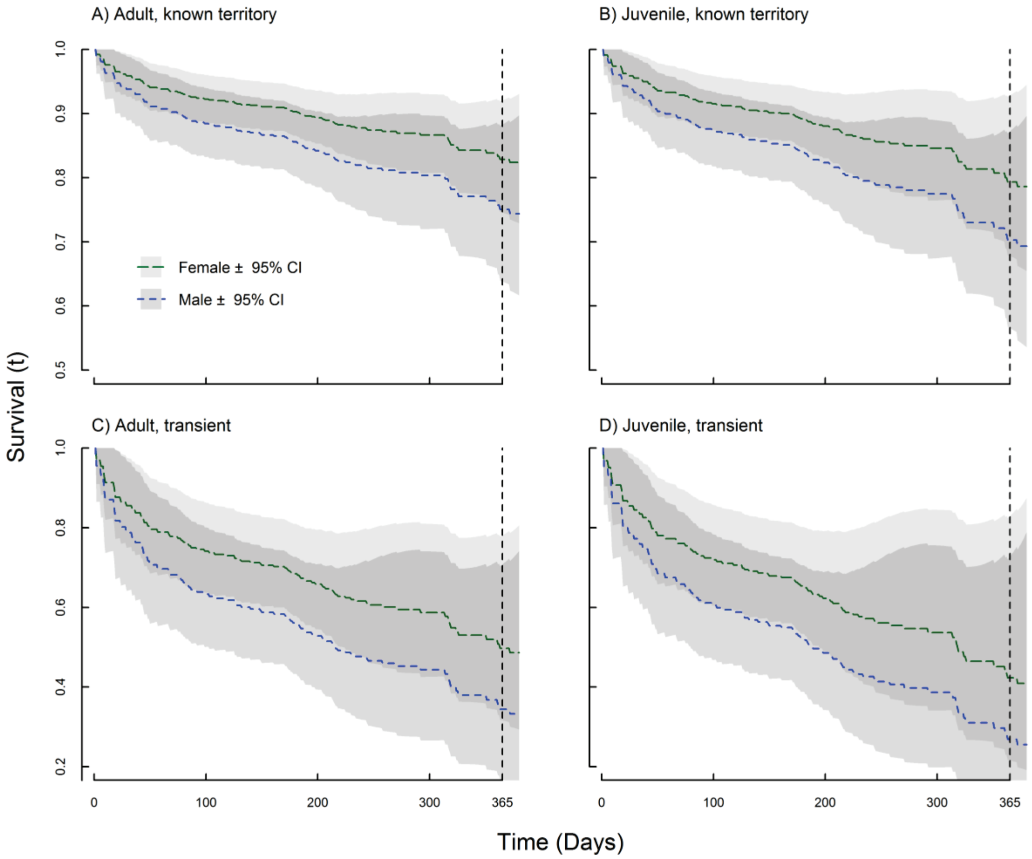

Figure 6.1. Predicted annual survival rates from a Cox Proportional Hazards (CPH) model comparing adult and juvenile wolves occupying territories (A, B) to adult and juvenile transient wolves (C, D) in Michigan, USA, 1992 – 2013. Females (green curves) had greater survival rates than males (blue curves), and survival varied seasonally based on a smoothed function of time (Julian day) with mortality risk greater in winter than in summer. Transient status was identified based on movements away from known territories without returning and was associated with lower predicted survival (C, D). Initial age was 1 year old for juveniles and 3.5 years old for adults; all

other covariates in the CPH were held constant at mean values for continuous variables or most common case for discrete or factor variables.

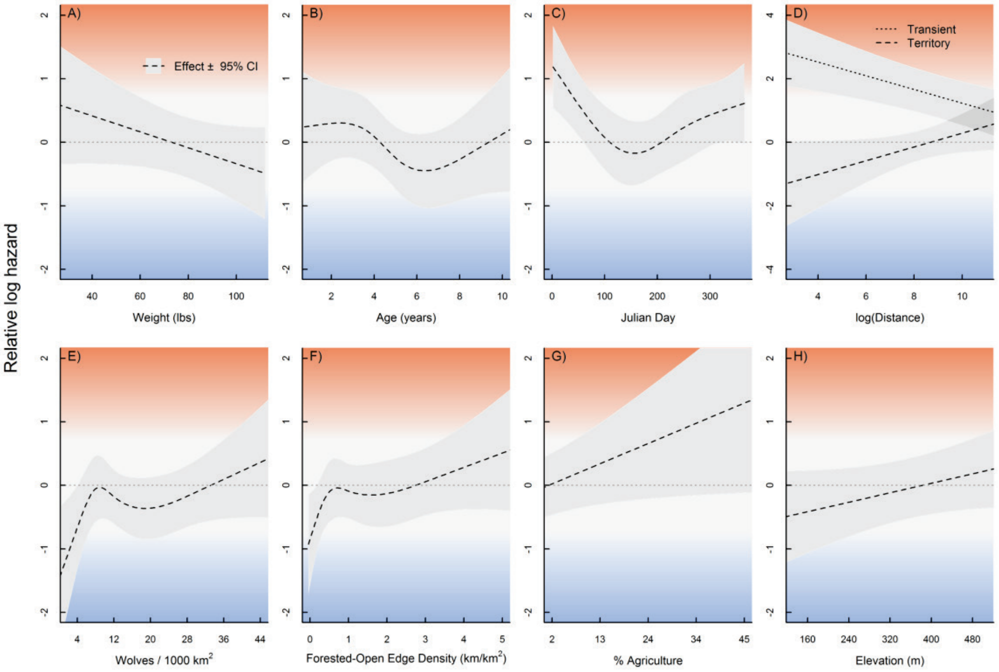

Figure 6.2. Relative log hazard effects from a Cox Proportional Hazards fit to time-varying predictors in Michigan USA, 1992 – 2013. Greater log hazard indicates greater mortality risk and shorter survival times (color-coded red) while lower hazards correspond to lower risk and longer survival times (color-coded blue).

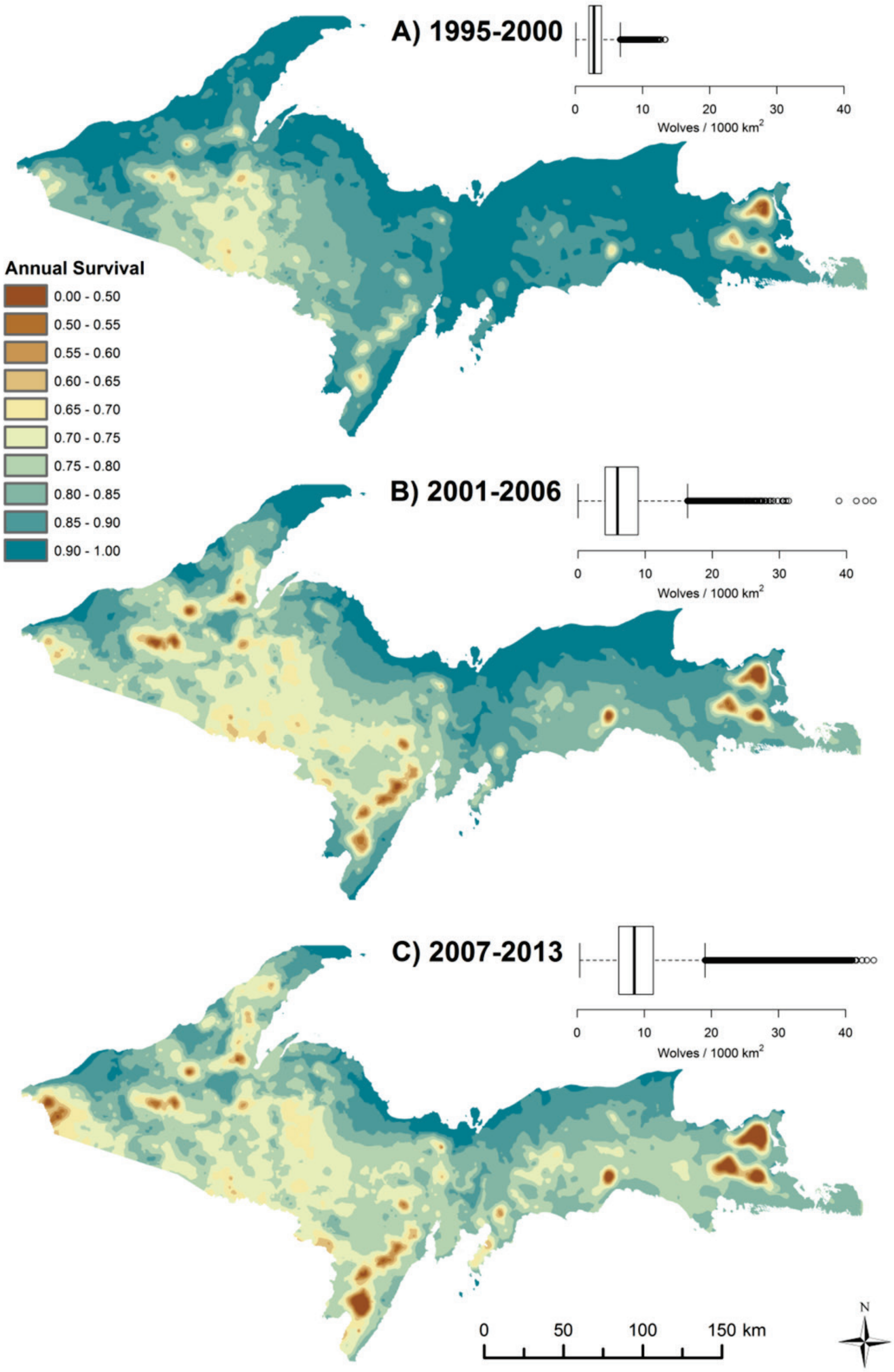

Fig. 6.3. Spatial representation of the ‘landscape of risk’ for wolves in Michigan, USA corresponding to three time periods: A) 1995 – 2000; early recovery, B) 2001 – 2006 (mid-recovery), and C) 2007 – 2013 (late recovery). Spatial and temporal variation in

predicted survival reflected density dependence (lower survival rates with increasing wolf density), and landscape effects associated with agriculture, open vs. forested edge densities, and elevation (increased mortality risk with greater proportions of agriculture, greater edge densities, and highest elevations). Annual survival estimates were for adult wolves (starting age = 3.5 years) and estimates were conditioned on the 1st day of the biological year (April 15).

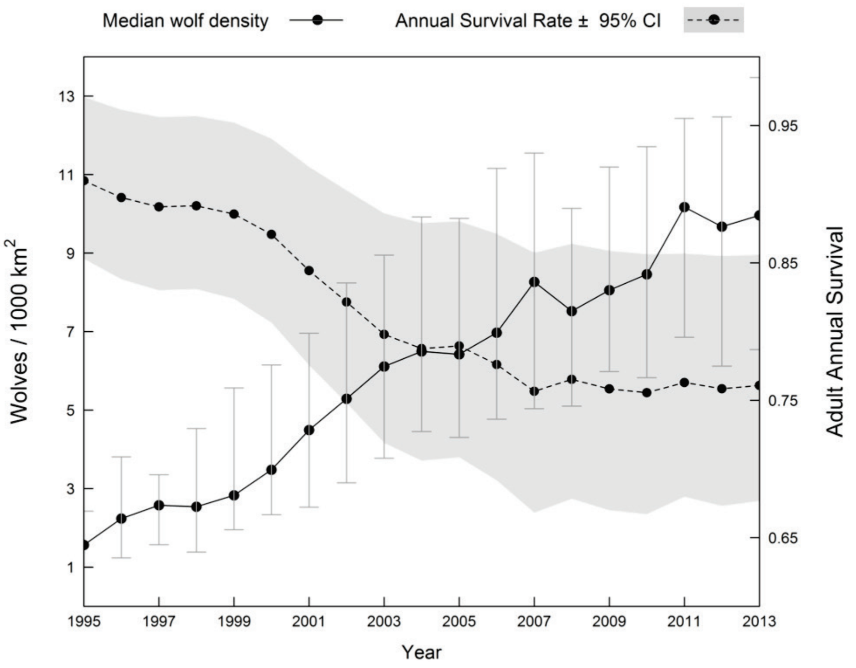

Figure 6.4. Time trend in predicted adult annual survival rates for an average adult wolf corresponding with changes in median wolf density in Michigan, USA, 1995 – 2013. Wolf abundance increased from 57 to over 600 during the study; declines in survival were related to increasing wolf density, as survival predictions were obtained from a Cox Proportional Hazards model with all predictors except wolf density held constant at their average (continuous variables) or most common values (factor variables) in the study. Error bars around the density estimates represent the interquartile range, while the shaded polygon around the survival estimates represents the 95% confidence interval.

# 7. Competing risks and partial compensation for human-caused mortality in Upper Peninsula wolves[6]

## Abstract

Conservation and management of wolves and other large carnivores requires monitoring and quantifying the effect that humans have on populations. Humans can either facilitate or limit range expansion and population growth of large carnivores. Quantifying the impacts of human-caused mortality on populations is essential for conservation and management, especially when goals involve facilitating range expansion. The primary mortality source for wolves is most commonly human-caused. The ability of wolves to withstand high rates of anthropogenic mortality is debated; although population growth has occurred with human-caused mortality near 30%, in many cases this has occurred in populations that have may have been sustained by immigration from outside populations. Human-caused mortality is often assumed to be compensated for by reductions in natural mortality or increased recruitment, but several studies have concluded that human-caused mortality is additive, or even "super-additive" to other mortality sources. I evaluated human-caused mortality in the Michigan wolf population. I focused specifically on estimating competing risks, exploring correlations between mortality sources, overall survival, density, and population growth. I also quantified compensatory-additivity metrics with respect to human caused mortality. Human causes contributed to 66% of reported wolf mortality in Michigan, and the most common cause of death was illegal killing. This translated to a rate of ~ 17% annual human-caused

---

[6] The material contained in this chapter is in preparation for submission to *Conservation Letters*

mortality. The compensatory-additivity statistic was 0.464, suggesting partial compensation, and growth rate was affected the most when both human and natural mortality rates were high (less compensation). In addition, human caused-mortality was density dependent. Although evidence for partial compensation is encouraging, informative censoring can bias survival estimates high if human-caused mortality is underestimated. Based on a sensitivity analysis, "cryptic poaching" of up to 20% of censored events could result in survival estimates ~ 6% lower than expected based on standard known fate analysis. States with connected populations should consider implementing interstate population models that borrow information from multiple data sources, thereby providing valuable information about immigration, emigration, larger scale population trends, and source-sink dynamics that have not been formally quantified.

## Introduction

Conservation and management of large carnivores requires monitoring and quantifying the effect that humans have on populations. Large carnivore populations have increased in certain areas of the United States (Bales et al. 2005, LaRue et al. 2012, Smith et al. 2014, Wilmers and Schmitz 2016), suggesting that recovery and reintroduction efforts have been successful in restoring top predators to ecosystems that were lacking them for several decades (Smith et al. 2003, Beschta and Ripple 2009, Mladenoff et al. 2009, Wydeven et al. 2009a, Ripple et al. 2014). However, increasing carnivore populations have come with new conservation policy challenges. Management and mitigation of wildlife-human conflicts are a key priority in state and federal management plans involving expanding predator populations. Current debates involve questions about the ethics and legality of large carnivore hunting (Bruskotter et al. 2014, Lute et al. 2014, Vucetich and Nelson 2014), the capacity for human tolerance of predators (e.g. "social carrying capacity"; Kellert et al. 1996 , Carpenter et al. 2000), and the impact that high rates of anthropogenic mortality can have on populations (Creel and Rotella 2010, Gude et al. 2012, Liberg et al. 2012). Humans play a key role in either facilitating or limiting range expansion and population growth for these species (Linnell et al. 2001, Musiani and Paquet 2004).

The gray wolf (*Canis lupus*) is an iconic top predator species that has re-established itself in the northern Rocky Mountains and northern Great Lakes through a combination of natural recolonization and human re-introduction efforts (Beyer et al. 2009, Smith and Bangs 2009, Wydeven et al. 2009a). Currently, Great Lakes populations have surpassed 3,000 wolves while Rocky Mountain populations have exceeded 1,500 and are expanding west and south into Washington, Oregon, and California (https://www.fws.gov/midwest/wolf/aboutwolves/WolfPopUS.htm). In nearly every study of wolf mortality to date, the primary mortality source for wolves has been death from human causes (Creel and Rotella 2010, Murray et al. 2010, Gude et al. 2012, Stenglein et al. 2015b). The only exceptions to this rule have been subpopulations inside Yellowstone and Isle Royale National Parks, where ~ 100 – 200 wolves collectively inhabit protected wilderness where hunting is prohibited and the only human presence is tourism (e.g. Cubaynes et al. 2014). In other areas, wolves have evidently sustained annual human-caused mortality rates of 30-50% (Fuller et al. 2003, Person and Russell

2008, Creel and Rotella 2010, Gude et al. 2012) , where killing occurs legally (e.g. depredation control or legal wolf hunt), illegally (poaching), and incidentally (hit by vehicles).

It is often suggested that wolf populations can continue to withstand human-caused mortality rates of up to 30% (Fuller et al. 2003, Gude et al. 2012). This assumption relies on evidence suggesting that human mortality is at least partially compensated for by reductions in natural mortality or increased reproduction (Murray et al. 2010). Evidence for this varies and often depends on context (Creel and Rotella 2010). Survival rates for wolves have historically been lowest where human influence is high. Annual estimates have ranged from 0.55 – 0.85 for wolves > 1 year old in generally unexploited populations (Fuller et al. 2003, Adams et al. 2008, Smith et al. 2010, Benson et al. 2014, Stenglein 2014). However, lower (0.34 – 0.54) survival estimates have been recorded for wolves subject to significant annual take (Person and Russell 2008), and lower estimates often correspond with areas of lower habitat quality (Smith et al. 2010, Stenglein 2014, Stenglein et al. 2015a). For example, wolves inhabiting areas with higher road densities and greater proportions of agricultural land cover relative to other (i.e. higher quality) habitats had lower survival and higher risks of human-caused mortality in Wisconsin (Stenglein 2014). This indicates that risk associated with human populations is may be an important regulating density-dependent factor for wolves in the Great Lakes Region. However, the nature of the linking mechanism has yet to be revealed by empirical data, hence the need for testing density-dependent habitat selection (Chapter 1) and relating it to survival rates and mortality factors over time (this chapter). While wolves apparently can sustain high levels of human take, additive increases in total mortality have been reported at rates lower than 30% (Creel and Rotella 2010, Stenglein 2014). The debate about the degree to which mortality from natural causes compensates for human causes is ongoing; recent evidence would seem to suggest that wolf populations, on average, can remain stable (i.e. zero growth) at approximately 22% annual human-caused mortality (Fuller et al. 2003, Stenglein 2014). However, there is much variation across space and time which suggests influences of other factors and potential source-sink dynamics between biologically connected populations. Given the policy implications, assessing the impacts of human-caused mortality on wolf populations remains an important analysis.

We estimated cause-specific mortality using data from recolonizing wolves in the Upper Peninsula (UP) of Michigan, USA during 1994 – 2013. We anticipated cause-specific mortality effects on survival that could be spatially variable, involving components such as proximity to humans (or road densities as a proxy for human conflict), and proportion of agricultural land cover associated with movements and territories (Murray et al. 2010, Smith et al. 2010). We expected these factors to vary across time in a manner that is consistent with density-dependent effects associated with the saturation of high quality habitats (Wydeven et al. 2009a, Murray et al. 2010). Our objectives were to estimate cause-specific mortality rates of UP wolves, evaluate the effects of spatial covariates influencing multiple mortality sources, and test for compensatory vs. additive effects of natural and human-caused mortality across time in UP wolves. Results provide important information for future management of a species that has been the subject of legal controversy ever since its initial Endangered Species Act delisting (Olson et al. 2015).

## Methods

### *Wolf monitoring and necropsy data*

Locations and encounter histories of radio-marked wolves were recovered from VHF radio telemetry. Data collection and methodology is fully described in previous chapters. The data we used for all models linking cause-specific mortality to covariates is also summarized in Chapter 6. Any necessary modifications to those data are explained in the analysis sections. We set procedures and definitions to assign specific causes of death to wolves (Stenglein 2014, Stenglein et al. 2015b). If possible, cause of death was initially determined in the field based on available evidence and condition of the carcass. Carcasses were typically sent to a wildlife disease lab so that necropsy results could be obtained. If necropsy results were not available or inconclusive, the determination in the field was used to assign cause of death (Stenglein et al. 2015b). Field notes and lab necropsy results were maintained in a wolf carcass database. To insure consistency and transparency in cause of death assignments, we set criteria for assigning cause and level of certainty at three levels: overall fate (level 1), cause of death (level 2; human vs. natural vs. unknown), and contributions to mortality (level 3; Table 7.1). Each level received a ranked certainty assignment (1=highly uncertain, 2 = uncertain, 3=somewhat certain, 4=certain). Two researchers independently made assignments and judgments of certainty; results were then compared. If assignments differed between researchers, we downgraded the certainty level for the assignment.

After initial assignments were made, results for any uncertain assignments (e.g. ultimate cause of death, uncertainty level 1, 2, or 3) were sent to the principal investigator (PI) for review. If additional information could be obtained by contacting field biologists and checking for updated necropsy information), the uncertainty level was upgraded and ultimate cause of death was assigned. Otherwise, the ultimate cause of death was assigned to ‘unknown.’ We used the following lines of evidence to assign the ‘illegal’ cause of death: 1) presence of fatal gunshot wound from an unknown source, and 2) retrieval of a cut or destroyed collar without a carcass. In the latter case, the collar was typically retrieved near a road or trail, or from a stream underneath a bridge. We interpreted this as the highest level of certainty that a wolf was killed illegally.

### *Competing Risks Analysis*

We used competing risks analysis to quantify separate sources of mortality influencing the wolf population. Competing risks seeks to identify the contributions of multiple hazard types affecting the overall mortality rate (Therneau and Grambsch 2000, Heisey and Patterson 2006). In our case, we considered two hierarchical levels of competing risks. The first level involved separating human vs. natural causes of death, which is an important distinction when evaluating the long-term growth potential of recovering wolf populations (Fuller et al. 2003, Murray et al. 2010) . The second level involved breaking down known causes of death from each class (human vs. natural) into specific events (Table 7.1; Fig. 7.1). A third overall category was death from unknown causes. We used Cumulative Incidence Functions (CIFs) to estimate competing mortality risks at both levels.

The CIF is an extension of common survival models such as the Cox Proportional Hazards (CPH) model. Survival models express the time to an event (typically death), often as a function of covariates (Therneau and Grambsch 2000, Klein and Moeschberger 2005). Survival times can be modeled using parametric regression approaches (e.g. Weibull or Exponentially distributed survival times; Moore 2016) or with semiparametric approaches where the baseline hazard function can take any form while covariates enter the model similar to linear regression (CPH models; Therneau and Grambsch 2000). Briefly, if *T* is a random variable with cumulative distribution function $P(t) = Pr(T \leq t)$ and probability density function $p(t) = dP(t)/dt$ , then the survival function *S(t)* is the complement $S(t) = Pr(T > t) = 1 - P(t)$. The hazard function is the instantaneous risk of an event (e.g. death) at time *t* conditional on survival up to that time:

$$h(t) = \lim_{\Delta t \to 0} \frac{\Pr\left(\left(t \leq T < \Delta t\right) \mid T \geq t\right)}{\Delta t} = \frac{f(t)}{S(t)} \tag{18}$$

The hazard function, or log hazard, implies an exponential distribution of survival times with density function $p(t) = ve^{-vt}$ (Fox 2002, Heisey and Patterson 2006). The hazard function is:

$$h_i(t) = h_0(t)\exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_p x_{ip}) \tag{19}$$

with hazard ratios

$$\frac{h_i(t)}{h_{i'}(t)} = \frac{h_0(t)e^{\eta i}}{h_0(t)e^{\eta i'}} = \frac{e^{\eta i}}{e^{\eta i'}} \tag{20}$$

(Heisey and Patterson 2006). To extend the model to incorporate competing risks, we considered *K*=8 overall causes of death occurring from human, natural or unknown sources (Table 7.1; Fig. 7.1). The cumulative risk function is then defined as the probability of an individual dying from cause *k* by time *t* (Moore 2016):

$$F_k(t) = \Pr(T \le t, C = k) = \int_0^t h_k(u)S(u)du \tag{21}$$

A cause-specific hazard is obtained from the hazard function defined previously, except that the probability of death from cause *k* is conditional on the individual surviving through time *t* (i.e. not dying from another cause):

$$h_j(t) = \lim_{\Delta t \to 0} \frac{\Pr\left(t \le T < \Delta t, C = j \mid T > t\right)}{\Delta t} \tag{22}$$

The hazard function defined previously becomes the sum of all cause-specific hazards at a given time (Moore 2016),

$$h(t) = \sum_{j=1}^{K} h_j(t) \tag{23}$$

and the CIF is obtained by:

$$\hat{F}_k(t) = \sum_{t_i \le t} \hat{S}(t_{i-1})\hat{h}_k(t_i) \tag{24}$$

To evaluate the CIF for all causes of death during the study, we extended the hazard function of a CPH model in its simplest form (i.e. hazard function without covariates). To evaluate influences on human- vs. naturally-caused death independently (Meira-Machado et al. 2008, Moore 2016), we used an existing Anderson-Gill CPH model framework (Chapter 6) to model the cause-specific hazard as a function of time-dependent spatial predictors. Specifically, survival times associated with all human causes were subset for the human-causes model, whereas survival times with all natural causes were subset for the natural-causes model. For each of these models, we fit one model with individual-level factors (sex, age, weight, depredation status, capture type, home range status, vaccination, and ivomec; see Chapter 6), one model with landscape predictors (see Chapter 6). For the latter model, we employed forward-backward stepwise variable selection based on AIC to only include the most useful predictors (Harrell 2015, Moore 2016). As a final step, we combined the first model with the second (reduced) model, and again employed stepwise selection. The resulting model was used to compare cause-specific influences driving wolf survival and mortality.

In addition to cause-specific hazards, we were interested in testing for potentially informative censoring. Several methods have been employed to indicate potential for informative censoring, including sensitivity analysis and a generalized linear model (GLM) with covariates and a binomial distribution (e.g. logistic regression) fit to right-censored vs. non-right-censored (known fate) encounter histories (Murray 2006, Murray et al. 2010). We implemented the logistic regression test for informative censoring using the same covariates that were used in cause-specific hazard models, except that in this case we used the median overall value for each individual's time-dependent covariates. In addition, we employed a sensitivity analysis by reassigning increasing proportions of censored events with a death event and re-estimating the annual survival rate. If this analysis affects survival estimates, then informative censoring is more likely (Murray 2006). We conducted the sensitivity analysis using a replacement range of 2.5% to 20% of censored events, as unobserved mortality is unlikely to exceed 25% (Liberg et al. 2012, Stenglein et al. 2015c)

Next, we extended the CIF corresponding to the first level (human, natural, and unknown mortality sources) to include a time covariate for use in an exploratory analysis of the relative impact of human-caused caused mortality on wolf survival and population growth rate (next section). Quantifying relationships between, e.g. human vs. natural causes, allows estimation of additivity of human-caused mortality to other causes of death (Creel and Rotella 2010, Peron 2013). We adjusted our time-scale for these models, as the AG approach may be less reliable for obtaining year-specific estimates. Specifically, we used a recurring time scale where each individual re-enters the study each year (Fieberg and DelGiudice 2009, DeCesare et al. 2014). We set the start date to the beginning of the biological year (April 15), and back-dated age estimates to match the appropriate time scale. Since individuals that lived through one year were re-entered into the study the next year, we used robust sandwich variance estimators to calculate standard errors (DeCesare et al. 2014).

### *Impact of Anthropogenic Mortality*

We extended the CIF to include biological year as a categorical fixed effect. As such, we obtained annual estimates of human and naturally-caused mortality, as well as overall annual mortality (e.g. 1 - annual survival rate; Murray 2006, Heisey and Patterson 2006). Quantifying inter-annual variation in the CIF allowed us to explore the degree to which reductions in natural mortality sources compensated for increases in human-caused mortality (Creel and Rotella 2010, Murray et al. 2010, Gude et al. 2012). To explore the potential impact of human-caused mortality on the population, we computed annual estimates of human-caused mortality (*h*), natural mortality (*n*), overall survival (*S*), population growth rate (*r*), and population density (*d*) for the years 1997 – 2012. We included data from early years (1992 – 1996) with 1997 because data were too sparse to obtain annual estimates of survival and mortality (e.g. $\leq 3$ individuals monitored per year prior to 1997). This analysis was cut off after biological year 2012 to avoid biases associated with censoring a large number of individuals at the end of the study (end of year 2013). We created a correlation matrix for (*h, n, S, r, d*) to explore relationships between the set of variables. We used Pearson's correlation and assessed statistical significance using non-parametric rank tests (Harrell Jr 2013, Hollander et al. 2013). We set $\alpha$ to 0.10 because our analysis was exploratory and small sample sizes can make effects difficult to detect statistically under conventional significance levels.

We fitted 8 candidate linear regression models with *r* as the response variable to explore hypotheses about the relative effects of mortality sources, survival, and wolf density on the growth rate. We included four models with single linear predictors (*h, n, S, d*) and four models with unique pairs of predictors (*h,n*), (*h,d*), (*n,d*), and (*S,d*). Since *h* and *n* are components of *S*, we did not include these pairs together in models. Further, since we were limited to 15 data points (one for each year), we did not include models with more than 2 predictors. We evaluated the best fit to the data by ranking models in terms of adjusted $R^2$ and AIC.

The relationships between temporal variation in $h$, $n$, and *S* can reveal important information about a population's ability to compensate for human-imposed perturbations that reduce population size (Creel and Rotella 2010, Servanty et al. 2010). The relationship between human mortality and overall mortality (i.e., 1-*S*) can be described by the formula $\beta/(1-\alpha)$ where $\alpha$ is the intercept and $\beta$ is the slope of a simple linear regression model relating overall annual mortality to human-caused mortality (Creel and Rotella 2010, Peron 2013). The resulting value indicates a measure of compensation for vs. additivity of human-caused mortality. An overall compensation rate was developed based on the temporal correlation coefficient between *h* and *n* (Sedinger et al. 2010, Peron 2013), where the decomposition of $corr(n,h)$ is rewritten in terms of *C*, the overall rate of compensation-additivity (Peron 2013):

$$C = -corr(n,h)\sqrt{\frac{Var(n)}{Var(h}} = -\frac{cov(n,h}{Var(h)} \approx \frac{\partial n}{\partial h}$$

In general, *C* is typically somewhere between 0 and 1, where 0 indicates complete additivity (*h* and *n* independent) and 1 indicates complete compensation (Peron 2013). *C* > 1 would suggest overcompensation, whereas C < 0 indicates over-additivity (Peron 2013). We estimated *C* for our study area using (eq. 1) and year-specific estimates of *h*, *n*, and *S* from the CIF model described previously.

## Results

The DNR captured 465 wolves overall during the study time period. Of these, 367 wolves were collared, relocated and monitored by aerial telemetry, and thus included in this analysis. The sex ratio was nearly balanced between males (52.0%; *n*=191) and females (48.0 %; *n*=176). The censoring rate was 51.5% (*n*=189) which was consistent with other radio telemetry studies of wolves (Murray et al. 2010, Stenglein 2014). We observed mortalities for the other 178 wolves, and were able to determine cause of death for 91.0 % (*n* = 162). Wolf mortality was primarily human caused (66.3% of mortality; *n* = 118), with the most likely cause of death from human causes being "*illegally killed*," followed by "*vehicle strike*," "*legally killed*," and "*other human cause*." Natural causes (24.7% of mortality; *n* = 44) were primarily "*disease*," followed by "*intraspecific conflict,*" and "*other natural cause*." All mortality sources are summarized in Table 7.1.

*Cumulative Incidence Functions*

The estimated Cumulative Incidence Function (CIF) revealed the contribution of each mortality type to population-level mortality risk during the study. The overall annual mortality rate based on CPH survival models was 25 ± 5%. For a given year, the expected mortality from human causes was broken down into *illegally killed* (9.0 ± 1.6%), *vehicle strike* (5.2 ± 1.3%), *legally killed* (2.4 ± 0.9%), and *other* (0.6 ± 0.4%). Thus, the cumulative expected mortality from human causes was ~ 17.0% annually. For natural causes, expected mortality was broken down into *disease* (3.2 ± 1.0%), *intraspecific conflict* (1.4% ± 0.7%), and *other* (1.3 ± 0.7%). Expected mortality from natural causes thus summed to ~ 5.9% annually. An additional 2.3 (± 0.8) % of expected annual mortality was from *unknown* cause. The CIF is summarized in Fig. 7.2 with the mortality rate (e.g. the CIF) plotted as a function of time, with each specific cause stacked such that the sum of all mortality types represents the overall estimated annual mortality during the study.

### *Cause-specific hazards and informative censoring*

Cause-specific hazards models fit to human and natural cause events independently revealed differences in covariate effects depending on death type. When survival times for death by human cause were isolated, the selected predictors included age, sex, capture type, transience status, wolf density, and edge density. Specifically, the human-caused hazard (i.e. risk of mortality) increased with greater wolf densities and greater open vs. forested edge densities and for males*, and decreased for research-trapped*, non-transient, and older individuals (Table 7.2). In contrast, the natural-caused hazard increased with age and for individuals treated with Ivomec and decreased for non-transients, individuals that were vaccinated, and in terrain with greater slope* (Table 7.2). Tests for informative censoring indicated that age class at capture was the only statistically significant predictor of censoring status. With adults being the reference age class, old adults were less likely to be censored ($\hat{\beta}$=-2.64, $p$=0.01) and pups were more likely to be censored ($\hat{\beta}$=-2.64, $p$=0.01), while juveniles were not more or less likely than adults to be censored ($\hat{\beta}$=-0.11, $p$=0.67). Notably, wolf density was nearly a statistically significant predictor of censoring status ($\hat{\beta}$=0.20, $p$=0.06). A non-parametric one-sided test of the hypothesis that survival times for *censored* endpoints were different (lower) than all other endpoint survival times was significant ($W$=1.48e$^{e04}$, $p$=0.024). Median time to censoring was 291 days (Interquartile range [IQR] = 144 – 794) while median time to death of any cause was 454 days (IQR = 177 – 1034). This result indicated that if censoring were informative (e.g. some censoring events actually deaths), then survival estimates would be overestimated.

*Temporal variation and compensation-additivity of mortality sources*

We observed temporal variation in competing mortality sources (Table 7.3, Fig. 7.2), which allowed us to explore the relationship between human- and naturally-caused deaths, overall annual survival, and population growth. Based on pairwise correlations, wolf growth rate was negatively correlated with human-caused mortality ($r$ = -0.630, $p$ = 0.009) and density ($r$ = -0.600, $p$ = 0.014), positively correlated with annual survival ($r$ = 0.611, $p$ = 0.012), and independent of natural mortality ($r$ = -0.02, $p$ = 0.931). The most explanatory correlates of growth rate in simple regression models were rates of human-caused and natural mortality ($R^2_{\text{adj}}$ = 0.534, $p$ = 0.003; $\hat{\beta}_{\text{human}}$ = -1.427, $p$ = 0.001, $\hat{\beta}_{\text{natural}}$ = -0.976, $p$ = 0.025), as opposed to wolf density and overall annual survival (Table 7.4A). Human-caused mortality, wolf density, and survival were confounded because each independently appeared to influence growth rate, but relationships also potentially existed among predictors (Table 7.4B).

A negative correlation between human- and natural-caused mortality suggested partial compensation, i.e. a reduction in natural mortality rate with increases in human-caused mortality rate (Péron 2013). The effect of human-caused mortality on overall mortality was $\hat{\beta}$ = 0.405 (SE = 0.201) and was significant at $\alpha$ = 0.10 ($t$ = 2.020, $p$ =

0.063). Based on Creel and Rotella (2010), the formula $\beta/(1-\alpha)$ can indicate a measure of compensation for vs. additivity of human-caused mortality, where $\alpha$ is the intercept and $\beta$ is the slope of a simple linear regression model relating overall annual mortality to human-caused mortality. In our system, $\hat{\beta}/(1-\hat{\alpha})$ = 0.491, indicating partial compensation/additivity. The compensation-additivity C estimate (Péron 2013) was 0.464, also suggesting partial compensation.

## Discussion

Human-caused mortality plays a major role in moderating population growth and range expansion for large carnivores such as wolves. Human-caused mortality generally has its most direct influence on annual survival rates, although it can influence other population vital rates as well (Brainerd et al. 2008, Borg et al. 2015). Despite documentation of human-caused mortality approaching 50% annually in some populations (Ballard et al. 1987, Person and Russell 2008), the prevailing thought has been that wolves can be resilient to these impacts at some range of offtake between 28 and 50% (Mech 2001, Haight et al. 2002, Fuller et al. 2003). To sustain high rates of mortality, wolves must be able to compensate for top-down pressure. This can occur through increased reproduction following downward perturbation (McCullough 1990, Stewart et al. 2005, Mills 2012), decreased natural mortality related to increases in human-caused mortality (Lebreton 2005, Sedinger et al. 2010, Servanty et al. 2010), and immigration from source populations that may be more protected from the risk of human mortality (Boyd and Pletscher 1999, Fuller et al. 2003, Adams et al. 2008, Smith et al. 2010).

Wolves' ability to compensate for human-caused mortality has varied. Further complications involve the variety of methods that have been implemented to evaluate compensatory vs. additive mortality in wolf populations (Stenglein 2014). It is generally agreed upon that population decline is likely to occur when overall mortality exceeds approximately one third of the overall population (Ballard et al. 1987, Fuller et al. 2003, Person and Russell 2008, Stenglein 2014). However, some have argued that human-caused mortality can reach 28% (Mech 2001) or 29% (Adams et al. 2008) without negatively impacting populations. Gude et al. (2012) showed that this can occur when recruitment compensates for high rates of human offtake. Depending on the analysis that is done, human-caused mortality can appear to be additive or super-additive to other causes (Creel and Rotella 2010) or partially compensated for (Murray et al. 2010, Gude et al. 2012). Regardless of the method, some degree of consensus has been reached that populations can be stable when human-caused mortality is not > 22% (Fuller et al. 2003, Creel and Rotella 2010, Murray et al. 2010, Stenglein 2014). However, this does not imply that human-caused mortality is being compensated for by reductions in natural mortality. In a population that generally increased over time, Perón (2013) re-evaluated existing data and estimated $C$ to be -0.122 which would imply over-additivity.

In the context of other wolf populations in the U.S., the rate of human-caused mortality that we reported (~ 17%) was relatively low. In addition, we observed a significant negative correlation between human and natural mortality causes, suggesting that natural deaths were reduced when human-caused mortality increased. Overall population growth rate was correlated with human-caused mortality, natural mortality, annual survival rate, and wolf density. Human and natural mortality rates together were the best predictors of wolf population growth, and performed better than models that included wolf density and overall survival rates. As shown in Table 7.5, human-caused mortality was strongly density-dependent (Pearson's $r$ = 0.68; human-caused mortality increased with increasing wolf densities). Hence, density-dependent population growth rate was manifested in part by increases in human-caused mortality, which has been observed in other increasing wolf populations subject to human exploitation (Murray et al. 2010, Smith et al. 2010). Wolves may self-regulate via inter- and intra- pack aggression at high densities when humans are not a strong top-down force (Cubaynes et al. 2014, Cassidy et al. 2015). This suggests that increased mortality, regardless of its source, can be a strong driver of density dependence in wolf populations. Since upper limits to wolf density are likely driven by available resources and nutrition (Fuller et al. 2003, Vucetich and Peterson 2004, Mcroberts and Mech 2014, Mech and Barber-Meyer 2015), it is possible that top-down regulatory mechanisms influence density dependence primarily once high quality habitat has become saturated (e.g. Chapters 5 & 6).

We estimated human-caused mortality to be partially compensated by associated reductions in natural mortality ($\hat{\beta}/(1-\hat{\alpha})$ = 0.491; $\hat{C}$ = 0.464; Creel and Rotella 2010, Perón 2013). Our estimates contrasted values for the same metrics reported elsewhere that suggest strongly additive human-caused mortality ($\hat{\beta}/(1-\hat{\alpha})$ = 1.34 [Northern Rocky Mountains, USA; Creel and Rotella 2010] and 1.38 [Wisconsin, USA, Stenglein 2014]; $\hat{C}$ = -0.122 [Northern Rocky Mountains; Murray et al. 2010, Perón 2013]). Despite lower human-caused mortality in our study area compared to others, overall survival rate was comparable. Natural mortality evidently played an important role in our study area, and apparently had a stronger influence on growth rate than has been observed in other areas subject to high rates of human-caused mortality. Key differences existed between our study area and others during this time period. First, the UP had relatively little agriculture and cattle farms, so lethal control contributed less to human-caused mortality than in other areas. Second, unique limitations in prey availability during winter may have contributed to greater natural mortality. However, evidence of compensation from our study and reports of greater rates of human mortality associated with similar survival rates suggest that moderate increases in human-caused mortality may not have a substantial effect on annual survival. Finally, it is possible that human-caused mortality was underestimated due to uninformative censoring. If this were to be the case, then actual survival rates may actually be lower than reported.

To address the question of potential informative censoring, we conducted a sensitivity analysis post-hoc. Informative censoring in wolves is most likely to be associated with unobserved mortality (e.g. illegal killing) where the collar is destroyed and never found. Thus, in this case the right-censored event is non-random and is a misclassified event in the observed data (Liberg et al. 2012, Stenglein et al. 2015c). High rates of such informative censoring can result in overestimates of annual survival (Liberg et al. 2012, Stenglein 2014, Stenglein et al. 2015c). We did not have reliable data on wolf recruitment, and thus were unable to provide estimates of such 'cryptic poaching' (Liberg et al. 2012, Stenglein et al. 2015c). However, given the estimated rates of misclassification from Wisconsin (Stenglein 2014, Stenglein et al. 2015c) and

Scandinavia (Liberg et al. 2012), it was possible to provide the potential effect of a range of informative censoring rates on wolf survival in our study. We considered rates of informative censoring of 2.5% –20% at 2.5% intervals, because 20% was the maximum possible estimate based on the posterior distribution reported in Liberg et al. (2012). To estimate the effects, we randomly sampled censored events, replaced their endpoints with death events, refit the basic CPH survival model to the partially simulated dataset, and re-evaluated the annual survival rate. Results suggested that misclassifications would bias estimates of survival, because censored survival times were shorter than known fate survival times. A 2.5% cryptic poaching rate (of all censored events) would have resulted in a survival rate estimate of 0.74 (95% CI 0.68 – 0.80), whereas 20% cryptic poaching would have resulted in annual survival = 0.69 (0.62 – 0.76). Possible rates of cryptic poaching have ranged from 0% to > 20% depending on the posterior distribution of the model considered (Liberg et al. 2012) and the time period of study (Stenglein et al. 2015c). It is also important to note that informative censoring can result in underestimation of survival if censored events in reality have longer survival times than known fate events (Murray 2006). This is possible but unlikely in monitored wolf populations because the most probable alternative event would be that the individual dispersed and left the study area, and dispersing wolves are typically at greater risk than resident wolves (Person and Russell 2008, Smith et al. 2010).

### *Conclusion*

Large carnivore populations are regulated primarily by human-caused mortality and evaluating the impacts of this mortality source is critical for facilitating population growth and expansion. Our analysis of cause-specific mortality for gray wolves in Michigan, USA adds to a growing body of literature that suggests wolves can sustain relatively high rates of human-caused mortality. We provide evidence that ~ 17% annual human-caused mortality is partially compensated for by decreases in natural mortality, and that human-caused mortality increases with subsequent increases in wolf density. Survival rates may have been overestimated due to potential for informative censoring and unobserved mortality, but quantifying these effects remains challenging. We urge wildlife managers in states with connected populations to consider combining available information from long term monitoring programs and developing interstate population models that borrow information from multiple data sources. Such an effort would provide valuable information about immigration, emigration, larger scale population trends, and source-sink dynamics that have not been formally quantified. Legal status has been controversial for species such as wolves, but cooperative multi-state management efforts (i.e. collaborative conservation; Duvall et al. 2017) have precluded the need for ESA listing in other species. Collaborative conservation at large spatial scales will likely be a necessary and critical component of promoting long-term recovery of large carnivore species.

Table 7.1. Categories of assigned mortality sources for radio-collared wolf carcasses retrieved in Michigan, USA, 1995-2013.

| **Mortality Cause**<br>Level 2 | Level 3 | Common examples |
|---|---|---|
| Human | Illegally killed | Shot, trapped illegally, cut or otherwise destroyed collar retrieved near road, trail, or bridge |
| | Vehicle strike | Hit by car, truck, or snowmobile on road or highway |
| | Legally killed | Depredation control case, legally hunted |
| | Other human | Unintentional death associated with incidental capture (coyote trap) |
| Natural | Disease | Sarcoptic mange, canine distemper, infection, canine parvovirus |
| | Intraspecific conflict | Killed by other wolves |
| | Other natural | Starvation, drowning, natural accident (death from fall or other trauma) |
| Unknown | Unknown | Carcass decomposed, scavenged, or otherwise deteriorated, labs results inconclusive |

Table 7.2. Summary of cause-specific mortality of gray wolves in Upper Michigan, USA, 1992–2013.

| Cause of Death | *n* | % of all endpoints | % of all mortality |
|---|---|---|---|
| Human – Illegal | 68 | 18.5 | 38.2 |
| Human – Vehicle Strike | 31 | 8.4 | 17.4 |

|  |  |  |  |
|---|---|---|---|
| Human – Legal | 14 | 3.8 | 7.9 |
| Human – Other | 5 | 1.4 | 2.8 |
| Natural – Disease | 26 | 7.1 | 14.6 |
| Natural – Intraspecific | 9 | 2.5 | 5.1 |
| Natural – Other | 9 | 2.5 | 5.1 |
| Unknown cause | 16 | 4.4 | 9.0 |

Table 7.3. Individual and environmental covariates retained in Cox Proportional Hazards models fit independently to wolves that died by human vs. natural causes. Each model was fit in the absence of other causes and variable selection was done using stepwise AIC comparisons. Variables in bold are statistically significant at α = 0.05.

| Hazard | Variable | $\hat{\beta}$ | se($\hat{\beta}$) | $\chi^2$ | *df* | *p* |
|---|---|---|---|---|---|---|
| Human causes | Sex = Male | 0.325 | 0.192 | 2.872 | 1.000 | 0.090 |
|  | **Age, main effect** | **-0.185** | **0.074** | **6.264** | **1.000** | **0.012** |
|  | Age, non-linear |  |  | 1.939 | 3.030 | 0.590 |
|  | Capture = Research | -0.439 | 0.233 | 3.495 | 1.000 | 0.062 |
|  | **Status = Transient** | **-1.572** | **0.266** | **34.680** | **1.000** | **0.000** |
|  | **Density, main effect** | **0.333** | **0.088** | **14.258** | **1.000** | **0.000** |
|  | Density, non-linear |  |  | 2.492 | 2.050 | 0.297 |
|  | **Edge, main effect** | **0.280** | **0.093** | **8.957** | **1.000** | **0.003** |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Edge, non-linear | | | 1.054 | 2.040 | 0.599 |
| Natural causes | **Age, main effect** | **0.171** | **0.074** | **5.256** | **1.000** | **0.022** |
| | **Status = Transient** | **-1.466** | **0.365** | **16.057** | **1.000** | **0.000** |
| | **Ivomec** | **0.936** | **0.449** | **4.318** | **1.000** | **0.038** |
| | **Vaccination** | **-1.248** | **0.482** | **6.686** | **1.000** | **0.010** |
| | Slope, main effect | -0.218 | 0.148 | 2.151 | 1.000 | 0.142 |
| | Slope, non-linear | | | 3.925 | 1.990 | 0.139 |

Table 7.4. Annual rates of wolf mortality from human and natural sources in the Upper Peninsula of Michigan, USA, 1997 – 2012. Results were obtained from Cumulative Incidence Functions based on individual wolf encounter histories (time-to-event data) and are compared to annual estimates of survival, population, and growth rate (*r*) to assess the potential impacts of human-caused mortality on the population.

| Biological Year | Human | Natural | Survival | Pop. | *r* |
|---|---|---|---|---|---|
| Pre-1998[1] | 0.046 | 0.151 | 0.804 | 113 | 0.203 |
| 1998 | 0.090 | 0.074 | 0.730 | 139 | 0.207 |
| 1999 | 0.060 | 0.098 | 0.842 | 169 | 0.195 |
| 2000 | 0.095 | 0.038 | 0.867 | 216 | 0.245 |
| 2001 | 0.132 | 0.088 | 0.780 | 249 | 0.142 |
| 2002 | 0.164 | 0.076 | 0.761 | 278 | 0.110 |
| 2003 | 0.190 | 0.034 | 0.776 | 321 | 0.144 |

| | | | | | |
|---|---|---|---|---|---|
| 2004 | 0.132 | 0.113 | 0.755 | 360 | 0.115 |
| 2005 | 0.142 | 0.110 | 0.748 | 405 | 0.118 |
| 2006 | 0.155 | 0.164 | 0.680 | 434 | 0.069 |
| 2007 | 0.162 | 0.064 | 0.774 | 509 | 0.159 |
| 2008 | 0.251 | 0.022 | 0.727 | 520 | 0.021 |
| 2009 | 0.220 | 0.000 | 0.780 | 577 | 0.104 |
| 2010 | 0.162 | 0.124 | 0.714 | 557 | -0.035 |
| 2011 | 0.140 | 0.090 | 0.770 | 687 | 0.210 |
| 2012[2] | 0.163 | 0.064 | 0.773 | 673 | -0.021 |

[1] Wolf monitoring efforts began in 1992 but few individuals (< 5) were monitored until 1997 – 1998; we included encounter histories dating back to 1992, but included all previous biological years in 1997's estimate.

[2] 2012's estimate includes some individuals that were monitored through biological year 2013 (the cutoff for the study). Most individuals monitored in 2013 were right-censored at the end of the study and were not included in analysis.

Table 7.5. **A)** Simple linear regression models correlating wolf annual growth rates (r) with annual rates of human-caused mortality (h), natural mortality (n), overall survival (*S*), and wolf density (d) in the Upper Peninsula of Michigan, 1997-2012; **B)** Pearson's correlation matrix showing relationships between r, h, n, *S*, and d, with bold indicating statistical significance at $\alpha = 0.10$.

**A.**

| Rank | Model | $R^2_{\text{adj}}$ | $p$ | *df* | AIC |
|---|---|---|---|---|---|
| 1 | $r$ = h + n | 0.534 | 0.003 | 2, 13 | -41.87 |
| 2 | $r$ = $S$ + d | 0.460 | 0.007 | 2, 13 | -39.49 |
| 3 | $r$ = h | 0.356 | 0.009 | 1, 14 | -37.49 |
| 4 | $r$ = h + d | 0.368 | 0.020 | 2, 13 | -36.99 |
| 5 | $r$ = $S$ | 0.328 | 0.012 | 1, 14 | -36.83 |
| 6 | $r$ = d | 0.315 | 0.014 | 1, 14 | -36.52 |
| 7 | $r$ = d + n | 0.292 | 0.042 | 2, 13 | -35.16 |
| 8 | $r$ = n | -0.071 | 0.931 | 1, 14 | -29.36 |

| | |
|---|---|
| h | model-estimated annual rate of human-caused mortality |
| n | model-estimated annual rate of natural mortality |
| $S$ | model-estimated annual survival rate |
| d | overall wolf density |
| $r$ | estimated annual growth rate |

**B.**

| | r | h | n | S | d |
|---|---|---|---|---|---|
| r | | **-0.63** | -0.02 | **0.61** | **-0.6** |
| h | **-0.63** | | **-0.55** | **-0.48** | **0.68** |
| n | -0.02 | **-0.55** | | -0.32 | -0.22 |
| S | **0.61** | **-0.48** | -0.32 | | -0.38 |
| d | **-0.6** | **0.68** | -0.22 | -0.38 | |

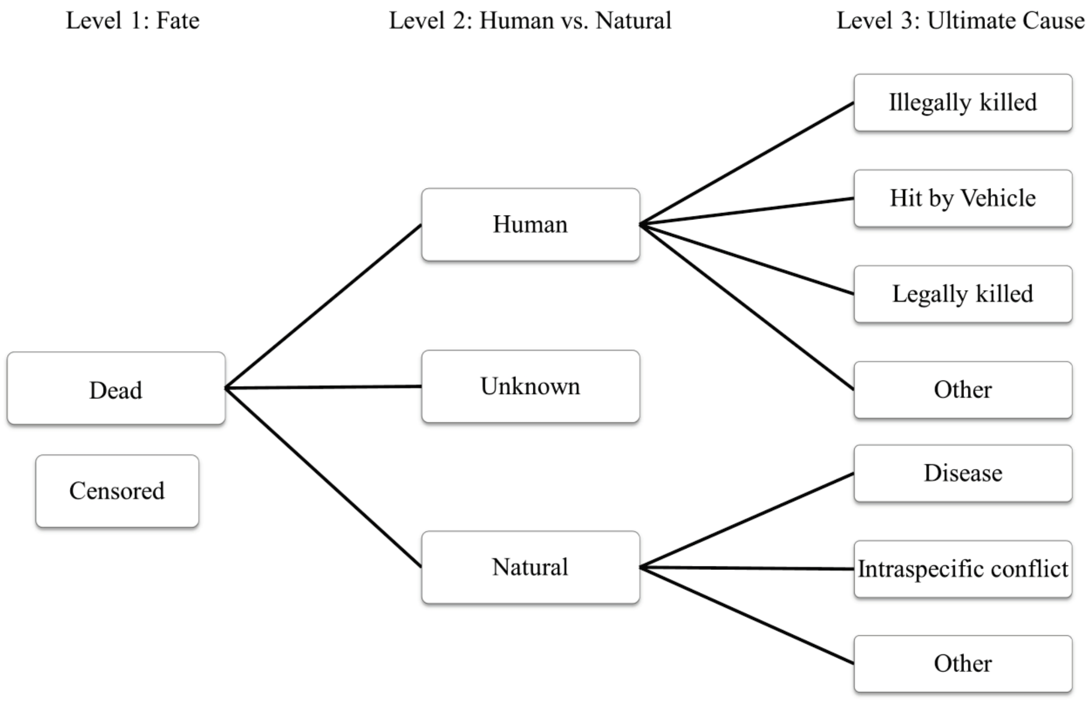

Figure 7.1. Hierarchy of competing risks analysis for wolves in Michigan, USA, where causes of death for known fates are separated into human vs. unknown vs. natural (level 2), and further broken down into specific mortality sources (level 3).

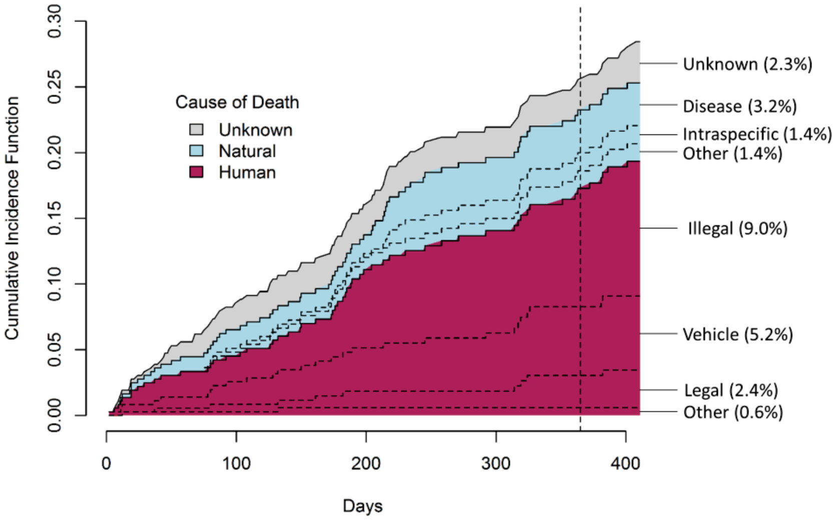

Figure 7.2. Stacked cumulative incidence function showing annual contributions of wolf mortality sources in Michigan, USA, 1995 – 2013. Overall annual mortality was ~ 25%, with primary causes being human-caused (dark red) followed by natural (light blue), and unknown (gray).

## Literature Cited

Aarts, G., J. Fieberg, S. Brasseur, and J. Matthiopoulos. 2013. Quantifying the effect of habitat availability on species distributions. Journal of Animal Ecology **82**:1135-1145.

Aarts, G., J. Fieberg, and J. Matthiopoulos. 2012. Comparative interpretation of count, presence-absence and point methods for species distribution models. Methods in Ecology and Evolution **3**:177-187.

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs:1-25.

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered Greater Sage-Grouse. Ecological Applications **17**:508-526.

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management **69**:298-310.

Anderson, K., and K. J. Gaston. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Frontiers in Ecology and the Environment **11**:138-146.

Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling **200**:1-19.

Bales, S. L., E. C. Hellgren, D. M. Leslie Jr, and J. Hemphill Jr. 2005. Dynamics of a recolonizing population of black bears in the Ouachita Mountains of Oklahoma. Wildlife Society Bulletin **33**:1342-1351.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs:1-54.

Barja, I., F. J. de Miguel, and F. Bárcena. 2004. The importance of crossroads in faecal marking behaviour of the wolves (Canis lupus). Naturwissenschaften **91**:489-492.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology **18**:1482-1491.

Beale, C. M., J. J. Lennon, J. M. Yearsley, M. J. Brewer, and D. A. Elston. 2010. Regression analysis of spatial data. Ecology Letters **13**:246-264.

Beguin, J., S. Martino, H. Rue, and S. G. Cumming. 2012. Hierarchical analysis of spatially autocorrelated ecological data using integrated nested Laplace approximation. Methods in Ecology and Evolution **3**:921-929.

Benson, J. F., B. R. Patterson, and P. J. Mahoney. 2014. A protected area influences genotype-specific survival and the structure of a Canis hybrid zone. Ecology **95**:254-264.

Besag, J., J. York, and A. Mollie. 1991. Bayesian Image-Restoration, with 2 applications In spatial statistics. Annals of the Institute of Statistical Mathematics **43**:1-20.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation **142**:2401-2414.

Beyer, D. E., R. O. Peterson, J. A. Vucetich, and J. H. Hammill. 2009. Wolf Population Changes in Michigan. Pages 65-85 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York.

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

Beyer, H. L., R. Ung, D. L. Murray, and M. J. Fortin. 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. Journal of Applied Ecology **50**:286-294.

Bivand, R. S., V. Gomez-Rubio, and H. Rue. 2015. Spatial Data Analysis with R-INLA with Some Extensions. Journal of Statistical Software **63**:1-31.

Blangiardo, M., M. Cameletti, G. Baio, and H. Rue. 2013. Spatial and spatio-temporal models with R-INLA. Spatial and spatio-temporal epidemiology **7**:39-55.

Blix, A. W., A. Mysterud, L. E. Loe, and G. Austrheim. 2014. Temporal scales of density-dependent habitat selection in a large grazing herbivore. Oikos **123**:933-942.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.

Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology **84**:177-187.

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

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

Boyd, D. K., and D. H. Pletscher. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management **63**:1094-1108.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, and O. Liberg. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management **72**:89-98.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy **80**:385-399.

Bruskotter, J. T., J. A. Vucetich, S. Enzler, A. Treves, and M. P. Nelson. 2014. Removing Protections for Wolves and the Future of the US Endangered Species Act (1973). Conservation Letters **7**:401-407.

Bump, J. K., R. O. Peterson, and J. A. Vucetich. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology **90**:3159-3167.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling **197**:516-519.

Carpenter, L. H., D. J. Decker, and J. F. Lipscomb. 2000. Stakeholder acceptance capacity in wildlife management. Human Dimensions of Wildlife **5**:5-19.

Cassidy, K. A., D. R. MacNulty, D. R. Stahler, D. W. Smith, and L. D. Mech. 2015. Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behavioral Ecology **26**:1352-1360.

Chapron, G., P. Kaczensky, J. D. Linnell, M. Von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, and O. Anders. 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science **346**:1517-1519.

Chapron, G., and A. Treves. 2016. Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. Page 20152939 *in* Proc. R. Soc. B. The Royal Society.

Coates, P. S., M. L. Casazza, M. A. Ricca, B. E. Brussee, E. J. Blomberg, K. B. Gustafson, C. T. Overton, D. M. Davis, L. E. Niell, S. P. Espinosa, S. C. Gardner, and D. J. Delehanty. 2016. Integrating spatially explicit indices of abundance and habitat quality: an applied example for greater sage-grouse management. Journal of Applied Ecology **53**:83-95.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. B. Gustafson, P. Ziegler, and M. L. Casazza. 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology & Management **70**:25-38.

Creel, S., and J. J. Rotella. 2010. Meta-Analysis of Relationships between Human Offtake, Total Mortality and Population Dynamics of Gray Wolves (Canis lupus). Plos One **5**.

Cromsigt, J. P., D. P. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology **50**:544-549.

Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). Journal of Animal Ecology **83**:1344-1356.

Dale, M. R., and M.-J. Fortin. 2014. Spatial analysis: a guide for ecologists. Cambridge University Press.

DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. Journal of Animal Ecology **83**:343-352.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M.

Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications **22**:1068-1083.

Doepker, R. V., D. E. Beyer, and M. L. Donovan. 1994. Deer population trends in Michigan's Upper Peninsula. Michigan Department of Natural Resources, Wildlife Division.

Donovan, M. L., G. M. Nesslage, J. J. Skillen, and B. A. Maurer. 2004. The Michigan GAP analysis final report. Wildlife Division, Michigan Department of Natural Resources, Lansing, MI.

Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography **16**:129-138.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J. R. Garcia Marquez, B. Gruber, B. Lafourcade, P. J. Leitao, T. Muenkemueller, C. McClean, P. E. Osborne, B. Reineking, B. Schroeder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography **36**:27-46.

Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X. Morin, C. Römermann, and B. Schröder. 2012. Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography **39**:2119-2131.

Duong, T. 2007. ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software **21**:1-16.

Duvall, A. L., A. L. Metcalf, and P. S. Coates. 2017. Conserving the Greater Sage-Grouse: A Social-Ecological Systems Case Study from the California-Nevada Region. Rangeland Ecology & Management **70**:129-140.

Eichenlaub, V. L., J. R. Harman, F. V. Nurnberger, and H. J. Stolle. 1990. The climatic atlas of Michigan. University of Notre Dame Press.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Pages 677-697 Annual Review of Ecology Evolution and Systematics.

Ellenwood, J., and F. Krist. 2007. Building a nationwide 30-meter forest parameter dataset for forest health risk assessments. Forests and remote sensing: methods and operational tools. Proceedings of ForestSat:5-7.

Engelbrecht, B. M., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature **447**:80-82.

Evans, J. S., J. Oakleaf, S. A. Cushman, and D. Theobald. 2014. An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0., http://evansmurphy.wix.com/evansspatial.

Falcy, M. R. 2015. Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. Journal of Animal Ecology **84**:545-553.

Fieberg, J., and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. Ecology **90**:1687-1697.

Fox, J. 2002. An R and S-Plus companion to applied regression. Sage, Thousand Oaks CA, Thousand Oaks, CA.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs **70**:539-590.

Frantz, A., S. Cellina, A. Krier, L. Schley, and T. Burke. 2009. Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? Journal of Applied Ecology **46**:493-505.

Frawley, B. J. 2010. Michigan deer harvest survey report 2009 seasons. 3513, Michigan Department of Natural Resources.

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

Friedman, J., T. Hastie, and R. Tibshirani. 2010. Regularization paths for generalized linear models via coordinate descent. Journal of Statistical Software **33**:1.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs:1-41.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf Population Dynamics. Pages 161-191 *in* L. D. Mech and L. Botani, editors. Wolves: behavior, ecology, and conservation. The University of Chicago Press.

Gaggiotti, O. E. 1996. Population genetic models of source–sink metapopulations. Theoretical Population Biology **50**:178-208.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2255-2265.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology **90**:699-710.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. Journal of Wildlife Management **76**:108-118.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. Ecology **94**:861-869.

Haight, R. G., L. E. Travis, K. Nimerfro, and L. D. Mech. 2002. Computer simulation of wolf-removal strategies for animal damage control. Wildlife Society Bulletin:844-852.

Harrell, F. 2015. Regression modeling strategies: with applications to linear models, logistic and ordinal regression, and survival analysis. Springer.

Harrell Jr, F. E. 2013. Hmisc: Harrell miscellaneous. R package version 3.12-2. Computer software]. Available from http://cran. r-project. org/web/packages/Hmisc.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology **45**:834-844.

Heinrichs, J. A., J. J. Lawler, and N. H. Schumaker. 2016. Intrinsic and extrinsic drivers of source–sink dynamics. Ecology and evolution **6**:892-904.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management **70**:1544-1555.

Held, L., B. Schrödle, and H. Rue. 2010. Posterior and cross-validatory predictive checks: a comparison of MCMC and INLA. Pages 91-110  Statistical modelling and regression structures. Springer.

Hirzel, A. H., and G. Le Lay. 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology **45**:1372-1381.

Hollander, M., D. A. Wolfe, and E. Chicken. 2013. Nonparametric statistical methods. John Wiley & Sons.

Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Alldredge. 2013. Reconciling resource utilization and resource selection functions. Journal of Animal Ecology **82**:1146-1154.

Hosmer Jr, D. W., and S. Lemeshow. 1999. Applied survival analysis: Regression modelling of time to event data (1999). Eur Orthodontic Soc.

Houle, M., D. Fortin, C. Dussault, R. Courtois, and J. P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (Canis lupus) in the boreal forest. Landscape Ecology **25**:419-433.

Hutchinson, G. E. 1957. Cold spring harbor symposium on quantitative biology. Concluding remarks **22**:415-427.

Jensen, N. R., C. R. Webster, J. C. Witt, and J. B. Grant. 2011. Ungulate winter habitat selection as a driver of herbaceous-layer heterogeneity in northern temperate forests. Ecosphere **2**:art67.

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

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**:65-71.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters **10**:690-700.

Keating, K. A., and S. Cherry. 2009. Modeling utilization distributions in space and time. Ecology **90**:1971-1980.

Kellert, S. R., M. Black, C. R. Rush, and A. J. Bath. 1996. Human culture and large carnivore conservation in North America. Conservation Biology **10**:977-990.

Kery, M., B. Gardner, T. Stoeckle, D. Weber, and J. A. Royle. 2011. Use of Spatial Capture-Recapture Modeling and DNA Data to Estimate Densities of Elusive Animals. Conservation Biology **25**:356-364.

Kittle, A. M., M. Anderson, T. Avgar, J. A. Baker, G. S. Brown, J. Hagens, E. Iwachewski, S. Moffatt, A. Mosser, B. R. Patterson, D. E. B. Reid, A. R. Rodgers, J. Shuter, G. M. Street, I. D. Thompson, L. M. Vander Vennen, and J. M. Fryxell. 2015. Wolves adapt territory size, not pack size to local habitat quality. Journal of Animal Ecology **84**:1177-1186.

Klein, J. P., and M. L. Moeschberger. 2005. Survival analysis: techniques for censored and truncated data. Springer Science & Business Media.

Kohn, B. E., E. M. Anderson, and R. P. Thiel. 2009. Wolves, Roads, and Highway Development. Pages 217-232 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York.

Kojola, I., J. Aspi, A. Hakala, S. Heikkinen, C. Ilmoni, and S. Ronkainen. 2006. Dispersal in an expanding wolf population in Finland. Journal of Mammalogy **87**:281-286.

Laforge, M. P., R. K. Brook, F. M. van Beest, E. M. Bayne, and P. D. McLoughlin. 2016. Grain-dependent functional responses in habitat selection. Landscape Ecology **31**:855-863.

Laforge, M. P., E. Vander Wal, R. K. Brook, E. M. Bayne, and P. D. McLoughlin. 2015. Process-focussed, multi-grain resource selection functions. Ecological Modelling **305**:10-21.

LaRue, M. A., C. K. Nielsen, M. Dowling, K. Miller, B. Wilson, H. Shaw, and C. R. Anderson. 2012. Cougars are recolonizing the midwest: Analysis of cougar confirmations during 1990-2008. Journal of Wildlife Management **76**:1364-1369.

Lebreton, J. D. 2005. Dynamical and statistical models for exploited populations. Australian & New Zealand Journal of Statistics **47**:49-63.

Lele, S. R., and J. L. Keim. 2006. Weighted distributions and estimation of resource selection probability functions. Ecology **87**:3021-3028.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology **82**:1183-1191.

Lesmerises, F., C. Dussault, and M. H. St-Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. Forest Ecology and Management **276**:125-131.

Lesmerises, F., C. Dussault, and M. H. St-Laurent. 2013. Major roadwork impacts the space use behaviour of gray wolf. Landscape and Urban Planning **112**:18-25.

Liberg, O., G. Chapron, P. Wabakken, H. C. Pedersen, N. T. Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proceedings of the Royal Society B-Biological Sciences **279**:910-915.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution **11**:131-135.

Lindgren, F., and H. Rue. 2013. Bayesian spatial and spatiotemporal modelling with r-inla. Journal of Statistical Software.

Linnell, J. D., J. E. Swenson, and R. Anderson. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation **4**:345-349.

Lute, M. L., A. Bump, and M. L. Gore. 2014. Identity-driven differences in stakeholder concerns about hunting wolves. Plos One **9**:e114460.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies, 2nd Edition. 2nd edition. Kluwer Academic Publishers, Boston, MA.

Marucco, F., L. Vucetich, R. Peterson, J. Adams, and J. Vucetich. 2012. Evaluating the efficacy of non-invasive genetic methods and estimating wolf survival during a ten-year period. Conservation Genetics **13**:1611-1622.

Massé, A., and S. D. Côté. 2009. Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover? Journal of Mammalogy **90**:961-970.

Massol, F., D. Gravel, N. Mouquet, M. W. Cadotte, T. Fukami, and M. A. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. Ecology Letters **14**:313-323.

Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat selection and animal population dynamics. Ecological Monographs **85**:413-436.

Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalized functional responses for species distributions. Ecology **92**:583-589.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography **28**:403-416.

Mattisson, J., H. Sand, P. Wabakken, V. Gervasi, O. Liberg, J. D. C. Linnell, G. R. Rauset, and H. C. Pedersen. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia **173**:813-825.

McCaffery, K. R., J. Tranetzki, and J. Piechura Jr. 1974. Summer foods of deer in northern Wisconsin. The Journal of Wildlife Management:215-219.

McClintock, B. T., R. King, L. Thomas, J. Matthiopoulos, B. J. McConnell, and J. M. Morales. 2012. A general discrete-time modeling framework for animal movement using multistate random walks. Ecological Monographs **82**:335-349.

McCullough, D. 1990. Detecting density dependence: filtering the baby from the bathwater. Pages 534-543 *in* Transactions of the North American Wildlife and Natural Resources Conference.

McDonald, L., B. Manly, F. Huettmann, and W. Thogmartin. 2013. Location-only and use-availability data: analysis methods converge. Journal of Animal Ecology **82**:1120-1124.

McDonald, T. L. 2013. The point process use-availability or presence-only likelihood and comments on analysis. Journal of Animal Ecology **82**:1174-1182.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society of London B: Biological Sciences **273**:1449-1454.

McLoughlin, P. D., K. Lysak, L. Debeffe, T. Perry, and K. A. Hobson. 2016. Density-dependent resource selection by a terrestrial herbivore in response to sea-to-land nutrient transfer by seals. Ecology **97**:1929-1937.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology **79**:4-12.

Mcroberts, R. E., and L. D. Mech. 2014. Wolf population regulation revisited—Again. The Journal of Wildlife Management **78**:963-967.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology **9**:270-278.

Mech, L. D. 2001. Managing Minnesota's recovered wolves. Wildlife Society Bulletin **29**:70-77.

Mech, L. D., and S. Barber-Meyer. 2015. Yellowstone wolf (Canis lupus) density predicted by elk (Cervus elaphus) biomass. Canadian Journal of Zoology **93**:499-502.

Mech, L. D., and L. Boitani. 2010. Wolves: behavior, ecology, and conservation. University of Chicago Press.

Meira-Machado, L. F., J. de Uña-Álvarez, C. Cadarso-Suárez, and P. Andersen. 2008. Multi-state models for the analysis of time-to-event data. Statistical methods in medical research.

Michigan Department of Natural Resources. 2008. Michigan Wolf Management Plan. 3484.

Michigan Department of Natural Resources. 2015. Michigan Wolf Management Plan Updated 2015. 3604, Michigan Department of Natural Resources.

Milakovic, B., K. L. Parker, D. D. Gustine, R. J. Lay, A. B. D. Walker, and M. P. Gillingham. 2011. Habitat selection by a focal predator (Canis lupus) in a multiprey ecosystem of the northern Rockies. Journal of Mammalogy **92**:568-582.

Mills, L. S. 2012. Conservation of wildlife populations: demography, genetics, and management. John Wiley & Sons.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management **70**:384-395.

Mladenoff, D. J., M. K. Clayton, S. D. Pratt, T. A. Sickley, and A. P. Wydeven. 2009. Change in Occupied Wolf Habitat in the Northern Great Lakes Region

Recovery of Gray Wolves in the Great Lakes Region of the United States. Pages 119-138 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Springer New York.

Mladenoff, D. J., and T. A. Sickley. 1998. Assessing potential gray wolf restoration in the northeastern United States: A spatial prediction of favorable habitat and potential population levels. Journal of Wildlife Management **62**:1-10.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes Region. Conservation Biology **9**:279-294.

Mobaek, R., A. Mysterud, L. E. Loe, O. Holand, and G. Austrheim. 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. Oikos **118**:209-218.

Moore, D. F. 2016. Applied Survival Analysis Using R. Springer.

Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2289-2301.

Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs **57**:269-281.

Morris, D. W. 1988. Habitat-dependent population regulation and community structure. Evolutionary Ecology **2**:253-269.

Morris, D. W. 1989. Density-Dependent habitat selection - testing the theory with fitness data. Evolutionary Ecology **3**:80-94.

Morris, D. W. 1994. Habitat matching: alternatives and implications to populations and communities. Evolutionary Ecology **8**:387-406.

Morris, D. W. 2002. Measuring the Allee effect: positive density dependence in small mammals. Ecology **83**:14-20.

Morris, D. W. 2003a. How can we apply theories of habitat selection to wildlife conservation and management? Wildlife Research **30**:303-319.

Morris, D. W. 2003b. Toward an ecological synthesis: a case for habitat selection. Oecologia **136**:1-13.

Morris, D. W. 2011. Adaptation and habitat selection in the eco-evolutionary process. Proceedings of the Royal Society B-Biological Sciences **278**:2401-2411.

Morris, D. W., and J. T. MacEachern. 2010. Active density-dependent habitat selection in a controlled population of small mammals. Ecology **91**:3131-3137.

Morrison, S. F., G. J. Forbes, S. J. Young, and S. Lusk. 2003. Within-yard habitat use by white-tailed deer at varying winter severity. Forest Ecology and Management **172**:173-182.

Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. Ecology Letters **12**:1050-1060.

Murray, B. D., C. R. Webster, and J. K. Bump. 2013. Broadening the ecological context of ungulate-ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology **94**:1317-1326.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management **70**:1530-1543.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, and T. J. Meier. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation **143**:2514-2524.

Musiani, M., and P. C. Paquet. 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. Bioscience **54**:50-60.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology **79**:1435-1441.

National Operational Hydrologic Remote Sensing Center. 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, Version 1. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center.

Nelson, M. E. 1998. Development of migratory behavior in northern white-tailed deer. Canadian Journal of Zoology-Revue Canadienne De Zoologie **76**:426-432.

Nelson, M. E., and L. D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. The Journal of Wildlife Management:471-474.

Nelson, M. E., L. D. Mech, and P. F. Frame. 2004. Tracking of white-tailed deer migration by global positioning system. Journal of Mammalogy **85**:505-510.

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

Nunes, M. A., S. L. Taylor, and I. A. Eckley. 2014. A multiscale test of spatial stationarity for textured images in R. A peer-reviewed, open-access publication of the R Foundation for Statistical Computing:20.

O'Neil, S., and J. Bump. 2014. Modeling habitat potential for elk expansion in Michigan, USA. Wildlife Biology in Practice **10**:111-131.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. Journal of Wildlife Management **70**:554-563.

Olson, E. R., J. L. Stenglein, V. Shelley, A. R. Rissman, C. Browne-Nuñez, Z. Voyles, A. P. Wydeven, and T. Van Deelen. 2015. Pendulum swings in wolf management led to conflict, illegal kills, and a legislated wolf hunt. Conservation Letters **8**:351-360.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist **137**:S29-S49.

Oro, D. 2008. Living in a ghetto within a local population: An empirical example of an ideal despotic distribution. Ecology **89**:838-846.

Panzacchi, M., B. Van Moorter, O. Strand, L. E. Loe, and E. Reimers. 2015. Searching for the fundamental niche using individual-based habitat selection modelling across populations. Ecography **38**:659-669.

Peron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. Journal of Animal Ecology **82**:408-417.

Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. Journal of Wildlife Management **72**:1540-1549.

Petty, J., and G. D. Grossman. 2010. Giving-up densities and ideal pre-emptive patch use in a predatory benthic stream fish. Freshwater Biology **55**:780-793.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**:231-259.

Pinheiro, J. C., D. M. Bates, S. Debroy, D. Sarkar, and R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models.

Potvin, M. J., T. D. Drummer, J. A. Vucetich, D. E. Beyer, R. O. Peterson, and J. H. Hammill. 2005. Monitoring and habitat analysis for wolves in upper Michigan. Journal of Wildlife Management **69**:1660-1669.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist:652-661.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters **3**:349-361.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection - a landscape perspective on population-dynamics. American Naturalist **137**:S50-S66.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.

Rich, L. N., M. S. Mitchell, J. A. Gude, and C. A. Sime. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. Journal of Mammalogy **93**:722-731.

Richard, Y., and D. P. Armstrong. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. Journal of Applied Ecology **47**:603-610.

Ridley, J., J. Komdeur, and W. J. Sutherland. 2004. Incorporating territory compression into population models. Oikos **105**:101-108.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, and M. P. Nelson. 2014. Status and ecological effects of the world's largest carnivores. Science **343**:1241484.

Roberts, D. W., and S. V. Cooper. 1989. Concepts and techniques of vegetation mapping. General technical report INT-US Department of Agriculture, Forest Service, Intermountain Research Station (USA).

Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, and M. Muller. 2011. pROC: an open-source package for R and S plus to analyze and compare ROC curves. Bmc Bioinformatics **12**.

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: A new synthesis. Ecology **78**:2025-2042.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology **62**:327-335.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. The American Naturalist **137**:S5-S28.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution **19**:256-263.

Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society Series B-Statistical Methodology **71**:319-392.

Schreuder, H. T. 1993. Sampling methods for multiresource forest inventory. John Wiley & Sons.

Sedinger, J. S., G. C. White, S. Espinosa, E. T. Partee, and C. E. Braun. 2010. Assessing Compensatory Versus Additive Harvest Mortality: An Example Using Greater Sage-Grouse. Journal of Wildlife Management **74**:326-332.

Sergio, F., and I. Newton. 2003. Occupancy as a measure of territory quality. Journal of Animal Ecology **72**:857-865.

Servanty, S., R. Choquet, E. Baubet, S. Brandt, J.-M. Gaillard, M. Schaub, C. Toigo, J.-D. Lebreton, M. Buoro, and O. Gimenez. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state-space modeling approach. Ecology **91**:1916-1923.

Shi, H., E. J. Laurent, J. LeBouton, L. Racevskis, K. R. Hall, M. Donovan, R. V. Doepker, M. B. Walters, F. Lupi, and J. G. Liu. 2006. Local spatial modeling of white-tailed deer distribution. Ecological Modelling **190**:171-189.

Smith, D. W., and E. E. Bangs. 2009. Reintroduction of wolves to Yellowstone National Park: history, values, and ecosystem restoration. Reintroduction of top-order predators. Oxford: Wiley-Blackwell:92-125.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management **74**:620-634.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience **53**:330-340.

Smith, J. B., C. K. Nielsen, and E. C. Hellgren. 2014. Illinois resident attitudes toward recolonizing large carnivores. Journal of Wildlife Management **78**:930-943.

Smith, J. B., C. K. Nielsen, and E. C. Hellgren. 2015. Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx:1-10.

Stenglein, J. L. 2014. Survival of Wisconsin's gray wolves from endangered to harvested, 1980–2013. Dissertation. University of Wisconsin–Madison.

Stenglein, J. L., J. H. Gilbert, A. P. Wydeven, and T. R. Van Deelen. 2015a. An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk. Ecological Modelling **302**:13-24.

Stenglein, J. L., T. R. Van Deelen, A. P. Wydeven, D. J. Mladenoff, J. E. Wiedenhoeft, N. K. Businga, J. A. Langenberg, N. J. Thomas, and D. M. Heisey. 2015b.

Mortality patterns and detection bias from carcass data: An example from wolf recovery in Wisconsin. The Journal of Wildlife Management **79**:1173-1184.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015c. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and evolution **5**:368-376.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia **143**:85-93.

Tardy, O., A. Masse, F. Pelletier, J. Mainguy, and D. Fortin. 2014. Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. Ecosphere **5**.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology:1828-1834.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer Science & Business Media.

Thomas, L., and E. M. Reyes. 2014. Tutorial: survival estimation for Cox regression models with time-varying coefficients using SAS and R. Journal of Statistical Software **61**.

Tibshirani, R., J. Bien, J. Friedman, T. Hastie, N. Simon, J. Taylor, and R. J. Tibshirani. 2012. Strong rules for discarding predictors in lasso-type problems. Journal of the Royal Statistical Society: Series B (Statistical Methodology) **74**:245-266.

Treves, A., K. A. Martin, J. E. Wiedenhoeft, and A. P. Wydeven. 2009. Dispersal of Gray Wolves in the Great Lakes Region. Pages 191-204 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York.

Turner, M. G. 2005. Landscape ecology: What is the state of the science? Pages 319-344 Annual Review of Ecology Evolution and Systematics.

Uboni, A. 2012. Wolf habitat selection at the territory level: seasonal and interannual variation and influence on reproductive success.

Uboni, A., D. W. Smith, J. S. Mao, D. R. Stahler, and J. A. Vucetich. 2015a. Long- and short-term temporal variability in habitat selection of a top predator. Ecosphere **6**:art51.

Uboni, A., J. A. Vucetich, D. R. Stahler, and D. W. Smith. 2015b. Interannual variability: a crucial component of space use at the territory level. Ecology **96**:62-70.

van Beest, F., P. McLoughlin, E. Vander Wal, and R. Brook. 2014a. Density-dependent habitat selection and partitioning between two sympatric ungulates. Oecologia **175**:1155-1165.

van Beest, F. M., P. D. McLoughlin, A. Mysterud, and R. K. Brook. 2015. Functional responses in habitat selection are density dependent in a large herbivore. Ecography.

van Beest, F. M., A. Uzal, E. Vander Wal, M. P. Laforge, A. L. Contasti, D. Colville, and P. D. McLoughlin. 2014b. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. Journal of Animal Ecology **83**:147-156.

Van Deelen, T. R., H. Campa, M. Hamady, and J. B. Haufler. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. Journal of Wildlife Management **62**:205-213.

Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A Comparison of Presettlement and Present-Day Forests in Two Northern Michigan Deer Yards. The American Midland Naturalist **135**:181-194.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management:893-901.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer Science & Business Media.

Vié, J.-C., C. Hilton-Taylor, and S. N. Stuart. 2009. Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species. IUCN.

Vucetich, J. A., B. A. Huntzinger, R. O. Peterson, L. M. Vucetich, J. H. Hammill, and D. E. Beyer. 2012. Intra-seasonal variation in wolf Canis lupus kill rates. Wildlife Biology **18**:235-245.

Vucetich, J. A., and M. P. Nelson. 2014. Wolf Hunting and the Ethics of Predator Control.*in* L. Kalof, editor. The Oxford Handbook of Animal Studies. Oxford University Press, Oxford, UK, Oxford Handbooks Online.

Vucetich, J. A., and R. O. Peterson. 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves Canis lupus. Oikos **107**:309-320.

Warton, D., and G. Aarts. 2013. Advancing our thinking in presence-only and used-available analysis. Journal of Animal Ecology **82**:1125-1134.

Watanabe, S. 2013. A Widely Applicable Bayesian Information Criterion. Journal of Machine Learning Research **14**:867-897.

Whittington, J., C. C. St Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

Wilmers, C. C., and O. J. Schmitz. 2016. Effects of gray wolf-induced trophic cascades on ecosystem carbon cycling. Ecosphere **7**.

Witt, J. C., and C. R. Webster. 2010. Regeneration dynamics in remnant Tsuga canadensis stands in the northern Lake States: Potential direct and indirect effects of herbivory. Forest Ecology and Management **260**:519-525.

Witt, J. C., C. R. Webster, R. E. Froese, T. D. Drummer, and J. A. Vucetich. 2012. Scale-dependent drivers of ungulate patch use along a temporal and spatial gradient of snow depth. Canadian Journal of Zoology-Revue Canadienne De Zoologie **90**:972-983.

Wunder, M. B. 2010. Using isoscapes to model probability surfaces for determining geographic origins.*in* J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, editors. Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping. Springer, New York, NY, USA.

Wydeven, A. P., J. E. Wiedenhoeft, R. N. Schultz, R. P. Thiel, R. L. Jurewicz, B. E. Kohn, and T. R. Deelen. 2009a. History, Population Growth, and Management of Wolves in Wisconsin. Pages 87-105 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York.

Wydeven, A. P., J. E. Wiedenhoeft, R. N. Schultz, R. P. Thiel, R. L. Jurewicz, B. E. Kohn, and T. R. Van Deelen. 2009b. History, population growth, and management of wolves in Wisconsin. Pages 87-105  Recovery of gray wolves in the Great Lakes Region of the United States. Springer.

Xian, G., C. Homer, J. Dewitz, J. Fry, N. Hossain, and J. Wickham. 2011. Change of impervious surface area between 2001 and 2006 in the conterminous United States. Photogrammetric Engineering and Remote Sensing **77**:758-762.

Yackulic, C. B., R. Chandler, E. F. Zipkin, J. A. Royle, J. D. Nichols, E. H. C. Grant, and S. Veran. 2013. Presence-only modelling using MAXENT: when can we trust the inferences? Methods in Ecology and Evolution **4**:236-243.

Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. To predict the niche, model colonization and extinction. Ecology **96**:16-23.

Zając, T., W. Solarz, and W. Bielański. 2006. Adaptive settlement in sedge warblers Acrocephalus schoenobaenus—focus on the scale of individuals. Acta Oecologica **29**:123-134.

Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology:aru134.

Zurell, D., F. Jeltsch, C. F. Dormann, and B. Schroeder. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? Ecography **32**:733-744.