RESOURCE SELECTION AND VIABILITY OF SHARP-TAILED GROUSE IN THE UPPER PENINSULA OF MICHIGAN

By

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A THESIS

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

Fisheries and Wildlife-Master of Science

2016

ABSTRACT

RESOURCE SELECTION AND VIABILITY OF SHARP-TAILED GROUSE IN THE UPPER PENINSULA OF MICHIGAN

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Sharp-tailed grouse (*Tympanuchus phasianellus*) have experienced declines and range contractions across their distribution. Within Michigan, sharp-tailed grouse expanded during European settlement but subsequently experienced declines and fragmentation. While populations were widespread, these grouse became an important species for hunters and wildlife viewers within the state. Uncertainty about their habitat requirements and how management may influence populations makes current management difficult. I modeled sharp-tailed grouse resource selection and mapped their relative likelihood of occurrence across Michigan's eastern Upper Peninsula. The best model, based on AICc, included the variables of openland, upland forestland, lowland forestland, and upland shrubland. Sharp-tailed grouse selected sections with higher proportions of openland and shrubland and lower proportions of forest and forested wetlands. The relative likelihood of occurrence of sharp-tailed grouse was highest in the eastern and central Upper Peninsula. I also created a spatially explicit metapopulation model and used the model to predict population response to alternative harvest and habitat management options. Scenarios using estimates of current harvest rates did not significantly impact extinction risk and simulations of range-wide harvest indicated lower metapopulation viability than when harvest was localized. Simulations of habitat improvement indicate greater increases in grouse viability when modeled in one large patch versus the addition of small scattered patches. My results suggest that harvest regulations should be implemented locally and not exceed a 25% harvest rate and habitat management scenarios should be ranked by area of contiguous habitat.

ACKNOWLEDGEMENTS

First, I would like to sincerely thank my advisors Dr. Michael Jones and Dr. David Luukkonen for their support, patience, and guidance throughout my research. Their combined expertise gave me excellent resources into any issue I encountered. I would also like to thank Dr. Gary Roloff for being on my committee and provided helpful guidance on resource selection studies.

I thank the faculty and students in the Quantitative Wildlife Center and Quantitative Fisheries Center. I would especially like to thank Dr. William Porter for welcoming me as a member of his lab and Dr. David Williams for his willingness to discuss my research at the drop of a hat and guidance throughout my endeavors into Geographic Information Systems. I thank the Michigan Department of Natural Resources for providing funding and data for this research and their staff; especially Al Stewart, Mike Donovan, Terry Minzey and Dave Jentoft. I also thank the Michigan Sharp-tailed Grouse Advisory Committee for their time and input which were instrumental in my research. I would also like to thank the Michigan Chapter of Safari Club International for funding.

Lastly, I would like to thank my family for their support and encouragement throughout this process. Specifically, without the faith, motivation and reassurance of my mother and sister I would not be the person I am today.

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INTRODUCTION

Openland habitats have been greatly reduced from their historic distributions across North America, and often do not receive the conservation attention that other habitats are given (Askins 2001). While much of eastern North America was forested pre-settlement, there were also large openings that likely supported native openland species (Askins 2001). These large open habitats have declined due to fire suppression, habitat conversion, forest plantings and natural succession (Ammann 1963, Askins 2001). As a result, many species that rely on these open habitats have declined substantially (Hunter et al. 2001). Because of the transitory nature and low conservation priority of open habitats, special effort must be made to ensure that these lands and the wildlife that they support persist (Ammann 1957, Askins 2001).

The prairie sharp-tailed grouse (*Tympanuchus phasianellus campestris*) relies heavily on grassland and shrubland habitats throughout their life history (Connelly et al. 1998). Similar to other openland species, sharp-tailed grouse have experienced population declines and range contractions throughout their distribution (Braun et al. 1994, Connelly et al. 1998). These declines have resulted in extirpation from 8 of the 21 states they originally occupied and many remaining populations have become isolated due to habitat fragmentation (Connelly et al. 1998).

Michigan is the eastern edge of the North American sharp-tailed grouse range (Connelly et al. 1998, Sjogren and Corace 2006). Sharp-tailed grouse occur in a variety of habitats in Michigan, including pine-barrens, non-forested wetlands, shrub lands, grasslands and hayfields, and early successional lands created by large clear-cuts and burns (Sjogren and Corace 2006). In the mid-1800’s there were likely over 32,000 ha of recently burned forested areas in the eastern Upper Peninsula of Michigan (Comer and Albert 1995), and these areas combined with barrens and forest blow downs amounted to approximately 7.5% of the eastern Upper Peninsula habitat (Lorimer 2001). It is believed that sharp-tailed grouse resided in these areas of Michigan before European settlement, but their prevalence is not well documented and many early sightings were likely recorded as prairie-chickens (Ammann 1957).

During the late 1800's and early 1900's the distribution of available grouse habitat expanded considerably throughout Michigan. Open areas were created in the state when timber harvest and burning was widespread (Ammann 1957). This allowed sharp-tailed grouse populations to spread eastward through the entire Upper Peninsula by the early 1940s and translocations during the winter of 1937-38 established populations in the Lower Peninsula (Ammann 1957). Coinciding with population increases, sharp-tailed grouse became a popular game bird in Michigan.

The openland habitat created during European settlement has since been reduced due to forest plantings, fire suppression, and natural succession (Ammann 1963). This reduction in habitat led to sharp-tailed grouse population declines and fragmentation. Because of these declines and uncertainty about population trends, the sharp-tailed grouse harvest season was halted in 1996. Sharp-tailed grouse are no longer present in the Lower Peninsula and there is uncertainty about whether they are still present in the western portion of the Upper Peninsula (Luukkonen 2012). Current occurrence records indicate that sharp-tailed grouse are present in scattered groups in the eastern half of the Upper Peninsula. Recent research focusing on monitoring methods have led to a better understanding of sharp-tailed grouse occupancy in the far eastern portion of Michigan's Upper Peninsula (Luukkonen et al. 2009). Populations in the eastern Upper Peninsula are believed to be stable enough to tolerate modest hunting pressure, and in 2010 a limited hunting season was reopened in this region (Frawley 2011).

While suitable habitat and populations have decreased from historic highs, there is still public interest in the status of sharp-tailed grouse in Michigan as these birds provide both hunting and viewing recreational opportunities for the public (Luukkonen et al. 2009). Maintaining populations of sharp-tailed grouse in Michigan is also important because they are on the periphery of the existing sharp-tailed grouse distribution (Connelly et al. 1998). Peripheral populations are important to conservation because their genetic diversity may be essential to the long term persistence of the species (Lesica and Allendorf 1995). Management for sharp-tailed grouse in Michigan may also benefit other species such as black-backed woodpecker (*Picoides arcticus*), sand-hill crane (*Grus canadensis*) and Kirtland's Warbler (*Setophaga kirtlandii)*; (Sjogren and Corace 2006). Because sharp-tailed grouse are area sensitive, openings large enough to sustain them may be used by these and other wildlife species.

Population declines have been documented for sharp-tailed grouse since they were widespread in Michigan, but uncertainties remain about current population trends, specific habitat requirements and the best management practices needed to sustain and/or rebuild populations. Maintaining sharp-tailed grouse in Michigan will require a concerted effort on the part of managers and a better understanding of habitat requirements and responses to habitat and harvest management options will aide in this management. The uncertainties surrounding sharp-tailed grouse in Michigan have prompted interest in additional research and monitoring to increase our knowledge of this species and its habitat requirements.

Sharp-tailed grouse are considered an indicator species and a species of special concern in Michigan and it is therefore important to be proactive about their management. In the past, prairie grouse management efforts have often been reactive (Aldridge et al. 2004), and Michigan has already seen the loss of the greater prairie-chicken (*Tympanuchus cupido*). The potential benefits of adaptive management, spatially explicit resource selection modeling and metapopulation modeling have been advocated throughout grouse research (Akcakaya et al. 2004, Aldridge et al. 2004, Niemuth 2011). These tools are especially helpful in situations where management uncertainties are present, but funding availability is limited.

Adaptive management was first described in the mid 1970's as a strategy for accounting for uncertainties associated with managing natural resource systems (Holling 1978, Walters 1986). The process includes generating models that represent competing hypothesis about how a system functions. Adaptive management promotes the involvement of stakeholders throughout the planning and implementation process (Lee 1994).

Adaptive management can be either passive or active. Active adaptive management is experimental in nature because the management is designed to test alternative hypotheses and decrease uncertainty about the system of interest (Aldridge et al. 2004). This approach may involve contrasting management actions (treatments) such as varying hunter harvest regulations in different regions of the study area. When management's main purpose is to achieve management objectives without being specifically designed to decrease uncertainty, it is considered passive (Aldridge et al. 2004).

Information gained through experimentation and/or management is then used to reevaluate and modify management practices (Holling 1978, Walters 1986). Monitoring a natural resource system's response to experiments and mangement is key to successfully implementing adaptive management. Failure to implement adequate monitoring has led to numerous unsuccessful adaptive management attempts (Aldridge et al. 2004).

The first steps in an adaptive management process are to identify management objectives and potential management options. Early in this study the Michigan Department of Natural Resources (MDNR) organized a group of sharp-tailed grouse stakeholders to develop a list of objectives and options to guide my work (Luukkonen and Jones 2011). The next step is to conduct an analysis and develop models that synthesize understanding about the management issue – in this case sharp-tailed grouse management in the Michigan Upper Peninsula – that help to identify critical uncertainties and highlight opportunities for active adaptive management. My thesis is focused on this critical step of the adaptive management cycle.

Understanding ecological requirements of a species is essential for making knowledgeable habitat management decisions. While broad habitat requirements for sharp-tailed grouse have been described (Ammann 1963, Berger and Baydack 1992), the wide range of habitats they occupy necessitate region specific studies that address habitat relationships at scales applicable to landscape-level management. Geographic information systems (GIS) have substantially enhanced our ability to characterize species-landscape relationships at varying spatial scales (Niemuth 2011). With GIS we are able to create spatially explicit models using digital landcover data to characterize landscape components and configuration specifically for the region of interest (Niemuth 2011).

Resource selection happens hierarchically beginning at a species range and narrowing to individual home ranges, habitats within an individual's home range and ultimately to specific resources (Johnson 1980). Resource selection studies often compare the selection of resources to their availability, looking for indications that resources are selected disproportionately to their availability (Manly et al. 2002). These studies are useful for natural resources managers because they give managers the ability to spatially represent information necessary for conservation planning using a resource selection function (RSF); (Boyce and McDonald 1999, Johnson et al. 2004). An RSF is any function proportional to the probability of use of a resource (Boyce and McDonald 1999). When resource selection is mapped it can be used to determine land best suited for preservation or restoration, and to identify sites that have value for connecting suitable habitat patches or meta-populations (Niemuth 2011). Determining the best sites for management can reduce management costs by limiting the restoration of habitats with little connectivity to current grouse populations or population-limiting habitat resources (Niemuth 2011). In addition, fine scale monitoring, such as radio telemetry and on the ground habitat assessments, which are often time consuming and expensive and are not always required to create useful spatially explicit habitat models (Niemuth 2011).

Metapopulation models are used to predict the trajectory of a species occurring in sub-populations that interact across a landscape (Akcakaya et al. 2004). These models can be useful when spatially-explicit habitat modeling is used to identify potential metapopulation structure on the landscape. Using this strategy, managers can assess the effects of manipulating habitat patches individually based on population status, dispersal patterns, and landscape configuration (Barnes 2007). Metapopulation models can also assist wildlife researchers in evaluating hypotheses that would be unrealistic or cost prohibitive to conduct at large spatial scales. In this way metapopulation theory and landscape habitat modeling can help design management experiments and associated population monitoring strategies.

Research Objectives

The objectives of this research were to (1) use land use/land cover and occupancy data to model sharp-tailed grouse resource selection, (2) construct a spatially explicit metapopulation model, (3) use the metapopulation model to predict population dynamics in response to alternative habitat and harvest management scenarios, and (4) provide recommendations for sharp-tailed grouse management in Michigan. We used available occurrence data to identify resources of importance to sharp-tailed grouse life history. We then identify spatially explicit habitat patches suitable for sharp-tailed grouse populations in Michigan and used these patches as the landscape structure for a meta-population model. This model is then used to test various habitat and harvest management scenarios that could be considered for future adaptive management experiments.

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CHAPTER 1. SHARP-TAILED GROUSE RESOURCE SELECTION IN MICHIGAN

Introduction

The prairie sharp-tailed grouse *Tympanuchus phasianellus campestris*, has experienced significant declines in numbers throughout the southern and eastern portions of its range, following a similar pattern to that seen in other prairie grouse species across North America (Connelly et al. 1998). This decline has often been attributed to loss of habitat through grassland conversion to farmland and fire suppression leading to habitat succession. Sharp-tailed grouse populations in Michigan have fluctuated extensively throughout the state since they were first recorded in 1904 (Ammann 1957). Deforestation in the 1800's and sharp-tailed grouse translocations between the 1930s and 1950s resulted in expanded populations in Michigan with occurrence records in at least 22 counties by 1957 (Ammann 1957). Since that time habitat loss due to vegetation succession, forest plantings, and fire suppression has substantially decreased their range and from 2009 to 2013 they were reported to occur in only the 6 easternmost counties of Michigan's Upper Peninsula.

Sharp-tailed grouse habitat has been described in the past (Hamerstrom 1939, Ammann 1957, Berger and Baydack 1992), and Geographic Information Systems (GIS) technology and remote sensing advances have facilitated the creation of landscape level habitat analyses (Hanowski et al. 2000, Niemuth and Boyce 2004, Goddard et al. 2009). These grouse generally inhabit areas consisting of grassland and shrub cover and many populations have become reliant on cropland when pre-settlement habitat types are not available (Connelly et al. 1998). Sharp-tailed grouse require large tracts of open habitat (Ammann 1957), although there is uncertainty about what opening sizes can support persistent populations (Niemuth and Boyce 2004).

To inform management and support spatially explicit modeling, it is important to understand the landscape-scale habitat selection of a species, and the likely distributional pattern resulting from that selection. Understanding this pattern can facilitate the identification of lands important for sharp-tailed grouse conservation. A quantitative analysis of sharp-tailed grouse habitat use has not been completed in Michigan since GIS technology and remote sensing data became widely used in habitat analyses. This research is especially important within Michigan because the state has recently reopened a hunting season in a portion of sharp-tailed grouse range. Michigan is also at the periphery of sharp-tailed grouse range, where morphological and genetic differences important for long-term conservation often occur (Lesica and Allendorf 1995) and habitat quality and availability may differ from core populations. Accounting for the possibility that peripheral populations select habitats differently than those within core populations may be helpful when trying to understanding limiting factors to species occurrence.

Many previous studies on grouse habitat use have focused on understanding habitat immediately surrounding leks, because of their importance as breeding habitat. I chose to look at landscape scale habitat selection because studies that look at fine scale resource selection are not always applicable to informing large-scale management decisions. Landscape scale habitat selection studies also allow for mapping areas of importance to the species across large expanses, which is not practical using habitat characteristics identified as important through local habitat measurements (on the ground data collection).

The study of resource selection in wildlife ecology has refined techniques to accommodate studies without credible information on where species are absent by comparing the characteristics at presence locations to those at locations considered available to the organism (used-available design) (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). Available locations are intended to describe the environment accessible to the species and should cover the range of environmental conditions found within the study region (Franklin 2010). Elith and Leathwick (2009) suggest that available locations are those that can be “reached by the animal”. A used-available study design helps to identify landscape characteristics important to a species by examining data for indications that resources are being used disproportionately to their availability (Manly et al. 2002, Johnson et al. 2006). When a resource’s use is disproportionate to its availability the use is said to be selective (Johnson 1980). The statistical analysis from used-available study designs results in a resource selection function (RSF), which is a function that is proportional to the likelihood of use of a resource unit (Manly et al. 2002). The used-available research approach has been used to identify critical winter habitats of sage-grouse throughout Wyoming, Montana, and Alberta, Canada (Doherty et al. 2008, Carpenter et al. 2010). These methods differ from the many statistical techniques used in wildlife habitat studies that compare characteristic of used locations to unused or random locations, under the assumption that these locations are not occupied by the species of interest (presence-absence design) (Guisan and Zimmermann 2000).

The objectives of this study were to 1) compare observed spring habitat use of sharp-tailed grouse with habitat availability to identify landscape characteristics (cover type and openland patch size) important to grouse at a 1-square-mile section scale in Michigan’s Upper Peninsula; and 2) create a spatially-explicit model predicting the relative likelihood of sharp-tailed grouse occurrence across the study area. This model identifies areas potentially important to sharp-tailed grouse management and may be used to inform habitat management, reintroductions, and identify additional survey locations. It was also the basis for spatially-explicit metapopulation modeling efforts (Chapter 3).

Methods

Study Area

Although all Upper Peninsula sections were considered, I delineated the study extent using the range of sections within the central and eastern Upper Peninsula of Michigan classified as “available” to sharp-tailed grouse (see Statistical Analysis) based on occurrence data for the most recent known occurrences (2009-2013) in the state (Fig. 1.1). This included portions of Chippewa, Mackinac, Luce, Alger, Schoolcraft, Delta, and Marquette counties (approximately 16,000 km^2) in the eastern Upper Peninsula. The study area is primarily forested (66%), with some large scrub/shrub and emergent wetland complexes (20%), agricultural lands (4%), grassland (4%), and the remainder comprised of barren lands, developed lands, and open water. Much of the forest and wetlands of the eastern Upper Peninsula are managed by the United States Forest Service, Michigan Department of Natural Resources (MDNR) and the United States Fish and Wildlife Service. The land in the far eastern portions of the Upper Peninsula is mainly privately owned and used for pasture and low-intensity agriculture (Eagle et al. 2005).

Occurrence Data

I identified sharp-tailed grouse occurrence by compiling lek and occupancy survey data collected by the MDNR and observations by the Michigan Natural Features Inventory between 2009 and 2013. Lek surveys were conducted in the early morning hours during the spring mating season, with most surveys being conducted between April 1 and May 15. During these surveys, observers would count dancing males while watching the dancing ground from a distance, and then approach the lek and count all birds flushed. The MDNR initiated occupancy surveys in 2009 to estimate sharp-tailed grouse occupancy rates and evaluate the Department’s monitoring process (Luukkonen et al. 2009). Occupancy surveys were conducted between 30 minutes before sunrise and 3 hours after sunrise from April 1 to May 5. Some occupancy surveys occurred as late as May 15 due to heavy snow cover in 2013. During occupancy surveys, observers visited eight points along road transects bordering 1-square-mile township sections. At each survey point observers listened and scanned for sharp-tailed grouse for 4 minutes. Although many observations came with geographic coordinates, I chose to model observations at the township section scale to include occupancy survey data which did not have specific spatial reference. Species distributions modeled with logistic regression have been shown to perform better with increasing sample size and simulations with at least 50 records of occurrence achieved relatively accurate results compared to other modeling techniques (Stockwell and Peterson 2002). To achieve an adequate sample size I pooled data from 2009 to 2013.

Combined survey data included 81 sections with occurrence records between 2009 and 2013. Thirty-one of 112 sections surveyed during this time resulted in records with no indication of sharp-tailed grouse occurrence. Luukkonen et al. (2009) estimated a detection probability of approximately 0.54 during occupancy surveys, indicating that surveyed sections without occurrence records may indicate non-detection of sharp-tailed grouse rather than non-occurrence. In addition, a higher than expected rate of occupancy was found in sections included in occupancy surveys initiated by the MDNR in 2009 (D. R. Luukkonen, MDNR, personal communication), suggesting that many unsurveyed sections may well be occupied. Therefore, rather than using a statistical method which requires locations without occurrence data to be assumed unoccupied, I chose to perform a used-available design analysis which follows a presence-only modeling framework.

Statistical Analysis

I used multiple logistic regression (generalized linear model with a logit link) under a used-available design to assess sharp-tailed grouse habitat selection at the 1-square-mile township section scale. I model the relationship between the binary dependent variable, used (1) or available (0) sections, and independent landscape variables using the logistic regression model:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \beta X + \varepsilon \qquad (1)$$

where p_i is the probability of sharp-tailed grouse use, α is the constant, βX are vectors of the independent covariates and their coefficients, and ε is the error term. I defined used sections as those with one or more sharp-tailed grouse detections between 2009 and 2013. When characterizing available locations it is important to inform decisions using the scale and characteristics of the system of interest (Elith and Leathwick 2009, Franklin 2010). I designated all sections within 21 miles of any occupied section (N = 6,518) as the distribution of available resource units (study extent, Fig. 1.1). This distance represented the maximum likely movement distance for sharp-tailed grouse (Hamerstrom and Hamerstrom 1951). Because some sharp-tailed grouse were observed in sections containing large proportions of forest land, I did not exclude largely forested sections from the available sections sample. To discern variations in characteristics of used versus available locations and to ensure negligible sampling errors, it is often necessary to select a substantial number of available locations (Manly et al. 2002). I randomly selected a sample of 2,500 available sections within the study extent, which I found accurately represented the habitat available to sharp-tailed grouse (Northrup et al. 2013) while ensuring that overlap of used locations within the available sample was limited to a level shown to produce unbiased coefficient estimates (Johnson et al. 2006).

One of the key assumptions of regression analysis is that model residuals are independent and identically distributed (Dormann et al. 2007). When model data contains spatial autocorrelation, a pattern where the values of a variable co-vary across space (Legendre and Fortin 1989, Legendre 1993), violations of this assumption may occur. Ecological data are very likely to exhibit patterns of spatially autocorrelated values because the factors influencing their distributions (e.g. temperature and dispersal capabilities) are often spatially autocorrelated (Sokal and Oden 1978, Legendre and Fortin 1989). Violations of the assumption of independence may lead to parameter estimates with decreased precision and an increased possibility of type 1 errors (Franklin 2010).

To assess whether spatial autocorrelation might be problematic in my analysis, I examined the spatial structure of sharp-tailed grouse survey locations using average nearest neighbor statistics. This method compared the observed versus expected average distance between locations to determine if they were distributed randomly or were clustered. My preliminary analysis showed evidence of clustering in survey locations, so I chose to take into account the spatial structure of my data by including a spatial covariate in the model using autologistic regression. Autologistic regression builds on traditional logistic regression models by incorporating an additional covariate to account for spatial autocorrelation (Augustin et al. 1996). With addition of this covariate, the autologistic regression model becomes:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \rho A + \beta X + \varepsilon \tag{2}$$

where ρ is the coefficient of the autocovariate (A) (Franklin 2010).

The autocovariate is an estimate of how occurrence at a location reflects occurrence at surrounding locations (Dormann et al. 2007). I modeled the autocovariate using the spatial dependence 'spdep' package in R as a distance-weighted sum:

$$A_n = \sum_{m \in \mathrm{N}_n} w_{nm} y_m \,, \tag{3}$$

where A_n is the autocovariation at section n, N_n is the set of sections within the neighborhood of section *n*, w_{nm} is the neighborhood weight of section m over section n, and y_m is the sharp-tailed grouse occurrence value at section *m* during the relevant time frame (Bardos et al. 2015). I set neighborhood distance to 13.36 km, the average movement of female sharp-tailed grouse (Ammann 1957), and based neighborhood weights on inverse distance.

Landscape Habitat Variables

I used the National Oceanic and Atmospheric Administration's (NOAA) Coastal Change Analysis Program (C-CAP) 2010 land cover layer to calculate all landscape variables (National Oceanic and Atmospheric Administration Coastal Services Center, 1995-present). This classification scheme included 24 land cover categories with 30 m x 30 m pixel resolution derived through mostly remote sensing techniques (Appendix B, Table 1.3). I used ArcMap 10.3.1 for all spatial analysis (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.). All proportion landscape variables were calculated at the 1-square-mile section scale, and because many survey locations were without precise spatial reference, I was unable to explicitly examine landscape variable influences at other scales. For all sections I calculated land cover proportion and opening size variables that I felt might be important for sharp-tailed grouse landscape scale habitat selection based on previous research examining landscape level relationships in the Great Lakes region (Appendix C, Table 1.4). Because land cover classification can significantly impact model outputs (Roloff et al. 2009) I used both individual land cover classes (e.g. cultivated crops) and groups of similar land cover classes (e.g. pr_open) for calculating variables (N=17).

Sharp-tailed grouse are known to occur in prairies and brushlands across their range (Connelly et al. 1998, Niemuth and Boyce 2004). While some research has found that landscapes around sharp-tailed grouse leks have greater amounts of shrub cover (Niemuth and Boyce 2004), other research indicates that both trees and shrubs may similarly limit the amount of openness perceived by sharp-tailed grouse (Ammann 1957, Hanowski et al. 2000). Therefore, I created proportion variables with land cover classes commonly considered to describe prairie landscapes (pr_grass, pr_hay, and pr_open), shrub landscapes (pr_srb and pr_srb2) and an openland grouping including shrub cover (pr_open2). The decline of early successional habitats in parts of sharp-tailed grouse range has led to many populations relying on cropland (Connelly et al. 1998). This is likely the case in Michigan, as stakeholders (Sharp-tailed Grouse Advisory Committee, personal communications) have frequently observed sharp-tailed grouse using lands classified as cultivated crops under the NOAA C-CAP classification scheme. This information prompted the inclusion of a cultivated crops variable (pr_cul) and openland grouping variable including the cultivated crops land cover class (pr_open3). Active sharp-tailed grouse leks have been shown to occur in areas with higher amounts of wetland cover classes than inactive and random locations (Hanowski et al. 2000) and the use of wetlands has been well documented in Michigan (Ammann 1957, Sjogren and Robinson 1997, Sjogren and Corace 2006). I examined individual land cover classes of emergent wetland (pr_em_wet) and scrub/shrub wetland (pr_srb_wet) and a grouped variable of wetland classes (pr_wet). Following Hanowski et al.

(2000) who found active sharp-tailed grouse leks associated with both hardwood and coniferous wetlands, I included a wetland forest variable (pr_forwet). Research has shown that sharp-tailed grouse leks in the Great Lakes region are negatively associated with forest land (Hanowski et al. 2000) but influence of the number of forest patches on lek locations is mixed depending on scale (Niemuth and Boyce 2004). Because sharp-tailed grouse utilize forest lands for ecological needs such as foraging and cover (Connelly et al. 1998) landscape scale selection analyses may not show the same relationship as fine scale analyses. Thus, I included a forest land cover class (pr_for) and its squared term (pr_for^2) to allow for a dome-shaped selection function and assess whether sharp-tailed grouse are selecting sections with intermediate proportions of forestland.

I calculated land cover proportion variables two ways to assess the influence of land cover within and surrounding the sections. First, I calculated the proportion of all land cover variable raster cells within each section (non-focal) and second I used a moving window analysis on all cells within a 1,400m radii circular neighborhood averaged to each section (focal). The moving window analysis calculates the average of all cell values within the designated neighborhood around each pixel, creating a raster of values relevant to the scale of interest (Piorecky and Prescott 2006). I chose the neighborhood size to approximate the average sharp-tailed grouse home range. I then took the average of all cells from the moving window analysis within each section for a proportion land cover metric influenced by land cover outside the section.

Sharp-tailed grouse are known to require large tracts of open land throughout their life history (Ammann 1957, Niemuth and Boyce 2004). To quantify the amount and connectivity of openland associated with each section I aggregated openland cover type pixels sharing at least one side into patches, based on the above openland grouped variables (pr_open, pr_open2, pr_open3). I then identified the largest patches of each openland grouping intersecting each section to create the sz_open, sz_open2 and sz_open3 variables.

I selected the final set of explanatory variables for modeling by conducting univariate logistic regression (Hosmer et al. 2013) and correlation testing on all variables (Appendix C, Table 1.4). I examined individual p-values and removed all variables with p-values greater than 0.25 and the least explanatory scale (either focal or non-focal) for all proportion variables. I conducted pairwise Pearson's correlation coefficient tests on all remaining variables and removed the variable with the highest p-value from any pairs with a correlation coefficient ≥ 0.60. I removed the predictor variable with the highest p-value when proportion variables included overlapping land cover classes (e.g. pr_wet and pr_forwet, see Appendix C, Table 1.4). I included only the opening size variable which best characterized sharp-tailed grouse habitat selection in the final models, based on the lowest univariate logistic regression p-value. To test the validity of including the quadratic variable of proportion forest (pr_for^2) I examined the p-value of the quadratic term in a model including both the proportion forest linear effect variable and quadratic variable (Osborne 2014).

I compared all possible main effects combinations of the candidate landscape variables and an autocovariate (N=64) with the glmulti package in RStudio (version 0.99.467, RStudio Inc., Boston, Massachusetts, USA). The glmulti package automates model building and selection by building all model possibilities under the constraints specified by the user (Calcagno and de Mazancourt 2010). Running all possible variable combinations allows for multi-model inferences while avoiding the pitfalls of stepwise regression analysis which may not always converge to the best model (Calcagno and de Mazancourt 2010). Because of the a priori ecological basis for predictor variables and subsequent variable selection procedures the inclusion of all remaining variable combinations is supported, and should control for overfitting pitfalls cautioned by Burnham and Anderson (2002). I evaluated relative model fit using Akaike Information Criterion (AICc) values for small sample sizes (Burnham and Anderson 2002). I used model averaging (Burnham and Anderson 2002) to estimate a final model from all candidates.

Predictive Modeling

Models of resource selection can also be used to map a resource selection function (RSF) predicting the relative likelihood of use of resources given their landscape characteristics (Johnson et al. 2006). I used model averaged coefficient estimates from the above logistic regression analysis to model a RSF in ArcGIS using an exponential model:

$$\mathrm{w(x)} = \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k) \quad (4)$$

where X_1 to X_k are predictor variables and β_1 to β_k their respective coefficients. The exponential model is preferable to the logistic function for creating an RSF with a used versus available design because it does not rely on the assumptions that the number of locations be proportional to their actual occurrence or that the available sections are unused (Johnson et al. 2006, Pearce and Boyce 2006). The exponential model results are also robust to relatively high levels of overlap between used and available locations (Johnson et al. 2006). I created mapped surfaces of all relevant predictor variables at the 1-square-mile scale across the study region before applying map algebra using the above equation. I mapped the predicted RSF in ArcGIS depicting areas from high to low relative likelihood of occurrence across the study region (Fig. 1.2). Because the proportion of locations occupied by a species is not known, the RSF predicts the relative likelihood of occurrence (Elith and Leathwick 2009) for sharp-tailed grouse for all sections within the study region.

I tested model prediction accuracy following k-fold cross validation procedures (Johnson et al. 2006), rather than using classification approaches such as confusion matrices and Receiver Operating Characteristics, which are more appropriate for used versus unused sampling designs (Boyce et al. 2002). I used this approach because it tests prediction accuracy and whether the RSF is approximately proportional to the likelihood of use by comparing the frequency of observed and expected observations within ranked groupings/bins of RSF values (Johnson et al. 2006). I separated occurrence locations into 4 random data folds and calculated new logistic regression coefficients based on 3 of the 4 folds and mapped the predicted RSF values in ArcGIS. I then grouped the full range of predicted RSF values into 6 ordinal bins classified using the geometric intervals classification method. I combined the two highest value RSF bins because their predicted area was small, which resulted in 5 bins. I then calculated the mid-point RSF value for each bin. I calculated a utilization value for each bin using the equation

$$U_{\mathrm{i}} = \quad w(x_i)A(x_i)/\sum_j w(x_j)\, A(x_j) \tag{5}$$

where $w(x_i)$ and $A(x_i)$ are the RSF midpoint value and area of all pixels within bin i, respectively. I then calculated the expected number of occupied sections within each RSF bin by multiplying the utilization value for each bin with the total number of testing locations. I compared the expected number of sections occupied with the actual number of testing sections from the remaining cross-validation fold that occurred in each bin using linear regression and a chi-square test. I evaluated whether the slope of the regression line was significantly different from 0, representing the null model that use was equivalent to availability, and 1, which would be the expected slope when the model is approximately proportional to the likelihood of use. I tested whether the intercept was significantly different from 0, which is the expected intercept when a model is proportional to the likelihood of use. Lastly, I examined the R^2 value of the linear regression and conducted a χ^2 goodness-of-fit test to asses model fit. A high R^2 value and a non-significant χ^2 goodness-of-fit test would indicate a model proportional to the likelihood of use. I iterated the above process 4 times, with each data fold used as testing data against all other folds and tested prediction accuracy for cross validation groups individually and combined.

Using model averaged coefficient estimates and the exponential function (Eq. 4), I calculated the relative predicted likelihood of occurrence of sharp-tailed grouse for important habitat proportion variables, by varying respective resource proportions (across observed values) while holding all other variables at their means (Fig. 1.3). I bounded the relative likelihoods between 0 and 1 using the equation:

$$\text{BoundedRSF} = \frac{(\text{RSF Value} - \text{Minimum RSF Value})}{(\text{Maximum RSF Value} - \text{Minimum RSF Value})} \qquad (6)$$

Results

The final set of landscape variables retained following univariate analysis were the focal scale variables pr_forwet and pr_srb, non-focal scale variables pr_open3, pr_for, and the maximum opening size variable sz_open2, hereafter also referred to as forested wetlands, shrubland, openland, forest, and patch size respectively (see Appendix C, Table 1.4 for variable descriptions). The pr_for^2 variable was not significant ($P = 0.30$), so no models with curvilinear relationships were considered. The openland variable pr_open3, which characterized the proportion of grassland, herbaceous cover, pasture, hay, and cultivated crops performed best during univariate analysis ($P \leq .001$).

Variables in the best AICc model included pr_open3, pr_for, pr_forwet, pr_srb and the autocovariate term (Table 1.1). This model received an evidence weight of 0.43 and two other models were within 2 ΔAICc values. The maximum opening size variable sz_open2 was also included in some top models, but did not strongly influence sharp-tailed grouse resource selection. Sharp-tailed grouse selected for sections with high proportions of openland and shrubland and against sections with high proportions of forest and forested wetlands compared to what was available in the study region (Table 1.2).

Mapping the RSF using model-averaged coefficients showed areas of high relative likelihood of occurrence in the eastern and central portions of the study region (Fig. 1.2). The predicted relative likelihood of sharp-tailed grouse occurrence increased sharply with increasing proportions of shrubland and openland at around 40% and 50% of each habitat type, respectively (Fig. 1.3). Increasing proportions of forest within sections caused declines in the relative likelihood of occurrence, with sections with greater than 50% forest having low relative probabilities (Fig. 1.3).

The RSF model's predictive ability performed well under model validation. The highest ranking RSF bin contained 75.3% of all used locations and accounted for 8.5% of the study region. The linear regressions between observed and expected number of validation locations in 5 RSF bins showed good model fit for each cross validation model (Fig. 1.4, a-d). All models had intercepts not significantly different from 0 and slopes significantly different from 0 but not from 1, indicating models were proportional to the true likelihood of occurrence. In addition, R^2 values (from 0.863 to 0.998) and insignificant $\chi 2$ goodness-of-fit tests indicated good model fit when predicting the relative likelihood of sharp-tailed grouse occurrence in sections within the study area and supported that models were proportional to the true likelihood of use (Fig. 1.4, a-d).

Discussion

The identification of how resources are selected is a key step in planning species management efforts. This study found the proportions of openland, shrubland, and forest to be important drivers of sharp-tailed grouse resource selection at the 1-square-mile scale in Michigan. Sharp-tailed grouse occurred in sections with higher proportions of shrubland than what was generally available in the study region. Previous research looking at the amount of shrubland near sharp-tailed grouse lek locations has been mixed. Hanowski et al. (2000) found that inactive lek locations in Minnesota had higher proportions of brush cover types than active lek locations. Research by Niemuth and Boyce (2004) in the Wisconsin pine barrens indicated that habitat near sharp-tailed grouse leks contained higher proportions of shrubland than unused locations. The maximum proportion of shrubland (focal scale) in all sections available within my study region was 0.69. Therefore, the range of shrubland proportion within the study region likely did not reached levels which would limit sharp-tailed grouse occurrence at the landscape scale and the selection of sections with higher proportions of shrub land is consistent with sharp-tailed grouse utilizing these lands for nesting and feeding (Ammann 1957). Michigan sharp-tailed grouse may also be selecting sections with higher proportions of shrubland compared to other populations because of their peripheral location, where increased snow depths may heighten the importance of these habitats.

The selection for sections with higher amounts of openland cover types is consistent with research on sharp-tailed grouse habitat use and lek locations (Hanowski et al. 2000, Niemuth and

Boyce 2004, Orth 2012). Openland habitats are important because they provide areas for loafing, foraging, and for breeding males to display (Ammann 1957). Areas of forest cover are used for winter foraging, refuge from extreme weather and escape cover, and it has been suggested that between 20 and 40 percent forest cover is ideal for sharp-tailed grouse in Michigan (Ammann 1957). The avoidance of locations with higher proportions of forest habitat than available throughout the study region and exclusion of the squared forest term supports that sections with both intermediate and high proportions of forest lands are not selected for by sharp-tailed grouse.

Hanowski et al. (2000) found forested wetlands associated with sharp-tailed grouse occurrence in Minnesota, but I did not find support for sections with higher proportions of forested wetlands having increased selection. Other wetland cover variables that I considered were not included in final model development due to low P-values or correlations with other predictor variables. Although there is evidence of sharp-tailed grouse wetland use in Michigan, especially around Seney National Wildlife Refuge (Sjogren and Corace 2006), the selection of these habitat types may be diminished outside of fall and winter months when grouse are focused on finding food and cover (Ammann 1957, Sjogren and Robinson 1997). The lack of evidence for wetland habitat selection may also be due to a higher amount of grassland and shrubland available to sharp-tailed grouse within our study region than compared to other locations in the Great Lakes states or an indication that survey data on these locations are lacking. Surveys of wetland cover types are known to be difficult due to limited access, and these findings do not necessarily indicate that these areas are not important for sharp-tailed grouse populations in Michigan.

Past research on the effects of landscape connectivity on sharp-tailed grouse occurrence has focused on metrics such as the number of land cover types or habitat patches associated with occurrence (Hanowski et al. 2000, Niemuth and Boyce 2004, Orth 2012). Although these studies have shown that the spatial patterning of the landscape is important to sharp-tailed grouse, these metrics are difficult for wildlife managers to manipulate. I attempted to assess whether openland patch size directly influenced occurrence, assuming that the largest intersecting patch would have the greatest influence on resource selection. Surprisingly, the opening size variables describing the amount and connectivity of openland were not good predictors of grouse occurrence at the section scale. This may be due to instances where large patches intersecting only a small portion of a section are inaccurately characterizing the openland connectivity available within that section. Using mean patch size or limiting patch size calculations to only openland within the section may provide a more useful explanatory variable. While I did not find strong support for these metrics, future research should attempt to assess the impacts of landscape composition with variables which can be realistically manipulated by habitat managers whenever possible.

Many of the previous studies on prairie grouse landscape modeling have addressed characteristics surrounding lek locations (Niemuth 2011). My research attempts to inform management by utilizing occurrence data collected through the broader scale occupancy surveys recently establish by the MDNR in the eastern Upper Peninsula of Michigan. This method of sampling was instituted to account for changes in grouse distribution and abundance that lek surveys may not adequately address (Luukkonen et al. 2009). The scale of occurrence data and environmental predictors I used allowed me to avoid the limitations of GIS mapping with local scale variables and create a mapped surface of relative likelihood of occurrence for an extensive study region. One issue with using these data was the lack of an explicit spatial location for occurrence within surveyed sections. In order to utilize the occupancy surveys it was necessary to assume the centroid location of sections as the location of occurrence. This limited the scale of inference to the 1-square-mile section and hindered the use of possibly important explanatory variables, including distance to forest edge which has been shown to be an important landscape scale predictor of sharp-tailed grouse occurrence (Niemuth and Boyce 2004).

Management Implications

Spatially explicit landscape model predictions are useful for planning the conservation and management of prairie grouse (Niemuth 2011). These maps can be used to guide translocation efforts, establish priority habitats and direct future survey efforts. The RSF model I created mapping relative likelihood of sharp-tailed grouse occurrence was a good predictor of grouse occurrence and should be useful for identifying areas at a landscape scale to focus future monitoring and management efforts. Once sections important for sharp-tailed grouse conservation have been identified effort should be made to keep the proportion of forest within those sections below 50%.

Combining this landscape scale research with large-scale studies utilizing habitat use information (e.g. metapopulation modeling), which are often constrained to informing modeling with general species-habitat relationships coming from locations far outside the study region, provides additional opportunities for informing management. My modeling has increased the understanding of sharp-tailed grouse resource selection within Michigan and was subsequently used to form the basis of metapopulation modeling experiments (Chapter 3).

APPENDICES

Appendix A. Tables and Figures.

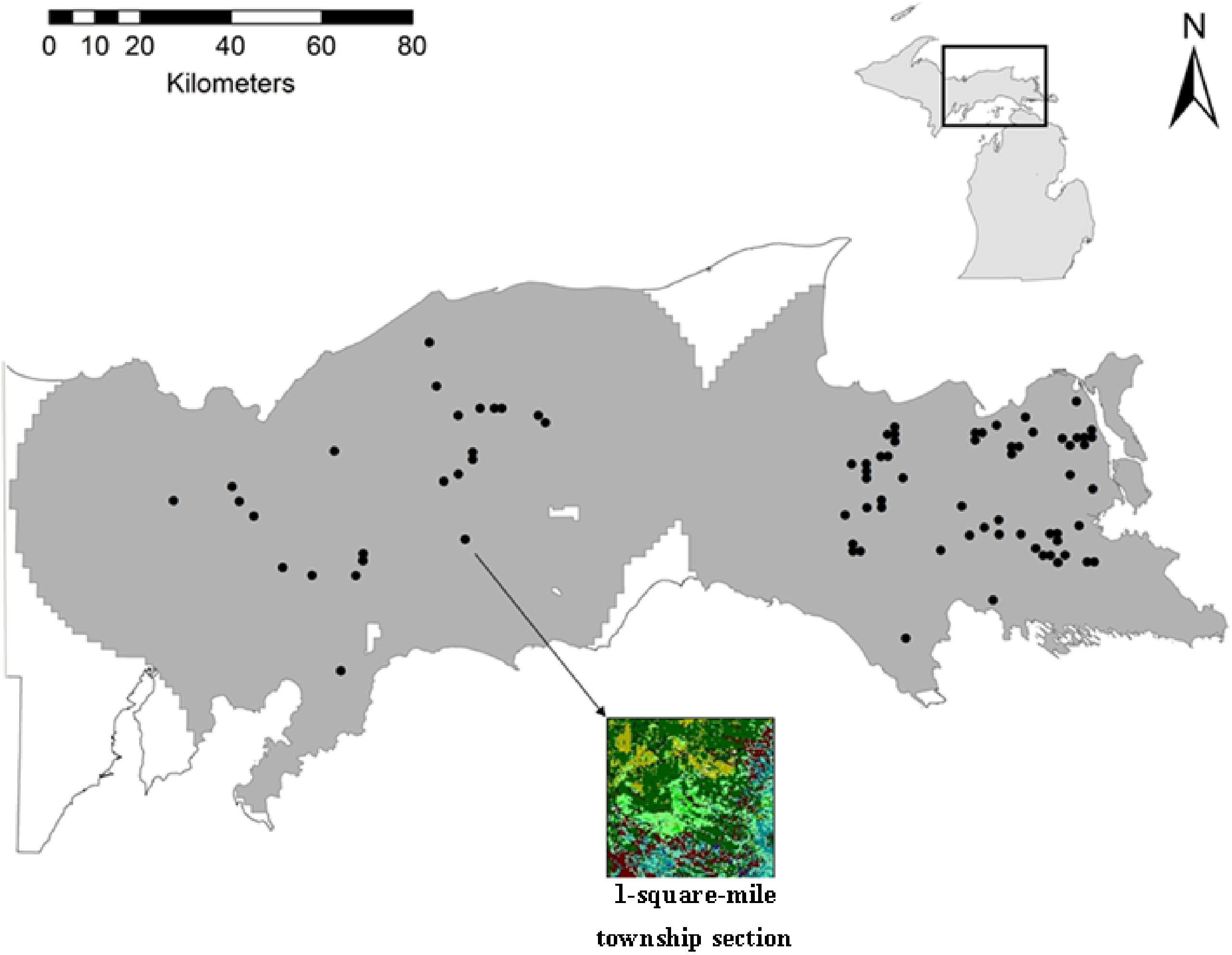


Figure 1.1 Location of study area in Michigan's Upper Peninsula. The black dots indicate 1-square-mile township sections with recorded occupancy between 2009 and 2013. The shaded area indicates the full distribution of sections designated as available resource units (study extent).

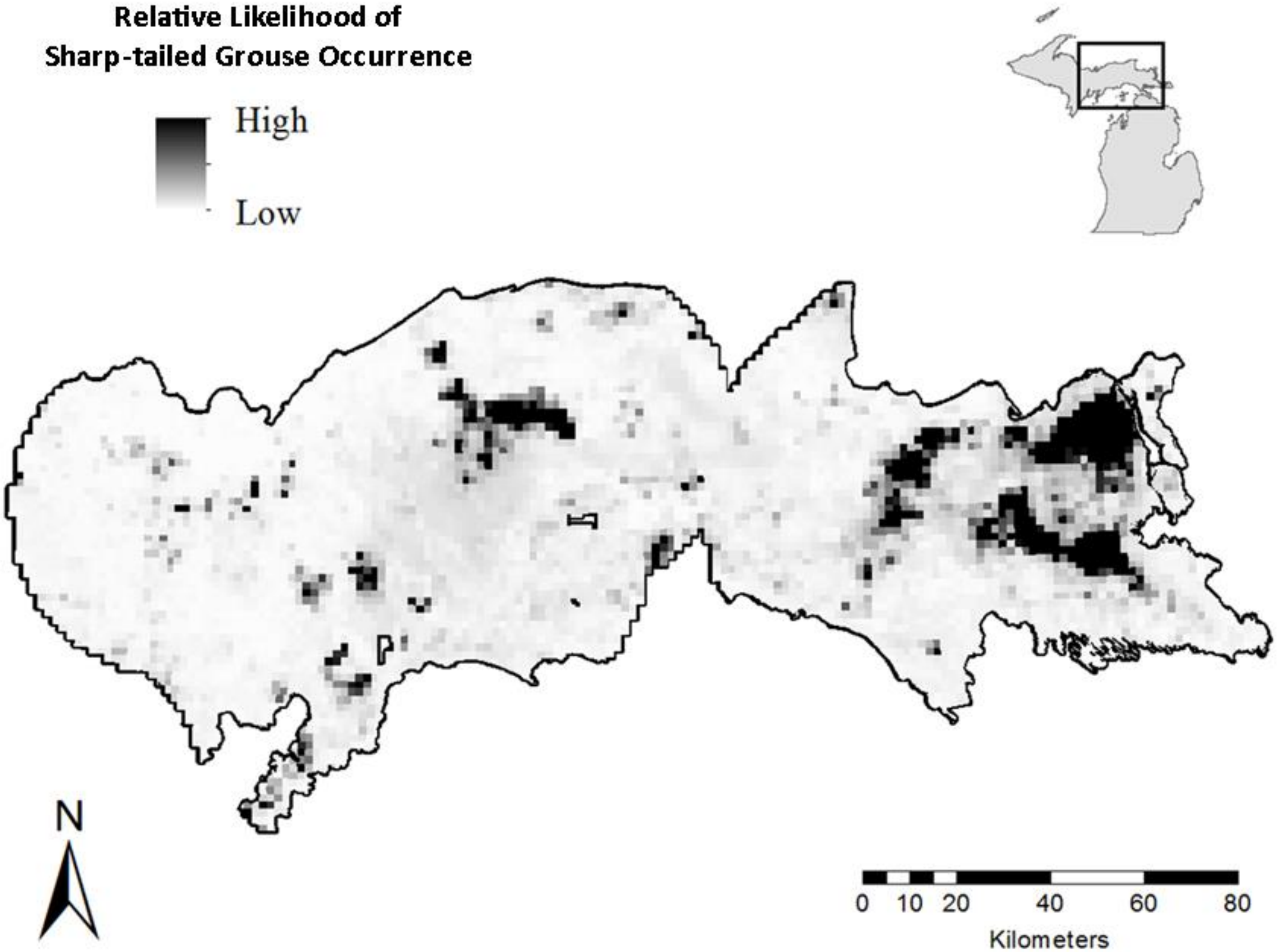


Figure 1.2 Map of predicted relative likelihood of occurrence of sharp-tailed grouse from 2009-2013 in the Upper Peninsula of Michigan, USA.

Table 1.1 Resource selection of sharp-tailed grouse modeled from 2009 to 2013 in Michigan's Upper Peninsula, USA. Reporting includes model independent variables (see Appendix C, Table 1.4 for variable descriptions), Akaike Information Criterion values corrected for small sample sizes (AICc), change in AICc from model with minimum AICc value (ΔAICc), and Akaike evidence weights (ω_i) (Burnham and Anderson 2002). Models within 4 ΔAICc of lowest AIC model are shown.

Model Variables	AICc	ΔAICc	ω_i
pr_open3, pr_forwet, pr_srb, pr_for, autoc	471.53	0.00	0.43
pr_open3, pr_srb, pr_for, autoc	472.57	1.04	0.25
pr_open3, sz_open2, pr_forwet, pr_srb, pr_for, autoc	473.37	1.84	0.17
pr_open3 + open2_ac + pr_srb + pr_for + autoc	474.50	2.97	0.10

Table 1.2 Model averaged habitat coefficient estimates, odds ratios, and variable importance for all models of sharp-tailed grouse resource selection in the Upper Peninsula of Michigan, USA.

Variable	β	Odds Ratio	Importance
pr_open3	3.537	34.364	1.00
pr_srb	6.872	964.876	1.00
pr_for	-2.110	0.121	1.00
autoc	595.394	3.77×10^{258}	0.95
pr_forwet	-1.414	0.243	0.61
sz_open2	3.460×10^{-6}	1.00	0.28

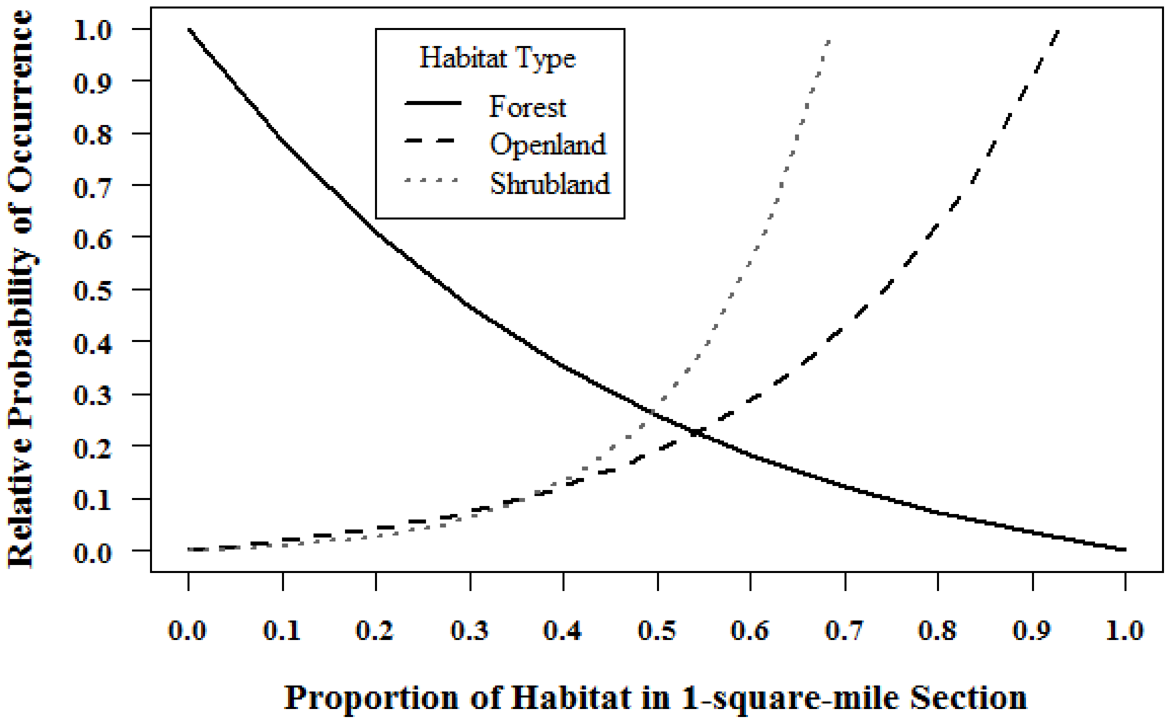


Figure 1.3 Relationship between relative likelihood of sharp-tailed grouse occurrence and the proportion of forest, openland, and shrubland in 1-square-mile township sections, Upper Peninsula of Michigan, USA. Relative likelihoods were calculated with model averaged coefficients (Table 1.2) by varying proportions of the relevant resource, while using mean values of all other variables. Relative likelihoods were bounded between zero and one.

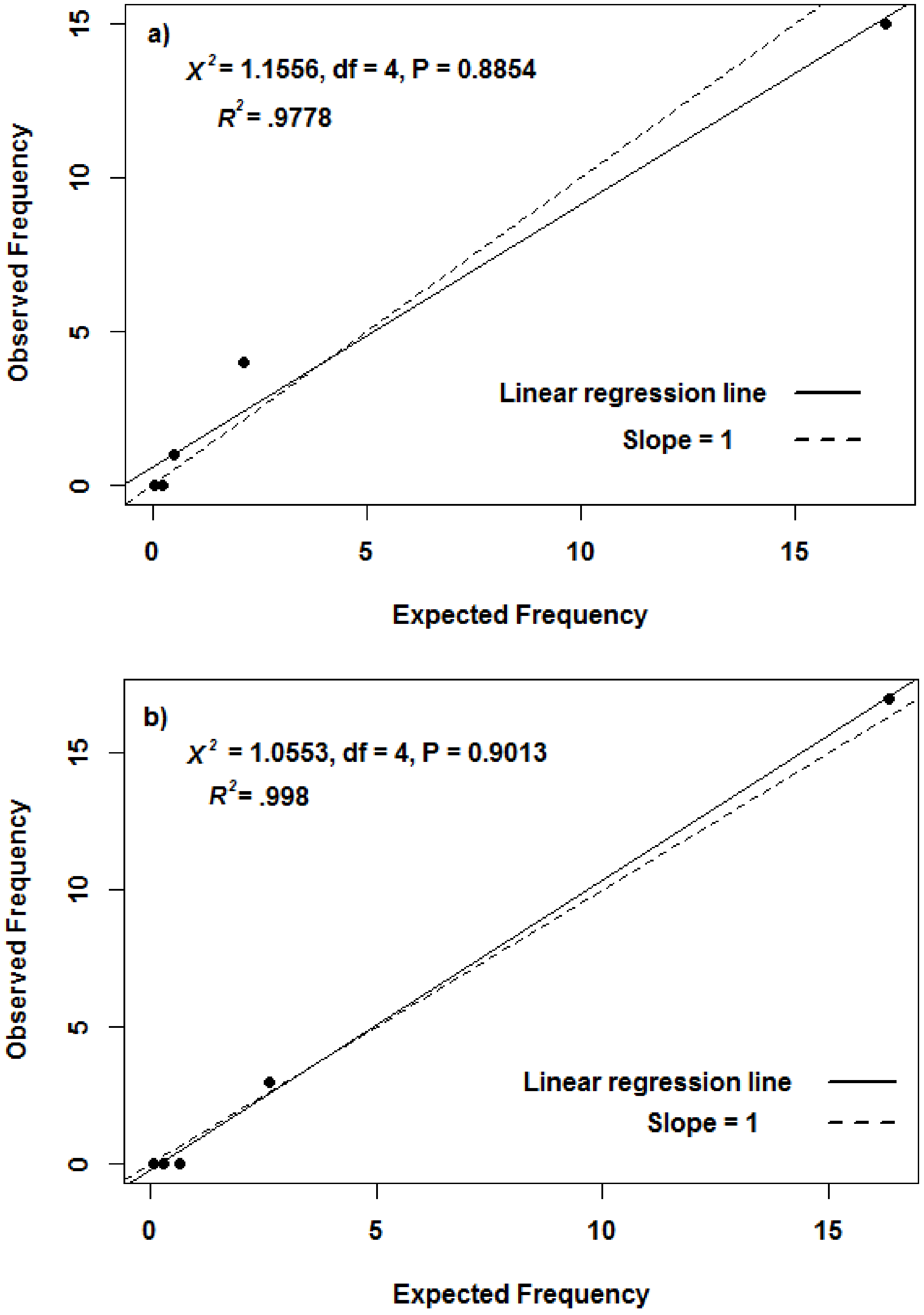
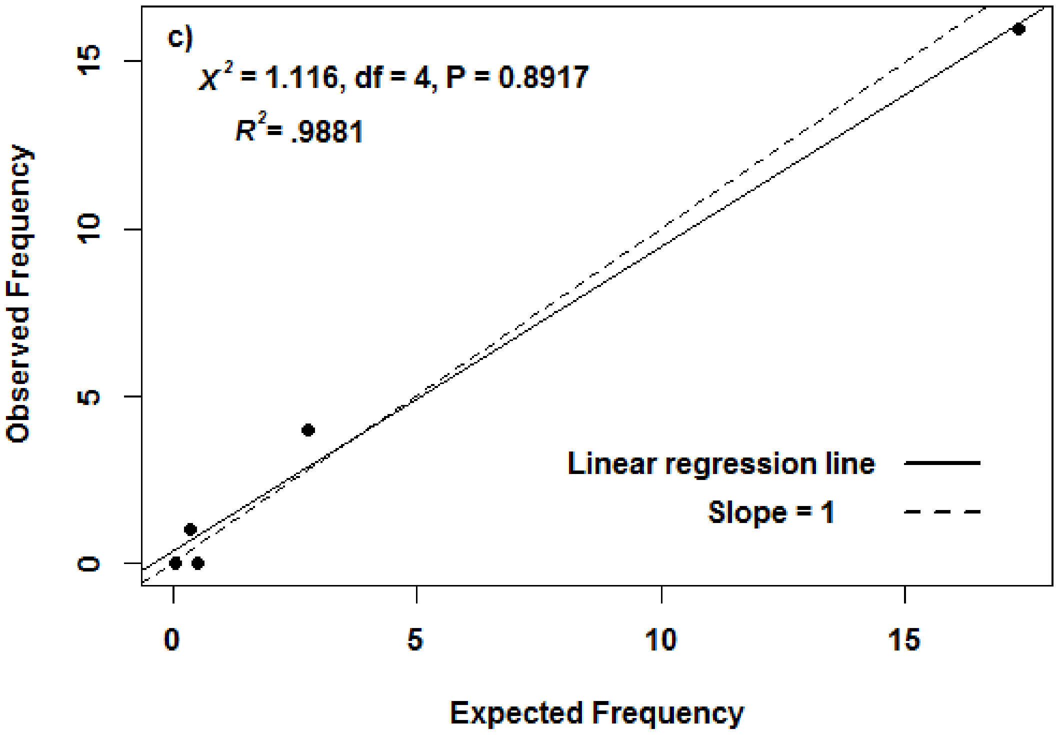
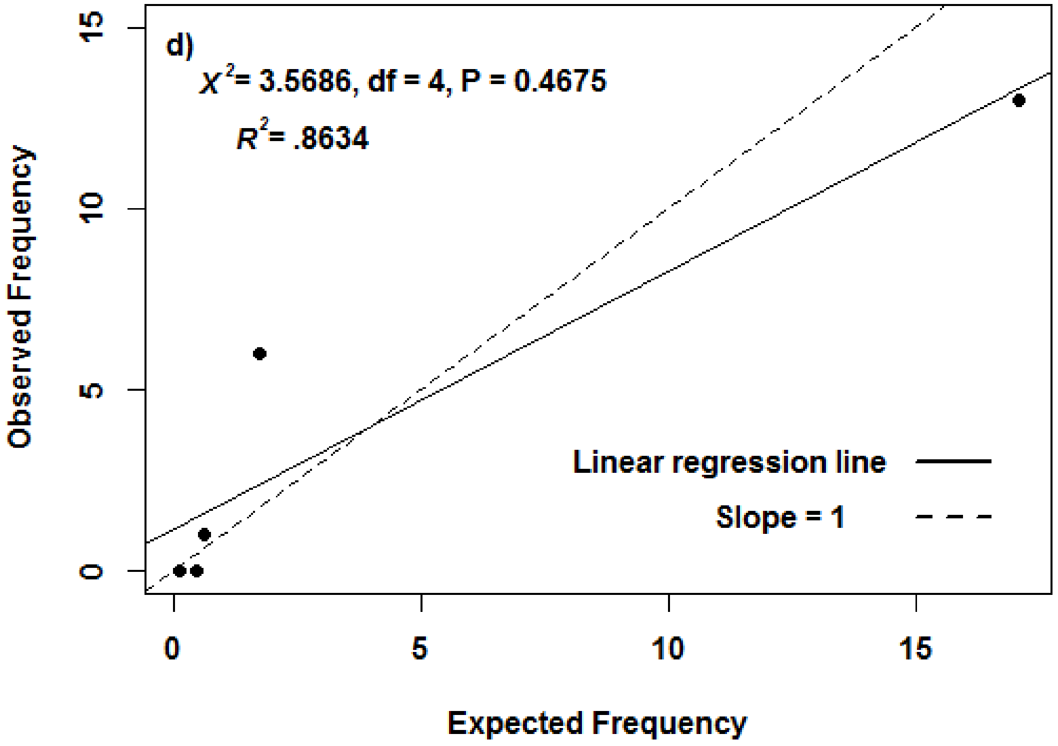


Figure 1.4 Linear regression of observed versus expected frequencies of validation locations in 5 resource selection function bins for each of 4 cross-validation folds (a-d).

Figure 1.4 (cont'd)





Appendix B. Land Cover Classification Scheme.

Table 1.3 Land cover classification scheme, modified from Coastal Change Analysis Program (C-CAP), NOAA Office for Coastal Management, Regional Land Cover Classification Scheme. Land cover classes not used in predictor variables are excluded.

Land Cover Class[a]	**Class**	**Description**
Cultivated Crops	6	Areas intensively managed for cultivated crops. Crop vegetation accounts for > 20% of total vegetation. Includes all lands being actively tilled.
Pasture/Hay	7	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle and not tilled. Pasture/hay vegetation accounts for > 20% of total vegetation.
Grassland/ Herbaceous	8	Areas dominated by grammanoid or herbaceous vegetation, generally > 80% of total vegetation. Not subject to intensive management such as tilling, but can be utilized for grazing.
Deciduous Forest	9	Areas dominated by trees generally > 5m tall and > 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change.
Evergreen Forest	10	Areas dominated by trees generally > 5m tall and > 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.
Mixed Forest	11	Areas dominated by trees generally > 5m tall and > 20% of total vegetation cover. Neither deciduous nor evergreen species are > 75% of total tree cover. Both coniferous and broad leaved evergreens are included in this category.
Scrub/Shrub	12	Areas dominated by shrubs < 5m tall with shrub canopy typically > 20% of total vegetation. Includes tree shrubs, young trees in an early successional stage, or trees stunted from an environmental condition.
Palustrine Forested Wetland	13	Tidal and nontidal wetlands dominated by woody vegetation ≥ 5m in height, and all such wetlands that occur in tidal areas in which salinity due to ocean-derived salts is below 0.5%. Total vegetation coverage is > 20%.
Palustrine Scrub/Shrub Wetland	14	Tidal and nontidal wetlands dominated by woody vegetation < 5m in height, and all such wetlands that occur in tidal areas in which salinity due to ocean-derived salts is below 0.5%. Total vegetation coverage is >20%. Species present could be true shrubs, young trees and shrubs, or trees that are small or stunted due to environmental conditions.
Palustrine Emergent Wetland	15	Tidal and non-tidal wetlands dominated by persistent emergent vascular plants, emerging mosses or lichens, and all such wetlands that occur in tidal areas where salinity due to ocean-derived salts is below 0.5%. Total vegetation cover is > 80%. Plants generally remain standing until the next growing season.

Appendix C. Explanatory Variables.

Table 1.4 Full set of potential explanatory variables considered in modelling sharp-tailed grouse resource selection in the Upper Peninsula of Michigan, USA. Focal and non-focal forms (see Methods) of all proportion variables were considered. Landscape variables included in model building are in bold.

Variable Name	Land Cover Classes	Description
pr_hay[b,c]	7	Pasture/hay vegetation
pr_grass[b,d]	8	Grassland and herbaceous vegetation
pr_open[a,c]	7,8	Upland openland including pasture/hay and grassland and herbaceous vegetation
pr_open2[a,c]	7,8,12	Upland openland including pasture/hay, grassland and herbaceous and scrub/shrub vegetation
pr_open3[a]	6,7,8	Upland openland including pasture/hay, grassland and herbaceous and cultivated crops
pr_srb[b]	12	Upland scrub/shrub vegetation
pr_srb2[b,d]	12,14	Upland and lowland scrub/shrub vegetation
pr_cul[b,c]	6	Cultivated crops
pr_for[a]	9,10,11	All upland forestland
pr_for^{2}[a,b]	9,10,11	Squared term for pr_for
pr_wet[b,c]	13, 14,15	All wetland including emergent, scrub/shrub, and forested
pr_forwet[b]	13	Lowland forest vegetation
pr_srbwet[a,c]	14	Lowland scrub/shrub vegetation
pr_emgwet[ab]	15	Lowland emergent vegetation
sz_open[c]	7,8	Maximum intersecting patch of aggregation of non-focal pr_open variable pixels
sz_open2	7,8,12	Maximum intersecting patch of aggregation of non-focal pr_open2 variable pixels
sz_open3[c]	6,7,8	Maximum intersecting patch of aggregation of non-focal pr_open3 variable pixels

[a] Focal variable removed from model development due to p-value

[b] Non-focal variable removed from model development due to p-value

[c] Variable removed from model development due to correlations ≥ 0.60

[d] Variable removed from model development due to overlapping land cover classes

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CHAPTER 2. EVALUATING POTENTIAL MANAGEMENT IMPACTS ON SHARP-TAILED GROUSE VIABILITY IN THE UPPER PENINSULA OF MICHIGAN

Introduction

It is widely believed that the distribution and abundance of sharp-tailed grouse in Michigan are limited by the supply of suitable habitat. In the previous chapter I developed a statistical model of sharp-tailed grouse resource selection that was informed by surveys of sharp-tailed grouse occurrence on the landscape along with detailed maps of habitat conditions associated with their occurrence. To forecast future changes to sharp-tailed grouse populations, either under status quo conditions, or in the face of management actions targeted at sharp-tailed grouse, I need to couple this model of habitat suitability with knowledge of sharp-tailed grouse demographics. In this chapter I develop such a model, using a spatially-explicit metapopulation modeling approach, and use this model to examine how Upper Peninsula sharp-tailed grouse populations might change in the future, and how such changes might be affected by management tactics such as changes to harvest regulations and habitat improvement.

Metapopulation models include a broad variety of models that can be helpful in understanding how landscape structure influences metapopulation dynamics (Beissinger et al. 2006). These models describe dynamics of species that occur in multiple populations linked by dispersal (subpopulations), often with the goal of assessing the ability for these populations to persist over some period of time (Akçakaya and Sjögren-Gulve 2000). There are several ways to conceptualize metapopulation models. My research involves models of the “patch” class as described by Beissinger et al. (2006). This class of models defines populations by distinct habitat patches, and any portion of the landscape not included within a patch is only available for individuals to use for dispersal (Beissinger et al. 2006). Beyond their use for assessing population viability, metapopulation models can also be used to assess impacts of environmental changes, prioritize data collection, and rank management options in terms of their performance at meeting management objectives (Akçakaya and Sjögren-Gulve 2000).

Previous attempts to model sharp-tailed grouse have been performed by Temple (1992) and Akcakaya et al. (2004) on Wisconsin populations. Temple (1992) modeled population viability by looking at minimum viable population size, minimum area requirements, and metapopulation viability. He found that to have a high probability of persistence, Wisconsin sharp-tailed grouse metapopulations needed to consist of at least 280 birds in each of five separate populations with suitable habitat of at least 4000 ha. Akcakaya et al. (2004) implemented a dynamic landscape and metapopulation model assessing the potential responses of sharp-tailed grouse populations to alternative forest management scenarios; varying stand harvest age, clear-cut size, and stand composition. They predicted that larger clearcut sizes would result in higher carrying capacities, and results were sensitive to fecundity values. This study illustrated the importance of combining spatially explicit landscape and metapopulation dynamics to inform sharp-tailed grouse management decisions, and that when both were incorporated into modeling it was possible to more completely evaluate management options (Akcakaya et al. 2004). Although informative, Temple (1992) did not incorporate spatially explicit habitat suitability and Akcakaya et al. (2004) modeled habitat suitability without local habitat selection data, and the landscape dynamics software (LANDIS) used did not predict reasonable dynamics within wildlife management areas where grouse were likely to occur.

To date, limitations in computational capacity and/or data availability have restricted analyses to geographic scales not ideally suited for evaluating large scale management options.

My previous work on sharp-tailed grouse habitat use (Chapter 2) makes large-scale metapopulation modeling possible within Michigan without characterizing habitat suitability based on habitat use information described in the literature, which often varies considerably (Connelly et al. 1998) or on fine scale vegetation data necessary for landscape dynamics programs but often not available across large areas.

Across much of their range, sharp-tailed grouse are a popular game species (Connelly et al. 1998). Beginning in 2010, the Michigan Department of Natural Resources (MDNR) reopened portions of Chippewa and Mackinac counties to sharp-tailed grouse hunting after 12 years without an open harvest season (Frawley 2011). Each year from 10 October to 31 October, hunters were allowed a daily limit of 2 birds per day and 6 birds per season. From 2010 to 2013 a minimum of 697 sharp-tailed grouse were harvested, averaging 174 birds per year (Frawley 2011, 2012, 2013, 2014). Because the MDNR recently increased the area open to sharp-tailed grouse hunting, metapopulation models that incorporate hunter harvest scenarios are useful for informing management decisions (D. R. Luukkonen, MDNR, personal communication).

The objectives of this chapter were to: (1) identify habitat patches with potential to support sharp-tailed grouse populations, (2) create a metapopulation dynamics model based on habitat size and configuration of these habitat patches, (3) create a baseline model forecasting grouse response to persistent habitat conditions without population management, (4) evaluate recent harvest management practices and potential increased harvest effects on population viability, (5) assess harvest impacts when broad and localized harvest strategies are employed and (6) evaluate the effects of habitat management alternatives on population persistence.

Methods

To model sharp-tailed grouse populations under potential management scenarios I used the population viability analysis software RAMAS GIS 6 (Applied Biomathematics, Setauket, New York). RAMAS GIS is designed to model population viability by combining a matrix-based stage/age metapopulation demographics model (RAMAS Metapop) with spatially explicit landscape data in a GIS (Akçakaya and Root 2013). This software has been used in studies evaluating management decisions under a variety of circumstances that may influence population dynamics. Examples include modeling Amur tigers (*Panthera tigris altaica*) and poaching (Tian et al. 2011), northern spotted owl (*Strix occidentalis caurina*) population responses to habitat loss (Akçakaya and Raphael 1998), snowy plover (*Charadrius alexandrinus*) responses to sea level rise (Chu-Agor et al. 2012) and forest management impacts on ruffed grouse (*Bonasa umbellus*) (Blomberg et al. 2012). RAMAS GIS has also been shown to be an effective tool for modeling prairie grouse populations in North America (Akcakaya et al. 2004, Lyons 2008, Pratt 2010).

RAMAS GIS allows the user to import GIS map layers that are used to calculate suitability values for all pixels in a layer, and to delineate landscapes into patches that subpopulations can occupy. I delineated population patches across the entire Upper Peninsula by mapping the resource selection pattern identified for sharp-tailed grouse in the central and eastern Upper Peninsula of Michigan (Chapter 2) and importing it into the Spatial Data subprogram. This map depicted the relative likelihood of occurrence for sharp-tailed grouse ranging from 0.07 to 345.36 at the 1-square-mile section scale. To evaluate suitability the program uses a habitat suitability threshold, which is the cutoff below which it assumes that pixels are not suitable for survival or reproduction (Akçakaya and Atwood 1997). I classified pixels as unsuitable if their predicted relative likelihood of occurrence was below 2.89, the minimum value of predicted relative likelihood within the two highest RSF classification bins (see Chapter 2). I chose to model potential habitat patches across the entire Upper Peninsula, to allow for sharp-tailed grouse expansion into currently unoccupied suitable locations. This also allows for modeling management scenarios that could occur across large expanses, such as translocations.

After identifying suitable pixels, I then aggregated pixels into habitat patches (i.e. populations) based on a "neighborhood distance". The neighborhood distance is the maximum distance between two pixels for them to be considered in the same patch. Following Akçakaya and Atwood (1997), I used the foraging distance of the species to define the neighborhood distance. Sharp-tailed grouse in Wisconsin have shown daily movements ranging from between 200 and 400 meters in the summer to between 800 and 1200 meters in the winter (Gratson 1983). I tested sensitivity of the program's patch delineation using neighborhood distances from 400 to 1200 meters and found it insensitive to this range of neighborhood distances. Following Akcakaya et al. (2004), I used a neighborhood distance equivalent to 500 meters (16.67 pixels) to aggregate suitable pixels into patches.

From the resulting habitat patch map, each patch's initial abundance, carrying capacity and a distance matrix were calculated based on patch characteristics (e.g. area, edge) and location and then exported for use into the metapopulation subprogram RAMAS Metapop. Distances between patches were calculated based on the center point of each patch. I established nonzero initial abundances for all patches that had a record of sharp-tailed grouse occurrence between 2009 and 2013. The recent sharp-tailed grouse distribution in Michigan includes sections of Chippewa, Mackinac, Alger, Schoolcraft, and Delta counties in the eastern Upper

Peninsula (Fig. 2.1). I set the initial abundances of these patches equivalent to 5 birds per square mile and assumed that carrying capacity varied linearly from 5 birds per square mile when habitat suitability was at 2.89 (suitability threshold) to 24 birds per square mile when habitat suitability was highest (345.36), based on post-breeding densities typical of multiple states (Edminster 1954).

Within the RAMAS Metapop module I developed a six stage demographic model with 1 year time steps, and a 100-year time horizon. Following Akcakaya et al. (2004) the stages included 0-year old, 1-year old, and 2-year old and older females (F0, F1, F2+) and males (M0, M1, M2+). The model included both demographic and environmental stochasticity, so each scenario was simulated 1,000 times to produce a distribution of outcomes. Because demographic data for Michigan were limited, rates from outside the state were used when necessary. Similar to Akcakaya et al. (2004) and due to the greater availability of demographic data at this time of year, I modeled post-breeding abundance.

Although there is evidence that female sharp-tailed grouse have higher mortality rates than males during the nesting season, differences in survival between sexes are likely offset by selective mortality of males displaying on breeding grounds (Ammann 1957). Similar survival rates between the sexes were found in South Dakota (Robel et al. 1972). I assumed the probability of surviving from hatching to breeding at one year of age was 0.26 (Temple 1992). Annual survival of sharp-tailed grouse in Washington was reported as 0.53 for an unhunted population (Connelly et al. 1998); I assumed this survival rate would apply to older grouse in our model in the absence of hunting.

While sharp-tailed grouse females most likely begin to breed during their first mating season (Connelly et al. 1998), first year males (MO) of polygynous tetraonid species do not generally breed (Wiley 1974). Therefore, I assumed they did not contribute to reproduction. On average, sharp-tailed grouse in Michigan produced 7.7 chicks per female (Ammann 1957). To calculate fecundity I multiplied this fertility by stage-specific survival and then divided equally between male and female offspring. Thus age zero fecundity equals 1.001, and later stages fecundities equal 2.041 (Table 2.1).

Unlike populations of sharp-tailed grouse that occur on extensive open prairies, those in the Great Lakes states do not often need to travel long distances to reach woody cover (Hamerstrom and Hamerstrom 1951). Among 120 sharp-tailed grouse recovered in Wisconsin, 79% dispersed within 3 miles and the longest dispersal distance observed was 21 miles (Hamerstrom and Hamerstrom 1951). While extensive movements have been observed in birds after translocation in Michigan, 98% of locally trapped sharp-tailed grouse recoveries were within 3 miles of the release location (Ammann 1957). Female sharp-tailed grouse translocated to Michigan from Wisconsin, Alberta and within higher abundance areas of the state traveled on average 13.36 km, while males were less mobile than females, with an average dispersal of 7.89 km (Ammann 1957). Although average distances based on translocation have been shown to be higher than distances traveled by native birds (Hamerstrom and Hamerstrom 1951, Ammann 1957), these values probably more closely approximate movement of Great Lakes birds than estimates of movement available from western states. Similar dispersal rates have been exhibited by sharp-tailed grouse in both South Dakota and Wisconsin, with 58.2% percent of birds traveling greater than 0.5 miles and 59.2% of birds traveling greater than 1 mile, respectively (Hamerstrom and Hamerstrom 1951, Robel et al. 1972). I used Robel et al. (1972) dispersal rate of 58.2% because the distance constituting a dispersal event (.5 miles) was more similar to our neighborhood distance (distance used to delineate patches) of 500 meters.

I modeled dispersal using an exponential decay function:

$$M_{ij} = a \exp(-D_{ij}/b), \tag{1}$$

where M_{ij} is the proportion dispersing from patch j to patch i, D_{ij} is the distance between patches, and a and b are scaling parameters calculated using the above movement data, with b equal to the rate of decline in dispersal with increasing distance and a equal to the maximum rate of dispersal. I calculated b as $-\ln(0.5)*13.36 = 9.26$ and a as $0.582/b= 0.063$; the total proportion of dispersers scaled by the rate of dispersal decline (Akçakaya and Raphael 1998). Following Akcakaya et al. (2004) I modeled differences in dispersal rates among sexes and life stages: juvenile females were assumed to have the highest rates, calculated from equation (1), with scalars reducing the rates for adult females (0.66), juvenile males (0.44), and adult males (0.33). I set the maximum possible dispersal distance to 34 km, above which dispersal is unlikely to be sufficiently common to affect population growth rates (Sjogren and Corace 2006).

Many external factors vary across time and can lead to fluctuations in vital rates. In particular, factors such as predator abundance, spring weather and prey availability are important drivers of sharp-tailed grouse demographics (Sjogren and Corace 2006, Goddard and Dawson 2009). Following Temple (1992), I simulated environmental stochasticity in vital rates using a coefficient of variation (CV) of 40% for fecundity, 30% for juvenile survival, and 20% for adult survival. Using these CVs, I then sampled the vital rates from a lognormal distribution. To account for demographic stochasticity, I allowed the number of survivors and dispersers of the ith stage to be drawn from a binomial distributions with parameters N_i (abundance) and S_i

(survival rate) or D_i (dispersal rate), respectively (Akçakaya and Root 2013). The number of young produced in the *i*th stage are drawn from a Poisson distribution with a mean of F_iN_i (fecundity·abundance) (Akçakaya and Root 2013).

Environmental factors, such as temperature and rainfall, tend to be correlated across space and can lead to spatially correlated population dynamics. Models that assume complete independence in correlation of vital rates among populations tend to underestimate the actual metapopulation extinction risk (Akçakaya 2000). The synchronous nature of environmental dynamics often extend large distances, and can result in synchronized declines in populations (Akcakaya and Brook 2008). Baines et al. (2007) found spatially correlated rates of black grouse fecundity (r = 0.64) in regions of the United Kingdom separated by around 250 km, but did not find significant evidence for correlation (r = 0.08) among regions separated by around 500 km. I modeled vital rate correlation with an exponential decay function:

$$C_{ij} = a \exp(-D_{ij}/b), \qquad (2)$$

where C_{ij} is the correlation coefficient between patch *i* and patch *j*, D*ij* is the distance between patch *i* and patch *j*, *a* is a function parameter equivalent to the maximum correlation rate at a distance of 0 km and *b* is a scaling parameter of the rate of correlation decline. I set *a* = 0.99 to model high correlation for populations separated by short distances and *b* = 573 where populations separated by 250 km would have a correlation coefficient equal to 0.64.

At the end of each time step RAMAS recorded the total number of male and female birds in all stages immediately after breeding. In Michigan peak activity on breeding grounds is roughly the third week in April (Drummer et al. 2011), and peak hatching occurs between June 6-10 (Ammann 1957). I used a ceiling type density dependence (Temple 1992), which allowed the populations to grow exponentially until patches reached carrying capacity. If a population's abundance exceeded carrying capacity during any time step it was set equal to the carrying capacity (Akçakaya and Root 2013).

Simulations

To predict basic metapopulation dynamics I simulated initial models assuming no population or habitat management efforts, with and without dispersal between populations (simulation 1 and 2, respectively). To simulate scenarios including hunter harvest, I estimated recently observed harvest mortality by increasing reported harvest values by 20% to account for unreported harvest and wounding loss. I then removed the equivalent harvest from either the two largest eastern Upper Peninsula populations, which are within the current hunt region (populations 53 and 98, Fig. 2.2 A) (localized harvest), or from across the entire metapopulation (range-wide harvest). I initiated harvest in the 10th time step, to allow populations to stabilize after increases from their initial abundances. I predicted sharp-tailed grouse response to a range of harvest mortality rates ranging from current rates to 4.5 times current rates (Table 2.2). I removed the harvest each time step in proportion to members in each age and sex class, before dispersal.

I simulated sharp-tailed grouse response to habitat management by adding patches of habitat, which I assumed were optimally managed for sharp-tailed grouse, to the Spatial Data subprogram input map. Pixels within these patches were set to the highest suitability value and consequently these patches had the maximum carrying capacity of 24 birds per square mile. I evaluated the influence of habitat patch size by creating both large and small patches, which were equal in total area (Table 2.3, Fig. 2.3 A-D). I compared the importance of patch location by creating equal area patches in a location chosen to increase population connectivity and a random location on the landscape (Fig. 2.3 A, E). I ran additional simulations that incorporated moderate localized harvest rates (2 times current levels) into each habitat management scenario to rank management strategies according to their ability to increase population viability (Table 2.2, simulations 24 to 28).

The MDNR has established a goal to "maintain a viable population of sharp-tailed grouse that supports both hunting and non-consumptive recreation in the Upper Peninsula" (Luukkonen et al. 2009) . While the MDNR has not established a specific population objective, according to Temple (1992), five populations of at least 280 individuals would be necessary for a 95% certainty of population persistence over a 50 year period. Therefore, simulations were evaluated based on their final average metapopulation abundance, expected minimum abundance (EMA), percentiles of final total abundance, and terminal quasi-extinction risk (risk that the metapopulation will be below 1400 birds at the end of the 100 year simulation) (Akçakaya and Root 2013). Because of the importance of maintaining a sharp-tailed grouse population than can support hunting, models including hunter harvest were also evaluated based on cumulative harvest.

Results

RAMAS GIS identified 143 suitable habitat patches totaling 2172 km^2, with the majority of suitable habitat in the central and eastern Upper Peninsula (Fig. 2.2 A-B). Patches ranged from 2 km^2 to 362 km^2, with an average patch area of 15 km^2. Many of the patches were small and the 4 largest patches accounted for 52.9% of the suitable habitat. Of these patches, 13 coincided with recorded sharp-tailed grouse occupancy between 2009 and 2013. Carrying capacity totaled 4976 birds for all patches, and initial abundance was 2526 birds. Under the dispersal assumptions and initial distribution settings, large patches in the central and eastern Upper Peninsula had a higher average number of time steps occupied and suitable habitat patches in the western Upper Peninsula did not become occupied during the 100 year simulation (Fig. 2.4).

The metapopulation's finite rate of increase was 1.53, without accounting for stochasticity and management actions. The metapopulation abundances of simulations 1 and 2, with no management actions, grew rapidly to near carrying capacity of occupied patches and then gradually increased throughout the remainder of the simulation or oscillated near carrying capacity, respectively (Fig. 2.5). Final average metapopulation abundance and EMA were highest for simulation 1, when compared to all simulations without addition of suitable habitat patches (Table 2.3). The terminal quasi-extinction risk of metapopulation abundance ending below 1400 was negligible for both base simulations 1 and 2 (Table 2.3).

Recent harvest mortality rate estimates were approximately 6% and 12% of the predicted metapopulation and localized patch abundances (average abundances of simulation 1, time step 10), respectively. Final average metapopulation abundance, EMA and percentiles of total abundance decreased with increasing localized and range-wide harvest rates (Table 2.3). Across all localized harvest simulations metapopulation abundance trends were relatively stable following a decrease due to harvest initiation in time step 10 (Fig. 2.6 A). Localized and range-wide harvest strategies had similar terminal quasi-extinction rates for simulations up to 3 times current harvest estimates (approx. 19.4% metapopulation harvest rate, Table 2.3). Simulations of large harvest rates resulted in lower quasi-extinction risks for localized harvest simulations than for range-wide harvest simulations. Range-wide harvest exceeding 3 times current harvest rates led to a declining metapopulation abundance trend (Fig. 2.6 B). Cumulative harvest increased with increasing localized and range-wide harvest up to 2 and 3.5 times current harvest rates, respectively (Fig. 2.7 A-B).

Metapopulation viability was higher for all simulations modeling the addition of suitable habitat (Simulations 19 to 24, Table 2.3) than for base simulations. Large habitat patches increased viability more than equal area smaller patches. The addition of habitat patches near important patches in the eastern Upper Peninsula and randomly placed (Fig. 2.3 A, E) showed similar metapopulation viability. Scenarios modeling combined harvest and habitat management resulted in higher abundance values and lower terminal quasi-extinction risks than comparable harvest scenarios without habitat management, with the exception of simulation 26.

Discussion

The rapid increase in sharp-tailed grouse abundance and range expansion following timber harvest and increased occurrence of fire coincident with European settlement in Michigan (Ammann 1957) is consistent with dynamics predicted under initial abundance and dispersal assumptions of my metapopulation model. The subsequent stable metapopulation dynamics predicted under the base and current harvest rate simulations are also consistent with occupancy surveys conducted in the eastern Upper Peninsula by the MDNR. These surveys have not indicated a declining trend in sharp-tailed grouse occupancy rates in sections with and without hunting since they were established in 2009 (D. R. Luukkonen, MDNR, personal communication).

The base simulation without dispersal was completely dependent upon the initial occupancy pattern on the landscape because patches not initially occupied and those that went extinct could not be colonized during simulations. While not truly realistic, this simulation served to illustrate the importance of dispersal to metapopulation viability by allowing occupied patches to recolonize extinct habitat patches within the maximum dispersal distance. Individual patch occupancy results indicated that the observed distribution of sharp-tailed grouse used to parameterize the model is not within dispersal proximity to suitable habitat patches in the western Upper Peninsula. This highlights the importance of understanding the current occupancy pattern when performing spatially-explicit modeling. Before management actions such as translocation can be recommended it would be useful to better understand current occupancy patterns in the western Upper Peninsula. Suitable habitat patches not overlapping known sharp-tailed grouse occurrences can inform additional survey locations.

Model results indicated that populations subjected to localized hunter harvest, which resulted in extinction of target populations when subjected to high harvest rates, had lower extinction risks than when harvested at similar rates across their entire range. While metapopulation viability was higher in these scenarios, the extirpation of subpopulations is problematic and decreases in hunter satisfaction and opportunities for people to view grouse would likely occur. Harvest results were similar to Akcakaya et al. (2004) research showing declining viability when simulated harvest rates increased from 20% to 30%. Therefore, harvest regulations using a localized framework, with harvest limited to no more than 2 times the estimated current rate (approx. 25% harvest) should exhibit low extinction risk for sharp-tailed grouse populations in Michigan’s Upper Peninsula.

Simulations of habitat management generally increased population viability, with larger patches having a greater benefit to sharp-tailed grouse viability than similar areas distributed among smaller patches. This pattern is similar to findings by Akcakaya et al. (2004) who found that scenarios with larger clear cut sizes increased carrying capacity of sharp-tailed grouse patches more than scenarios with small clear cuts. Research by Blomberg et al. (2012) also indicated that large suitable habitat patches were more beneficial to ruffed grouse viability than small patches of the same total area. Interestingly, under moderate hunting pressure, simulation of the addition of 9 mi^2 suitable habitat with several small patches resulted in lower viability than similar hunting pressure without the addition of habitat. This may be due to source-sink dynamics among populations where birds from these small patches are dispersing to locations where reproduction does not keep up with mortality rates (i.e. nearby hunter harvested patches) (Pulliam 1988) and therefore not contributing to metapopulation viability.

While this study did not find a high risk of sharp-tailed grouse decline under simulations approximating recent harvest trends, these results are based on the current landscape configuration of the Upper Peninsula. The Upper Peninsula of Michigan was historically predominantly forested and the favorable landscape created in Michigan through forest clearing and slash fires has seen dramatic declines since the mid-1900s (Maples and Soulliere 1996). This trend is continuing within the Great Lakes region and management efforts such as timber harvest and prescribed fire are necessary to control the expansion of succession (Sjogren and Corace 2006). Additional simulations modeling the effects of habitat loss on sharp-tailed grouse are needed to further inform habitat management goals within Michigan. Based on the current habitat management simulations I would recommend that locations for sharp-tailed grouse habitat management are ranked based on the area of contiguous habitat managed rather than total area of managed habitats.

APPENDIX

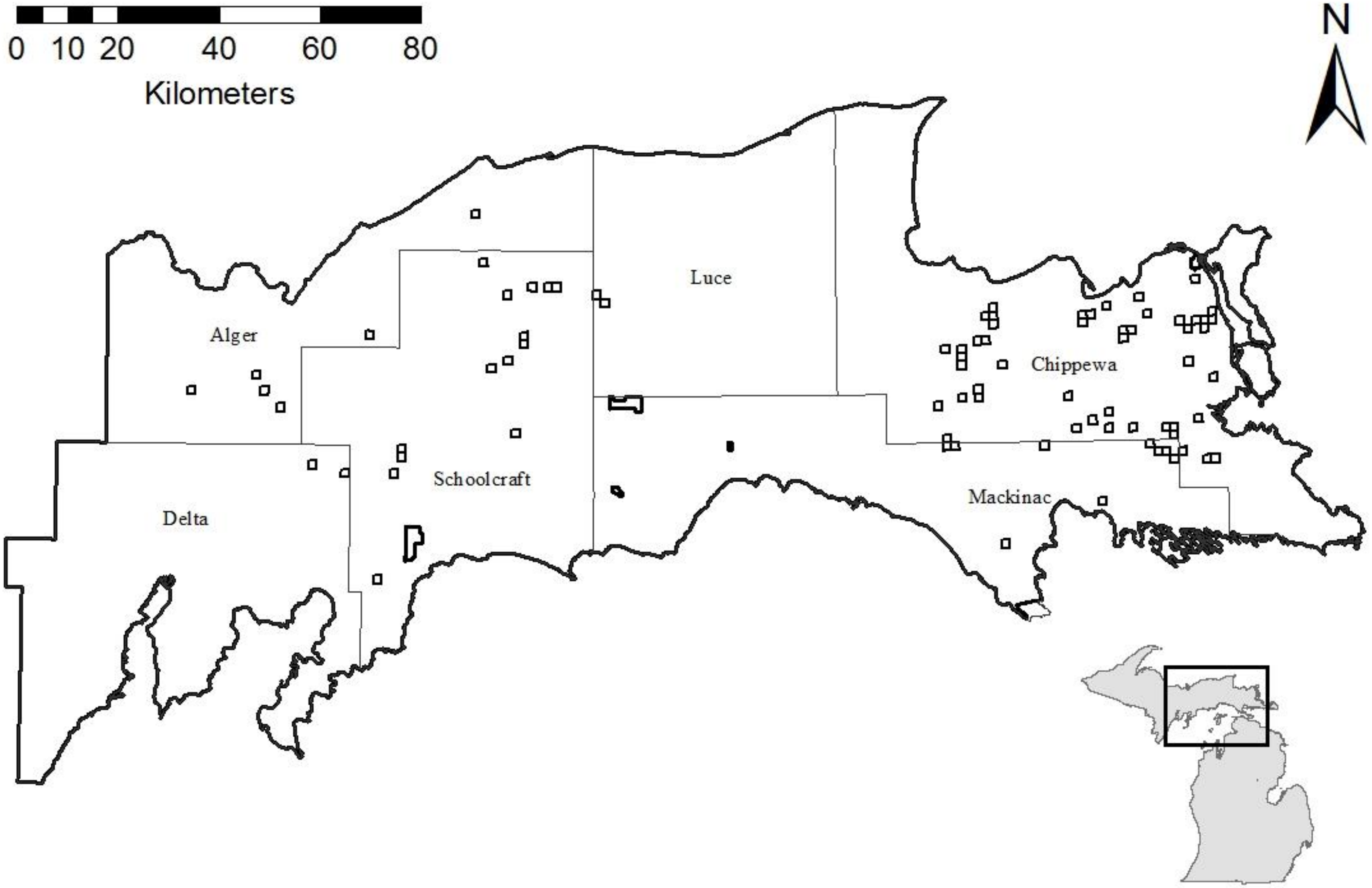


Figure 2.1 Locations of recent observations (2009-2013) of sharp-tailed grouse in 1mi² township sections within Michigan's Upper Peninsula.

Table 2.1 Population projection matrix showing average female offspring per breeding female (upper left quadrat top line), average male offspring per breeding female (lower left quadrat top line) and stage specific survival rates (remaining non-zero cells) for sharp-tailed grouse metapopulation modeling in the Upper Peninsula of Michigan, USA.

Stage Matrix						
	F0	**F1**	**F2+**	**M0**	**M1**	**M2+**
F0	1.001	2.041	2.041	0	0	0
F1	0.26	0	0	0	0	0
F2+	0	0.53	0.53	0	0	0
M0	1.001	2.041	2.041	0	0	0
M1	0	0	0	0.26	0	0
M2+	0	0	0	0	0.53	0.53

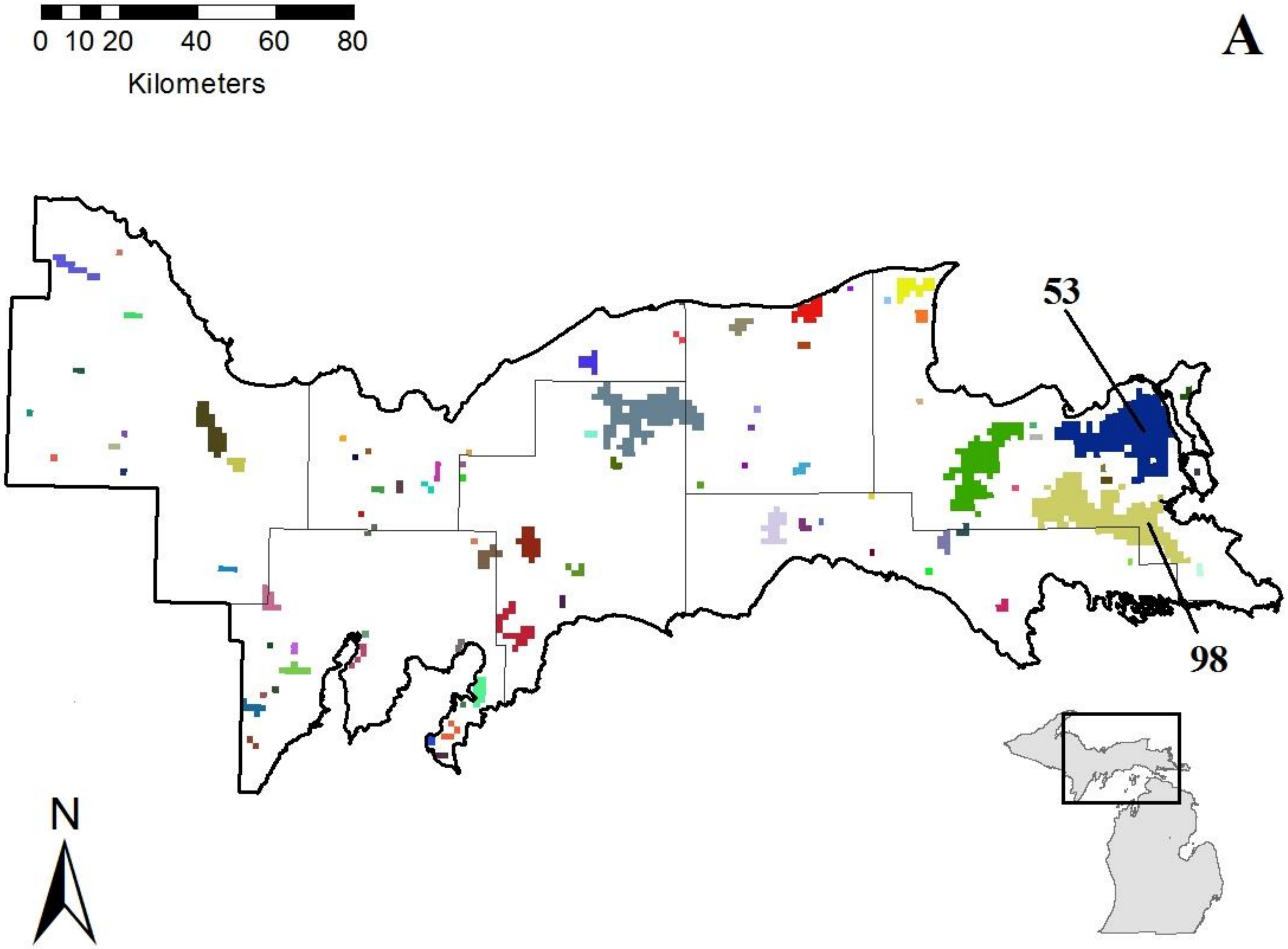


Figure 2.2 Locations of potentially suitable habitat patches in the (A) eastern and (B) western Upper Peninsula of Michigan, identified by RAMAS GIS Spatial Data program. Populations 53 and 98 were used for localized harvest scenarios.

Figure 2.2 (cont’d)

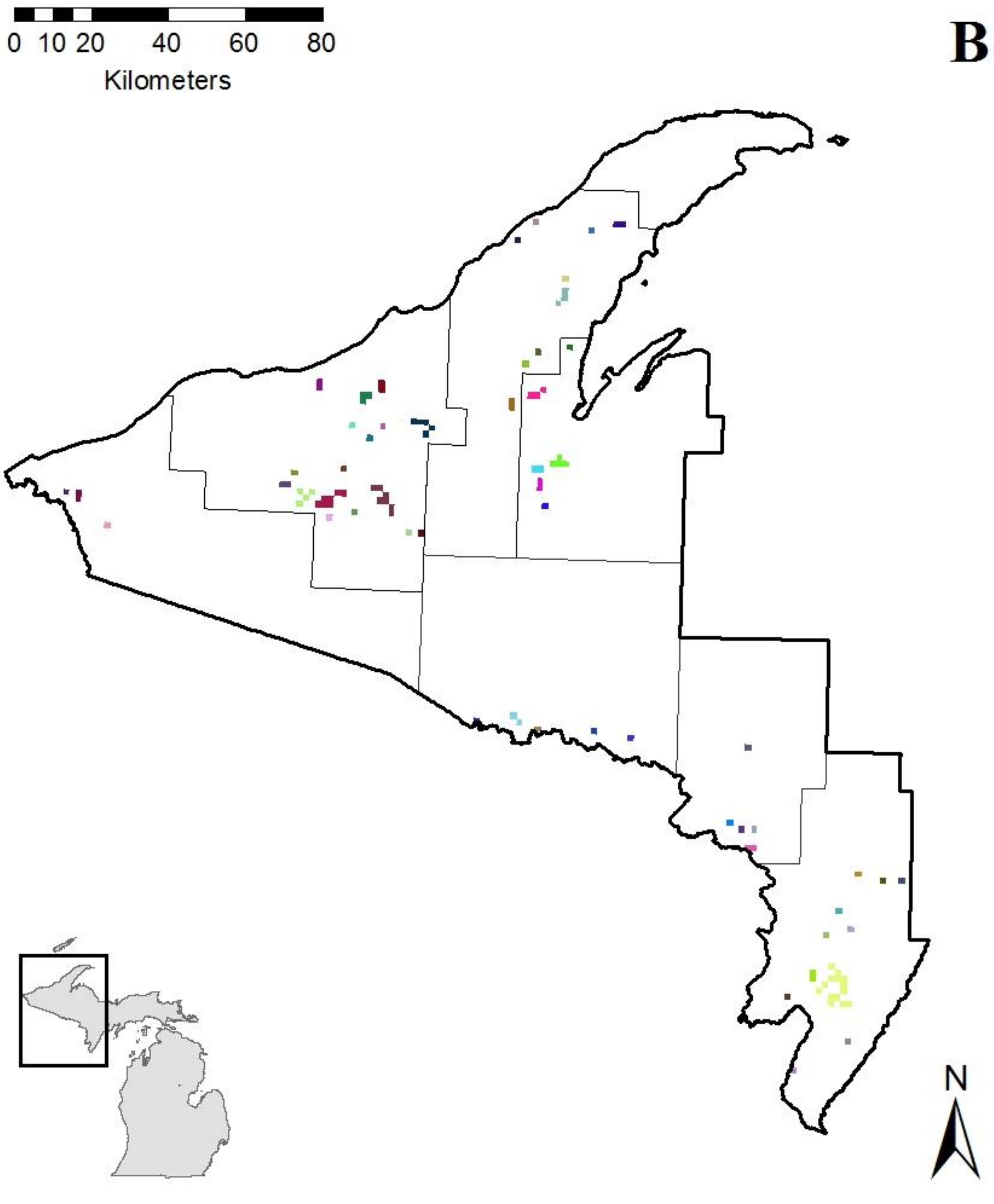


Table 2.2 Localized and range-wide harvest rates used in simulations of sharp-tailed grouse metapopulation viability in the Upper Peninsula of Michigan, USA. Localized harvest was removed from two largest eastern Upper Peninsula populations within the current hunt region (populations 53 and 98).

Simulation	Population 53 harvest rate	Population 98 harvest rate	Metapopulation harvest rate
1	N/A	N/A	N/A
2[a]	N/A	N/A	N/A
3	0.1238	0.1248	N/A
4	0.1856	0.1872	N/A
5	0.2475	0.2496	N/A
6	0.3094	0.3120	N/A
7	0.3713	0.3743	N/A
8	0.4331	0.4367	N/A
9	0.4950	0.4991	N/A
10	0.5569	0.5615	N/A
11	N/A	N/A	0.0646
12	N/A	N/A	0.0969
13	N/A	N/A	0.1291
14	N/A	N/A	0.1614
15	N/A	N/A	0.1937
16	N/A	N/A	0.2260
17	N/A	N/A	0.2583
18	N/A	N/A	0.2906
19	N/A	N/A	N/A
20	N/A	N/A	N/A
21	N/A	N/A	N/A
22	N/A	N/A	N/A
23	N/A	N/A	N/A
24	N/A	N/A	N/A
25	0.2475	0.2496	N/A
26	0.2475	0.2496	N/A
27	0.2475	0.2496	N/A
28	0.2475	0.2496	N/A
29	0.2475	0.2496	N/A
30	0.2475	0.2496	N/A

[a] Simulation assumed no dispersal between populations

Table 2.3 Number of patches, patch area, total area managed, patch location and harvest for simulations of sharp-tailed grouse metapopulation viability under habitat management scenarios in the Upper Peninsula of Michigan, USA.

Simulation	Number of Patches	Patch Area (mi^2)	Total Area (mi^2)	Harvest
19	1	9	9	No
20	9	1	9	No
21	1	25	25	No
22	25	1	25	No
23	1	9	9	No
24	25	1	25	No
25	1	9	9	Yes
26	9	1	9	Yes
27	1	25	25	Yes
28	25	1	25	Yes
29	1	9	9	Yes
30	25	1	25	Yes

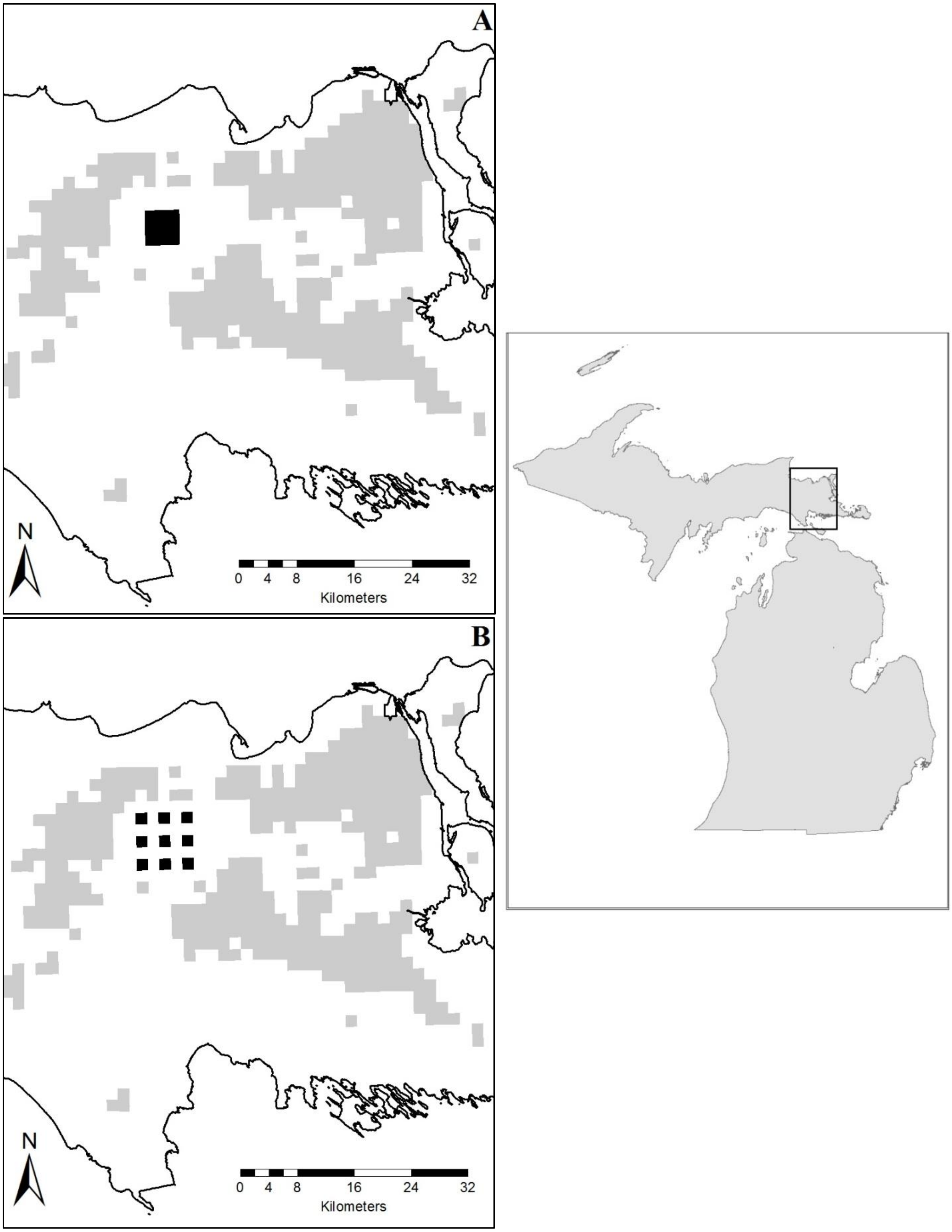


Figure 2.3 Locations of habitat patches (black) added for habitat management simulations 19 through 24 (A-F, respectively) and 25 through 30 (A-F, respectively).

Figure 2.3 (cont'd)

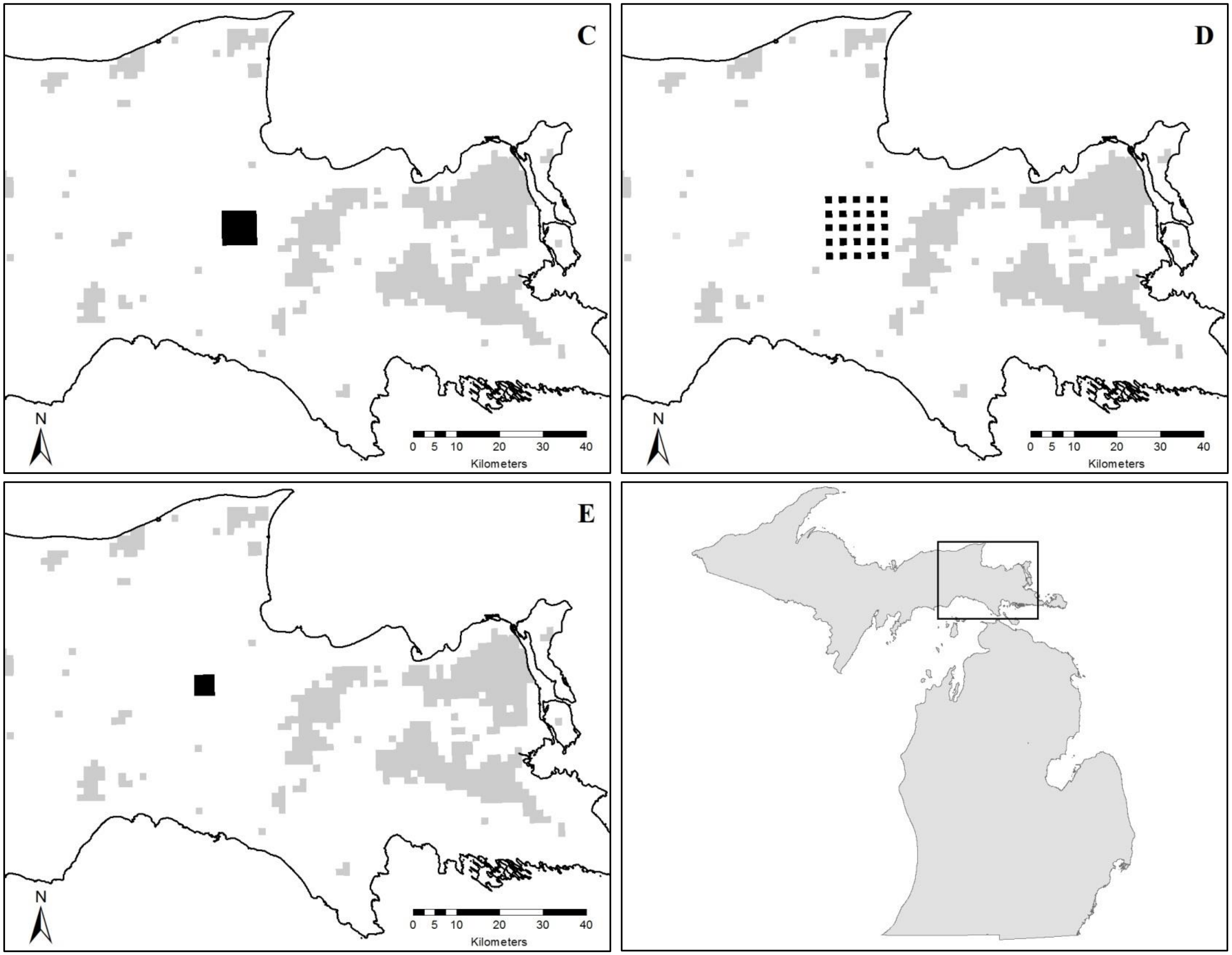
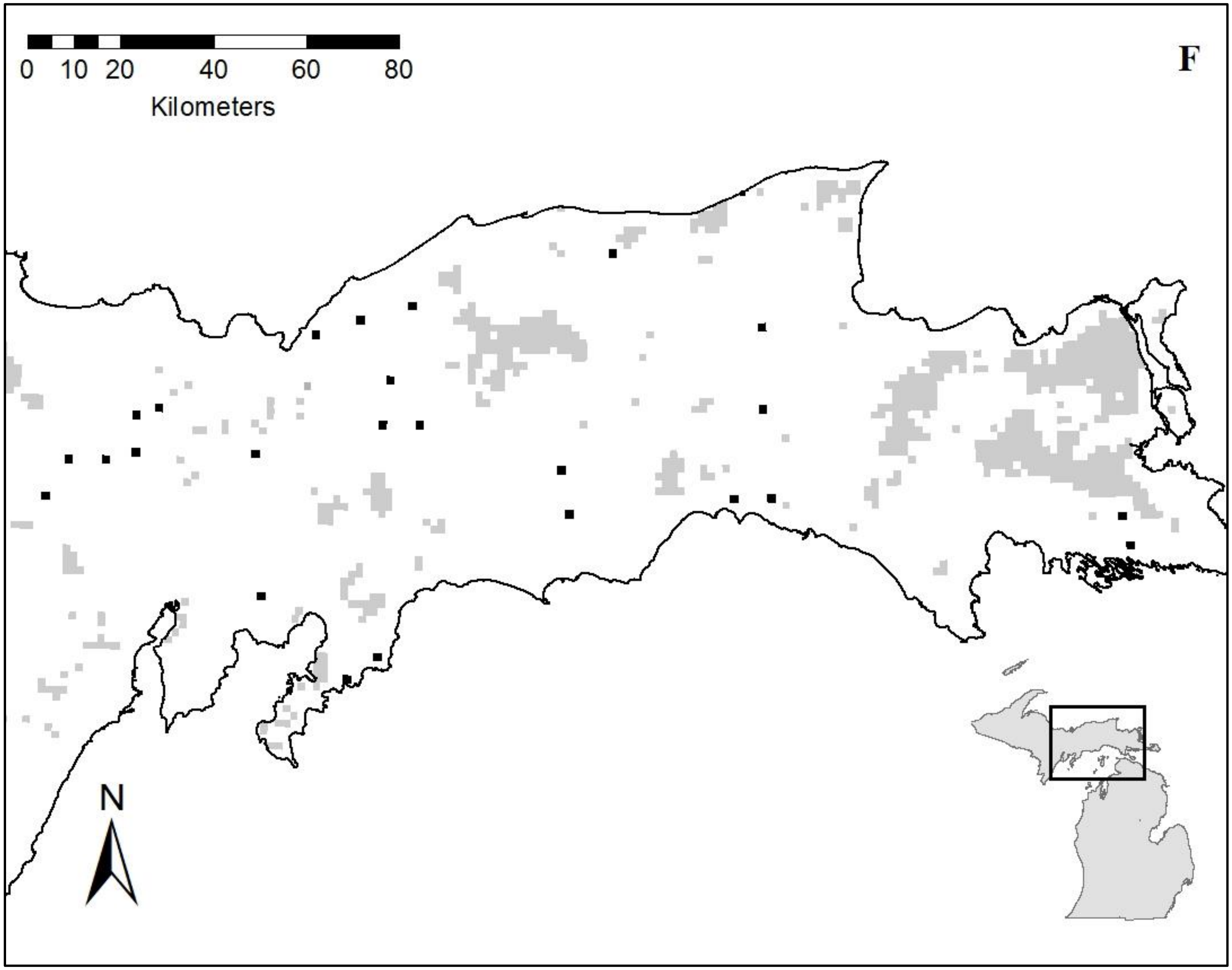


Figure 2.3 (cont'd)



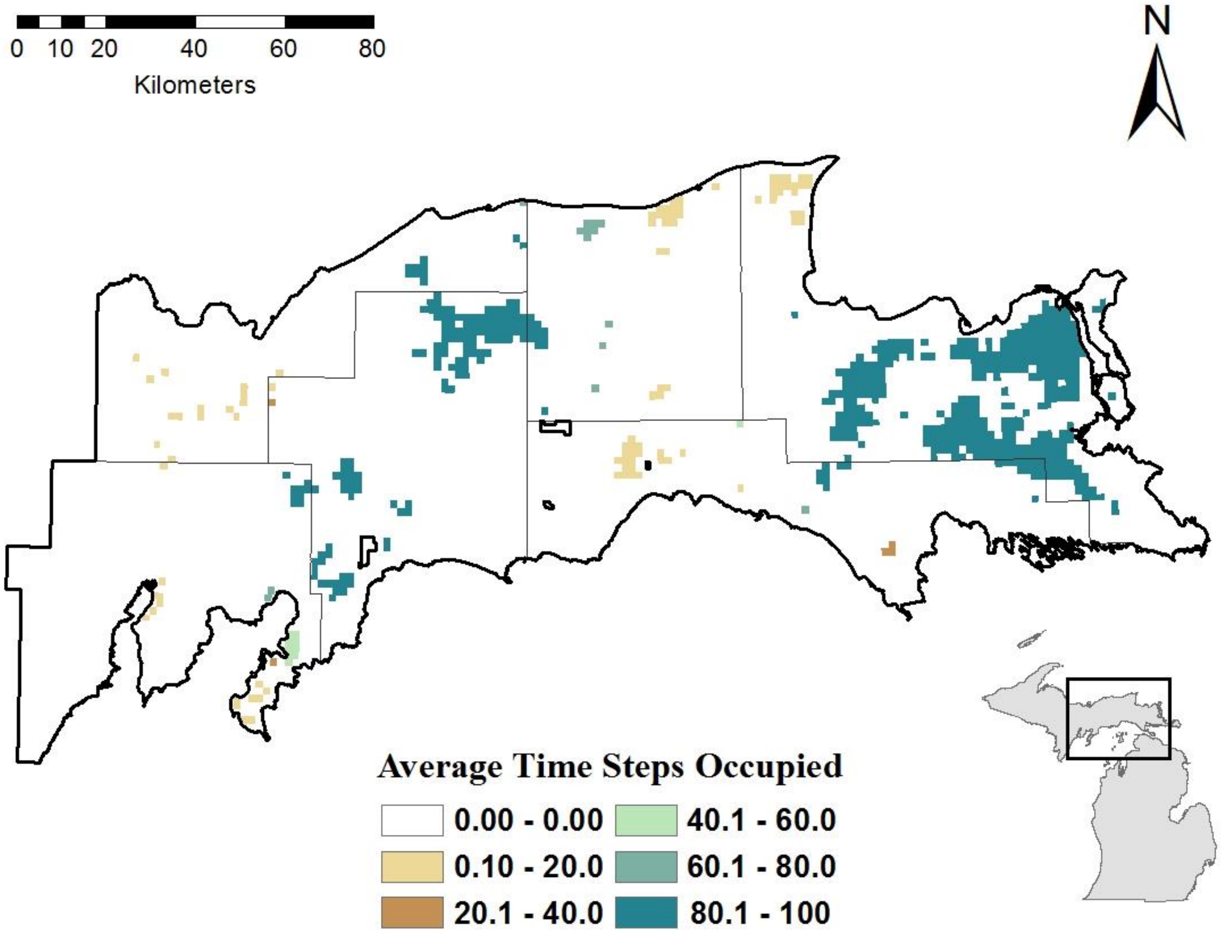


Figure 2.4 Average number of time steps (100 time steps total) metapopulation patches were occupied during Simulation 1, with 2009-2013 initial occupancy pattern and no population management actions in Michigan's Upper Peninsula, USA. Populations outside map extent did not become occupied during simulations.

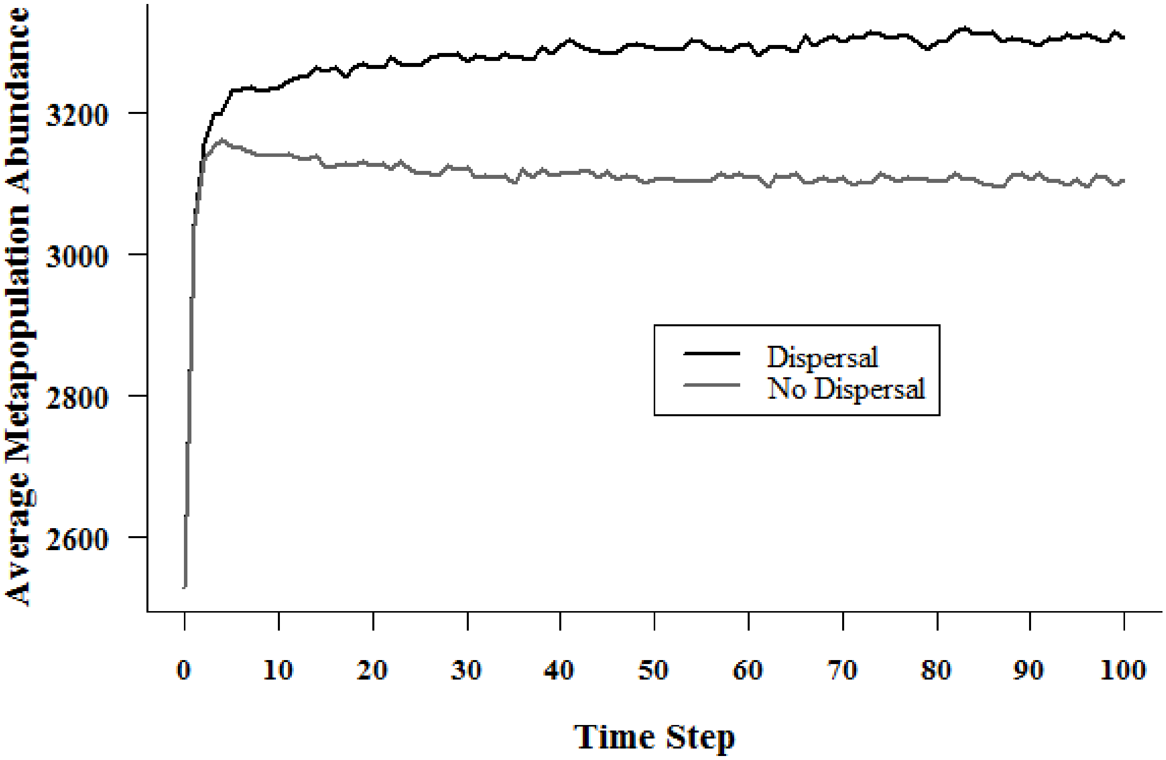


Figure 2.5 Average metapopulation abundance dynamics of base sharp-tailed grouse metapopulation modeling simulations (without population management), with (black) and without (grey) dispersal in the Upper Peninsula of Michigan, USA.

Table 2.4 Final average metapopulation abundance, expected minimum abundance (EMA), percentiles of final total abundance, and terminal quasi-extinction risks (N=1400) for all simulations.

Simulation	Final average metapopulation abundance	EMA	Percentiles of final total abundance					Terminal quasi-extinction risk
			5th	25th	50th	75th	95th	
1	3308	2240	2754	3315	3382	3425	3481	0
2	3106	2218	2798	3123	3165	3168	3171	0
3	3025	1928	2399	2928	3144	3195	3256	0
4	2776	1711	2052	2559	2932	3061	3133	0.004
5	2359	1463	1603	1995	2397	2766	2987	0.009
6	1547	1116	1259	1488	1542	1593	1817	0.107
7	1510	1046	1267	1483	1537	1573	1631	0.12
8	1509	1035	1267	1489	1536	1575	1621	0.112
9	1506	1042	1239	1486	1535	1572	1635	0.127
10	1511	1028	1273	1484	1535	1576	1635	0.115
11	3064	1936	2545	3039	3156	3205	3257	0.001
12	2884	1770	2149	2820	3023	3075	3131	0.001
13	2698	1552	1893	2603	2858	2924	2983	0.004
14	2506	1351	1672	2304	2667	2801	2867	0.009
15	2186	1058	1233	1863	2348	2583	2705	0.076
16	1789	771	662	1379	1882	2318	2557	0.256
17	991	392	21	434	922	1476	2194	0.714
18	299	123	0	0	103	423	1293	0.957
19	3528	2346	3015	3532	3606	3648	3701	0
20	3472	2296	2904	3436	3580	3630	3695	0
21	3953	2511	3384	3948	4028	4083	4172	0
22	3839	2482	3231	3736	3932	4042	4152	0
23	3556	2341	3024	3556	3625	3677	3751	0
24	3607	2357	2931	3570	3693	3767	3866	0

Table 2.4 (cont’d)

Simulation	Final average metapopulation abundance	EMA	Percentiles of final total abundance					Terminal quasi-extinction risk
			5th	25th	50th	75th	95th	
25	2579	1604	1831	2192	2636	3000	3199	0.005
26	2276	1426	1597	1909	2206	2617	3114	0.018
27	2995	1852	2255	2643	3026	3411	3638	0.001
28	2883	1725	1926	2490	2919	3355	3639	0.005
29	2609	1579	1843	2238	2637	3046	3250	0.004
30	2625	1594	1811	2229	2637	3074	3329	0

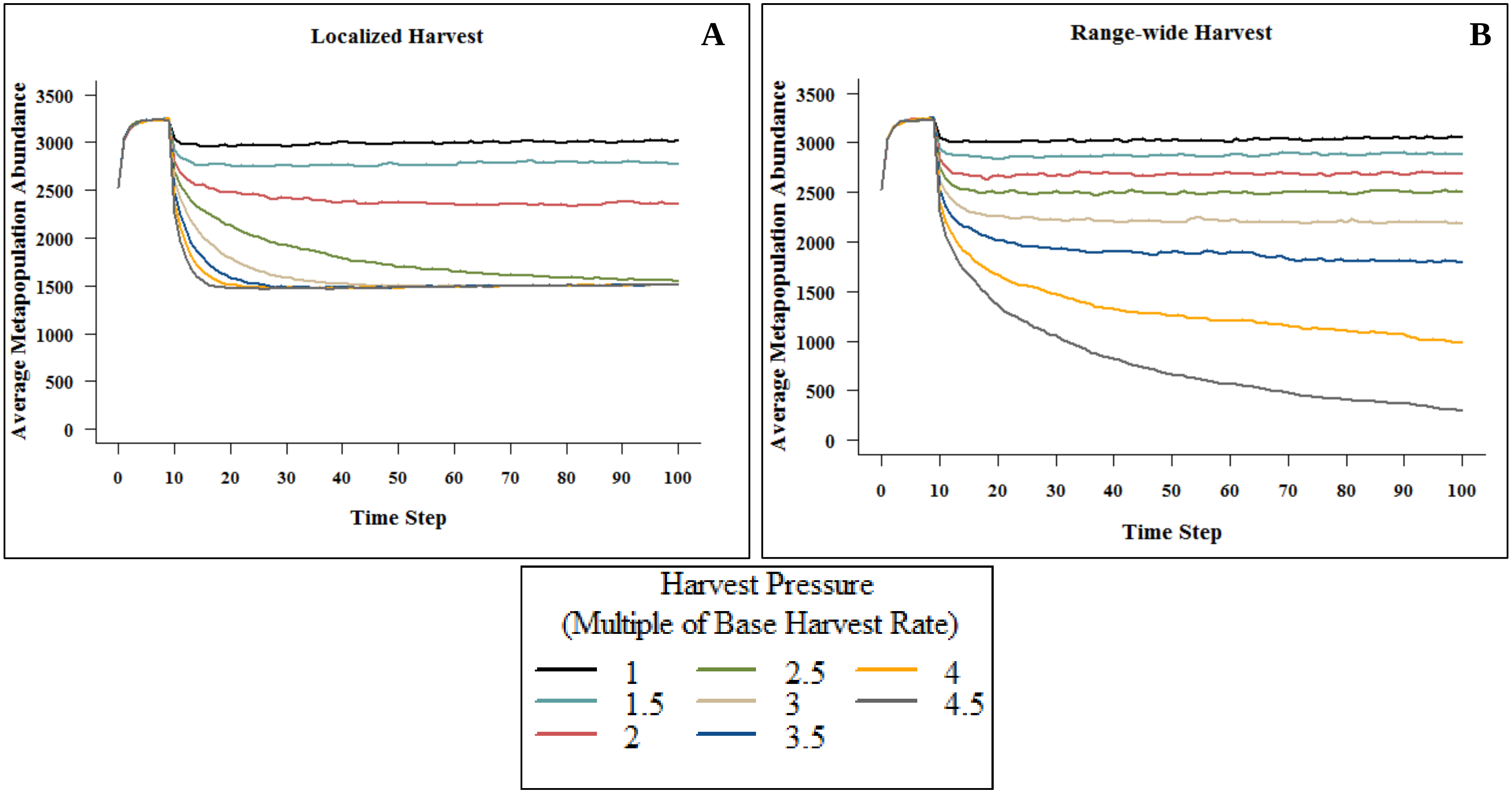


Figure 2.6 Effects of localized (A) and range-wide (B) harvest of sharp-tailed grouse on average metapopulation abundance dynamics in the Upper Peninsula of Michigan, USA. Harvest was initiated in time step 10.

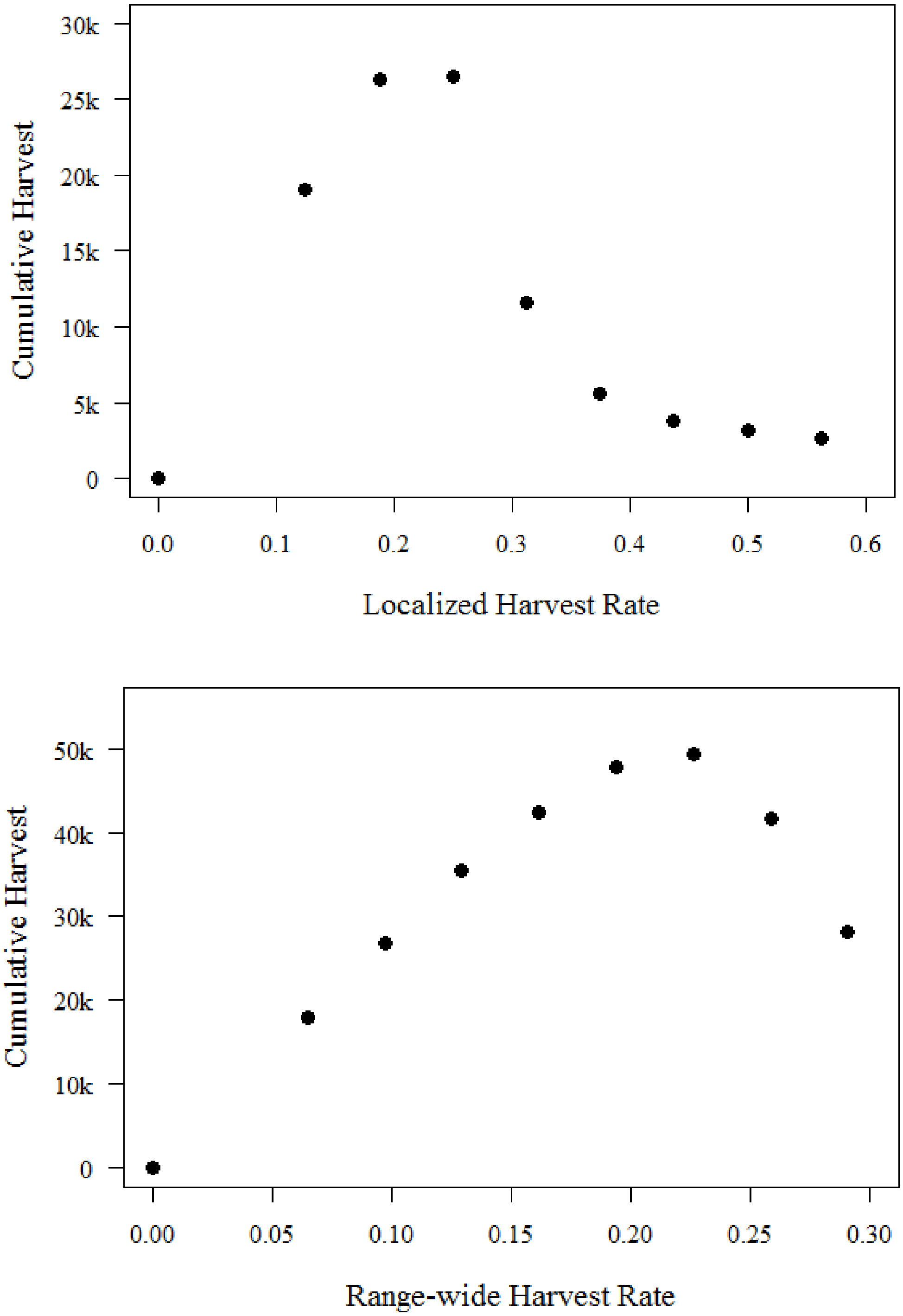


Figure 2.7 Effects of localized (A) and range-wide (B) harvest rate on cumulative harvest (time step 10 to 100) in the Upper Peninsula of Michigan, USA. Localized harvest rates are from subpopulation 98

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