

BOBCAT (*Lynx rufus*) SPATIAL ECOLOGY AND HARVEST IN MINNESOTA

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Paul Michael Kapfer

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Ronald L. Tilson

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## **Dedication**

For Kaia and Kendall, my inspiration in all things.

## Abstract

The bobcat (*Lynx rufus*) is the most widely distributed and abundant felid in North America, whose status is primarily monitored via harvest and associated data. I used a combination of harvest and field data to investigate factors affecting spatiotemporal dynamics of bobcat harvest and spatial ecology in Minnesota.

In chapter one, I investigate the socioeconomic and ecological factors that affected the number of bobcats harvested in Minnesota. Management of game animals requires understanding of factors that affect harvest levels. Although influenced by international law, bobcat management is the responsibility of state or provincial agencies, and jurisdictional environmental, ecological, and regulatory differences may alter which variables influence harvest. Consequently, our understanding of the factors driving bobcat harvest should be at a scale similar to that at which they are managed. I associated 32 years of bobcat harvest data from Minnesota with socioeconomic (e.g., pelt prices, license sales) and ecological variables (e.g., prey abundance, bobcat-specific index of winter severity) to determine what variables most strongly influenced annual bobcat harvest. I constructed candidate negative binomial generalized linear models based on an information-theoretic approach and used quasi-likelihood Akaike's Information Criterion adjusted for small sample size to assess the relative performance of each model. My best model suggested that annual bobcat harvest in Minnesota was positively related to the proportion of scent stations visited by bobcats and season length, and negatively related to the proportion of days when the maximum temperature remained below the bobcat's lower critical temperature. My results differ from those of other studies examining factors

influencing furbearer harvest that have suggested furbearer harvest is driven primarily by pelt price, and suggest that managers can influence the annual harvest of bobcats by changing season length.

In chapter 2, I examine the factors affecting the spatial distribution of bobcat harvest in northeastern Minnesota. Understanding which factors limit species distributions is fundamental to predicting their response to and impact under environmental change. For species that are difficult to monitor, the spatial distribution of their harvest represents a common tool used for monitoring populations and can, with caution, be used to infer ecological relationships. Despite a nearly three-fold increase in abundance over the last 15 years and coincident increase in harvest, the spatial distribution of bobcat harvest in Minnesota has remained relatively static. Of particular interest is the near total absence of bobcat harvest in the northeastern portion of the state because it represents one of five regions designated critical habitat for the federally-threatened Canada lynx (*Lynx canadensis*), and anecdotal accounts suggest bobcats may threaten the persistence of Canada lynx populations. To explore potential explanations for the lack of bobcat harvest in this region I developed candidate binomial generalized linear models comparing townships where male and female bobcats were and were not harvested to determine whether hunter access and effort, climate, competition, prey abundance, or some combination thereof, accounted for the absence of bobcat harvest in this region. As judged by Akaike's Information Criterion corrected for small samples sizes, top-ranked models for males and females suggest that the distribution of bobcat harvest in northeastern Minnesota is primarily determined by bobcat ecology rather than

hunter effort and access. The probability that a male or female bobcat was harvested in a township increased with white-tailed deer (*Odocoileus virginianus*), density and decreased with coyote (*Canis latrans*) density; harvest of females was also positively related to the proportion of a township composed of regenerating forest, an index of snowshoe hare (*Lepus americanus*) abundance. My results correspond with those of previous studies suggesting that bobcat populations can be suppressed by coyotes, that females are more reliant on snowshoe hare than males, and that white-tailed deer form an important component of the diet of bobcats at northern latitudes. Furthermore, my results suggest that reductions in winter-related mortality of white-tailed deer as predicted by climate change and consequent increases in deer density may remove one of the barriers to further colonization of the Arrowhead by bobcats, potentially increasing Canada lynx exposure to competition and genetic introgression.

In chapter 3 I use data from two GPS radio-collared sibling adult female bobcats and compare estimated home range and core area size to previously published studies of bobcat space use in Minnesota and Wisconsin and provide the first published estimate of space use overlap among sibling adult females. Social organization influences carnivore demography, space use, density and abundance. In bobcats, social organization is thought to be affected by multiple interacting factors including relatedness, sex, and prey and conspecific density. To provide baseline data on the effect of relatedness on bobcat social organization, I examined space use and overlap among two sibling, adult female bobcats in east-central Minnesota, and compared these results to previously published research. Estimated bobcat home range size was similar to that of previous studies, suggesting

stability in home range size across several decades and reliability in our estimates. Home range and core area overlap was within the range of previous studies. Importantly, the use of two different methods for estimating core area suggested that the subjective use of the 50% utilization distribution would have underestimated core area size and overlap.

In the 4<sup>th</sup> and final chapter, I estimate how environmental features affect the suitability of habitat for bobcat reproduction and kitten survival and estimate the extent and distribution of bobcat breeding habitat in Minnesota. Distribution models have seen widespread adoption for a diversity of conservation applications because they require minimal data yet have proven highly predictive of the environmental features tolerated by animals. However, there has been limited integration of demography and distribution modeling despite empirical evidence suggesting that the environmental conditions supportive of reproduction are a subset of those supporting survival. I developed a maximum entropy distribution model of habitat suitable for bobcat reproduction and kitten survival using locations where kittens were harvested. My distribution model had good predictive ability and results suggest that the distribution of riparian forest is the preeminent environmental feature explaining the distribution of bobcat reproduction in Minnesota. Coyote abundance, row-crop agriculture and prairie were negatively associated with habitat suitability, mirroring the results of previous studies. Percentage of the study area providing suitable habitat for bobcat reproduction ranged from 23-76%, depending on the threshold used to discriminate between suitable and unsuitable habitat. Notably, I used data that agencies charged with managing bobcat populations largely already gather to develop a highly predictive model of the suitability of habitat for bobcat

reproduction. Conservationists without access to harvest data can gather similar data from incidental observations of reproduction to provide better insight into the relative importance of environmental features for conservation planning and prioritization.

## Table of Contents

LIST OF TABLES .....	xi
LIST OF FIGURES .....	xiii
CHAPTER ONE: SOCIOECONOMIC AND ECOLOGICAL CORRELATES OF BOBCAT HARVEST IN MINNESOTA	
INTRODUCTION .....	1
METHODS .....	2
<i>Study Area</i> .....	2
<i>Explanatory Variables</i> .....	4
<i>Statistical Analysis</i> .....	7
RESULTS .....	9
DISCUSSION .....	10
<i>Variable Effects</i> .....	10
<i>Management Implications</i> .....	13
CHAPTER TWO: CONSTRAINTS ON THE DISTRIBUTION OF BOBCAT HARVEST IN NORTHEASTERN MINNESOTA: IMPLICATIONS FOR CANADA LYNX CONSERVATION	
INTRODUCTION .....	14
METHODS .....	17
<i>Study Area</i> .....	17
<i>Variable Selection and Data Collection</i> .....	18
<i>Statistical Analysis</i> .....	20
RESULTS .....	21
DISCUSSION .....	22
<i>Bobcat Harvest Distribution</i> .....	22
<i>Conservation Implications for the Canada lynx</i> .....	25

CHAPTER THREE: WINTER HOME RANGE AND CORE AREA SIZE AND OVERLAP OF SIBLING ADULT FEMALE BOBCATS IN EAST-CENTRAL MINNESOTA

INTRODUCTION .....27

METHODS .....28

*Study Area* .....28

*Field Methods* .....28

*Data Analysis*.....29

*Genetic Analysis* .....31

RESULTS .....31

DISCUSSION .....32

CHAPTER FOUR: INTEGRATING DEMOGRAPHY AND DISTRIBUTION MODELING: BOBCAT BREEDING HABITAT IN MINNESOTA

INTRODUCTION .....35

METHODS .....38

*Study Area* .....38

*Distribution Records* .....39

*Environmental Data* .....40

*Model Building* .....42

*Model Evaluation* .....44

RESULTS .....45

DISCUSSION .....46

FIGURES .....51

TABLES .....61

LITERATURE CITED .....70

## List of Tables

Table 1.1 A priori generalized linear models of the effects of socioeconomic and ecological variables on bobcat harvest .....	61
Table 1.2 Negative binomial generalized linear model maximum-likelihood estimates (log link) of factors affecting the number of bobcats harvested .....	62
Table 2.1 Description, mean and range of variables used to model distribution of bobcat harvest from 2001 to 2010 in northeastern Minnesota .....	63
Table 2.2 Candidate variables included in binomial generalized linear models to explain bobcat absence in the Arrowhead region of northeastern Minnesota. Model variables for each variable category were based on explanations as interpreted from the references .....	64
Table 2.3 Binomial generalized linear models of the effects of prey abundance (regenerating forest, deer), climate (snow depth, temperature), hunter access (minor roads, snowmobile trails) and interspecific competition (coyote, fisher) on male and female bobcat presence as determined by harvest records. Models are ranked according to differences in Akaike's Information Criterion corrected for small sample size ( $\Delta AIC_C$ ).....	65
Table 2.4 Maximum likelihood parameter estimates (logit link), standard errors and 95% confidence intervals for the best model describing the distribution of bobcat harvest .....	66

Table 3.1 Reference, method for delineating home range and core areas and % overlap for adult female bobcats.....67

Table 3.2 Percentage and utilization distribution overlap index (UDOI) of 95, 50, and core area utilization distributions of two adult sister bobcats.....68

Table 3.3 Mean home range area (km<sup>2</sup>) for female bobcats in Minnesota and Wisconsin, methods used for estimating home range, season when data were collected, number of bobcats monitored and reference.....69

## List of Figures

Figure 1.1 Bobcat range in Minnesota as determined by townships where bobcats were harvested during the 2009-2010 season.....	51
Figure 1.2 Reported harvest of bobcats in Minnesota from 1977-1978 through 2008-2009 seasons .....	52
Figure 1.3 Effect of the percent of scent stations visited by bobcats, season length, and the proportion of days when the maximum temperature < the bobcat’s lower critical temperature on the number of bobcats harvested. Solid line indicates maximum likelihood estimate holding other variables constant at their mean. Dashed lines indicate 95% pointwise bootstrap confidence intervals .....	53
Figure 2.1 Bobcat range in the Arrowhead region of northeastern Minnesota as estimated by townships where bobcats were harvested during the 2001 to 2010 seasons. Inset indicates location of Arrowhead in Minnesota .....	54
Figure 3.1 Winter adaptive kernel home ranges, core areas and overlap of two, sibling adult female bobcats in east-central Minnesota. Star on inset indicates study area location.....	55
Figure 4.1 Study area as delineated by 100% minimum convex polygon (hatched area) of sections where kittens were harvested (circles).....	56
Figure 4.2 Estimates of the importance of environmental features for predicting the suitability of habitat for supporting bobcat reproduction based on 1000 bootstrapped replicates. Error bars represent $\pm 1$ standard error .....	57

Figure 4.3 Marginal response curves of the four environmental features that were most influential in predicting the suitability of habitat for bobcat reproduction. Red curve represents mean response curve from 1000 bootstrapped replicates and blue  $\pm 1$  standard error .....58

Figure 4.4 Distribution of bobcat breeding habitat as delineated by the threshold probability of suitable environmental features within a section  $\geq 0.055$  (minimum probability associated with kitten presence in light blue) and probability  $\geq 0.90$  (gray). Red circles indicate sections where kittens were harvested; white area represents probability of suitable environmental features  $< 0.055$  .....59

Figure 4.5 Probability that habitat provides suitable environmental features for bobcat reproduction and kitten survival in northern Minnesota as delineated by locations where kittens were harvested from 2008 to 2010 (red dots) .....60

## CHAPTER ONE

### Socioeconomic and ecological correlates of bobcat harvest in Minnesota

#### 1.1. Introduction

Harvest management requires an understanding of which socioeconomic and ecological variables influence harvest. Socioeconomic variables include harvest regulations, numbers of hunters, cost of licenses, and monetary value of harvested animals (Tumilson & McDaniel 1986; Elsken-Lacy et al. 1999; Gehrt et al. 2002; Conroy et al. 2005). Ecological variables include weather, sex- and age-class distributions, and the abundance of the harvested animal or its food (Noyce & Garshelis 1997; Norman & Steffen 2003; Diefenbach et al. 2004; Ryan et al. 2004). Often, variables from both of these categories interact to determine harvest. For example, in a study examining factors affecting black bear (*Ursus americanus*) harvest in Pennsylvania, Diefenbach et al. (2004) found that both socioeconomic (i.e. hunter density) and ecological variables (i.e. bear age, sex distributions, and snow cover) jointly predicted harvest. For species harvested primarily for their pelts (e.g. furbearers), economic values strongly influence harvest. For example, Gehrt et al. (2002) documented that raccoon (*Procyon lotor*) harvest in Illinois was highly correlated with pelt prices. Likewise, in analyses of gray fox (*Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*) harvest in Arkansas, harvest rates were explained by pelt prices (Peck & Heidt 1985; Tumilson & McDaniel 1985; Elsken-Lacy et al. 1999). However, harvest regulations that limit the number of furbearers harvested may outweigh the importance of economics (Fortin & Cantin 2004; Hiller et al. 2011).

Bobcats are the most heavily traded felid on the international market (UNEP WCMC 2009) and the most valuable wild fur resource in portions of their range (Wilson 2007). In recent years demand for bobcat pelts has increased numerically and geographically, and is approaching the historic highs that occurred in the late 1970's and early 1980's following the bobcats' inclusion in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In many states, harvest statistics are the sole means used for monitoring bobcats (Roberts 2008); hence, an understanding of the factors affecting harvest, including abundance, will be important for informing local and national management of bobcat harvest and international oversight of bobcat trade. My objective in this study was to examine factors influencing harvest dynamics of bobcats in Minnesota.

## **1.2 Methods**

### *1.2.1 Study Area*

I used data describing 32 years (1977-2008) of environmental conditions and bobcat harvest in Minnesota, which lies near the northern edge of bobcat range (Anderson & Lovallo 2003). In the last decade, bobcat range in Minnesota has expanded slightly to the northwest and southeast and, according to harvest records, currently encompasses the northern half of the state (Fig. 1.1). Vegetation in this region consists primarily of mixed hardwood, conifer and deciduous forests, and conifer bogs and swamps (Coffin & Pfannmuller 1988). Topography generally consists of gently rolling hills with a few rocky outcrops; elevation ranges from 274 to 700 m, with the highest elevations in the northeast. Climate in Minnesota is continental with cold winters and hot summers: winter

(December-February) mean temperatures range from -12° C to -16° C and summer (June-August) means range from 14° C to 19° C (Minnesota Climatology Working Group 2010). Average annual precipitation ranges from 53 cm to 81 cm, with higher precipitation occurring in the east. Snow cover typically lasts from mid November through late March to mid April (Kuehnast et al. 1982).

Other than a state-wide bounty in place from 1951-1965, bobcat harvest in Minnesota was unregulated until 1977, when the Minnesota legislature designated the bobcat a game animal. Subsequently, the Minnesota Department of Natural Resources (MNDNR) established a limited season and a harvest quota of 5 bobcats per license (from 1977-83, the quota of 5 was for any combination of bobcats and Canada lynx [*Lynx canadensis*]). Between the 1977-1978 and the 2008-2009 seasons, reported annual bobcat harvest ranged from 84 to 890 bobcats (Fig. 1.2). The MNDNR monitors bobcats in Minnesota based on scent station and winter track surveys, harvest trends, and a stage-based population model that uses estimates of survival and fecundity and age and sex ratios of harvested bobcats to estimate pre-birth spring population size (Erb 2009a). Currently, a limited season, typically spanning 6 weeks from late November to early January (1977-2008:  $\bar{x} = 43$  days,  $SD = 10$ ), and the quota of 5 bobcats per license remain in place. The harvest of bobcats is limited to roughly the northern 1/2 of the state, which corresponds approximately with current bobcat range, although a few bobcats have recently been confirmed in the southeast corner of the state (J. Erb, personal communication). In Minnesota, the majority of bobcats are harvested using traps, though as many as 46% of bobcats are shot by hunters (Erb 2009b).

### *1.2.2 Explanatory variables*

I used available literature on bobcat biology and ecology and studies of socioeconomic factors influencing the harvest of bobcats and other species to select variables that may affect bobcat harvest. Socioeconomic variables in the model included bobcat harvest season length (range 16-62 days), inflation-adjusted mean pelt price for each season and the previous season, the number of trapping licenses sold, and unemployment rates. Pelt prices have been shown to influence furbearer harvest (Peck & Heidt 1985; Tumilson & McDaniel 1986; Elskén-Lacy et al. 1999; Gehrt et al. 2002), presumably by affecting trapper effort, although effort is rarely monitored. To account for this influence, I included the mean pelt price, as calculated by the MNDNR from surveys of licensed in-state fur buyers. I adjusted pelt prices using the Consumer Price Index (U.S. Department of Labor, Bureau of Labor Statistics) with a baseline of 2008 to account for inflation. I also included pelt prices from the previous season because, until the recent increase in the availability of fur market forecasts, trappers would have to base current season pelt prices on prices from previous years. I included unemployment to account for possible increased effort resulting from greater unemployment. I calculated the season-specific unemployment rate as the mean of the monthly non-seasonally adjusted unemployment rate in MN (U.S. Department of Labor, Bureau of Labor Statistics) for the months during the season, weighted by the number of days in each month when harvest was allowed. Because the MNDNR does not currently track harvest effort for bobcats, I included the number of furbearer licenses sold as an index of effort.

Ecological variables potentially important to understanding harvest included bobcat abundance, bobcat age and sex ratios, abundances of primary prey, and an index of winter severity. As an index of bobcat abundance I included the proportion of scent stations visited by bobcats during scent-station surveys conducted each fall by the MNDNR (Erb 2008). I included the proportion of harvest consisting of adults, yearlings and juveniles, and the proportion of each age-class consisting of males as determined through the examination of the cementum annuli in combination with internal and external examination of harvested bobcats (Crowe 1975) because there may be differences in the susceptibility of different sex- and age-classes to harvest (Chamberlain et al. 1999; Blankenship et al. 2006). I classified adults as bobcats > 2 years of age, yearlings as about 1.5 years old, and juveniles as < 1 year old (Erb 2007, Erb 2009b). Survival estimates from Mississippi suggest that males are more susceptible to harvest by hunters, presumably due to their higher movement rates (Chamberlain et al. 1999). In addition, many hunters that use hounds may refrain from harvesting females. Conversely, female bobcats more intensively use a small area and more frequently return to the same areas making them more predictable and potentially easier to harvest. Transients (generally dispersing juveniles) appear less susceptible to harvest than resident adults, possibly because their movements are less predictable as they disperse (Blankenship et al. 2006).

I included indices of snowshoe hare (*Lepus americanus*) abundance, calculated from the number of hares harvested and observed during grouse (*Bonasa* spp.) drumming surveys (Larson 2009), and pre-fawn white-tailed deer (*Odocoileus virginianus*) density

for the forested region (the primary range of bobcats), as modeled by the MNDNR (Lenarz 2010). These two species are the primary prey of bobcats in Minnesota (Rollings 1945; Berg 1979), and studies have shown that during prey shortages, bobcats make extraterritorial forays, increase the size of their home range, and may be more prone to risky behavior (e.g. approaching traps and human settlements; Knick 1990).

Using data from the Minnesota Climatology Working Group Website ([www.climate.umn.edu](http://www.climate.umn.edu), accessed 15 September 2010), I calculated the proportion of days from 14 days prior to season opener until the end of bobcat season when snow depth exceeded 15 cm (hereafter snow depth). I did the same for the proportion of days when the maximum temperature failed to exceed the bobcat's lower critical temperature of  $-2^{\circ}\text{C}$  (Mautz & Pekins 1989; hereafter temperature). I arbitrarily chose the 2 week buffer prior to season opener to capture lagged effect of cold temperatures and snow depth on bobcat behavior. To ensure that I captured geographical variation in weather conditions, I identified 4 weather stations near the periphery of bobcat range in the 4 intercardinal directions. I then calculated Pearson product-moment correlation coefficients ( $r$ ) for paired stations, and if  $r < 0.70$ , added another weather station located approximately halfway between the two stations. I did this until both climatic variables at a given station exhibited collinearity ( $r \geq 0.70$ ) with those at 1 other station. To account for missing data, I adopted 2 rules. If data were missing for  $\leq 5$  days in a given month, I assigned the missing day(s) the mean of the day immediately prior to and following the missing day(s). If  $> 5$  days were missing data in a given month, I used data from the nearest weather station with data on those days. Studies of bobcats in Maine and Idaho indicate

that bobcat movements are constrained by snow depths  $\geq 15$  cm (McCord 1974; Koehler & Hornocker 1989), which, combined with restricted trapper access from deep snow, could reduce susceptibility of bobcats to harvest. Alternatively, deep snow may result in more stereotyped movements (McCord 1974), making bobcats easier to detect and thus harvest. Bobcats have a relatively high lower critical temperature of  $-2^{\circ}\text{C}$ ; bobcat metabolism increases approximately 4% per degree below this temperature (Mautz & Pekins 1989). In comparison, the smaller fisher (*Martes pennanti*) has a lower critical temperature of  $-20^{\circ}\text{C}$  (Powell 1979). Consequently, low temperatures increase the bobcats' energetic requirements. To fulfill temperature-mediated energy requirements, bobcats must increase their foraging, likely resulting in increased movement rates, which have been correlated with harvest probability (Chamberlain et al. 1999), or may be more prone to approach trap baits, depredate domestic animals, or approach human settlements (Petraborg & Gunvalson 1962; Applegate & Bahrt 1993), thereby increasing their exposure to harvest. Alternatively, bobcats may mitigate cold temperatures by reducing their activity, a behavior observed in least weasels (*Mustela nivalis*) in Poland (Zub et al. 2009).

### *1.2.3 Statistical analysis*

To reduce collinearity among explanatory variables, I calculated Pearson product-moment correlation coefficients ( $r$ ) for each pair of variables. If  $|r| > 0.70$  for a pair of variables, I used only 1 variable from that pair in a given model. Collinearity was detected between proportion of days with snow depth  $> 15$  cm and days when the maximum temperature  $<$  the bobcat's lower critical temperature; proportion of days with

snow depth > 15 cm and the number of licenses; and inflation-adjusted mean pelt price paid per pelt at year  $t$  and  $t-1$ . These variables were subsequently not allowed to inhabit the same model.

To assess whether a single category of explanatory variables (e.g. social, economic, environmental or ecological) or a combination thereof best explained bobcat harvest dynamics I constructed 7 a priori candidate models; 6 models contained variables from only one of these categories (due to collinearity 2 models containing only economic and environmental variables were required) whereas the 7<sup>th</sup> model included a single variable from each category (Table 1). I adopted a negative binomial error structure to account for overdispersion (i.e. harvest variance exceeded harvest mean) because failing to do so can increase Type I error rates (Zuur et al. 2009). Models took the form of:  $Y = \exp(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)$ , where  $Y$  is the number of bobcats harvested,  $\beta_0 \dots \beta_n$  are the regression coefficients, and  $X_1 \dots X_n$  are observed covariate values. I used quasi-likelihood adjusted Akaike's Information Criterion adjusted for small sample size (QAIC<sub>C</sub>; Burnham & Anderson 2002) to assess the relative performance of each model. I subsequently eliminated uninformative parameters from the model with the lowest QAIC<sub>C</sub> (*sensu* Arnold 2010) by sequentially removing the variable with the minimal absolute value of  $\beta/SE$  and calculating QAIC<sub>C</sub> for the reduced model (e.g. Pagano & Arnold 2009). I continued this process until further variable removal resulted in an increase in QAIC<sub>C</sub>.

Density estimates for deer were not available for some years so I did not include this variable in my GLM because doing so would have considerably reduced my sample

size. To examine the relationship between deer density and bobcat harvest, I instead used simple linear regression of deer density against the residuals of my top-ranked model. All analyses were conducted in program R v2.11.1 ([www.r-project.org](http://www.r-project.org), accessed 1 Sept 2010)

### **1.3 Results**

Reported bobcat harvest totaled 10,435 and ranged from 87 to 983 per year during the 1977 to 2008 seasons (Fig. 1.2). My global model, which included all variables except snow depth and pelt prices (due to their collinearity with other variables) exhibited mild overdispersion ( $\hat{c} = 1.8$ ), but residuals did not indicate any systematic trends.

As indicated by QAIC<sub>C</sub> and model weights, my top-supported model included an index of bobcat abundance, season length, temperature, and pelt price from the previous season, but was only marginally better than the null model (Table 1.1). Subsequent examination of this model revealed that pelt prices were uninformative, and removal of this variable resulted in a reduction in QAIC<sub>C</sub> of 2.45; removal of additional parameters caused QAIC<sub>C</sub> to increase. According to parameter estimates from the best approximating model after removal of an uninformative parameter (inflation-adjusted price pelt at year-1; Table 1.2) and holding other variables constant at their mean, increasing the percent of scent stations visited by bobcats from 1% to 1.5% resulted in a 62% increase in bobcat harvest. Increasing season length from 40 to 60 days resulted in a 55% increase in harvest, and increasing the proportion of days when the maximum temperature < the bobcat's lower critical temperature from 0.5 to 0.6 resulted in a 11% decrease in the number of bobcats harvested (Fig. 1.3). The results of linear regression

indicated that deer density failed to improve upon my top-fitted model ( $R^2 = 0.01$ ,  $P = 0.73$ ,  $n = 12$ ).

## **1.4 Discussion**

### 1.4.1 Variable effects

My results indicate that bobcat managers can manipulate the number of bobcats harvested by altering season length (Fig. 1.3). However, I caution that harvest rates may not be temporally homogeneous throughout the season, and managers should be aware of any temporal patterns of harvest rates. For example, data from the 2008-2009 season in Minnesota indicate that approximately 33% of bobcats are harvested during the first week of the 5-week season and that reducing the season by 1 week at the end of the season would decrease harvest by only approximately 12% (Erb 2009*b*). It is likely that temporal heterogeneity in harvest arises for several reasons, including weather, trapper success, and whether the last week occurs during the holidays in late December and early January. Furthermore, if season length is shortened, hunters and trappers may compensate by increasing their effort accordingly and ultimately harvest the same number of bobcats, although there will be limits to the extent of this response. Nonetheless, managers should be aware of these temporal patterns and may need to make a large reduction in season length to achieve a desired harvest reduction.

The lack of relationship between inflation-adjusted pelt prices and harvest in this study contradicts results from some studies (Peck & Heidt 1985; Tumilson & McDaniel 1986; Elskén-Lacy et al. 1999; Gehrt et al. 2002), but corroborates others (Fortin & Cantin 2004; Hiller et al. 2011). There are two explanations for these differing results.

First, studies that have identified a relationship between pelt price and harvest (Peck & Heidt 1985; Tumilson & McDaniel 1986; Elsken-Lacy et al. 1999; Gehrt et al. 2002) did not adjust pelt prices for inflation, which has the effect of overestimating current values and underestimating distant ones. For example, \$100 in 1977 is equivalent to \$360 today (US Department of Labor Statistics, Bureau of Labor Statistics). Alternatively, harvest regulations that restrict the number of licenses (e.g. Fortin & Cantin 2004; Hiller et al. 2011) or the number of animals a license holder can harvest (this study) will limit the economic potential of a particular species. In Wisconsin for example, bobcat licenses are distributed through a lottery system in which participants typically receive a bobcat license that allows them to harvest a single bobcat once every three or four years (Dhuey & Olson 2008). Due to these regulations, harvested bobcats are highly prized by hunters and trappers in Wisconsin, and not a viable source of income. Indeed, most bobcats harvested in Wisconsin are turned into taxidermy mounts and are not exported (Dhuey & Olson 2008). Unfortunately, no comparable data exist on the ultimate disposition of bobcats harvested in Minnesota. Surveys indicate that approximately 40% of harvested bobcats are sold to instate fur buyers (Abraham & Dexter 2008) and it is likely an additional number are also sold outside the state, suggesting economics might influence harvest in Minnesota more than in Wisconsin. However, I suggest that the pattern in Wisconsin, where bobcats are not sold because regulations restrict the number of bobcats harvested, may be similar to that observed in Minnesota, where bobcat harvest is limited by an individual quota, because in both states, bobcats are unlikely to provide substantial income. Therefore regulations influence harvests more than economics, mirroring the

results of our study and those in which harvest was limited, and contradicting results from studies in which regulations were relatively liberal.

The negative relationship between harvest and cold temperatures (Fig. 1.3) may indicate two things: colder temperatures either decrease bobcat susceptibility to harvest, potentially by reducing movement rates, or else cold temperatures decrease harvest effort. I suspect the former is more likely because the majority of bobcats in Minnesota are trapped (Erb 2009*b*), and therefore do not require trappers to spend long periods outdoors. Taken in conjunction with the bobcat's relatively high lower critical temperature ( $-2^{\circ}\text{C}$ ; Mautz & Pekins 1989) it seems unlikely that my variable would capture the effect of decreased effort and the relationship is most likely due to the decreased susceptibility of bobcats to harvest when temperatures fall below their lower critical temperature.

The failure of the number of furbearer licenses sold (my index of harvest effort) to explain bobcat harvest, and its non-correlation with mean pelt price, is surprising because it is assumed that pelt price drives effort, which in turn drives harvest (Fortin & Cantin 2004). However, as bobcats are relatively difficult to trap relative to other furbearers, and license-holders are allowed only 5 bobcats, it is possible bobcat harvest will only be influenced by fur markets if prices change dramatically and that sales of licenses that are not specific to bobcats may be primarily influenced by pelt prices for species for which there are no quotas. Alternatively, it is possible that license sales do accurately reflect effort, but fails to exhibit a relationship with harvest because bobcat abundance in Minnesota has not changed to the degree that it would result in appreciable changes in

effort. Future research should attempt to assess whether harvest adjusted by effort is an accurate index of bobcat abundance.

#### *1.4.2 Management implications*

In my study, season length and bobcat abundance as indexed by scent station indices were the best predictors of bobcat harvest, but cold weather mitigated this relationship. Importantly my results differ from those of other studies examining the influence of pelt price on harvest, suggesting that jurisdictional regulatory, environmental and ecological differences may alter which variables influence harvest. Where bobcat harvest regulations are more liberal and bobcat pelts more valuable (e.g. in the intermountain west), pelt prices may exert a greater influence on harvest. Cold temperatures reduced bobcat harvest, most likely due to the effect of cold on bobcat behavior, but are unlikely to affect bobcat harvest in warmer climates. Consequently, knowledge of local factors affecting harvest may be required.

## CHAPTER TWO

### **Constraints on the distribution of bobcat harvest in northeastern Minnesota: Implications for Canada lynx conservation**

#### **2.1. Introduction**

Climate change has facilitated the poleward and upward range expansion of numerous species (Forsman & Mönkkönen 2003; Parmesan & Yohe 2003; Hitch & Leberg 2007). For species whose trailing range edge is defined by climate, poleward and upward range contraction has been documented and is expected to continue (Pounds et al. 2005; Anderson et al. 2009; Copeland et al. 2010). However, for species whose trailing edge is not defined by climate, the consequences of a changing climate are less clear. Biogeographical theory (MacArthur 1972) suggests that, in the absence of physical barriers, the trailing edge of many species distributions are constrained by biotic factors such as competition, predation, or disease. Consequently, the primary impact of climate change on these species may be the geographic or temporal range expansion of competitors, predators, and parasites released from climatic constraints (Hersteinsson & MacDonald 1992; Buskirk et al. 2000; Pounds et al. 2006), rather than physiological stress caused by changes in temperature and precipitation regimes.

With the possible exception of remotely-sensed data, information gathered from harvested game animals likely represents the most abundant and wide-scale ecological data available and is commonly used as an index for monitoring populations (Caughley 1977). The bobcat (*Lynx rufus*) is the most widely distributed and abundant felid in North America (Sunquist & Sunquist 2002) and a popular game animal whose status is largely

tracked using harvest data (Roberts & Crimmins 2010). Despite an estimated 3-fold increase in abundance over the last 15 years and a similar increase in harvest (Kapfer & Potts 2012), the geographical distribution of bobcat harvest in Minnesota has remained relatively static (Erb 2009). Notably, harvest of bobcats remains rare in the west, a region of intensive row-crop agriculture, to the south, a region of increasing suburbanization, and to the northeast (Fig. 2.1; hereafter the Arrowhead). Of particular interest is the lack of harvest in the Arrowhead, partially because, unlike the other two regions, human influence remains minimal, and harvest of other furbearers is common, suggesting that the lack of bobcat harvest in the region may be indicative of a non-human ecological limitation to bobcat range.

Bobcat biology in combination with the winter climate of the Arrowhead provide a compelling hypothesis for the bobcats' rarity. The Arrowhead experiences colder temperatures, greater snowfall and greater snow depth than the rest of Minnesota (Minnesota Climatology Working Group 2010). Relative to similarly-sized mammals of northeastern Minnesota, bobcats exhibit high lower critical temperatures during winter (Mautz & Pekins 1989). Consequently, when ambient temperatures fall below  $-2^{\circ}\text{C}$ , bobcats must increase their metabolism and ultimately their food consumption, representing an increase in energy expenditure of approximately 4% per degree below their lower critical temperature (Mautz & Pekins 1989). In comparison the winter lower critical temperatures of red fox (*Vulpes vulpes*), porcupine (*Erethizon dorsatum*), fisher (*Martes pennanti*) and coyotes (*Canis latrans*) are  $-13$ ,  $-12$ ,  $-20$  and  $-10^{\circ}\text{C}$ , respectively (Irving et al. 1955; Shield 1972; Powell 1979). Consequently, bobcats suffer reduced

stores of body fat following periods of deep snow and cold temperatures (Litvaitis et al. 1986b), and frequently succumb to starvation during winter (Knick 1990). In addition, bobcats have a higher mass:footpad (footload) than do snowshoe hare (*Lepus americanus*), one of their primary prey (Rollings 1945; Berg 1979), or sympatric carnivores (e.g. Canada Lynx (*Lynx canadensis*), fisher, marten, Buskirk et al. 2000). Bobcats have adapted behaviorally by avoiding areas of deep snow (McCord 1974), even when those areas have abundant prey (Petrauborg & Gunvalson 1962), and by restricting their movements to the relatively snow-free southern facing slopes and lower elevations in winter (Koehler & Hornocker 1989).

If bobcat distribution is constrained by winter climate, climate change may yield consequences for the federally threatened Canada lynx. The Arrowhead encompasses one of five regions designated as critical habitat for the federally-threatened Canada lynx, and anecdotal accounts suggest that Canada lynx are competitively excluded (Parker et al. 1983; Hoving et al. 2003; but see Hoving et al. 2005) or may experience gene-swamping (Homyack et al. 2008) where they occur sympatrically with bobcats. If bobcat harvest in the Arrowhead is indicative of bobcat distribution, determining the factors limiting the northern boundary of bobcat harvest is of great importance for predicting the potential effect of environmental change on the future of Canada lynx in Minnesota.

My goal was to identify factors important to predicting the spatial distribution of bobcat harvest in the Arrowhead. Specifically, I sought to determine which factors—hunter access and effort, interspecific competition, prey abundance, climate, or some

combination thereof—were most important to predicting the distribution of bobcat harvest in the Arrowhead.

## **2.2. Methods**

### *2.2.1. Study Area*

Multiple definitions of the area included in the Arrowhead exist but for the purposes of this study I defined the Arrowhead region as the region encompassed by Cook, Lake and St. Louis counties in northeastern Minnesota. These three counties fall primarily within the Northern Superior Uplands ecological section and hence exhibit similar ecological characteristics (Cleland et al. 1997). Combined, these counties cover ~ 27,500 km<sup>2</sup>. Locations of harvested bobcats during the last decade suggest that bobcat distribution encompasses ~ 36% of this region, or 9,900 km<sup>2</sup>, with most harvest occurring in the southwestern portions of St. Louis County (Fig. 2.1). Vegetation within the Arrowhead consists primarily of conifer (*Picea* spp.) and deciduous forests (*Betula papyrifera*, *Populus* spp.), and conifer bogs and swamps (*Thuja occidentalis*; Friedman and Reich, 2005). Topography generally consists of rolling hills with a few rocky outcrops which increase in frequency and area to the northeast, and both the highest (701 m) and lowest (183 m) elevations in Minnesota occur in the Arrowhead. Mean temperatures in this region range from 14 to 17 °C from June to August and -14 to -11 °C from December to February (Minnesota Climatology Working Group, 2010). Precipitation ranges from 68 to 78 cm, with ~ 180 cm of snow per year. Snow cover generally lasts from 140 to 160 days (Kuehnast et al. 1982). In addition to bobcats and Canada lynx, this region also supports moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), American

black bears (*Ursus americanus*), American martens (*Martes americana*), fishers, gray wolves (*Canis lupus*), and coyotes.

### *2.2.2. Variable selection and data collection*

I used townships where bobcats were harvested during the 2001 to 2010 hunting seasons as my sample of bobcat presences. All bobcats harvested in Minnesota must be turned over to the Minnesota Department of Natural Resources (MN DNR), with the majority being turned over during scheduled furbearer registration dates. Bobcats were subsequently sent to a MN DNR laboratory where their sex was determined by external and internal examination of reproductive tracts.

I created a data layer containing townships where bobcats were harvested within a geographic information system (ArcGIS v. 9.2, ESRI, Redlands CA, USA). I selected townships without a harvest record during the last decade that were contiguous with townships with a recorded harvest as a sample of bobcat absences, excluding townships that would not have been subject to presence sampling (i.e. municipalities and state parks where hunting was not allowed). For each township I used the ArcGIS extension Hawth's Tools (Beyer 2004) to calculate explanatory variable values (Table 2.1). Because townships varied in size, I calculated the proportion rather than absolute area within each township consisting of each spatial explanatory variable. In cases where townships overlapped multiple polygons of an explanatory variable coverage I calculated the explanatory variable as the area-weighted mean value and calculated density ( $m / km^2$ ) for linear features (e.g. minor roads, snowmobile trails).

I used literature on bobcat ecology and harvest distribution to identify explanatory variables relevant to predicting bobcat distribution owing to their effect on bobcat vital rates and hunter access and effort (Table 2.2). Prey abundance has been linked to mortality, emigration, and fecundity rates in bobcats (Bailey 1974; Knick 1990). Snowshoe hare (*Lepus americanus*) and white-tailed deer are the primary prey of bobcats in this region (Rollings 1945; Berg 1979) and I included deer density as modeled by the MN DNR (Lenarz 2010) and regenerating forest because in Minnesota snowshoe hare are most abundant in this covertype (McCann & Moen 2011). I used regenerating forest from the 2008 refresh of LANDFIRE spatial layers (LF 1.1.0), a 30 m raster dataset produced by the United States Geological Survey and Department of Agriculture primarily used to map fire hazard. Coyotes (*Canis latrans*) kill bobcats (Gipson & Kamler 2002) and competition with coyotes (Nunley 1978; Henke & Bryant 1999) and fisher (Gilbert & Keith 2001) may suppress bobcat abundance and fecundity. I included coyote and fisher densities as indices of competition intensity. I used inverse-distance weighting of the proportion of scent stations visited along transects during annual scent station surveys conducted by the MN DNR to interpolate coyote density using the spatial analyst extension in ArcGIS. I estimated fisher density by using fisher harvest per township (MN DNR unpublished data), recognizing that fisher harvest may also indicate hunter effort and the accessibility of townships given some overlap in the methods typically used to trap bobcats and fishers. To estimate hunter access, I used road and snowmobile layers available on the MN DNR GIS website (<http://deli.dnr.state.mn.us/>, accessed 1 Feb 2011). I selected a subset of road classes from the roads layer based on a subjective

expectation of traffic volume and reclassified these roads as minor roads; road classes classified as minor roads included state forest, reservation, and organized and unorganized township roads.

Because no continuous coverages of snow depth (as an index of sinking depth) or maximum daily temperature relevant to bobcat biology were available I created coverages using data from individual weather stations scattered throughout bobcat range and the Arrowhead (Minnesota Climatology Working Group, 2010). I identified weather stations with  $\geq 3$  complete years of data from 2001 to 2010 and calculated the proportion of days when snow depth  $\geq 15$  cm (hereafter snow depth) and maximum temperature  $< -2^{\circ}\text{C}$  (the bobcat's lower critical temperature; Mautz & Pekins, 1999; hereafter temperature) for each station from 1 Oct to 30 Apr.

### *2.2.3. Statistical analyses*

I developed a linear model of snow depth and temperature relative to the latitude, longitude and elevation of each weather station. Because I was interested in maximizing model fit rather than parsimony I took a fully exploratory approach and examined all possible interactions and additive model forms but did not include quadratic terms because visual inspection of scatterplots failed to indicate any non-linear relationships. I chose the top model for each response based on its coefficient of determination and used model coefficients to estimate snow depth and temperature for each section in MN. I examined model residuals for autocorrelation and normality.

I developed binomial generalized linear models comparing townships where male or female bobcats were harvested to contiguous townships where they were not. Prior to

analysis I standardized all variables so they would have a mean of zero and a standard deviation of one. I prescreened explanatory variables for collinearity using Pearson product-moment correlation coefficients ( $r$ ) and in cases when  $|r| > 0.70$  did not use correlated variables in the same model. I took a two-step approach for model selection. First I combined non-correlated variables into candidate models to determine whether hunter access, interspecific competition, climate, or prey abundance best explained bobcat harvest and ranked these models using Akaike's Information Criterion adjusted for small sample size ( $AIC_C$ ; Burnham & Anderson 2002). Secondly, I added all non-correlated variables into a single model and sequentially deleted the least informative variable (sensu Arnold 2010) as judged by minimal absolute value of  $\beta/SE$ , and continued this process until further variable removal resulted in an increase in  $AIC_C$  (e.g. Pagano & Arnold 2009). I used Somers' Dxy to measure the predictive ability of the resulting models. Somers' Dxy estimates the rank correlation between model predictions and observed responses and is related to the area under the receiver operating curve commonly used to assess the predictive ability of distribution models. Somers' Dxy ranges in values from 0 to 1, with Dxy = 0 indicating that model predictions are no better than random, and Dxy = 1 indicating that model predictions are perfect. I adopted the approach of Giudice et al. (2012) and used bootstrapping to calculate a bias-corrected version of Dxy. I visually assessed correlograms of Pearson residuals to determine if spatial autocorrelation was present (Zuur et al. 2009). All statistical analyses were conducted using program R v2.11.1 ([www.r-project.org](http://www.r-project.org), accessed 1 Sep 2010).

### **2.3. Results**

As assessed by their coefficient of determination, the best model explaining the proportion of days when the maximum temperature  $< -2^{\circ}\text{C}$  contained additive terms for latitude, longitude, and an interaction between longitude and elevation ( $R^2 = 0.64$ ,  $P = < 0.001$ ,  $n = 43$ ). The best model explaining the proportion of days when snow depth  $> 15$  cm also contained additive terms for latitude, longitude and elevation but also included an interaction term between latitude and elevation ( $R^2 = 0.7903$ ,  $P = < 0.001$ ,  $n = 38$ ). Model residuals fit assumptions of normality and did not exhibit autocorrelation.

From 2001 to 2010 female and male bobcats were harvested in 89 and 75 townships in the Arrowhead and I compared these to 113 and 106 contiguous townships, respectively, wherein no females or males were harvested. As indicated by  $AIC_C$  and model weights, the category of variables that best explained where females were harvested was prey abundance (Table 2.3). Subsequent combination of all variables into a single model and elimination of uninformative parameters decreased the lowest category-based model by  $> 5 AIC_C$  units (Table 2.3), with the resulting model for females containing terms for deer, coyote and snowshoe hares (Table 2.4). The model that best explained the distribution of male harvest was also prey abundance, but subsequent elimination of uninformative variables from the full model decreased  $AIC_C$  by  $> 5$  and contained terms for deer and coyotes (Table 4). Predictive ability of the female model ( $D_{xy} = 0.46$ ) was slightly lower than the male model ( $D_{xy} = 0.50$ ). Examination of correlograms revealed non-significant autocorrelation among Pearson residuals.

## **2.4. Discussion**

### *2.4.1. Bobcat harvest distribution*

Although I used townships where bobcats were harvested as an index of bobcat distribution, hunter access, as measured by the density of snowmobile trails and minor roads, was not predictive of the distribution of bobcat harvest, suggesting that accessibility does not explain the distribution of bobcat harvest in the Arrowhead. Previous studies have shown that temporal trends in bobcat harvest in Minnesota are primarily driven by bobcat abundance (Kapfer & Potts 2012), and annual snow track and scent stations surveys support the conclusion that bobcats are as rare in the Arrowhead as harvest indicates (MN DNR, unpublished data). Conversely, the variables that were predictive of bobcat harvest distribution were related to bobcat ecology rather than hunter access. In combination, these three factors provide compelling evidence that the distribution of bobcat harvest in Minnesota is indicative of bobcat distribution rather than hunter access and effort.

My results add to the growing evidence that coyotes suppress bobcat populations (Nunley 1978; Henke & Bryant 1999) but challenge the suggestion that fishers may (Gilbert & Keith 2001). Bobcats and coyotes are sympatric throughout bobcat range at coarse scales, but at finer scales coyotes exclude bobcats (Thorton et al. 2004), and control of coyotes has consistently resulted in increases in bobcat populations (Nunley 1978; Henke & Bryant 1999). The suppression of bobcat populations by fisher predation on bobcat kittens was hypothesized by Gilbert and Keith (2001). However, my results suggest that fisher harvest density does not affect the distribution of bobcat harvest. Because I used fisher harvest as an index of fisher density and harvest locations of bobcats as an index of bobcat distribution, a positive relationship between the two may

have suggested that fisher harvest is reflecting hunting effort or accessibility or, alternatively, that bobcats and fishers have similar ecological requirements not accounted for in the other explanatory variables because fisher and bobcat niches overlap extensively (Gilbert & Keith 2001). The lack of either relationship suggests that fishers do not suppress bobcat populations or capture hunter effort and access as it pertains to the harvest of bobcats.

My results concur with analyses of the diet of bobcats at northern latitudes that have indicated a heavy reliance on white-tailed deer (Rollings 1945; Berg 1979) and the propensity for female bobcats to consume more snowshoe hare and less white-tailed deer than males (Litvaitis et al. 1986*a*; Gilbert and Keith 2001; but see McLean et al. 2005). Because white-tailed deer provide greater energy (kcal/g) and digestible dry matter than do snowshoe hare (Powers et al. 1989), can provide bobcats with food for multiple days (McCord 1974), and are more vulnerable to predation during winter (Nelson & Mech, 1986), their importance during energetically-expensive winters (Mautz & Pekins 1989) is unsurprising. Interestingly, the expansion of bobcats into northern Minnesota (Rollings 1945) coincided with increased densities of white-tailed deer populations in the northern forests of Minnesota (Erickson et al. 1961) following the extensive conversion of mature mixed conifer-broadleaf forests to earlier successional stages thereby improving deer forage (Alverson et al. 1988; Schulte et al. 2007), providing further evidence of the bobcat's reliance on deer at northern latitudes. I speculate that bobcat colonization of northern Minnesota was the result of increased deer densities resulting from the land-clearing and succession of northern forests.

#### *2.4.2. Conservation implications for the Canada lynx*

Contrary to my predictions, bobcat distribution in northeastern Minnesota does not appear to be directly limited by snow depth or winter temperature. Nonetheless, bobcat colonization of the Arrowhead may still be facilitated by climate change, presenting serious implications for the persistence of Canada lynx in the region. The population growth rates of white-tailed deer in northern Minnesota have been linked to winter severity (Mech et al. 1987; Post & Stenseth 1998). Climate change predictions for this region suggest that winter temperatures and precipitation will increase (Galatowitsch et al. 2009). If the temperature increases sufficiently, precipitation may fall as rain rather than snow and snow melt may increase, suggesting that while precipitation may increase, snow fall and hence snow depth may not. This prediction is supported by snow fall predictions in Wisconsin, wherein winter precipitation is expected to increase while snow fall, depth and the length of the snow season decrease (Notaro et al. 2011). If snow depth and duration decrease in the Arrowhead, it will reduce deer mortality in the region, and potentially bring about increased densities (Thompson et al. 1998), as has been hypothesized to have occurred in Alberta (Latham et al. 2011). If deer density increases in the Arrowhead, my results suggest one of the barriers to bobcats in this region (i.e. low deer densities) will be removed, and subsequent expansion further into the Arrowhead may occur. Whether this expansion will affect the resident population of Canada lynx is debatable (Parker et al. 1983; Buskirk et al. 2000; Hoving et al. 2003; Hoving et al. 2005; Murray et al. 2008). Current management plans for this region call for maintaining deer at low densities owing to their putative effect on declining moose populations (MN DNR,

2011) which may simultaneously benefit Canada lynx. Ironically, the coyote, another putative competitor of the Canada lynx (Buskirk et al. 2000), may limit bobcat colonization of the Arrowhead, and provide respite for lynx in Minnesota.

## CHAPTER THREE

### Winter home range and core area size and overlap of sibling adult female bobcats in east-central Minnesota

#### 3.1. Introduction

Bobcats (*Lynx rufus*) are solitary, territorial carnivores that range from southern Canada to the mid-latitudes of Mexico. Home range and core area size and overlap have been the focus of multiple studies of bobcat spatial ecology. Results have generally suggested that although male space use overlaps considerably, female space use tends to be more exclusive (Bailey 1974; Knick 1990; Lovallo & Anderson 1996; Diefenbach et al. 2006), especially at the scale of the core area (Chamberlain & Leopold 2001; Nielsen & Woolf 2001). However, the extent of overlap varies substantially among studies, as do the methods for estimating it (Table 3.1; Thornton et al. 2004; Diefenbach et al. 2006). The reasons for this variation in overlap are unknown, but the degree of space use overlap among bobcats has been hypothesized to be affected by multiple, interacting factors including sampling intensity (e.g. location frequencies or whether all bobcats within a study area are monitored), relatedness (mother-offspring or siblings; Chamberlain & Leopold 2001; Thornton et al. 2004), and conspecific (Benson et al. 2006; Cochrane et al. 2006; Diefenbach et al. 2006) or prey density across time and space (Bailey 1974; Knick 1990).

Evidence supporting the relatedness hypothesis comes from bobcat social organization, in which female offspring exhibit philopatry (Janečka et al. 2007; Croteau et al. 2010), whereby female offspring establish home ranges within or contiguous with

their maternal home range, and from the differences among home range and core area overlap among individuals within populations inhabiting similar ecological conditions (bobcat and prey densities) and subject to similar monitoring effort (Chamberlain & Leopold 2001). Genetic analyses make it possible to ascertain familial relationships, and the only study to date employing telemetry and genetic data suggests little relationship between pairwise relatedness and overlap among parent-offspring dyads (Janečka et al. 2006), but as of yet, no published studies have documented home range overlap among adult siblings. Herein I provide the first published data on home range and core area overlap among full sibling adult female bobcats and compare estimates of home range and core area size to previously published results.

### **3.2. Methods**

#### *3.2.1. Study Area*

This study took place in Saint Croix State Park, located in east-central Minnesota (Fig. 3.1) Uplands in the study area were dominated by stands of deciduous forest containing aspen (*Populus tremuloides*), northern red oak (*Quercus rubra*) and jack pine (*Pinus banksiana*). Lowland areas were dominated by gray alder (*Alnus incana*), ash (*Fraxinus spp.*) and tamarack (*Larix laricina*). Climate in the study area is continental with cold, dry winters and hot, humid summers; temperature means range from -13 C in January to 21 C in July and mean precipitation is 76 cm (Minnesota Climatology Working Group 2010). Topography in the area is characterized by gently rolling hills with elevation ranging from 100 to 350 meters asl.

#### *3.2.2. Field Methods*

I trapped bobcats using cage traps baited with beaver meat and commercially-available lures. I used a jabstick to administer an intramuscular injection of tiletamine-zolazepam at 10 mg / kg estimated weight (Kreeger & Arnemo 2007). I classified bobcats as adults based on weight (Crowe 1975) and tooth wear, and fit the bobcats with a 350g GPS collar (Advanced Telemetry Systems) programmed to acquire a location every four hours. I took an ear punch for subsequent DNA analysis. I monitored bobcats until they had recovered from anesthesia. All trapping and immobilization procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (0803A28826).

### *3.2.3. Data Analysis*

I prescreened collar locations to improve (decrease) location error by removing those acquired with < 4 satellites or with horizontal dilution of precision values > 5 (Dussault et al. 2001). I modeled adaptive and fixed kernel utilization distributions (UDs; Worton 1989) and assessed how well they fit location data using likelihood cross-validation criterion (CVC; Horne & Garton 2006) in program Animal Space Use (Version 1.3). To prevent over- and under-smoothing I used the *ad hoc* method for choosing the smoothing parameter for 95% UD (sensu Berger & Gese 2007). This method involves choosing the smallest reference bandwidth that produces a contiguous 95% UD. Whereas the typical method for delineating core areas entails estimating 50% isopleths or MCPs, I estimated core areas as the “area within which an animal spends a maximum amount of time” (VanderWal & Rodgers 2012) because, as pointed out by VanderWal and Rodgers (2012) this definition of a core area is both repeatable and biologically relevant. This method

defines the core area by taking the first derivative of a non-linear least squares curve of an animal's UD against isopleth volume to determine when the slope equals one, at which point the proportional area of a UD increases at a greater rate than isopleth volume. Analysis of the inflection points was conducted in the base package of R (Version 2.11.1, R Development Core Team). I also used the Home Range Tools extension (Rodgers & Kie 2007) in ArcGIS (Version 9.2, ESRI) to estimate area-added (White & Garrott 1990) 95% minimum convex polygons (MCP) and 50% UDs for comparison to previous studies and to qualitatively compare differences in overlap arising from different definitions of core areas. I assessed the effect of the number of locations on MCP home range size by constructing area-accumulation curves using the software BIOTAS (Version 2.0, Ecological Software Solutions).

I estimated home range and core area overlap as the percentage of each bobcat's 95%, 50% and core area UD isopleths that were encompassed by the corresponding isopleth of the other bobcat because use of this method is intuitive and directional (i.e. estimated overlap differs for each individual). Because this measure does not account for overlap in isopleth volumes it will produce biased estimates of the overlap in space use (Fieberg & Kochanny 2005). Consequently, I also calculated the UD overlap index (UDOI) which is a function of the product of isopleth volumes for both animals and indicates the extent to which shared areas are used. The UDOI equals zero if UDs do not overlap and  $> 1$  if overlap in space use is greater than expected given uniform space use. I estimated movement rates by dividing the distance moved by the number of hours between successive locations.

#### 3.2.4. Genetic analysis

Nineteen microsatellite markers were amplified using standard techniques with estimated population allele frequencies taken from concurrent research being conducted on the landscape genetics of bobcats in the Midwest (Reding 2011). Maximum-likelihood estimation of relatedness was accomplished using the program ML-RELATE (Kalinowski et al. 2006).

### 3.3. Results

Two adult female bobcats were trapped and fitted with radio-collars during the winter of 2008. Bobcat F1 weighed 10 kg and F2 weighed 9.5 kg. Both bobcats shed their collars prior to the date they were programmed to fall off. F1 retained her collar for 150 days (Oct. 2008-Mar. 2009) and F2 retained her collar for 66 days (Feb.-Apr. 2009) resulting in 188 and 70 locations suitable for use, respectively.

Based on 999 simulations, the relationship best fit by analysis of the 19 microsatellites indicated the bobcats were full-siblings, i.e. offspring of the same parents ( $P < 0.05$ ).

Examination of area-accumulation curves indicated that ~40-60 locations were sufficient to estimate MCP home ranges; however, home ranges continued to increase with more locations but with a decreasing slope. Cross-validation criterion indicated that adaptive UD outperformed fixed UD estimators for both bobcats ( $\Delta\text{CVC} > 7$ ). The isopleths at which proportional area increased faster than volume occurred at 58 and 66% for bobcats F1 and F2, respectively. Bobcat F1's 95%, core area, and 50% UD encompassed 26.84, 6.19, and 2.63 km<sup>2</sup>, respectively, and F2's encompassed 29.01, 6.50

and 4.68 km<sup>2</sup>, respectively. Percentage overlap of core areas was greater than 50% UDs (Table 3.2).

Mean hourly movement rates were similar and highly variable for both bobcats; F1's mean movement rate was 108.09 m hr<sup>-1</sup> (SE = 122.58) and F2's was 92.97 (SE = 93.76).

### **3.4. Discussion**

Estimated MCP home ranges from this study were comparable to those of other studies conducted in this region (Table 3.3) suggesting both a consistency in home range sizes among bobcats in Minnesota and Wisconsin across several decades and a reliability of home range estimates, at least at the 95% MCP level. Although home range estimates from this study are slightly smaller, this disparity is likely due to methodological differences, e.g. the inclusion of all points in the home range estimate (Lovallo & Anderson 1996; Gilbert & Keith 2001) or the inclusion of transient individuals (Fuller et al. 1985). Subsequent calculation of 100% MCPs for this study resulted in a mean home range estimate of  $25.16 \pm 2.28$  km<sup>2</sup>, which is not significantly different than the estimates from Wisconsin and fall within the range reported by Fuller et al. (1985; no SE presented). Because both bobcats shed their collars after only a few months, and area-accumulation curves never reached an asymptote, it is possible that estimated MCP home range sizes would have been larger had bobcats retained their collars longer. However, female bobcat home ranges are larger in winter (Lovallo & Anderson 1996) and the number of locations achieved during this study was as large as or larger than those obtained during the previous two studies. Consequently, despite only having data

covering 3-6 months, estimated home range and core areas are likely accurate.

Additionally, although all locations were taken during winter months, it is likely these estimates accurately reflect annual home ranges because bobcat summer home ranges tend to be smaller and fall within the limits of winter home ranges (Lovallo & Anderson 1996).

Movement rates of the two female bobcats in this study were high relative to those observed in southern populations (Chamberlain et al. 2003), but similar to those of bobcats at similar latitudes (Bailey 1974; Knick 1990), likely reflecting the greater movements required to patrol larger home ranges and acquire more dispersed prey (Anderson & Lovallo 2003). In Idaho, female bobcats used small patches intensively for several days prior to moving rapidly to another patch, presumably because local resources (i.e. prey) had fallen to a level at which movement to a new patch with more resources provided a positive energy balance (Bailey 1974). The pattern of multiple locations occurring in a single habitat patch followed by sudden movement to a different one was apparent in my data (Fig. 3.1) and consistent with the high variability in movement rates.

Overlap in space use is an important component of animal social organization which can influence demography (Wielgus et al. 2001; Diefenbach et al. 2006; Cooley et al. 2009) and be used to infer behavior in cryptic species. Moreover, in combination with information on home range size and distribution, overlap in space use provides a basis for estimating density, and ultimately abundance (Barlow et al. 2011). Although estimated core area and home range overlap from this study are comparable to those reported

elsewhere (Table 3.1), my results also indicate that the use of the common method of defining an animal's core area as that enclosed within the 50% UD may underestimate overlap in space use, particularly in the case when percent area of UD's are used as the overlap index. This suggests that, at least for related individuals, bobcats may be less territorial, and thereby less solitary, than previously suggested (Bailey 1974) and that the delineation of a core area using biologically-based methods (VanderWal & Rodgers 2012) rather than arbitrary isopleth volumes may better capture spatial relationships among individuals. The low UDOI values for all UDs suggest that the sibling bobcats in this study were using the overlapping areas of their home ranges and core areas less than uniformly (Fieberg & Kochanny, 2005). Future research should examine whether overlap of space use varies among half-siblings, siblings and parent-offspring, as would be predicted by kin selection theory.

Although limited by small sample size, my results provide the first estimates for home range and core area overlap among adult sibling bobcats, and are a useful starting point for furthering our understanding of the role of relatedness in structuring bobcat societies. Genetic techniques make it possible to discern relatedness among individuals and future research should aim to integrate this information with other putative factors affecting space use overlap to discern how each affects patterns in overlap of space use.

## CHAPTER FOUR

### **Integrating Demography and Distribution Modeling: Bobcat Breeding Habitat in Minnesota**

#### **4.1. Introduction**

Mammalian reproduction is an energetically expensive endeavor (Oftedal & Gittleman 1989; Thompson 1992), requiring greater resources than survival alone. For polygynous species with altricial offspring, this cost is amplified by lactational and rearing demands (Ackerman et al. 1986; Laundre 2005). Therefore, the range of environmental features that support reproduction will oftentimes be a subset of those supporting survival (Fernandez et al. 2003).

Distribution models have seen much utility in recent years having been used for conservation prioritization and reserve selection (Rodríguez-Soto et al. 2011), predicting the dynamics of invasions (Loo et al. 2007), recolonizations (Mladenoff et al. 1995), and the suitability of sites for reintroductions (Thatcher et al. 2006), niche evolution (Warren et al. 2008), and the response of species to climate change (Araújo et al. 2005).

Distribution model methodology has much in common with that of habitat selection (Baasch et al. 2010; Hoffman et al. 2010) but is particularly useful when data are limited to single locations per individual, the sampling unit is a territory (Mladenoff et al. 1995; Fernandez et al. 2003), or other methods are unfeasible (e.g. detection rates too low).

The putative impetus for the development of presence-only distribution models, which are developed by identifying the environmental variables associated with a species presence in combination with randomly-selected background data (akin to the selection

of available habitat in models of habitat selection) and uses these relationships to predict the suitability of the environment in areas where the species' status is unknown, was the desire to take advantage of the extensive presence-only datasets available in herbariums and museum collections (Elith et al. 2006). Specimens from these institutions rarely include absence data but are nonetheless invaluable because they frequently represent a large proportion of the total number of locations known for rare species (Marino et al. 2011). For many questions fundamental to species conservation, such as the environmental features that support reproduction, there is a similar lack of "absence" data because of the difficulty associated with documenting non-occurrences. Consequently, whereas presence-absence data will always be preferable for making inferences (Elith et al. 2011), presence-only methods provide a means for making informed decisions when data are deficient yet urgency is high. However, owing to their use of background rather than absence data, the interpretation of presence-only distribution modeling differs fundamentally from presence/absence and occupancy models in that it can only predict the probability that a suite of environmental variables are suitable rather than the probability that a species is present (Phillips et al. 2006).

Because of their crypticism, naturally low densities and a general paucity of even basic knowledge of their ecology, members of the Felidae make natural candidates for the use of distribution modeling. However, although there has been considerable effort directed at the development of predictive distribution models for felids (Monterroso et al. 2009; Wilting et al. 2010; Marino et al. 2011; Rodríguez-Soto et al. 2011), there has only been a single attempt to predict their breeding distribution. Fernandez et al. (2003) used

logistic regression to map the breeding habitat of the critically-endangered Iberian lynx (*Lynx pardinus*) in Doñana National Park, Spain. The model of Fernandez et al. (2003) was successful at discriminating breeding and non-breeding habitat because it was calibrated on an intensively monitored population over a small area. However, most felids are less intensively monitored and have distributions that encompass much larger areas, necessitating a more accessible method for predicting breeding distribution.

Currently, the spatial distribution and dynamics of bobcat harvest are the primary means used to monitor bobcats (Roberts & Crimmins 2011), under the assumption that a numeric or geographic expansion of harvest is correlated with increasing population size. However, occurrence does not necessarily equal suitability, just as population density does not always indicate habitat quality (Van Horne 1983; Mosser et al. 2009). As furbearers, bobcats are harvested for the monetary value of their pelts, which may result in a decoupling of the relationship between abundance and harvest (Tumlison & McDaniel 1986; but see Kapfer & Potts 2012). Bobcat movement rates, which affect their vulnerability to harvest (Chamberlain et al. 1999) and probably their observability, fluctuate with prey abundance (Knick 1990). Furthermore, bobcats, primarily juvenile males, frequently disperse > 100 km (Knick & Bailey 1986; Nielsen & Woolf 2003) from their natal home range. During dispersal juveniles frequently traverse unsuitable habitat (e.g. roads, developed areas; Nielsen & Woolf 2003) as they seek a suitable area to establish a permanent home range. Consequently, simply recording locations where bobcats are observed or harvested without regard to reproductive status will likely include large areas that are unable to support bobcat reproduction. This inflated estimate

of range can result in overly optimistic estimates of their distribution and the environmental features predictive of suitable habitat.

Several distribution models have been developed to predict suitable bobcat habitat (Lovallo 1999; Woolf et al. 2002; Nielsen & Woolf 2002; Preuss & Gehring 2007).

Lovallo (1999) developed the first distribution model for bobcats and mapped suitable habitat within Pennsylvania. Similar models have since been developed for Illinois (Woolf et al. 2002; Nielsen & Woolf 2002) and Michigan (Preuss & Gehring 2007). Data used in the calibration of these models includes radiolocations and core areas of collared bobcats as well as locations where bobcats have been sighted, harvested or killed in automobile collisions. None of these previous efforts attempted to predict bobcat breeding habitat.

## **4.2. Methods**

### *4.2.1. Study Area*

The study area was delineated by 100% minimum convex polygon containing all sections where bobcat kittens were harvested (Fig. 4.1). The study area encompasses approximately 76,000 km<sup>2</sup>. The majority of the study area falls within the Laurentian mixed forest province (Cleland et al. 1997). This area consists primarily of conifer (*Picea* spp., *Pinus* spp., *Thuja occidentalis*) and deciduous (*Betula papyrifera*, *Populus* spp., *Fraxinus* spp.) forests, bogs and swamps (~71%) intermixed with agricultural fields (~6%), pasture (~7%), open water (~7%) and rural, suburban and urban development (~3%). Topography is characterized by gently rolling hills and elevation increases from west to east, ranging from 180 to 590 m asl. Climate is continental with cold dry winters

and hot humid summers. Normal mean temperatures range from -15 to -13 C during the winter (Dec. to Feb.) and 17 to 20 C during the summer (Jun. to Aug.). Normal mean precipitation ranges from 15 to 30 cm during the winter and 25 to 33 cm during the summer (Minnesota Climatology Working Group, 2012).

#### *4.2.2. Distribution Records*

Hunters and trappers that harvest bobcats in Minnesota are required to register their harvest with the MN Department of Natural Resources (MN DNR) within 48 hours of the close of the season. Data collected by the DNR includes sex, date, and the township of harvest. I asked MN DNR personnel responsible for registering harvested bobcats and hunting and trapping associations to voluntarily label bobcat carcasses turned in during the registration with tags indicating the section where they were harvested. Carcasses of harvested bobcats were subsequently sent to a MN DNR office where they were aged using cementum annuli counts and sexed via visual examination of external and if necessary, internal reproductive tracts. Kittens (< 1 year old) were discriminated from adults (> 1 year old) based on open root foramina of extracted canines (Crowe 1972).

Whereas biases in presence data associated with non-random sampling (e.g. sampling near roads) are theoretically cancelled out when compared to biased absence data (Phillips et al. 2009; Elith et al. 2011), models using biased presence and randomly selected background data will retain any bias associated with the presence data (Phillips et al. 2009). Because my data consisted of sections where bobcats were harvested, it is possible they reflect hunter access and effort rather than bobcat ecology. However, previous research has shown that in Minnesota the number of bobcats harvested is

primarily the result of bobcat abundance (Kapfer & Potts 2012) and the absence of bobcat harvest in the northeast portion of the state the result of inadequate prey rather than hunter access or effort (see Chapter 2). Consequently, I assumed that harvest locations were indicative of bobcat habitat use. Nonetheless, I inspected the relationship between environmental features and habitat suitability skeptically in light of this potential bias. However, whereas some relationships may be obvious in this regard, others may be equivocal. For example, a linear, negative relationship between the density of rural roads and habitat suitability is likely the result of avoidance of roads of this type. However, a positive or quadratic relationship between rural road density and habitat suitability that initially increases then decreases would be harder to interpret. In these cases, I explored alternative hypotheses for these relationships in the discussion. Furthermore, whereas most distribution models use data spread across time as well as space, my data were limited to the bobcat season, which generally occurs from late Nov. to early Jan. (Kapfer & Potts 2012). Bobcat habitat use varies seasonally (Fuller et al. 1985a; Lovallo & Anderson 1996), likely due to seasonal variation in resource availability (e.g. hibernating prey species are not available during the winter). Although my inferences are therefore limited to this time period, it is likely a limiting period for bobcat reproduction and survival because of lower prey abundance coupled with increased energetic requirements (Mautz & Pekins 1989), as indicated by the larger space requirements of bobcats (Lovallo & Anderson 1996; Tucker et al. 2008).

#### *4.2.3. Environmental Data*

I used published literature to identify environmental features potentially important for affecting bobcat reproduction and kitten survival, either through direct (e.g. insufficient food, coyote predation) or behavioral mechanisms (e.g. avoidance). I quantified environmental features hypothesized important for bobcat survival and reproduction at each presence and background location using the extension Hawth's Tools (Beyer 2004) in ArcGIS 9.2 (ESRI). I used road, snowmobile trail, stream and GAP landcover datasets from the MN DNR GIS website (<http://deli.dnr.state.mn.us/>). Because data on traffic volume are incomplete, I reclassified roads into highways and minor roads based on the metadata associated with the layer and a subjective expectation of traffic volume. I combined the GAP level 4 covertypes lowland deciduous shrub, lowland evergreen shrub, lowland black spruce and lowland white cedar into a single category (lowland). Because the GAP dataset is > 20 years old, I randomly selected 100 locations to compare its accuracy relative to the Forest Stand Inventory coverage of the MN DNR, a continuously updated dataset. Accuracy of the lowland coverage was high (96%) so I retained it as an explanatory variable. All other covertypes were either single categories or combinations of categories from the 2008 refresh of the LANDFIRE dataset (LF 1.1.0), a 30 m raster dataset produced by the United States Geological Survey and Department of Agriculture (<http://www.landfire.gov/>). I created layers of white-tailed deer (*Odocoileus virginianus*) and coyote (*Canis latrans*) density using estimated deer density as modeled by the MN DNR (Lenarz 2010), and inverse distance weighting of the proportion of scent stations with coyote visitations observed during annual scent station surveys (Erb 2008) using the Spatial Analyst extension. I developed a continuous

coverage of the proportion of days when snow depth  $\geq 15$  cm using data from weather stations throughout bobcat range (see Chapter 2 for more details). I calculated Riparian forest by intersecting all forest types in the LANDFIRE dataset with the MN DNR streams coverage. Sections where bobcats were harvested varied in size, so I calculated areas as proportions and linear dimensions as densities.

#### *4.2.4. Model Building*

I used maximum entropy (Maxent, Version 3.3.1; Phillips et al. 2004; Phillips et al. 2006) to model bobcat breeding habitat. Maxent is a machine learning approach that estimates the most uniform distribution that adheres to all that is known about a species distribution subject to the constraint that the expected value of each environmental feature matches its empirical average (Phillips et al. 2006). The defined probability distribution is thus the one exhibiting maximum entropy (i.e. closest to uniform) while remaining faithful to all available data. To estimate the probability distribution, Maxent uses environmental data from sites where a species is present in combination with environmental data from the rest of the study area (frequently referred to as the “background”). Because Maxent uses presences with background data, it produces estimates of the probability that the environmental characteristics of a location are suitable rather than modeling the probability of occurrence (Phillips et al. 2006). Consequently, estimate interpretation is the probability that a suite of environmental features at a geographic location are suitable yet may be uninhabited for various reasons (e.g. delayed colonization). I chose Maxent for several reasons. First, case studies have consistently indicated it outperforms other, including parametric methods for estimating distributions, particularly in cases when

presence data are limited and when a species does not occupy all available suitable habitat (Elith et al. 2006; Pearson et al. 2007; Hernandez et al. 2008). The former justification is based on our relatively small sample (n=122) and the latter on the basis that an estimated 20-30% of the bobcat population in Minnesota is harvested annually (Erb 2009), likely resulting in numerous suitable patches of habitat remaining vacant.

I randomly split the presence data into training data (80%), used for model development, and evaluation data (20%), used for evaluating the model's predictive performance (see Model Evaluation below). Because both the number (Phillips & Dudik 2008) and spatial extent (Anderson & Raza 2010) of background locations influence predictive accuracy of distribution models, I selected 10,000 random background circles with an area equal to that of the average section where kittens were harvested constrained to fall within the 100% minimum convex polygon of all bobcat harvested. Because hunting is not allowed in municipalities and state parks, I excluded these areas from my random background sample.

Empirical investigations and simulations have shown that overly complex or simple distribution models suffer reduced predictive abilities (Anderson & Gonzalez 2011; Warren & Seifert 2011). Maxent controls model complexity via regularization, wherein users can penalize the addition of parameters by controlling how closely expected values of probability distributions conform to empirical averages (Phillips et al. 2006). Although the default value for regularization was tuned on an extensive data set encompassing presence and absence data for 226 species, recent investigations have indicated that model performance can be improved by changing this value (Warren &

Seifert 2011). I used Akaike's Information Criterion adjusted for small sample size ( $AIC_C$ ) to adjust the regularization parameter, therefore balancing model complexity and fit (Warren & Seifert 2011). Initially, I varied the regularization parameter from 1 to 20; upon finding the integer value with the lowest  $AIC_C$  I varied the regularization parameter by tenths. I used the regularization parameter with the lowest  $AIC_C$  and ran 1000 bootstrapped replicates with a random seed, but left all other Maxent settings at their default values.

I prescreened explanatory variables for collinearity using Pearson product-moment correlation coefficients ( $r$ ) and in cases when  $|r| > 0.60$  chose one variable to retain based on a priori expectations of its importance.

#### *4.2.5. Model Evaluation*

I evaluated model performance using the area under the receiving operating characteristic curve (AUC) of the test data set. AUC typically uses presence and absence evaluation data to estimate a model's ability to successfully predict where a species is present and absent. When absence data is not available (as in this study) AUC assesses whether model predictions are better than random (Phillips et al. 2006). AUC scores range from 0 to 1, with 1 indicating that the model predicts presences perfectly and 0.5 indicating that the model predictions are equivalent to random guesses (Elith et al. 2006).

To estimate the total area considered suitable for bobcat reproduction in the study area, I selected the threshold with the lowest predicted value associated with the presence of a kitten, which identifies sections that are at least as suitable as where a kitten was harvested (Pearson et al. 2007). For a more conservative estimate of the total area

considered suitable for reproduction I classified all sections with a logistic probability of suitability  $\geq 0.9$  as high quality.

Because spatial autocorrelation in residuals can inflate estimates of predictive accuracy (Segurado et al. 2006; Veloz 2009), I examined autocorrelation of model residuals at all presence localities using a spline correlogram (Zuur et al. 2009).

### **4.3. Results**

During the 2008 to 2010 bobcat seasons I gathered section-specific locations for 122 kittens of which 98 were used for model development and 24 for model evaluation. Similar to previous studies (Anderson & Gonzalez 2011; Warren & Seifert 2011), the optimal regularization parameter was of intermediate value (6.4). Based on 1000 bootstrapped replicates, the test AUC indicated the model predicted the suitability of habitat for supporting reproduction well ( $\bar{x} = 0.874$ , SE = 0.047). Examination of model residuals indicated no spatial autocorrelation.

Estimates of variable importance for the four most influential environmental features indicated that riparian forest was the most important feature for predicting whether habitat was suitable for bobcat reproduction, followed by row-crop agriculture, prairie and coyote abundance (Fig. 4.2). All other environmental features contributed less than 5% to the model. Marginal response curves for the four most important variables indicated a positive relationship between habitat suitability and riparian forest, and negative relationships between habitat suitability and row-crop agriculture, prairie and coyote abundance (Fig. 4.3).

The minimum logistic prediction associated with the harvest of a kitten was 0.055 (SE = 0.016). Using this threshold the total area predicted suitable for bobcat reproduction in the 75,214 km<sup>2</sup> study area was 57,251 km<sup>2</sup>, representing approximately 76% of the total study area (Fig. 4.4). Sections containing high quality habitat included 34% of all sections where kittens were harvested (n = 42). The total area of high quality habitat in the study area encompassed 17,679 km<sup>2</sup>, or approximately 23% of the total study area.

#### **4.4. Discussion**

Presence-only distribution models are commonly used to estimate the potential distribution of species of conservation concern when data are sparse or impractical to acquire. With a few exceptions (Fernandez et al. 2003) practitioners have neglected to account for habitat quality in demographic terms. By making minor changes to data collection protocols already implemented by the MN DNR, I was able to develop a highly predictive distribution model of suitable breeding habitat of bobcats in Minnesota. Because many state agencies already gather data on the distribution of bobcat harvest (Roberts & Crimmins 2011), it would require little additional effort to gather the requisite information to develop similar models of breeding distribution. However, the methods outlined herein can also be adapted for endangered species that are not harvested extensively. In these cases, use of confiscated carcasses, roadkill and sightings of dependent-young could be used as presences instead of harvested individuals. If these methods do not provide adequate sample-sizes of dependent-young, internal examination of reproductively-aged females for placental scars or other indicators of past reproduction

could also be used. However, although I would have increased my sample size several times over by using locations where adult females bearing placental scars were harvested, I was remiss to do so because of the unknown relationship between the number of placental scars and litter size; i.e. it is unclear whether bobcats bearing placental scars have actually given birth or reabsorbed fetuses. Furthermore, use of kittens that are presumably born during the birth pulse in May or June (Crowe 1975) allows identification of the environmental features important to kitten survival, a period that is difficult to study using telemetry and typically associated with high mortality rates in felids (Mowat et al. 1996; Boutros et al. 2007), in addition to bobcat reproduction. However, I acknowledge that for some species of conservation concern, even these methods may result in too great of data loss.

In human-modified landscapes naturally-vegetated riparian corridors provide important movement corridors and habitat patches for carnivores (Virgós 2001; Hilty & Merenlender 2004; Triska et al. 2011). Although much of bobcat range in Minnesota occurs in areas with minimal human disturbance, the large home ranges of bobcats doubtlessly expose them to roads, agriculture and the openspace surrounding human developments, three of the factors that had a negative effect on the suitability of habitat for supporting bobcat reproduction. In addition to serving as corridor between patches of natural habitat, riparian forest likely also provides the travel routes of reduced snow depth (Mowat & Slough 2003), vegetative cover (Kolowski & Woolf 2002) and prey (Buehler & Keith 1982) that is particularly important during winter, when bobcat survival is lowest (Fuller et al. 1985*b*), and consequently, may be particularly important for supporting

reproduction. Snowshoe hare (*Lepus americanus*) are more abundant in spruce (*Picea spp.*)-fir (*Abies spp.*; Fuller et al. 1986) and regenerating conifer forests (McCann & Moen 2011) than riparian forests. However, the unimportance of these cover types relative to riparian forest suggests that, although previous studies have identified snowshoe hare as the primary prey of bobcats in Minnesota (Rollings 1945; Berg 1979), this is likely the result of the location where these studies were conducted. Both studies were located near the northeastern edge of bobcat range where it overlaps with the southwestern edge of snowshoe hare range. Eastern cottontails (*Sylvilagus floridanus*), important prey of other northern bobcat populations (Koehler & Hornocher 1989; McLean et al. 2005), occur throughout most of bobcat range in Minnesota, and are most abundant in willow (*Salix spp.*)-alder (*Alnus spp.*) thickets of riparian forest (Buehler & Keith 1982). Consequently, the snowshoe hare is probably replaced by the eastern cottontail as the bobcat's primary prey across an NE to SW gradient, and this is reflected by the high importance of riparian forest for bobcat reproduction and the relative unimportance of both regenerating and spruce-fir forests. Notably, the response curve to riparian forest plateaued at approximately 600 m km<sup>-1</sup>, suggesting that densities of riparian forest higher than this do not increase habitat suitability. Future research should aim to understand whether bobcat diet varies geographically in Minnesota.

As ambush predators, bobcats require thick vegetative cover (Biggins & Biggins 2006). Numerous studies have documented bobcat avoidance of open habitats, be they anthropogenic (row crops; Tucker et al. 2008) or natural (prairie; Lovallo & Anderson 1996), and selection for understory cover (Anderson 1990; Litvaitis et al. 1986; Kolowski

& Woolf 2002). Because row-crop agriculture and prairies provide neither understory cover nor prey during the winter, it is not surprising that they were negatively related to the distribution of bobcat breeding habitat. Similarly, although males are known to disperse the vast row-crop agriculture of the upper Midwest (Reding 2011) the absence of resident populations in the cornbelt (Anderson & Lovallo 2003) is likely explained by its inability to support reproduction. Although bobcat prey and cover can be abundant along row-crop edges during the fall when crops begin to mature, both decline following crop harvest and the onset of winter (Larson et al. 1978; Swihart & Yahner 1982). Although my results suggest that bobcat breeding is incompatible with row-crop agriculture, the current amount of row-crop agriculture in northern Minnesota does not appear to be hindering connectivity of breeding habitat (Reding 2011). However, row-crop agriculture does appear to hinder gene flow between bobcats of the northern Great Lakes and regions south of the corn belt (Reding 2011). If row-crop agriculture expands in this region due to climate change or the development of new crop varieties, managers will need to monitor the connectivity of breeding populations.

Competition among carnivores can have large effects on the population dynamics of subordinate competitors (Palomares & Caro 1999). Coyotes are exploitative competitors with bobcats (Litvaitis & Harrison 1989), have been documented killing bobcats (Knick 1990; Gipson & Kamler 2002) and correlative (Robinson 1961; Nunley 1978; Litvaitis & Harrison 1989) and experimental (Henke & Bryant 1999) studies have consistently indicated that coyotes can suppress bobcat populations. Although coyotes do kill both adult and juvenile bobcats, adult bobcats are nearly as large as coyotes.

Consequently, competition with coyotes may be primarily experienced by small (i.e. females and juveniles; Gipson & Kamler 2002) bobcats and suppression of bobcat populations by coyotes the result of depredation on kittens and reproductive females. My results provide further correlative evidence of the impact of competition with coyotes on bobcat populations and provide a possible mechanism (depression of reproduction and kitten survival) by which bobcat populations are limited.

The extent of habitat predicted to be suitable for bobcat reproduction in Minnesota is dependent on the probability threshold chosen as the cutoff for what determines breeding and non-breeding habitat (Fig. 4.5). Use of the minimum presence threshold suggests that a large percentage of the study area (76%) can support reproduction whereas use of the more conservative estimate of breeding habitat as sections with an associated probability  $\geq 0.90$  resulted in vastly different estimates of the percentage suitable for reproduction (23%). However, because a typical bobcat home range is larger than a section (Fuller et al. 1985a) it is likely that kittens were harvested within unsuitable habitats as they moved between suitable patches. Consequently, more conservative estimates of the threshold used to identify habitat as suitable may be warranted, particularly when dealing with endangered species.

Figure 1.1. Bobcat range in Minnesota as determined by harvest locations during the 2009-2010 season. Locations of harvested bobcats are accurate to the township.

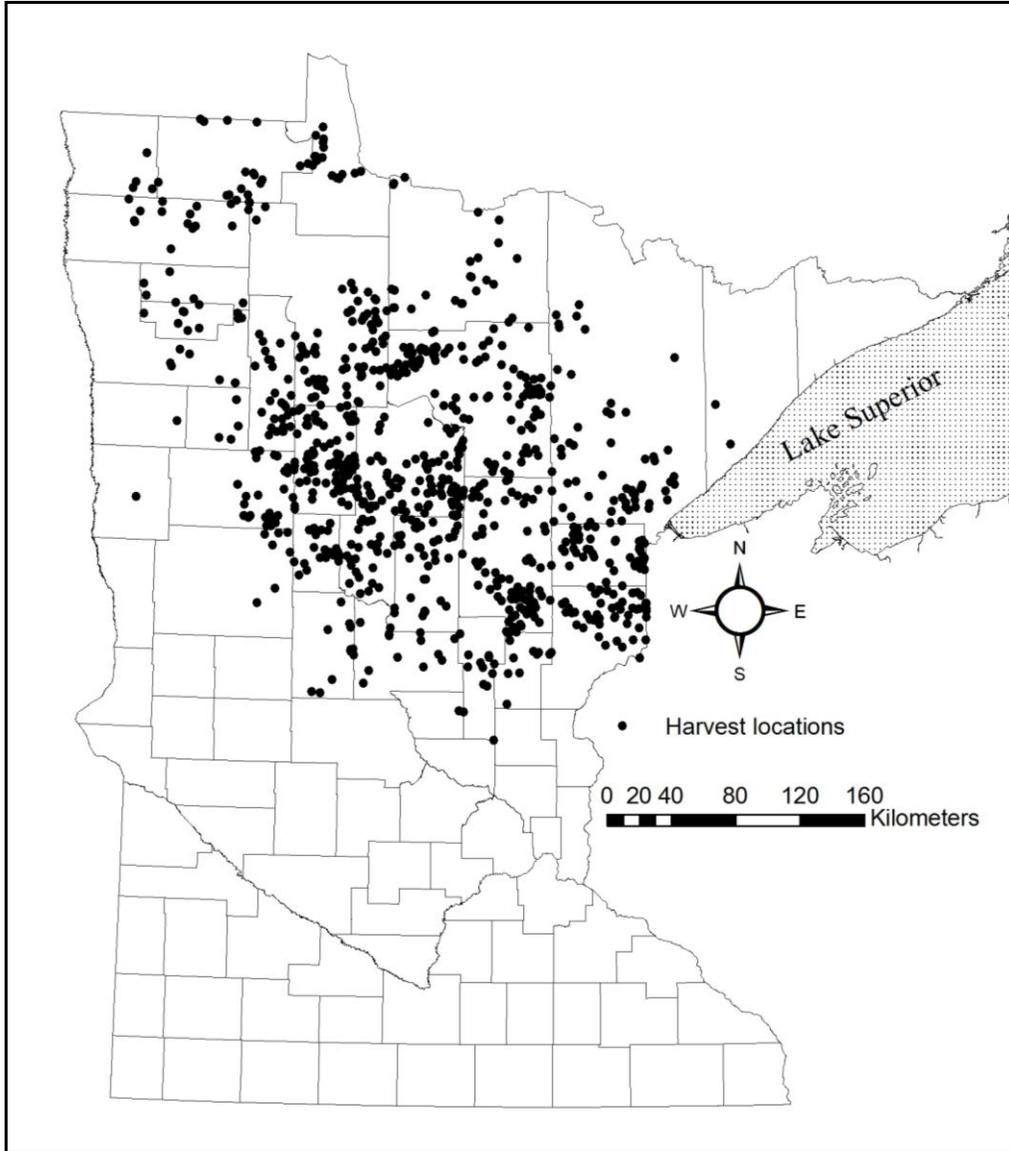


Figure 1.2. Reported harvest of bobcats in Minnesota from 1977-1978 through 2008-2009 seasons.

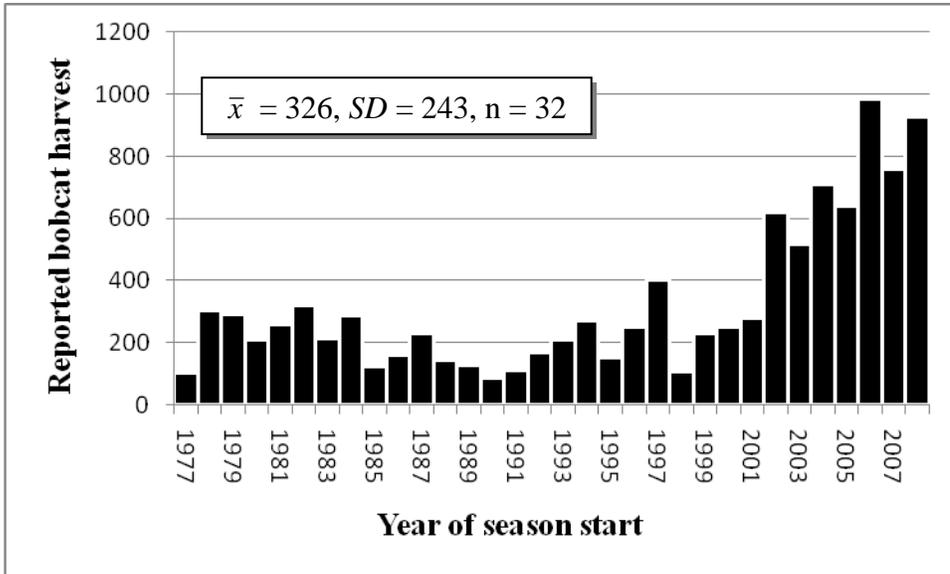


Figure 1.3. Effect of the percent of scent stations visited by bobcats, season length, and the proportion of days when the maximum temperature < the bobcat's lower critical temperature on the number of bobcats harvested. Solid line indicates maximum likelihood estimate holding other variables constant at their mean. Dashed lines indicate 95% pointwise bootstrap confidence intervals.

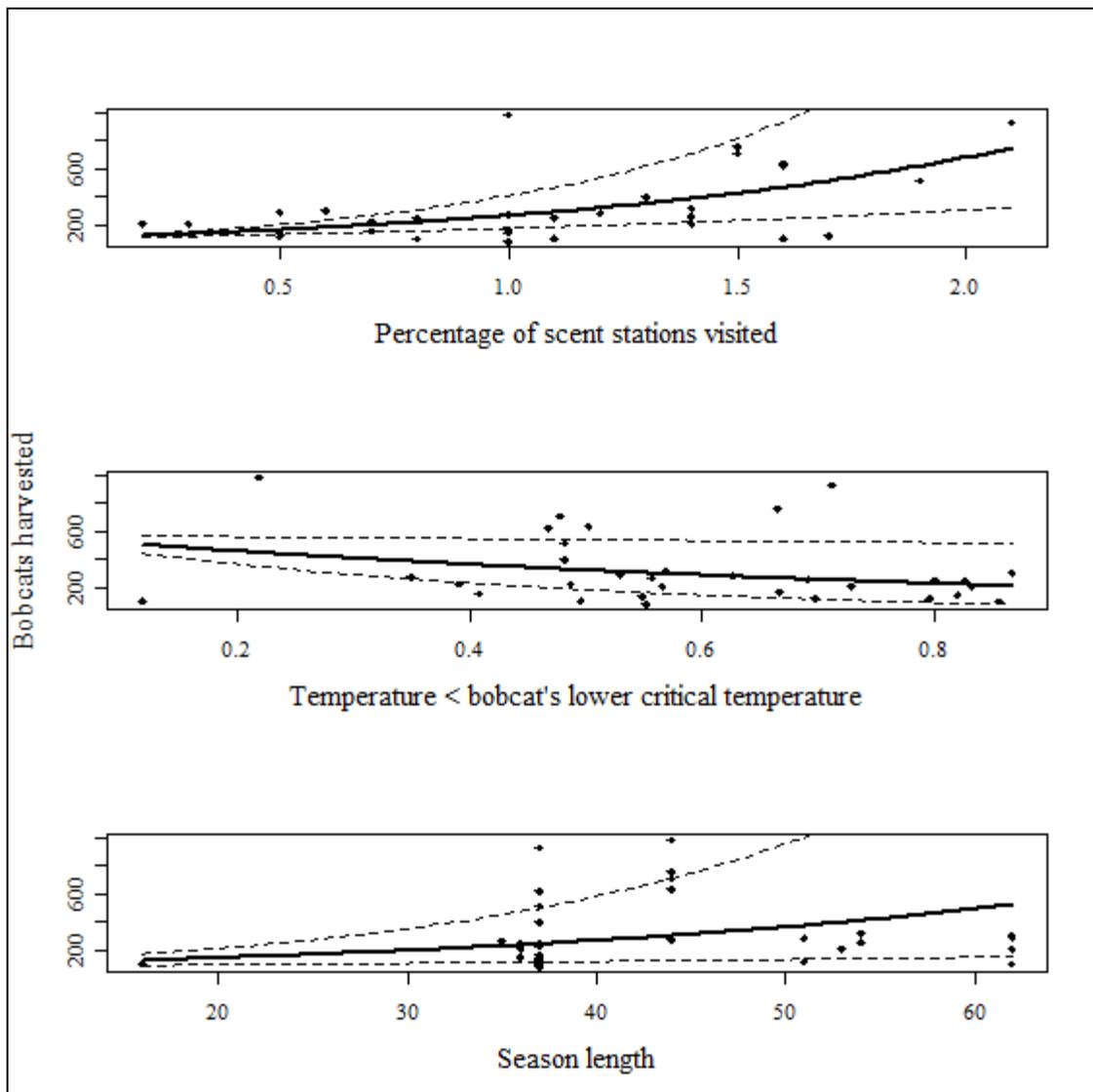


Figure 2.1. Bobcat range in the Arrowhead region of northeastern Minnesota as estimated by townships where bobcats were harvested during the 2001 to 2010 seasons. Inset indicates location of Arrowhead in Minnesota.

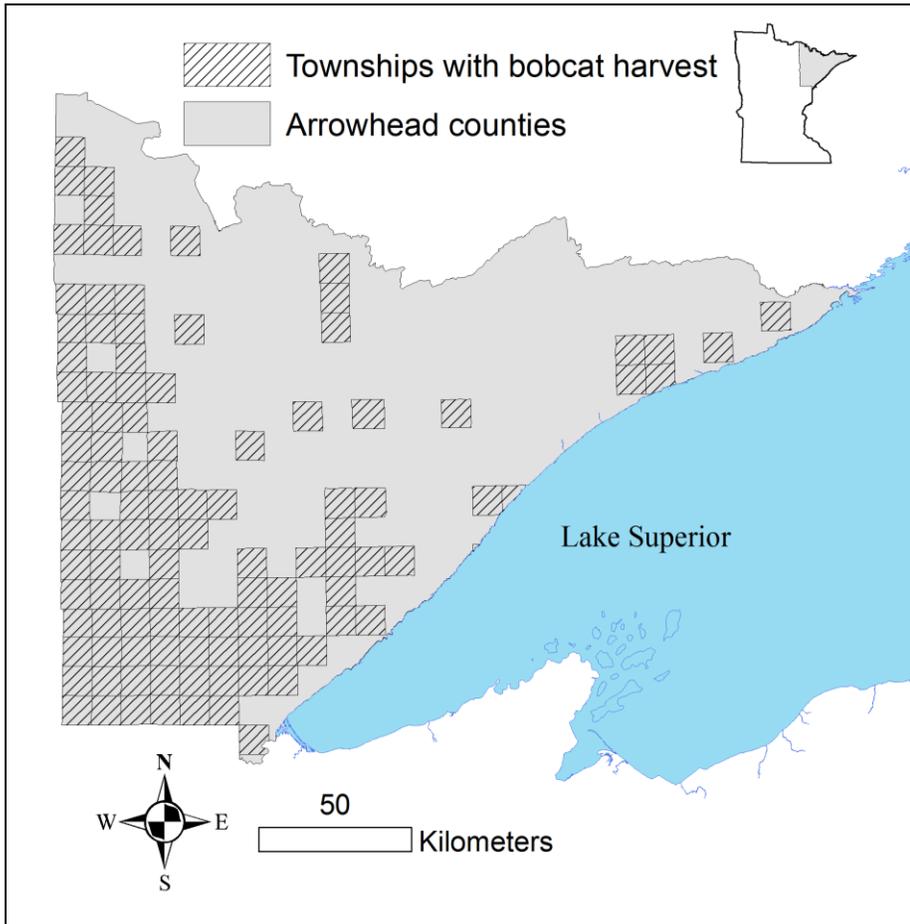


Figure 3.1. Winter adaptive kernel home ranges, core areas and overlap of two, sibling adult female bobcats in east-central Minnesota. Star on inset indicates study area location.

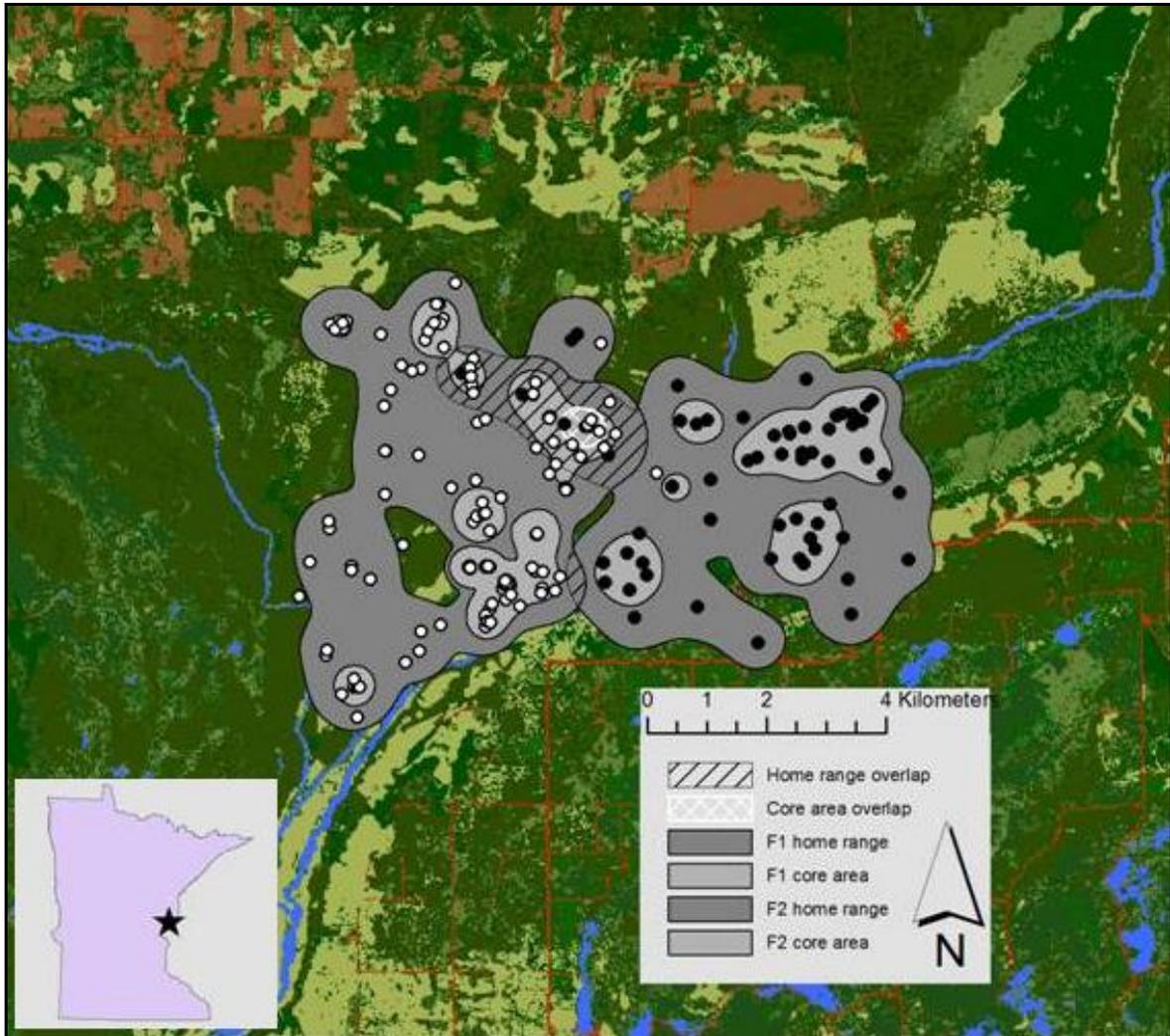


Figure 4.1. Study area as delineated by 100% minimum convex polygon (hatched area) of sections where kittens were harvested (circles).

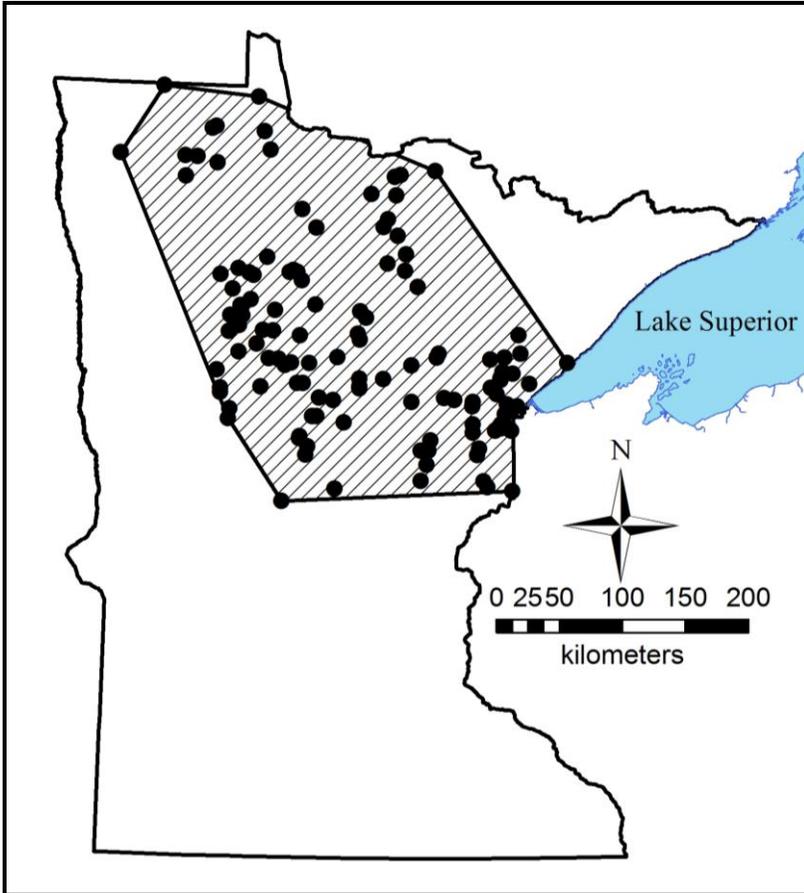


Figure 4.2. Estimates of the importance of environmental features for predicting the suitability of habitat for supporting bobcat reproduction based on 1000 bootstrapped replicates. Error bars represent  $\pm 1$  standard error.

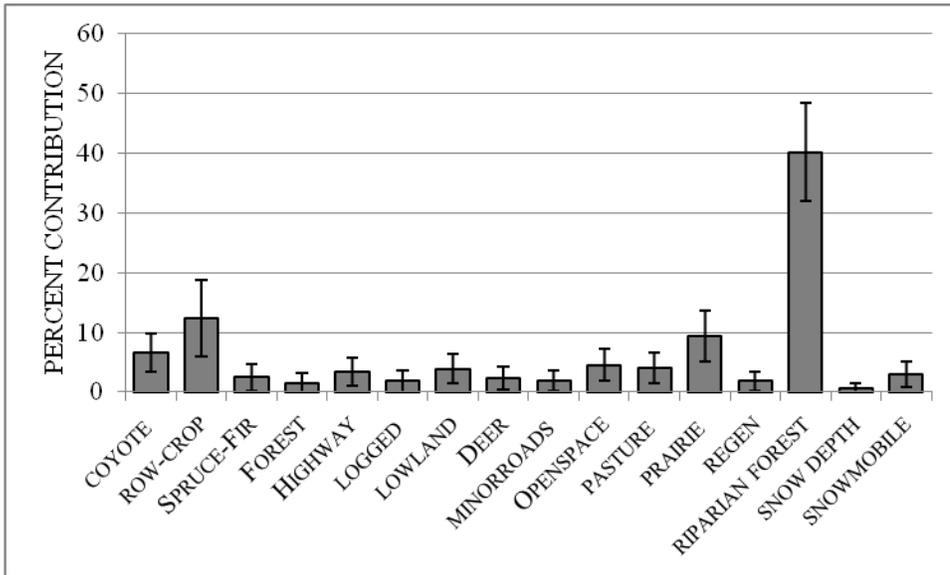


Figure 4.3. Marginal response curves of the four environmental features that were most influential in predicting the suitability of habitat for bobcat reproduction. Red curve represents mean response curve from 1000 bootstrapped replicates and blue  $\pm 1$  standard error.

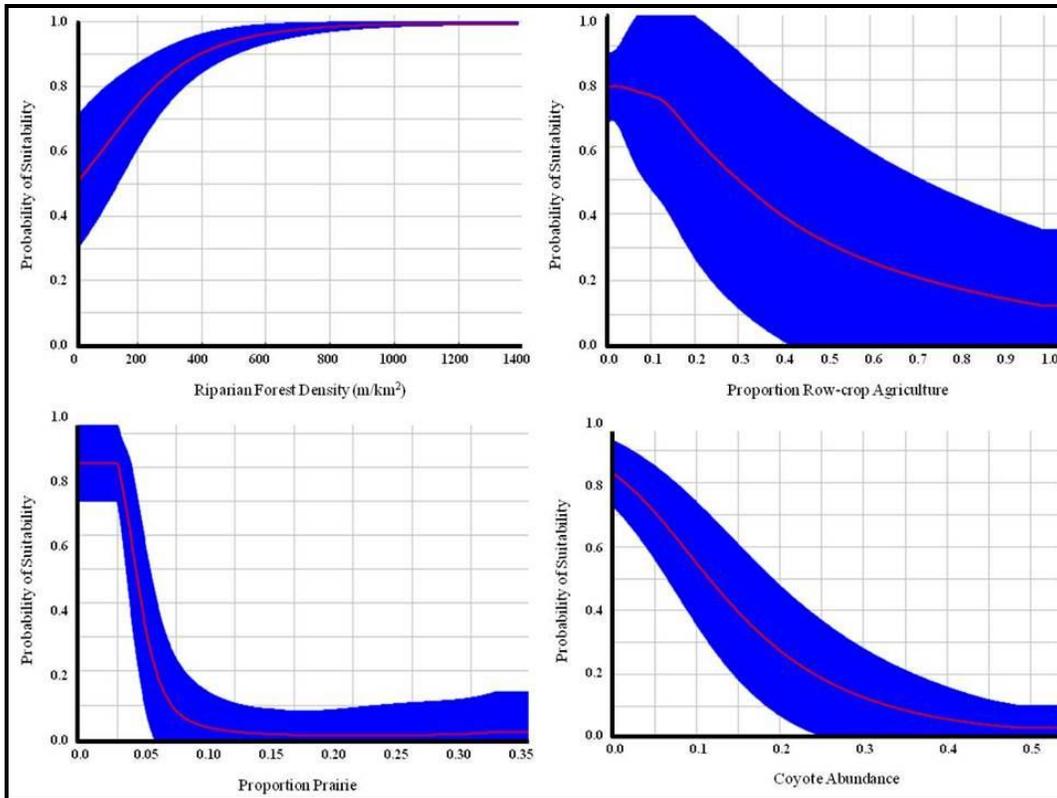


Figure 4.4. Distribution of bobcat breeding habitat as delineated by the threshold probability of suitable environmental features within a section  $\geq 0.055$  (minimum probability associated with kitten presence in light blue) and probability  $\geq 0.90$  (gray). Red circles indicate sections where kittens were harvested and white area represents probability of the environmental features being suitable for bobcat reproduction  $< 0.055$ .

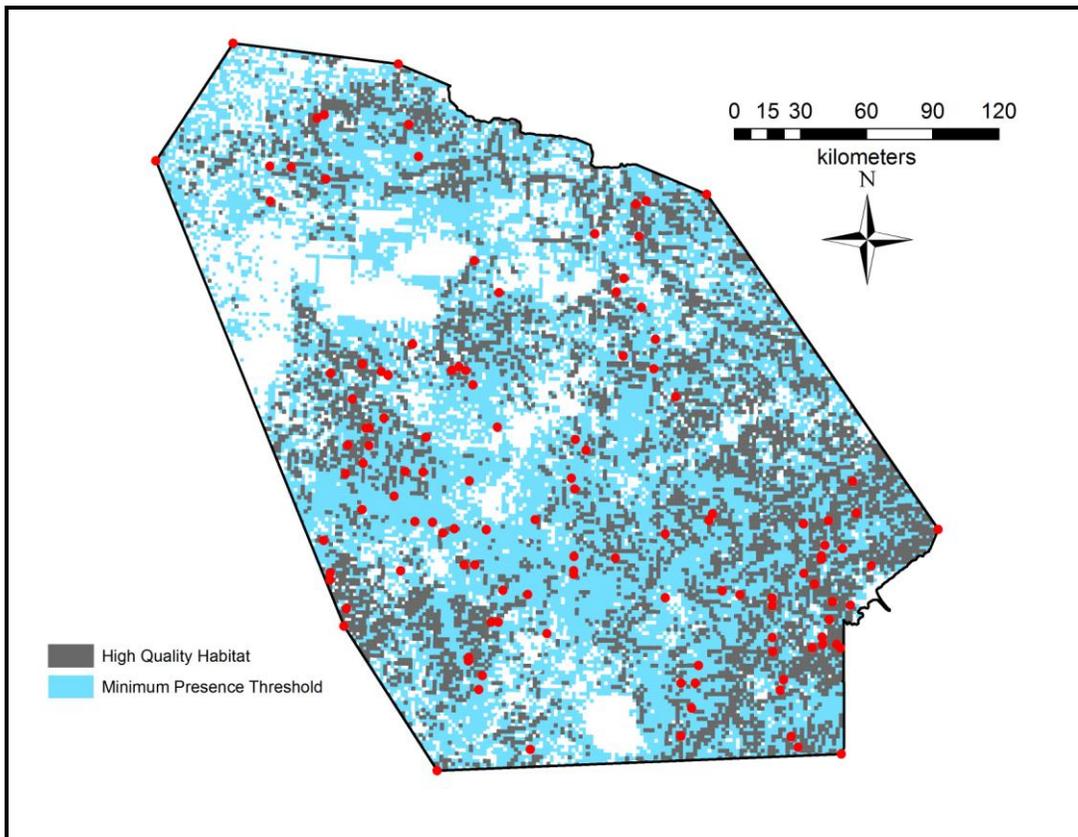


Figure 4.5. Probability that habitat provides suitable environmental features for bobcat reproduction and kitten survival in northern Minnesota as delineated by locations where kittens were harvested from 2008 to 2010 (red dots).

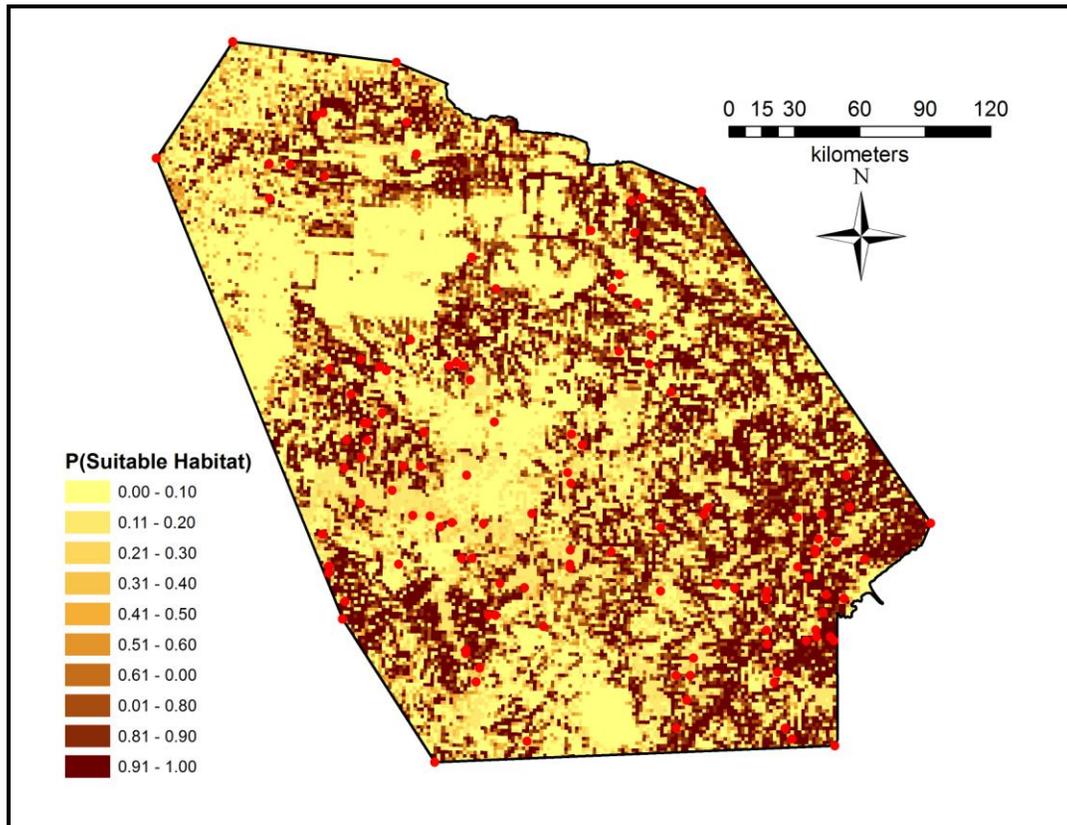


Table 1.1. A priori generalized linear models of the effects of season length, inflation-adjusted mean pelt price for bobcats harvested during the current (price) and the previous season (price-1), unemployment during bobcat season, proportion of scent stations visited (scent), proportion of days from two weeks prior to season end when snowdepth > 15 cm (snow) and maximum temperature < bobcat's lower critical temperature (temp), and indices of hare abundance (hare), on the number of bobcats harvested annually. Models are ranked according to differences in quasi-likelihood Akaike's Information Criterion corrected for small sample size ( $\Delta\text{QAIC}_C$ ).

Model	K <sup>a</sup>	$\Delta\text{QAIC}_C$ <sup>b</sup>	wt <sup>c</sup>	Dev <sup>d</sup>
scent + temp + season + price-1	7	0.00	0.42	33.14
null	3	0.47	0.33	34.15
licenses + season	5	2.92	0.10	33.84
hares + snow	5	3.96	0.06	33.95
hares + temp	5	4.46	0.04	34.00
price-1 + unemployment	5	5.35	0.03	34.08
price + unemployment	5	5.67	0.02	34.12
scent + adult + adult male + yearling + yearling male + juvenile male	9	9.94	< 0.01	33.28

<sup>a</sup> No. parameters, including estimate of dispersion.

<sup>b</sup> Top model  $\text{QAIC}_C = 252.90$ .

<sup>c</sup> Relative likelihood of model.

<sup>d</sup> Model deviance.

Table 1.2. Negative binomial generalized linear model maximum-likelihood estimates (log link) of factors affecting the number of bobcats harvested in Minnesota, USA, from 1977 through 2008 (32 seasons).

<b>Parameter<sup>ab</sup></b>	<b>Estimate</b>	<b>SE</b>	<b>95% CI</b>
$\beta_0$	4.036	0.544	2.877 to 5.252
$\beta_{\text{SCENT}}$	0.938	0.203	0.553 to 1.329
$\beta_{\text{TMX}}$	-1.154	0.531	-2.101 to -0.223
$\beta_{\text{SEASON}}$	0.030	0.010	0.009 to 0.051

<sup>a</sup> SCENT = proportion of scent stations visited during annual MN DNR surveys; TMX = proportion of days from 2 weeks prior to season start through season end when the maximum temperature < bobcat's lower critical temperature; SEASON = season length in days.

<sup>b</sup> Estimates for  $\beta_0$ ,  $\beta_{\text{CPI-1}}$ ,  $\beta_{\text{SCENT}}$ ,  $\beta_{\text{TMX}}$  and  $\beta_{\text{SEASON}}$  based on top-ranked model according to QAIC<sub>C</sub> following deletion of uninformative parameters.

Table 2.1. Description, mean and range of variables used to model distribution of bobcat harvest from 2001 to 2010 in northeastern Minnesota.

Variable	Description	$\bar{x}$	Range
Regenerating Forest	Proportion of township consisting of regenerating forest	0.001	0.000-0.011
Deer Density	Pre-fawn deer density as estimated by MN DNR	15.206	1.44-26.11
Coyote Density	Interpolated estimate of proportion of scent stations visited by coyotes during annual surveys	0.026	0.001-0.131
Fisher Harvest	Density of fisher harvest (fisher harvest/km <sup>2</sup> )	13.8	0.023-1202
Snowmobile trails	Density (m/km <sup>2</sup> ) of snowmobile trails in township	246	0-1510
Minor roads	Density (m/km <sup>2</sup> ) of minor roads in township	309	0-2122
Snow Depth	Proportion of days when snow depth > 15 cm	0.448	0.281-0.700
Temperature	Proportion of days when maximum temperature < -2°C	0.357	0.259-0.448

Table 2.2. Candidate variables included in binomial generalized linear models to explain bobcat absence in the Arrowhead region of northeastern Minnesota. Model variables for each variable category were based on explanations as interpreted from the references.

<b>Variable Category</b>	<b>Explanation</b>	<b>Model Variables</b>	<b>References</b>
Prey Abundance	Prey availability linked to increased mortality and emigration and reduced fecundity	Regenerating Forest Deer Density	Bailey 1974 Knicks 1990 McCann & Moen 2011
Competition	Interspecific competition suppresses bobcat populations	Coyote Density Fisher Density	Gilbert & Keith 2001 Henke & Bryant 1999 Nunley 1978
Hunter Access	Harvest distribution influenced by hunter access	Snowmobile Trails Minor Roads	Boer 1990 Diefenbach et al. 2005
Climate	Bobcat adaptations to winter climate relatively weak compared to sympatric carnivores; extreme winter weather linked to increased mortality and emigration	Snow Depth > 15 cm Temp < Bobcat's lower critical temperature	Knicks 1990 Mautz & Pekins 1989 McCord 1974 Petraborg & Gunvalson 1962

Table 2.3. Binomial generalized linear models of the effects of prey abundance (regenerating forest, deer), climate (snow depth, temperature), hunter access (minor roads, snowmobile trails) and interspecific competition (coyote, fisher) on male and female bobcat presence as determined by harvest records. Models are ranked according to differences in Akaike's Information Criterion corrected for small sample size ( $\Delta AIC_C$ ).

Model	K <sup>a</sup>	AIC <sub>C</sub>	$\Delta AIC_C$	wt <sup>b</sup>	Dev <sup>c</sup>
Females					
Deer + Coyote + Regenerating Forest	5	244.32	0.00	0.94	236.12
Deer + Regenerating Forest	4	249.76	5.43	0.06	243.64
Snow Depth	3	260.51	16.18	0.00	256.45
Fisher + Coyote	4	268.93	24.61	0.00	262.81
Temperature	3	273.94	29.61	0.00	269.88
Minor Roads + Snowmobile Trails	4	277.24	32.92	0.00	271.12
Null	2	279.19	34.87	0.00	277.17
Males					
Deer + Coyote	4	213.2502	0.00	0.94	207.12
Deer + Regenerating Forest	4	218.7584	5.51	0.06	212.62
Snow Depth	3	224.5062	11.26	0.00	220.44
Temperature	3	238.8366	25.59	0.00	234.77
Fisher + Coyote	4	242.0746	28.82	0.00	235.94
Snowmobile trails + Minor Roads	4	245.4493	32.20	0.00	239.31
Null	2	248.6721	35.42	0.00	246.65

<sup>a</sup> No. parameters.

<sup>b</sup> Relative likelihood of model.

<sup>c</sup> Model deviance.

Table 2.4. Maximum likelihood parameter estimates (logit link), standard errors and 95% confidence intervals for the best model describing the distribution of bobcat harvest using the lowest Akaike's Information Criterion adjusted for small sample size.

	Parameter <sup>a</sup>	Estimate	SE	95% CI
Females	Intercept	-0.2609	0.1584	-0.574 to 0.048
	Coyote Density	-0.4970	0.1965	-0.907 to -0.134
	Regenerating Forest	0.2912	0.1630	-0.030 to 0.618
	Deer	0.8719	0.1841	0.526 to 1.251
Males	Intercept	-0.4032	0.1697	-0.741 to -0.074
	Coyote Density	-0.4395	0.2050	-0.880 to -0.070
	Deer Density	0.9229	0.1897	0.566 to 1.313

<sup>a</sup> Parameter estimates based on top-ranked models based on minimum Akaike's

Information Criterion corrected for small sample size (AICc) following deletion of uninformative parameters.

Table 3.1. Reference, method for delineating home range and core areas and % overlap for adult female bobcats.

Reference	Method for delineating home range <sup>1</sup>	% Overlap	
		Home range	Core area
Chamberlain & Leopold 2005	95 & 50% FK	21	3
Bailey 1974	Irregular polygon	0	n/a
Cochrane et al. 2006	95% MCP	14	n/a
Lawhead 1984	Modified minimum area method	10	n/a
Thornton et al. 2004	95 & 50% FK	2	0
Nielsen & Woolf 2001	95 & 50% FK	28	6
Rucker et al. 1989	Minimum area method	5	n/a

<sup>1</sup> FK=Fixed Kernel, MCP=Minimum Convex Polygon

Table 3.2. Percentage and utilization distribution overlap index (UDOI) of 95, 50, and core area utilization distributions of two adult sister bobcats in east-central Minnesota.

Bobcat	95% Overlap*	50% Overlap *	Core Area Overlap*	95% UDOI	50% UDOI	Core Area UDOI
F1	17.12	0.00	5.92	0.02	0.00	0.00
F2	14.86	0.00	5.32	N/A	N/A	N/A

\*Percent of utilization distribution of bobcat  $i_1$  overlapped by that of bobcat  $i_2$  using adaptive kernel home range estimates.

Table 3.3. Mean home range area (km<sup>2</sup>) for female bobcats in Minnesota and Wisconsin, methods used for estimating home range, season when data were collected, number of bobcats monitored and reference.

State	Method <sup>1</sup>	Season	<i>n</i>	$\bar{x}$	Reference
Minnesota	VHF, 95% MCP	Combined	11	36.6	Fuller et al. 1985
Minnesota	GPS, 95% MCP	Winter	2	21.4	This Study
Wisconsin	VHF, 100% MCP	Winter	5	30.6	Lovallo & Anderson 1996
Wisconsin	VHF, 100% MCP	Winter	9	24.8	Gilbert & Keith 2001

<sup>1</sup> GPS=Global positioning system radio-collar, VHF=Very high frequency radio-collar, MCP=minimum convex polygon.

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