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Spatial and Habitat Responses of Canada Lynx in Maine to a Decline in Snowshoe Hare Density

David G. Mallett

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SPATIAL AND HABITAT RESPONSES OF CANADA LYNX IN MAINE TO A

DECLINE IN SNOWSHOE HARE DENSITY

By

David G. Mallett

B.S. Fisheries & Wildlife, University of Missouri, 2007

B.S. Forestry, University of Missouri, 2007

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

May 2014

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By David G. Mallett

Thesis Co-Advisors: Dr. Daniel J. Harrison
Dr. Angela K. Fuller

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
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Previous studies of Canada lynx (*Lynx canadensis*) within the northern boreal forest region have documented that lynx respond spatially to a decline in snowshoe hare (*Lepus americanus*) density, as exhibited by expansion of territories and changes in social structure. I compared home range area and spatial overlap in the southeastern portion of their geographic range during periods of relatively high and relatively low hare density. Home range areas of lynx did not change between periods of high and low hare density, except that home ranges of females during the denning season expanded during the low period. The presence of kittens constrained home range areas of reproductive females during denning because females were attending kittens. Intra- and intersexual overlap did not change as hare density declined, with the exception of a decrease in overlap between females. This decrease was likely caused by decreased reproduction during the low period, which reduced potential for territorial overlap among mothers and daughters. Hare density during the nadir of cycles in more northerly populations can reach levels nearly a magnitude lower than reported for Maine during my study. This may have

prevented breakdowns in territories and changes in social structure by lynx, which may have shifted life history strategies towards territorial maintenance and reduced reproduction as hare densities declined.

I also investigated changes in use of high-quality hare habitat (HQHH) at the landscape scale, and habitat selection of HQHH within home ranges of lynx between periods of high and low hare density. Lynx did not change their extent of use of HQHH at the landscape scale, suggesting lynx had adequate amounts of HQHH within their home ranges to encounter hares during both the high and low periods of hare density. Lynx exhibited stand-scale selection for HQHH during both hare density periods, but the intensity of female selection for HQHH declined as hare density declined. This suggests that lynx continued to remain focused on foraging for hares during both periods, but that females may become more generalized in habitat and prey selection during the period of lower hare density.

Lynx monitored during this study wore GPS collars during a period of low hare density and VHF collars during a period of high hare density. This presented methodological challenges when I compared lynx responses between hare density periods. Errors associated with VHF collars were known for this study, but errors associated with GPS collars were not. Failed fix attempts and location inaccuracy caused by environmental and satellite configurations can bias habitat selection and spatial analyses. I evaluated fix success and location error of GPS collars in 7 habitat classes during 2 seasons in northern Maine. I also used an information-theoretic modeling approach to investigate covariates influencing fix success and location error. Canopy cover had the greatest influence on fix success and the configuration of available

satellites had the greatest influence on location error. Results were used to compensate for habitat bias and location error caused by GPS collars worn by lynx during a period of low hare density.

PREFACE

Understanding the spatial responses of the U.S. federally threatened Canada lynx (*Lynx canadensis*) to changes in densities of their primary prey, the snowshoe hare (*Lepus americanus*), is important for future management efforts to conserve and recover the species. This is particularly relevant for populations that exist in the Acadian Forest region at the southeastern extent of their geographic range. Lynx and hares occur sympatrically from northern Alaska and Canada into the northern portion of the contiguous United States, including the states of Maine, New Hampshire, Colorado, Idaho, Minnesota, Montana, Washington, and Wyoming (McKelvey et al. 2000, Mowat et al. 2000). Hare populations in the boreal forests of northern Canada and Alaska exhibit population cycles every 8-11 years (Hodges 2000a), and lynx populations follow with a 1-3 year lag (Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979, Mowat et al. 2000). Lynx in the northern portion of their geographic range have been documented to increase their home range area and extent of overlap during the decline phase of hares (Ward and Krebs 1985, Poole 1995, Slough and Mowat 1996). Additionally, lynx have been documented to emigrate as social structure breaks down (Poole 1995) and declines in reproduction and recruitment have been recorded as hare densities decline (Poole 1994, Mowat et al. 1996).

Spatial ecology of lynx in their southern range has been hypothesized to be characteristic of lynx in the boreal forests of their northern range during a cyclic low in hare populations (Koehler and Aubry 1994, Aubry et al. 2000), which includes large home range areas of individual lynx and hare densities similar to populations typical at

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the low of hare cycles in the north (Mech 1980, Koehler 1990, Apps 2000). To the contrary, research conducted in the Acadian Forest region in Maine during a period of relatively high hare density did not support the hypothesis that southern populations of lynx exhibit similar spatial and demographic characteristics to northern populations during periods of low hare density (Vashon et al. 2008a). To date, however, little research has been conducted on lynx during a period of low hare densities within the southeastern portion of the geographic range of lynx. This is particularly relevant because it may influence management activities designed for conserving and recovering the largest population of U.S. federally threatened Canada lynx across temporal scales with fluctuating hare densities. My research goals were to investigate the spatial and habitat ecology of Canada lynx at the southeastern extent of their geographic range by evaluating how spatial characteristics (Chapter 2) and patterns of habitat use and selection (Chapter 3) of lynx changed from periods of relatively high to relatively low density of snowshoe hares.

My research utilized both VHF and GPS collars to collect location data on lynx to evaluate their spatial and habitat responses to changes in relative hare densities. GPS collars offer the advantage of decreased effort to record more locations than VHF collars, and, thus, are being utilized more frequently (Rodgers et al. 1996). However, GPS collars present potential errors in location success and accuracy that may bias results from habitat analyses and spatial modeling. Specific problems include missed location attempts and location errors, caused by environmental, topographic, and variable satellite configurations (Moen et al. 1996, Rempel and Rodgers 1997, D'Eon 2003, Hebblewhite et al. 2007). In Chapter 1, I evaluated the degree of fix success and location error of GPS

collars across habitat classes in northern Maine. Additionally, I investigated the specific

causes of fix success and location error to determine the environmental factors,

topographic factors, or effects of satellite configuration that may be contributing to errors.

Investigating the errors associated with GPS collars was necessary before evaluating

spatial and habitat responses of lynx. My results were used to mitigate the potential bias

in estimates of habitat use by lynx from GPS-derived locations, and to account for

locational inaccuracies presented by GPS collars.

I attempted to correct for spatial inaccuracy associated with GPS collars in

analyses conducted in Chapters 2 and 3 by developing a screening criterion to remove all

2D locations with ≥10 dilution of precision (DOP) for Lotek collars and locations with

≥10 DOP for Sirtrack collars (Sirtrack collars did not give a 2D/3D classification). DOP

is a measure of the geometry of satellites and a 2D/3D classification refers to the number

of satellites used to calculate a location (Rempel et al. 1995, Moen et al. 1996, Rodgers et

al. 1996, Moen et al. 1997). Screening removes locations with unacceptably large

location errors (i.e., outliers) and increases overall accuracy (D'Eon and Delparte 2005,

Lewis et al. 2007).

Vegetative variables, such as canopy cover can cause missed locations from GPS

collars (Rempel et al. 1995, Moen et al. 1996), which can cause bias in habitat selection

analyses (D'Eon 2003, Frair et al. 2004, Hebblewhite et al. 2007).   I attempted to correct

for habitat biases caused by missed locations in habitat analyses conducted in Chapter 3.

Using rates of fix success (i.e., percentage of successful location attempts) associated

with each habitat class (Chapter 1), I estimated missed locations by dividing the observed

locations from each collar by the percentage of fix success according to season and

habitat class. The resulting number of estimated missed locations was then added to the observed locations for each lynx.

In Chapter 2, I compared the change in annual and reproductive season-specific home range areas of lynx between 2 consecutive periods of high and low hare density. Denning rates of females were documented during both periods of hare density and I investigated whether presence of kittens had an influence on home range area. Additionally, I compared extent of intra- and intersexual overlap of home range areas of lynx between periods of high and low hare density. These analyses provided insight into the comparative spatial ecology, social structure, and reproductive success of lynx during a period of relatively high and relatively low hare density.

In Chapter 3, I compared the habitat ecology of lynx between the periods of relative high and low hare density. First, I evaluated how use of high-quality hare habitat (HQHH) at the home range scale changed between periods of high and low hare density. Second, I evaluated the change in direction and intensity of selection for patches of HQHH within home ranges between periods of high and low hare density. I discuss how changing hare density influences lynx habitat choices at 2 spatial scales within the transitional Acadian Forests of northern Maine.

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CHAPTER 1

FIX SUCCESS AND LOCATION ERROR OF GPS COLLARS ACROSS HABITATS USED BY CANADA LYNX: INFLUENCES OF ENVIRONMENTALLY INDUCED BIAS

ABSTRACT

Increasingly, GPS collars are replacing traditional VHF collars in many wildlife research applications, where accurate estimates of an animal's spatial location and habitat use are required. Although GPS collars offer advantages over VHF collars, they can be influenced by vertical structure (e.g., tree boles), horizontal structure (e.g., overhead canopy), and topography (e.g., slope) which affect the percentage of location attempts that are successful (i.e., fix success) and the accuracy of GPS locations. Influences of topography, vegetation, season, satellite configuration, frequency between location attempts, and manufacturer can bias fix success and accuracy of GPS derived location data. Evaluated in many regions of Canada and the United States, these influences have never been investigated in the mesic, heavily forested region of the Acadian forest in eastern North America. Additionally, during companion studies (Chapters 2 & 3) conducted in northern Maine, GPS collars were equipped on federally threatened Canada lynx (*Lynx canadensis*) to evaluate spatial requirements, habitat composition of home ranges, and resource selection. Thus, I evaluated whether fix success and location error of GPS collars differed across habitat classes to be later used in habitat analyses, and I used an information-theoretic approach to model the effects of within habitat structure, slope, aspect, and satellite configuration on fix success and location error. I measured location error and fix success during the leaf-on (May 15 – October 14) and leaf-off

(October 15 – May 14) seasons using two manufacturers of GPS collars (Sirtrack and Lotek), which I deployed at 66 test sites, representing 7 habitat classes, based on tree height, coniferous and deciduous tree composition, and harvest history. Fix success differed across habitat classes during the leaf-on season ($P < 0.001$); fix success was 87% for collars manufactured by Lotek and 80% for collars manufactured by Sirtrack. During the leaf-off season, however, fix success did not differ by habitat ($P = 0.123$), and was 95% for Lotek and 100% for Sirtrack collars. Fix success was lowest during the leaf-on season in deciduous-dominated regenerating stands for Lotek and in conifer-dominated stands for Sirtrack. The top AICc model for describing fix success in both seasons was the single variable model canopy cover (CC). Location error differed across habitat classes for Lotek ($P < 0.006$), but not for Sirtrack collars ($P \geq 0.364$) during both seasons. Both manufacturers averaged <21 m location error during both seasons. The number of satellites used to calculate a location (SATS) and their geometry (DOP) had the greatest influence on location error. The influence of CC, SATS, and DOP on fix success and location error may cause habitat and spatial bias. This study was conducted to evaluate influences of missed locations to be able to correct bias in estimates of habitat use of Canada lynx in the Acadian Forest of northern Maine (see Chapter 3). Additionally, it was conducted to evaluate the inaccuracies of GPS locations on results of habitat and movement studies to avoid inflation of estimated lynx home ranges during companion studies (see Chapters 2 and 3).

INTRODUCTION

Global positioning system (GPS) collars have become an important tool in wildlife research. Compared to more traditional VHF collars, they can provide more

continuous data as they are not limited by daylight or weather, and increased efficiency by reducing the number of man hours needed to record locations (Rodgers et al. 1996). Additionally, GPS collars can have increased location accuracy over VHF collars (Rodgers et al. 1996). Aerial telemetry errors associated with research in my study area were <80 m (Vashon et al. 2008a), but GPS locations can have errors <1 m (Moen et al. 1996) and <31 m for 95% of locations (Rempel et al. 1995, D'Eon et al. 2002, Hebblewhite et al. 2007).

Data collected using GPS collars, however, may be compromised by missed locations and extreme outliers, causing a reduction in accuracy (Moen et al. 1996, Rempel and Rodgers 1997, D'Eon 2003, Frair et al. 2004, Hebblewhite et al. 2007, Lewis et al. 2007). These errors can be influenced by environmental factors (e.g., vegetation and topography) that can impede communication between GPS collars and satellites, as well as technical factors (e.g., collar programming, available satellites, and satellite geometry) that can reduce accuracy of the locations; these errors can induce bias and reduce accuracy in subsequent spatial and habitat analyses. Testing to determine the error and bias associated with GPS collars should precede applications of GPS derived spatial data, particularly in environments with steep topography or high vertical and horizontal vegetative structure (Cain et al. 2005, Lewis et al. 2007, Sager-Fradkin et al. 2007).

Location error describes the difference between the recorded location from the GPS collar and the true location. Large location error can lead to misclassification of habitats used in habitat selection analyses, depending upon the magnitude of location error and habitat juxtaposition (Frair et al. 2004, Lewis et al. 2007). Additionally, large

location errors (i.e., outliers) may reduce the accuracy of spatial analyses, such as home range estimation.

Fix success (i.e., proportion of successful location attempts) across space and time can be an additional source of bias for habitat selection analyses (Rettie and McLoughlin 1999, D'Eon 2003, Frair et al. 2004, Hebblewhite et al. 2007), perhaps more so than location error (Johnson et al. 1998). This bias tends to occur differentially across habitat types, potentially leading to incorrect conclusions in habitat selection analyses (Frair et al. 2004). To prevent inaccurate conclusions in habitat and spatial analyses using locations from GPS collars, it is necessary to identify and correct for factors that cause errors.

Fix success and location error have been evaluated in the forests of the western United States and Canada, but there has been relatively little focus in eastern North American forests (but see Dussault et al. 1999;2001). Specifically, no research has been conducted in the dense, mesic Acadian forests (Seymour and Hunter 1992) of Maine which are characterized by stands of deciduous and conifer trees that have high vertical and horizontal vegetative structure and can exceed 12,000 stems/ha (Homyack et al. 2004). Overhead canopy closure near 100% is also common in regenerating clearcuts (Payer and Harrison 2000, Homyack et al. 2004) and deciduous dominated stands. These characteristics of the Acadian forest may impede satellite signals, thus influencing fix success and location error.

Previous studies have suggested that vegetation variables such as canopy cover (Rempel et al. 1995, Moen et al. 1996, Frair et al. 2004, Hansen and Riggs 2008, Jiang et al. 2008), tree height (Moen et al. 1996, Rempel and Rodgers 1997, Dussault et al. 1999),

and basal area (Rempel et al. 1995, Belant 2009) can negatively influence fix success. Further, interactions between vegetation variables such as canopy cover, basal area, and terrain obstructions have been documented to reduce fix success (Edenius 1997, D'Eon et al. 2002). Topographical variables such as GPS collar visibility to the sky (Cain et al. 2005), steep slopes (Frair et al. 2004), and aspect (D'Eon and Delparte 2005) can negatively influence fix success, especially in areas with significant elevation change. Other factors that may influence fix success are technical variables such as fix interval (i.e., programmed time between fix attempts) (Cain et al. 2005, Mills et al. 2006, Sager-Fradkin et al. 2007) and collar manufacturer and model (Di Orio et al. 2003, Frair et al. 2004, Hebblewhite et al. 2007).

Variables that influence fix success interact to influence location error because a successful fix is needed before location error can be determined. Thus, variables influencing fix success such as canopy cover (Di Orio et al. 2003, Hansen and Riggs 2008), tree height (Rempel and Rodgers 1997), and topography (Cain et al. 2005) have the potential to influence both fix success and location error. Additional to vegetative and topographical variables, geometry and availability of satellites can affect location error (Rempel et al. 1995, Edenius 1997, Bowman et al. 2000, D'Eon et al. 2002, Di Orio et al. 2003). Poor satellite geometry may result in an inaccurate estimation of the location of the GPS collar, with ≥3 satellites required to estimate a location (Rempel et al. 1995).

Models have been developed to predict and correct for habitat bias resulting from missed locations using landscape covariates for habitat selection analyses (D'Eon 2003, Frair et al. 2004, Hebblewhite et al. 2007). Those models, however, may not be widely

transferrable because errors were likely specific to the habitats and study areas where developed (but see Nielson et al. 2009). The habitats in Maine may have a greater density of woody stems or less mountainous terrain than previous studies, causing unique bias for GPS collars in Maine. Consequently, the unique vegetative structure and topography of Maine will make it necessary to test GPS collars to develop models and procedures to correct for missed locations caused by environmental variables.

Data screening can be used to reduce location error associated with GPS collars. GPS generated locations use an estimate of accuracy termed dilution of precision (DOP) that measures the quality of the satellite geometry, where a lower DOP value is generally considered more accurate (Rempel et al. 1995, Moen et al. 1997). A 2D or 3D classification may also be given to each location that corresponds to how many satellites are used to calculate a position. A 2D location uses 3 satellites, but a 3D location will use ≥4 satellites (Rempel et al. 1995, Moen et al. 1996, Rodgers et al. 1996). These two types of classifications of GPS locations have been used to screen locations to remove large outliers and to increase the overall accuracy of locations. However, an optimal balance among strict and liberal screening criteria is needed to avoid excessive data loss and to maintain location accuracy consistent with study objectives (D'Eon and Delparte 2005, Lewis et al. 2007). One approach is to plot location errors versus DOP values to determine acceptable levels of location error and data loss (Lewis et al. 2007), or a data loss threshold can be established prior to data screening.

The goal of my research was to understand how the performance of GPS collars in Maine was affected by vegetative, topographical, and satellite influenced variables and to apply those results in companion studies on Canada lynx. Specifically, my goal was to

improve the general understanding of individual and interacting roles of vertical and horizontal vegetation structure, phenology, topography, DOP, and number of intersecting satellite-derived azimuths (SATS) on fix success and location error in the Acadian forests of northeastern North America. Further, I developed a data screening method to increase overall location accuracy while minimizing data loss. Finally, I applied my findings to reduce location error and account for missed locations in spatial and habitat analyses (Chapters 2 & 3) on Canada lynx within the same study area.

STUDY AREA

My study area included 5 townships in northwestern Maine (T11 R13 WELS, T11 R12 WELS, T11 R11 WELS, T12 R11 WELS, T12 R12 WELS). Topography was minimal (250-550 m) relative to other study areas where the influences of topographic variables on fix success and location error of GPS collars have been previously studied (D'Eon et al. 2002, Cain et al. 2005). Total annual rainfall in the study area was 94.26 cm and total snowfall was 167.13 cm during 2009 (Clayton Lake weather station located in T11 R14 WELS, 46°37'N, 69°31'W, 304.8 m elevation, National Climatic Data Center, National Oceanic and Atmospheric Administration). The greatest rainfall occurred in July (4.72 cm) and the largest snowfall occurred during January (53.84 cm).

Natural disturbances in the Acadian forest, such as a spruce budworm (*Choristoneura fumiferana*) outbreak, are capable of killing millions of acres of spruce-fir forest. A spruce budworm epidemic in the 1970's and 1980's led to large salvage cuts (i.e., clearcuts) in spruce-fir forests of northern Maine (McWilliams 2005). These stands were sprayed with herbicide 4-21 years after being clearcut to reduce deciduous species, thus decreasing competition for coniferous species. The regenerating clearcut stands

were primarily composed of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) or black spruce (*P. mariana*), and often contained white spruce (*P. gluca*), eastern white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), pin cherry (*Prunus pennsylvanica*), and raspberry (*Rubus sp.*).

The 5 township study area was owned by private timber companies and investor organizations (McWilliams 2005) and the land was intensively managed primarily for pulpwood and saw timber. Forestry activities included timber harvesting in the form of clearcutting and various forms of partial harvesting. Clearcuts are defined as a removal of an entire stand with residual trees over 11.4 cm diameter at breast height (DBH) and a residual basal area <6.9 cm²/ha (Maine Forest Service 1990). Partial harvesting is a broad term that describes shelterwood, selection, and overstory removal harvests. Shelterwood harvests are the removal of overstory trees to promote regeneration under partial shade (Smith et al. 1997), selection harvests are multiple entries in a stand that removes single or small groups of trees to create an uneven age stand (Smith et al. 1997), and an overstory removal is a re-entry into a stand to harvest overstory trees and to promote regeneration. Stands that had been partially harvested primarily contained residual trees represented by sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch, and yellow birch (*Betula alleghaniensis*), with other species occurring less frequently that included red spruce, white pine, red maple, pin cherry, striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*). Partial harvest stands and regenerating stands that did not receive an herbicide treatment are capable of high canopy cover during the leaf-on season.

METHODS

I included 7 habitat classes (Table 1.1) that represented different silvicultural treatments and vegetation characteristics that have been previously identified in habitat selection studies of Canada lynx conducted in the same study area (Fuller et al. 2007, Vashon et al. 2008b). I selected two habitat classes that represented regenerating stands following a clearcut harvest, separated by the extent of conifer and deciduous regeneration. Conifer dominated regenerating clearcuts typically occur on relatively poorly drained sites, or in areas sprayed by herbicide (e.g., glyphosate). Deciduous dominated regenerating clearcuts typically occur on higher quality sites with no herbicide application. Mature forest was classified as conifer dominated (>75% conifer trees in overstory) or deciduous dominated (>75% deciduous trees in overstory) stands without a recent harvest (>35 years), trees ≥12 m tall, and closed canopies. Partial harvests were separated into two temporally distinct habitat classes to represent the change in structure of understory vegetation after competing overstory trees were removed. Recent partial harvests were stands 1-10 years post-harvest and established partial harvests were 11-21 years post-harvest. All roads were built for logging access and were unpaved. Roads typically included a 30 m area maintained as bare ground and shrub-stage vegetation on each side; therefore, a buffer was needed to represent the transition zone between habitat classes caused by the edge effects of a road (Murcia 1995). I used satellite imagery (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono, *In preparation*) to supplement existing landcover maps from Fuller (2007) and Vashon et al. (2008b) and used ArcMap 9.3 (Environmental Science Research Institute [ESRI], Inc., Redlands, California, USA) to identify habitat classes.

Table 1.1. Description of habitat classes in northern Maine, USA (T11 R13 WELS, T11 R12 WELS, T11 R11 WELS, T12 R11 WELS, T12 R12 WELS) evaluated for their potential to influence fix success and location error of GPS collars.

Habitat class	Code	Description
Regenerating conifer	CR	<12 m tall, conifer dominated (>75%)
Regenerating deciduous	DR	<12 m tall, deciduous dominated (>75%)
Mature conifer	CM	≥12 m tall, conifer dominated (>75%)
Mature deciduous	DM	≥12 m tall, deciduous dominated (>75%)
Recent partial harvest	PHR	1-10 yr postharvest, mixed deciduous-coniferous forest
Established partial harvest	PHE	11-21 yr postharvest, mixed deciduous-coniferous forest
Road edge	RD	Unpaved logging roads, 30 m buffer on each side

I established 59 test sites in 7 habitat classes during the leaf-on (July – October) season and 40 test sites in 4 habitat classes during the leaf-off (November – February) season, 2009-2010. The true location was measured by averaging 30-50 locations per site (estimated accuracy <2 m) with a Trimble GeoExplorer CE GPS unit, equipped with an external antenna mounted on a tripod to increase accuracy. Test sites were randomly chosen and placed >75 m from a road or other adjacent habitat patches to minimize all edge effects. At each test site I measured canopy cover, slope, aspect, basal area, and height of trees (Table 1.2) and then deployed a test GPS collar for 7 days. Canopy closure was measured from the center point of each test site by averaging four readings taken in each cardinal direction using a spherical densitometer (Lemmon 1956). Basal area was measured separately for conifer and deciduous trees (≥7.6 cm DBH) and saplings (<7.6 cm DBH and >1.5 m tall) using a 2 m^2/ha wedge prism. I used a point-centered quarter method to select trees to measure for total height (Cottam and Curtis 1956, Mitchell 2007). Heights were measured using a Häglof Vertex laser VL400 or Haglöf Vertex III hypsometer (Haglöf Sweden AB, Långsele, Sweden). To simulate actual field conditions as accurately as possible, I tested the same manufacturers and models of GPS collars that have been deployed on lynx in northern Maine between 2004 and 2011 by the Maine Department of Inland Fisheries and Wildlife (MDIFW). I used Sirtrack G2C 181B and Lotek 3300SL collars originally, but because of limited availability of these collars, I also used Sirtrack Custom G2C 181 and Lotek 3300S collars for testing. These collars use the same number of channels, GPS engine, antenna manufacturer, and antennae ground plane as the collars deployed by MDIFW, and were

Table 1.2. Vegetation characteristics and location accuracy data recorded by test GPS collars at 66 test sites in northern Maine, USA 2009-2010.

Code	Variable	Units	Measurement Method	Transformation
CC	Canopy cover	m^2/ha	Densitometer	Arcsine
Slope	Slope	degrees	Clinometer	Square root
Tr_BA	Basal area of live trees[a]	m^2/ha	2 m^2/ha wedge prism	Square root
H	Average height of live trees	meters	Hypsometer, 4 per plot[b]	Square root
D_To	Total basal area of deciduous trees and saplings[c]	m^2/ha	2 m^2/ha wedge prism	Square root
C_Tr	Basal area of conifer trees	m^2/ha	2 m^2/ha wedge prism	None
C_To	Total basal area of conifer trees and saplings[c]	m^2/ha	2 m^2/ha wedge prism	Square root
Aspect	Aspect	Cardinal and intermediate directions	Compass	None
SATS	Number of satellites used to calculate a location	N/A	GPS collar data	Logarithmic
DOP	Dilution of precision	N/A	GPS collar data	Logarithmic

[a] Includes coniferous and deciduous species. Trees are considered ≥7.6 cm DBH.
[b] Point-centered quarter method was used (Mitchell 2007). Measurements were taken on the nearest tree in each of the four quarters around the plot center.
[c] Saplings were considered <7.6 cm DBH and >1.5 m tall.

expected to perform identically (C. Kochanny, Sirtack, *personal communication,* Lotek Wireless, *personal communication*).

Each test collar was fitted with a 9 cm diameter foam insert that would support the collar and simulate a lynx neck. Each foam insert had two holes that would allow it to slide onto dowels attached to a wooden support stake, and were deployed at approximately the average shoulder height of a lynx (45 cm, J. Vashon, MDIFW, unpublished data). Stakes and collars were oriented in random directions.

Both brands of GPS collars were deployed on lynx by MDIFW personnel using different schedules for fix attempts. Sirtrack collars were programmed to attempt a fix every 4.5 hours every day of the week, and Lotek collars were programmed to attempt a fix once per day, Sunday through Friday, with no location attempts on Saturday. Sunday locations for Lotek GPS collars were attempted at 0200, Monday at 0800, Tuesday at 1400, Wednesday at 2000, Thursday at 0400, and Friday at 1000. The discrepancy of fix schedules between manufacturers was caused by battery life considerations and the Lotek schedule was designed to prolong battery life. I used the same manufacturer-specific fix schedule in my test GPS collars, given that previous researchers have documented that different fix schedules can influence fix success (Cain et al. 2005, Jiang et al. 2008).

I deployed 7 GPS collars at 7 test sites, each representing a different habitat class, starting in late July of 2009. After 1 week the GPS collars were collected, locations were downloaded, and the collars were redeployed at new test sites. GPS test collars were deployed in all 7 habitat classes during the leaf-on season (May 15-October 15) for a 10 week testing period and in 4 habitat classes during the leaf-off season (October 14-May 14) for a 7 week testing period. Similar habitat classes, based on fix success results from

the leaf-on season and vegetation characteristics, were combined from 7 to 4 classes for the leaf-off season because of a limited number of available test collars.

Fix Success

I tested for differences in fix success among habitat classes for both manufacturers of collars during the leaf-on and leaf-off seasons using a χ^2 test of independence with correction for continuity. When a significant difference among habitat types was observed, I conducted *post-hoc* tests for equality of proportions to evaluate pairwise differences between habitat classes, and used a Bonferroni correction to control for Type I errors.

To determine which variables had the greatest influence on fix success (successful or not successful), I developed mixed effects logistic regression models to consider effects of both fixed (vegetation and topographic) and random (test site) variables. I considered test sites a random variable because I observed that there was non-independence between each attempted fix due to changes in weather, satellite position, and satellite availability (Hebblewhite et al. 2007). Predictor variables were transformed (Table 1.2) to meet assumptions of normality. Prior to modeling, I tested for multicollinearity among all variables using a Pearson correlation matrix and I retained all variables with $r < |0.9|$ per the recommendation of Burnham and Anderson (2010).

I identified 3 vegetation variables (canopy cover, basal area, and height) and two topographic variables (slope and aspect) that were reported to influence fix success during previous research (Moen et al. 1996, Dussault et al. 1999, Di Orio et al. 2003, Frair et al. 2004, D'Eon and Delparte 2005). I also included two vegetation variables (basal area of conifer trees and basal area of conifer trees + saplings) unique to my study

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area (e.g., regenerating, conifer dominated clearcuts). I chose 17 *a priori* models to be considered for the leaf-on season and 16 for the leaf-off season, omitting the total deciduous basal area variable. I evaluated the most plausible models using Akaike's information criterion for small sample sizes (AICc), because the number of estimable parameters was <40 for the model with the largest k (Anderson and Burnham 2002). Models with a ΔAICc <2.0 were considered top models (Burnham and Anderson 2010). I assessed the Akaike weights (w_i) and their goodness-of-fit using receiver operating characteristic (ROC) curves (Murtaugh 1996, Pearce and Ferrier 2000).

I was not interested in using the top model from the AICc analysis to predict fix success, but instead to determine which variable had the greatest influence on fix success. I tested whether the variable with greatest influence differed among habitat classes using one-way analysis of variance (ANOVA); where differences existed ($P < 0.10$) I used a Tukey Honestly Significant Difference (HSD) statistic to test for pairwise differences among habitat classes.

Location Error

I estimated the average error between true and estimated locations in each habitat class using ArcMap 9.3 and calculated the distance between each test site's true location and the estimated location using Hawth's Analysis Tools for ArcMap 9.3. I averaged distances across all test sites in the same habitat class. I compared average location error for each habitat class and location errors among habitat classes using a one-way ANOVA.

Data screening can reduce the overall location error, but if the screening process is too restrictive, excessive data loss can occur. To determine the best criteria for data

screening, I plotted the distance (i.e., location error) between the true location of each test

site and the locations recorded by test collars, against the corresponding DOP for each

location to determine if there was a visual breakpoint (Moen et al. 1996). I also evaluated

screening data using a combination of DOP and 2D/3D classifications by comparing the

data loss and reduction of location error for all habitat classes using different

combinations of DOP and 2D/3D. To ensure data loss was not severe, I decided *a priori*

that data loss exceeding 10% would be unacceptable. After screening the data, I

recalculated average location errors for each habitat class and tested for differences in

location error among all habitat classes using a one-way ANOVA; I used a Tukey HSD

post-hoc test to determine which pairs of habitat classes were significantly different.

Like fix success, environmental and topographic variables can influence location

error. Variables that block communication between satellites and GPS collars can reduce

fix success and cause an increase in location error by decreasing the number of available

satellites. Additionally, blocking satellites from view may also alter the satellite

geometry available to the GPS unit, potentially increasing the location error due to poor

satellite geometry. Therefore, I used the same environmental and topographic variables

used to evaluate fix success and added two variables describing the number of satellites

and their geometry (SATS, DOP, Table 1.2). I constructed 23 *a priori* mixed effects

linear regression models for the leaf-on season and 22 for the leaf-off season, omitting

total deciduous basal area. Similar to the fix success models, I considered mixed effects

models incorporating both fixed (vegetation, topographic, and satellite) and random (test

sites) variables. I tested for multicollinearity among variables using Pearsons's

correlation matrix. I used AICc to determine the most plausible model that influenced

location error.   Models with a ΔAICc <2.0 were considered top models, and Akaike

weights (w_i) were used to rank the models (Burnham and Anderson 2010).

RESULTS

Fix Success

I deployed Sirtrack collars at 10 test sites located within 6 habitat classes, during a

5 week (July-August) period in the leaf-on season in 2009 (Table 1.3). In contrast, Lotek

collars were deployed at 59 test sites representing 7 habitat classes during 10 weeks

(July-October) in the leaf-on season of 2009 (Table 1.3). During leaf-off, I deployed

both Lotek (n = 40 test sites) and Sirtrack (n = 7 test sites) collars in 4 habitat classes for

7 weeks (Table 1.4). Limited availability of Sirtrack test collars caused the discrepancy

in sampling effort between the manufacturers.

Total fix success (i.e., combined among all habitat classes) was significantly

different between Sirtrack and Lotek collars, using the specified fix schedule, for the leaf-

on season (P = 0.044) and the leaf-off season (P = 0.001). For Lotek collars, during the

leaf-on season (1 fix attempt per day schedule), lowest fix success was in the deciduous

regeneration habitat class (63%) and highest success occurred in the road habitat class

(100%, Table 1.5). In contrast, Sirtrack collars (4.5 hour fix attempt schedule), had the

lowest fix success in conifer dominated habitat classes (CM 67%, CR 69%) and highest

in the deciduous regeneration habitat class (100%, Table 1.5). During the leaf-off season,

Lotek collars had a range of 90-100% fix success across all habitat classes, whereas

Sirtrack had 100% fix success in all habitat classes (Table 1.5). Fix success was

significantly different across all habitat classes during the leaf-on season for both Lotek

Table 1.3. Number of test sites sampled and number of fix attempts for each habitat class separated by brand of GPS collar during the leaf-on season. Testing was conducted in northern Maine, USA during July – October 2009.

	Habitat classes[a]										
	CM		CR		DM		DR		PHR		PHE	
GPS collar brands	Sites	Fixes	Sites	Fixes	Sites	Fixes	Sites	Fixes	Sites	Fixes	Sites	Fixes
Lotek	10	60	10	60	9	54	5	30	9	54	7	40
Sirtrack	1	30	3	83	3	34	1	32	1	25	N/A[b]	N/A[b]

Table 1.3 continued

	Habitat classes[a]			
	RD		Total	
GPS collar brands	Sites	Fixes	Sites	Fixes
Lotek	9	54	59	352
Sirtrack	1	26	10	230

[a] Habitat class abbreviations: CM = mature conifer, CR = conifer regeneration (<12 m tall), DM = mature deciduous, DR = deciduous regeneration (<12 m tall), PHR = recent partial harvest (1-10 years postharvest), PHE = established partial harvest (11-21 years postharvest), RD = road edge
[b] Sirtrack collars were not tested in established partial harvest habitat classes because of limited number of collars

Table 1.4. Number of test sites sampled and number of fix attempts for each habitat class separated by brand of GPS collar during the leaf-off season. Testing was conducted in northern Maine, USA during November – December 2009 and February 2010.

	Habitat classes[a]									
	C		DM/PH		DR		RD		Total	
GPS collar brands	Sites	Fixes	Sites	Fixes	Sites	Fixes	Sites	Fixes	Sites	Fixes
Lotek	10	60	10	60	10	60	10	60	40	240
Sirtrack	1	36	2	68	2	66	2	69	7	239

[a] Habitat class abbreviations: C = conifer (combination of mature conifer and conifer regeneration), DM/PH = combination of mature deciduous and recent and established partial harvest, DR = deciduous regeneration (<12 m tall), RD = road edge

Table 1.5. Fix success a) of Lotek and Sirtrack collars in habitat classes during the leaf-on and leaf-off seasons and b) P-values from post hoc pairwise comparisons of fix success (Lotek only) for 11 habitat class pairs during the leaf-on season in northern Maine, USA 2009-2010.

a)

GPS collar brands	Habitat classes												
	Leaf-on[a]								Leaf-off[b]				
	CM	CR	DM	DR	PHR	PHE	RD	Total	C	DM/PH	DR	RD	Total
Lotek	83%	85%	89%	63%	93%	90%	100%	87%	90%	95%	93%	100%	95%
Sirtrack	67%	69%	82%	100%	88%	N/A[c]	92%	80%	100%	100%	100%	100%	100%

b)

GPS collar brand	CM-CR	CM-DM	CR-DR	DM-DR	PHE-PHR	CM-RD	CR-RD	DM-RD	DR-RD	PHE-RD	PHR-RD
Lotek	1	0.56	0.039	0.012	0.943	0.005	0.009	0.036	<0.001[d]	0.063	0.126

[a] Habitat class abbreviations: CM = mature conifer, CR = conifer regeneration (<12 m tall), DM = mature deciduous, DR = deciduous regeneration (<12 m tall), PHR = recent partial harvest (1-10 years postharvest), PHE = established partial harvest (11-21 years postharvest), RD = road edge

[b] Habitat class abbreviations: C = conifer (combination of mature conifer and conifer regeneration), DM/PH = combination of mature deciduous and recent and established partial harvest, DR = deciduous regeneration (<12 m tall), RD = road edge

[c] Sirtrack collars were not tested in established partial harvest habitat classes because of limited number of collars

[d] Indicates significance difference (P < 0.10 using a Bonferroni adjusted α < 0.002)

(P = 0.022) and Sirtrack (P ≤ 0.001). However, there was no difference during the leaf-off season for either Lotek (P = 0.123) or Sirtrack (100% fix success).

I evaluated pairwise differences in fix success for Lotek collars between 11 habitat class pairings during the leaf-on season (Table 1.5). The results of this analysis were used to determine habitat classes that were suitable to combine for the leaf-off season. Road was significantly different from deciduous regeneration (P ≤ 0.001, Bonferroni adjusted α < 0.002), had equivocal p-values with both mature conifer (P = 0.005) and conifer regeneration (P = 0.009), and therefore, was not combined with other habitat classes during the leaf-off season. Deciduous regeneration was evaluated independently of other habitat classes for the leaf-off season because it had the lowest fix success (63%) and there were few sites sampled (n = 5), increasing the chances of making Type II errors. I created a conifer habitat class (C) for the leaf-off season by combining mature conifer and regenerating conifer because they had similar fix success (P = 1.00) and were both conifer dominated. Recent and established partial harvests had similar fix success (P = 0.943) and were both composed of mixed or deciduous dominated vegetation, thus I combined those two classes with DM to create the DM/PH habitat class for the leaf-off season.

The top ranked mixed effects model was composed of canopy cover (CC) as the single variable, which carried >0.25 of the weight of evidence during both seasons (Tables 1.6 and 1.7). The ROC score for the CC model for both seasons was 0.7, which suggests acceptable model fit (Hosmer and Lemeshow 2000). Canopy closure occurred in the top 8 models in the leaf-on season, the top 6 models in the leaf-off season, and all of those models had ROC scores ≥0.7. The top four models in the leaf-on season and the

Table 1.6. Model selection results ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) for the leaf-on season among 17 *a priori* candidate models used to examine the influence of vegetation and topographical variables on fix success of GPS collars in northern Maine, USA 2009-2010.

Model[a]	Rank	K[c]	Log-L[c]	AICc[c]	ΔAICc[c]	Model Likelihood	w_i[c]
CC	1	3	-116.7	239.8	0.0	1.000	0.292
CC + Tree_BA	2	4	-115.8	240.3	0.5	0.777	0.227
CC + C_To	3	4	-116.4	241.5	1.7	0.426	0.125
CC + H	4	4	-116.5	241.7	1.9	0.386	0.113
CC + C_Tr	5	4	-116.7	242.1	2.3	0.316	0.092
CC + Tree_BA + H	6	5	-115.7	242.5	2.7	0.260	0.076
CC + H + C_To	7	5	-116.3	243.7	3.9	0.143	0.042
CC + H + C_Tr	8	5	-116.5	244.1	4.3	0.117	0.034
C_To	9	3	-125.9	258.2	18.4	<0.001	<0.001
1 + Test_site[b]	10	2	-127.3	258.8	19.0	<0.001	<0.001
C_Tr	11	3	-126.5	259.4	19.6	<0.001	<0.001
Slope	12	3	-126.6	259.6	19.8	<0.001	<0.001
Tree_BA	13	3	-126.8	260.0	20.2	<0.001	<0.001
D_To	14	3	-126.9	260.2	20.4	<0.001	<0.001
H	15	3	-127.3	261.0	21.2	<0.001	<0.001
Global	16	25	-94.29	278.0	38.1	<0.001	<0.001
Aspect + Slope + (Aspect×Slope)	17	19	-109.3	276.1	36.3	<0.001	<0.001

Table 1.6. continued

[a] Model abbreviations: Canopy cover (CC), basal area of coniferous and deciduous trees (Tree_BA), average tree height (H), slope of each test site (Slope), aspect of each test site (Aspect), basal area of conifer trees (C_Tr), total basal area of conifer trees and saplings (C_To), and total basal area of deciduous trees and saplings (D_To).

[b] The random variable, Test_site, is only listed in the 10th ranked model, but is a part of each model.

[c] Number of estimable parameters (K), log likelihood (Log-L), AIC adjusted for small sample size (AICc), AICc difference of each model relative to the model with the smallest AICc (ΔAICc), and the Akaike weight, which is the probability that the model is the best model (w_i).

Table 1.7. Model selection results ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) for the leaf-off season among 16 *a priori* candidate models used to examine the influence of vegetation and topographical variables on fix success of GPS collars in northern Maine, USA 2009-2010.

Model[a]	Rank	K[c]	Log-L[c]	AICc[c]	ΔAICc[c]	Model Likelihood	w_i[c]
CC	1	3	-47.6	101.9	0.0	1.000	0.256
CC + C_To	2	4	-47.31	103.8	1.9	0.387	0.099
CC + H	3	4	-47.33	103.8	1.9	0.380	0.097
CC + Tree_BA + H	4	5	-46.08	103.9	2.1	0.357	0.092
CC + Tree_BA	5	4	-47.46	104.1	2.2	0.334	0.085
CC + C_Tr	6	4	-47.51	104.2	2.3	0.317	0.081
C_To	7	3	-48.91	104.5	2.6	0.270	0.069
1 + Test_site[b]	8	2	-50.47	105.3	3.4	0.183	0.047
Tree_BA	9	3	-49.42	105.5	3.6	0.162	0.042
C_Tr	10	3	-49.55	105.8	3.9	0.142	0.036
CC + H + C_To	11	5	-47.05	105.9	4.0	0.135	0.035
CC + H + C_Tr	12	5	-47.33	106.4	4.6	0.102	0.026
Slope	13	3	-50.29	107.2	5.4	0.068	0.017
H	14	3	-50.36	107.4	5.5	0.063	0.016
Aspect + Slope + (Aspect×Slope)	15	17	-40.18	142.2	40.3	<0.001	<0.001
Global	16	22	-35.5	174.5	72.7	<0.001	<0.001

Table 1.7. continued

[a] Model abbreviations: Canopy cover (CC), basal area of coniferous and deciduous trees (Tree_BA), average tree height (H), slope of each test site (Slope), aspect of each test site (Aspect), basal area of conifer trees (C_Tr), and basal area of conifer trees and saplings (C_To).

[b] The random variable, Test_site, is only listed in the 8th ranked model, but is a part of each model.

[c] Number of estimable parameters (K), log likelihood (Log-L), AIC adjusted for small sample size (AICc), AICc difference of each model relative to the model with the smallest AICc (ΔAICc), and the Akaike weight, which is the probability that the model is the best model (w_i).

top three models in the leaf-off season had ΔAICc <2.0. Additionally, the same top

models in both seasons had 0.76 total weight of evidence in the leaf-on season and 0.45

during the leaf-off season.

Canopy cover was the only variable to appear in all models with ΔAICc <2.0 and

therefore had the greatest influence on fix success during both seasons. Because CC had

the greatest influence on fix success, I conducted post hoc tests to compare CC among

habitat classes during each season. Values of CC were significantly different across all

habitats during both the leaf-on ($P \leq 0.001$) and leaf-off ($P = 0.001$) seasons. During the

leaf-on season, road habitat had the lowest canopy cover ($\bar{x} = 65.8\%$, SE = 11.9, Table

1.8) and was significantly different from all other habitat classes ($P \leq 0.015$). Pairwise

comparisons among habitat classes did not indicate any other significant differences ($P \geq$

0.888). During the leaf-off season, the conifer habitat class had the highest canopy cover

($\bar{x} = 90\%$, SE = 6.8, Table 1.8) and was significantly different from all other habitat

classes ($P \leq 0.023$). No other significant differences among habitat classes were evident

($P \geq 0.815$).

Location Error

I plotted location error vs. DOP for all four combinations of collar manufacturer

and season to determine a global DOP cutoff value to use for data screening (Figure 1.1).

Dilution of precision values ≥10 for Sirtrack (leaf-on season) and Lotek (leaf-off season)

collars represented 75% and 63% of all locations with location error ≥100 m,

respectively. During the leaf-on season, DOP ≥10 for Lotek collars only represented

44% of all location errors ≥100 m, but a DOP ≥6 represented 66% of location errors ≥100

m. During the leaf-off season, there was not a logical DOP cutoff value for Sirtrack

Table 1.8. Mean values of vegetative variables above test collars measured in 7 habitat classes during the leaf-on season (May 15 – October 14) and 4 habitat classes during the leaf-off season (October 15 – May 14) in northern Maine, USA 2009-2010. Overhead canopy cover was the only variable in all top models (ΔAICc <2.0) during both seasons.

Variables[a]	Leaf-on							Leaf-off			
	CM[b]	CR[b]	DM[b]	DR[b]	PHR[b]	PHE[b]	RD[b]	C[b]	DM/PH[b]	DR[b]	RD[b]
CC (%)	99.3	90.9	99.3	99.8	96.8	97.4	65.8	90	50.9	44.1	39.5
± SE	0.3	4.8	0.3	0.2	1.5	1.9	11.9	6.8	12	8.2	8.9
H (m)	14.8	8.7	16.5	10.9	12.9	12.3	10.8	13.2	15.5	11.0	10.7
± SE	1.3	0.6	1.0	0.8	1.0	1.4	1.1	1.6	1.2	0.7	1.1
Tr_BA (m^2/ha)	37.6	12.8	35.4	18.9	18.0	20.6	10.6	20.0	29.4	18.0	10.6
± SE	4.3	1.6	2.6	2.4	2.7	4.1	3.6	4.9	4.1	2.4	3.6
D_To (m^2/ha)	3.0	5.4	24.4	19.1	13.3	16.3	7.6	2.6	18.6	18.6	7.6
± SE	1.0	2.5	3.6	3.1	2.3	3.8	2.7	1.3	4.5	3.0	2.7
C_Tr (m^2/ha)	32.2	10.6	6.2	6.2	4.2	6.9	4.6	24.2	9.4	6.0	4.6
± SE	3.9	2.8	2.4	1.5	1.9	1.9	1.9	6.0	2.4	1.5	1.9
C_To (m^2/ha)	36.8	26.8	7.6	7.3	9.1	10.3	7.2	34.6	11.8	7.0	7.2
± SE	3.6	4.4	2.5	1.7	3.6	2.9	2.2	4.6	3.4	1.7	2.2

Table 1.8. continued

[a] Variable abbreviations: Canopy cover (CC), basal area of coniferous and deciduous trees (Tree_BA), average tree height (H), basal area of conifer trees (C_Tr), total basal area of conifer trees and saplings (C_To), and total basal area of deciduous trees and saplings (D_To).

[b] Habitat class abbreviations: CM = mature conifer, CR = conifer regeneration (<12 m tall), DM = mature deciduous, DR = deciduous regeneration (<12 m tall), PHR = recent partial harvest (1-10 years postharvest), PHE = established partial harvest (11-21 years postharvest), RD = road edge, C = conifer (combination of mature conifer and conifer regeneration), DM/PH = combination of mature deciduous and recent and established partial harvests

Figure 1.1. Location error (m) across a range of dilution of precision (DOP) values for 2 collar manufacturers during leaf-on and leaf-off seasons in northern Maine, USA 2009-2010.

a) Lotek leaf-on (59 test sites in 7 habitat classes)
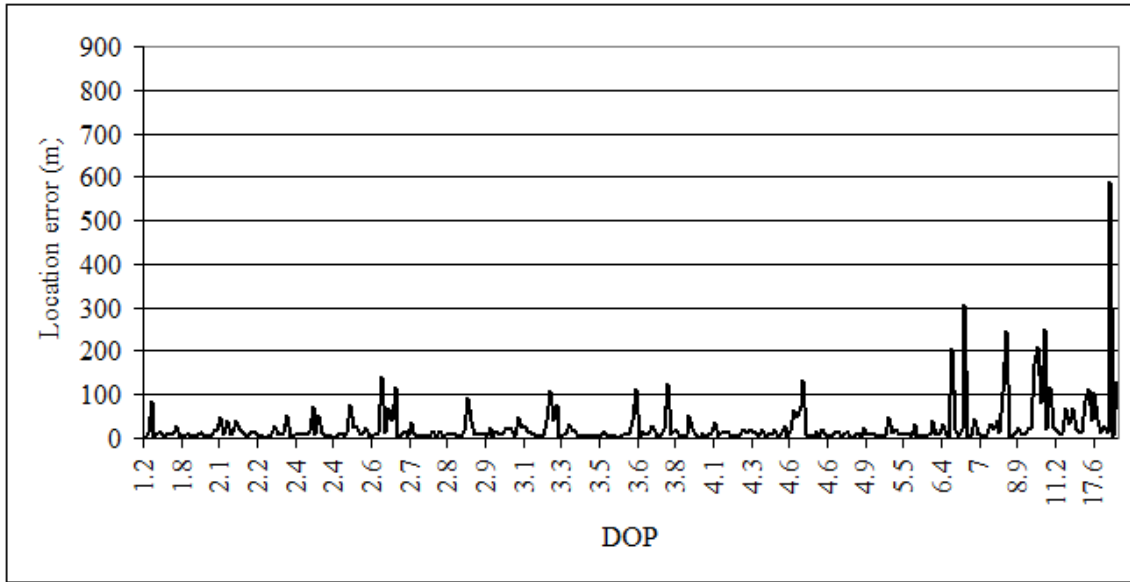
b) Sirtrack leaf-on (10 test sites in 6 habitat classes)
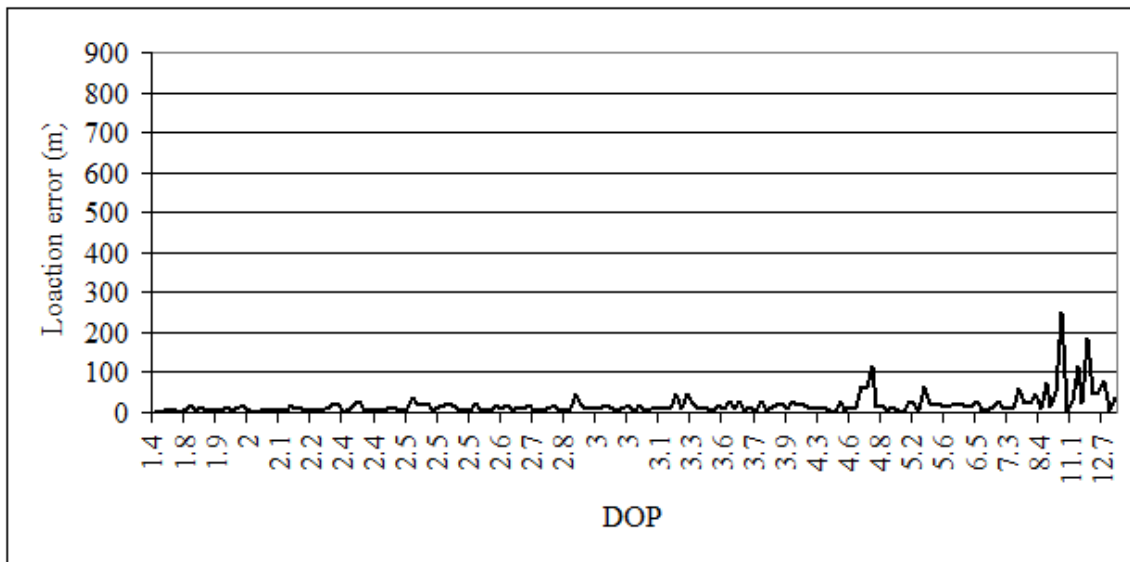
Figure 1.1. continued

c) Lotek leaf-off (40 test sites in 4 habitat classes)
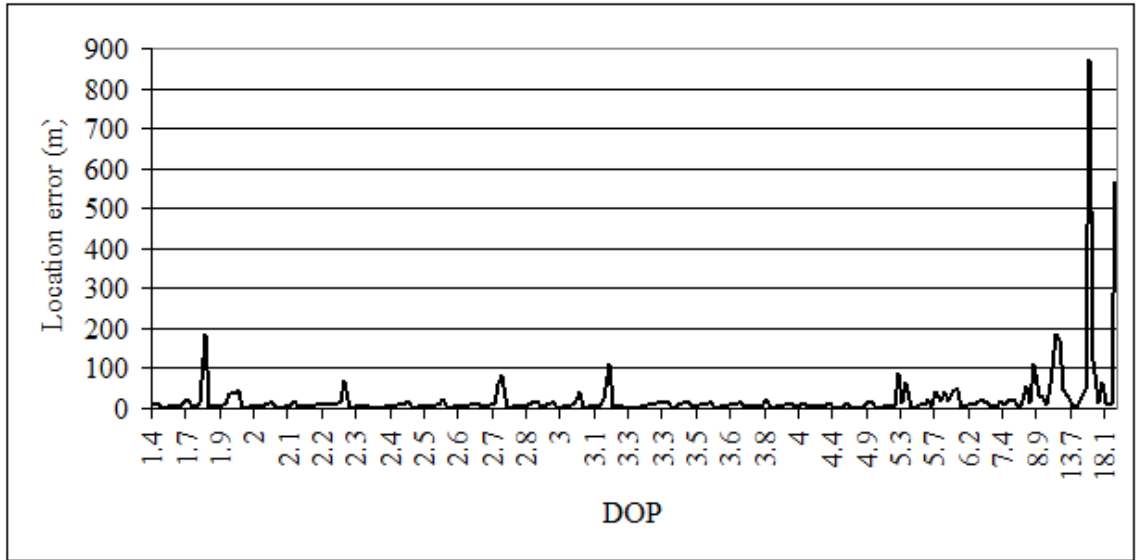
d) Sirtrack leaf-off (7 test sites in 4 habitat classes)
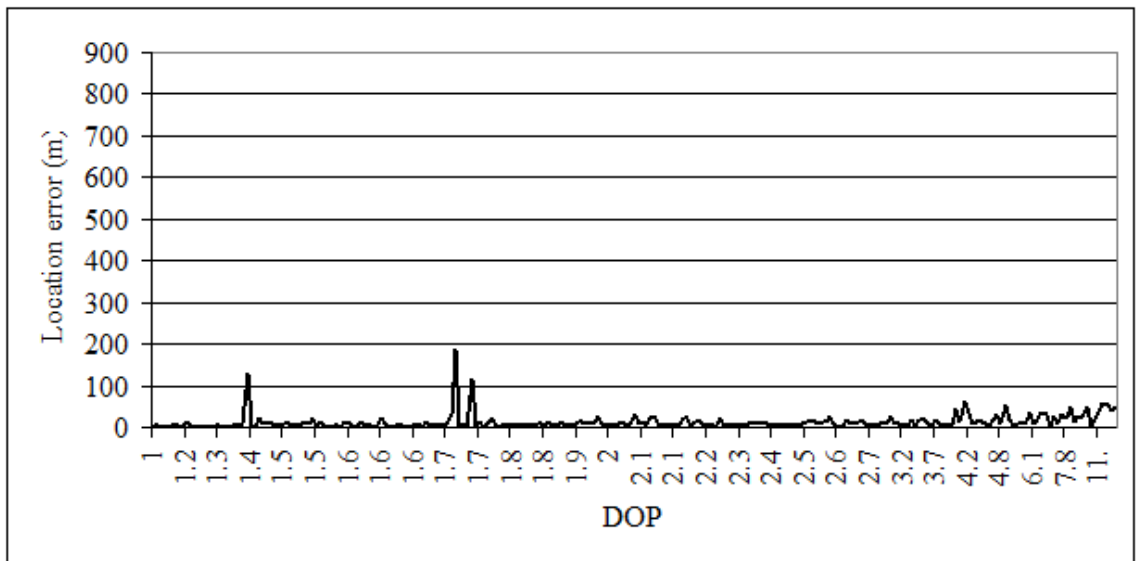
collars. I selected DOP ≥10 as a global cutoff value to eliminate large location errors

because it appeared to be the best visual breakpoint (Moen et al. 1996) for two

combinations (Lotek leaf-on and Sirtrack leaf-off) to balance data loss and decrease

location error. Prior to screening, 3.4% of the total number of locations from all seasons

and collar manufacturers had a location error of ≥100 m. After screening with a cutoff of

DOP ≥10, only 1.8% of all locations had a location error ≥100 m. The screening process

resulted in a 3.8% loss of locations and 46.9% of locations ≥100 m were removed.

I used the 2D/3D classification reported by Lotek collars to further screen

locations. Two dimensional locations are less likely to be accurate than 3D locations

because they utilize only 3 satellites, whereas 3D locations use ≥4 satellites (Rempel et

al. 1995, Moen et al. 1996, Rodgers et al. 1996). For data collected using Lotek collars, I

combined the DOP ≥10 cutoff with the 2D/3D classification to remove 2D locations with

DOP ≥10. This resulted in data loss of only 3.6% for the leaf-on season and 3.5% for the

leaf-off season (Table 1.9). Sirtrack collars do not distinguish between 2D and 3D

locations; therefore, only locations with DOP ≥10 were removed. For each combination

of season and manufacturer, data loss never exceeded 6% and location error decreased by

as much as 8.1 m after data screening (Table 1.9).

Total location error after screening (i.e., combined among all habitat classes) was

not significantly different between Sirtrack and Lotek collars during the leaf-on (P =

0.663) or the leaf-off (P = 0.5) seasons. Additionally, there were no significant

differences in location error among all habitat classes during both seasons for Sirtrack

collars (leaf-on P = 0.498, leaf-off P = 0.364); however, location errors for Lotek collars

were significantly different across habitat classes during both seasons (leaf-on P = 0.006,

Table 1.9. Mean location error (m) during leaf-on and leaf-off seasons for Lotek and Sirtrack brands of GPS collars before (top value for each habitat class) and after (bottom value for each habitat class) data screening in northern Maine, USA 2009-2010. Screening criteria for Lotek collars removed locations classified as 2D and DOP ≥10. Screening criteria for Sirtrack collars removed locations classified as DOP ≥10.

Leaf-on season			Leaf-off season		
Habitat class[a]	Lotek Mean ± (SE)	Sirtrack Mean ± (SE)	Habitat class[b]	Lotek Mean ± (SE)	Sirtrack Mean ± (SE)
CM	23.2 (4.98) 18.4 (3.19)	18.1 (2.9) 18.1 (2.9)	C	13.1 (3.37) 9.5 (1.46)	12.8 (1.79) 12.8 (1.79)
CR	14.3 (2.71) 12.2 (1.78)	18.9 (3.15) 16.3 (2.71)	DM/PH	19.5 (4.08) 16.3 (2.92)	11.2 (1.9) 10.1 (1.8)
DM	27.1 (6.32) 24.6 (6.09)	40.8 (8.89) 16.1 (2.84)	DR	49.6 (18.41) 24.4 (4.76)	10.8 (2.09) 9.7 (2)
DR	10.3 (1.88) 8.7 (0.98)	20.5 (5.83) 15.2 (2.55)	RD	6.8 (0.65) 6.8 (0.65)	15.4 (3.13) 14.9 (3.14)
PHE	41.8 (16.32) 26.1 (4.94)	N/A[c] N/A[c]	Total	22.1 (4.82) 14 (1.48)	12.5 (1.22) 11.8 (1.2)
PHR	34 (6.71) 31.3 (6.26)	13 (2.12) 11.7 (1.98)	Data loss[d]	3.5%	2.5%
RD	21.5 (7.22) 17.3 (6)	10.5 (2.05) 10.5 (2.05)			
Total	25.3 (2.89) 20.5 (1.96)	20.3 (2.03) 15 (1.15)			
Data loss[d]	3.6%	6%			

[a] Habitat class abbreviations: CM = mature conifer, CR = conifer regeneration (<12 m tall), DM = mature deciduous, DR = deciduous regeneration (<12 m tall), PHR = recent partial harvest (1-10 years postharvest), PHE = established partial harvest (11-21 years postharvest), RD = road edge

Table 1.9 continued

leaf-off P ≤ 0.001). Recent partial harvests had the largest location error ($\bar{x}$ = 31.32 m,

SE = 6.26) for Lotek collars during the leaf-on season, and was significantly different

from conifer regeneration ($\bar{x}$ = 12.2 m, SE = 1.78, P = 0.006) and road edge ($\bar{x}$ = 17.3 m,

SE = 6, P = 0.006), but all other habitat pairs were not significantly different. For Lotek

collars during the leaf-off season, deciduous regeneration had the largest location error

($\bar{x}$ = 24.4 m, SE = 4.76) and was different from conifer ($\bar{x}$ = 9.5 m, SE = 1.46, P =

0.004) and road edge ($\bar{x}$ = 6.8 m, SE = 0.65, P ≤ 0.001). Location error for road edge

was significantly lower than for mature deciduous and both partial harvest habitat classes

($\bar{x}$ = 16.3 m, SE = 2.92, P = 0.006), but did not differ significantly from other habitat

classes for Lotek collars during the leaf-off season.

I ranked 23 mixed effects models for the leaf-on season (Table 1.10) and 22

models for the leaf-off season (Table 1.11) using AICc to examine their influence on

location error. The top ranked model in both seasons was SATS + DOP, with Akaike

weights of 0.71 in the leaf-on season and 0.745 in the leaf-off season, indicating the

probability these are the top models out of the model set in each season are 71% and

75%, respectively.   The second ranked model was CC + DOP + SATS in both seasons,

with Akaike weights of 0.29 in the leaf-on season and 0.149 in the leaf-off season.

Similarly, the variables with the greatest influence on location error during both seasons

were SATS and DOP, with both variables appearing in all models ΔAICc <2.0 (Table

1.11). Of all vegetative and topographical variables considered, canopy cover had the

greatest influence on location error.

Table 1.10. Model selection results ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) for the leaf-on season among 23 *a priori* candidate models used to examine the influence of vegetation, topographical, and satellite variables on location error in northern Maine, USA 2009-2010.

Model[a]	Rank	K^c	Log-L^c	$AICc^c$	$\Delta AICc^c$	Model Likelihood	w_i^c
SATS + DOP	1	4	-421.3	851.341	0.00	1.000	0.71
CC + DOP + SATS	2	5	-421	853.132	1.79	0.408	0.29
SATS	3	3	-430.1	866.636	15.30	<0.001	<0.001
CC + SATS	4	4	-429.8	868.341	17.00	<0.001	<0.001
CC + DOP	5	4	-435.1	878.941	27.60	<0.001	<0.001
DOP	6	3	-437.6	881.636	30.30	<0.001	<0.001
CC	7	3	-441.4	889.236	37.90	<0.001	<0.001
Tree_BA	8	3	-442.3	891.036	39.70	<0.001	<0.001
1 + Test_site[b]	9	2	-443.5	891.214	39.87	<0.001	<0.001
H	10	3	-442.5	891.436	40.10	<0.001	<0.001
CC + H	11	4	-441.5	891.741	40.40	<0.001	<0.001
D_To	12	3	-442.9	892.24	40.90	<0.001	<0.001
CC + Tree BA	13	4	-442.3	893.341	42.00	<0.001	<0.001
CC + C_To	14	4	-443.4	895.541	44.20	<0.001	<0.001

Table 1.10. continued

Model[a]	Rank	K[c]	Log-L[c]	AICc[c]	ΔAICc[c]	Model Likelihood	w_i[c]
Slope	15	3	-445	896.436	45.10	<0.001	<0.001
CC + Tree_BA + H	16	5	-442.8	896.732	45.39	<0.001	<0.001
C_To	17	3	-445.9	898.236	46.90	<0.001	<0.001
CC + H + C_To	18	5	-443.7	898.532	47.19	<0.001	<0.001
CC + C_Tr	19	4	-445.3	899.341	48.00	<0.001	<0.001
C_Tr	20	3	-447.6	901.636	50.30	<0.001	<0.001
CC + H + C_Tr	21	5	-445.3	901.732	50.39	<0.001	<0.001
Aspect + Slope + (Aspect×Slope)	22	19	-438.7	934.887	83.55	<0.001	<0.001
Global	23	27	-424.1	950.97	99.63	<0.001	<0.001

[a] Model abbreviations: Canopy cover (CC), basal area of coniferous and deciduous trees (Tree_BA), average tree height (H), slope of each test site (Slope), aspect of each test site (Aspect), basal area of conifer trees (C_Tr), total basal area of conifer trees and saplings (C_To), total basal area of deciduous trees and saplings (D_To), number of satellites used to calculate a location (SATS), and the dilution of precision (DOP).

[b] The random variable, Test_site, is only listed in the 9th ranked model, but is a part of each model.

[c] Number of estimable parameters (K), log likelihood (Log-L), AIC adjusted for small sample size (AICc), AICc difference of each model relative to the model with the smallest AICc (ΔAICc), and the Akaike weight, which is the probability that the model is the best model (w_i).

Table 1.11. Model selection results ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) for the leaf-off season among 22 *a priori* candidate models used to examine the influence of vegetation, topographical, and satellite variables on location error in northern Maine, USA 2009-2010.

Model[a]	Rank	K[c]	Log-L[c]	AICc[c]	ΔAICc[c]	Model Likelihood	w_i[c]
SATS + DOP	1	4	-305.1	619.343	0.00	1.000	0.7451
CC + DOP + SATS	2	5	-305.4	622.565	3.22	0.200	0.1488
SATS	3	3	-308.5	623.667	4.32	0.115	0.0858
CC + SATS	4	4	-308.7	626.543	7.20	0.027	0.0204
DOP	5	3	-319.3	645.267	25.92	<0.001	<0.001
CC + DOP	6	4	-320	649.143	29.80	<0.001	<0.001
Slope	7	3	-323.5	653.667	34.32	<0.001	<0.001
H	8	3	-323.5	653.667	34.32	<0.001	<0.001
1 + Test_site[b]	9	2	-324.9	654.124	34.78	<0.001	<0.001
Tree_BA	10	3	-324	654.667	35.32	<0.001	<0.001
CC + Tree BA	11	4	-324	657.143	37.80	<0.001	<0.001
CC + H	12	4	-324.2	657.543	38.20	<0.001	<0.001
CC	13	3	-325.5	657.667	38.32	<0.001	<0.001
C_To	14	3	-326.8	660.267	40.92	<0.001	<0.001

Table 1.11. continued

Model[a]	Rank	K[c]	Log-L[c]	AICc[c]	ΔAICc[c]	Model Likelihood	w_i[c]
CC + Tree_BA + H	15	5	-324.5	660.765	41.42	<0.001	<0.001
CC + C_To	16	4	-326	661.143	41.80	<0.001	<0.001
CC + H + C_To	17	5	-325.2	662.165	42.82	<0.001	<0.001
C_Tr	18	3	-328.7	664.067	44.72	<0.001	<0.001
CC + H + C_Tr	19	5	-326.3	664.365	45.02	<0.001	<0.001
CC + C_Tr	20	4	-328.9	666.943	47.60	<0.001	<0.001
Aspect + Slope + (Aspect×Slope)	21	17	-317.6	697.018	77.68	<0.001	<0.001
Global	22	24	-304.7	737.400	118.06	<0.001	<0.001

[a] Model abbreviations: Canopy cover (CC), basal area of coniferous and deciduous trees (Tree_BA), average tree height (H), slope of each test site (Slope), aspect of each test site (Aspect), basal area of conifer trees (C_Tr), and basal area of conifer trees and saplings (C_To), number of satellites used to calculate a location (SATS), and the dilution of precision (DOP).

[b] The random variable, Test_site, is only listed in the 9th ranked model, but is a part of each model.

[c] Number of estimable parameters (K), log likelihood (Log-L), AIC adjusted for small sample size (AICc), AICc difference of each model relative to the model with the smallest AICc (ΔAICc), and the Akaike weight, which is the probability that the model is the best model (w_i).

DISCUSSION

Overhead canopy cover was the most influential variable on fix success during both leaf-on and leaf-off seasons, and is consistent with previous studies which concluded that fix success decreases as canopy cover above GPS collars increases (Moen et al. 1996, Frair et al. 2004, Hebblewhite et al. 2007, Hansen and Riggs 2008). During the leaf-on season, road edge had the lowest canopy cover (67%), and the highest fix success (100%) of all habitat classes. During the leaf-off season, conifer habitat had the highest canopy cover (90%) and the lowest fix success (90%) among all habitat classes. Other studies have presented evidence that terrain can also influence fix success (D'Eon et al. 2002, Cain et al. 2005), but topographic variables did not influence fix success in my study where little elevation change (250-550 m) and moderate slope ($\leq 38°$) were present.

The number of satellites used to calculate a fix and their geometry had the greatest influence on location error. Similar results were reported in Minnesota, where a key factor affecting location error was a decrease in the number of satellites (Moen et al. 1997), and in Quebec where satellite geometry was related to location error (Dussault et al. 2001). Other studies have evaluated the number of satellites used to calculate a fix and their geometry on location error, but my consideration of both variables in mixed models is unique (but see Moen et al. 1997). Accuracy of locations increased with greater numbers of satellites, and there was a distinct advantage of using ≥ 4 satellites. A fourth satellite enables a location to be calculated using elevation data, which greatly increases accuracy (Rempel et al. 1995), and ≥ 5 satellites allows the GPS collar to choose the best satellite geometry (Moen et al. 1997, Dussault et al. 2001). Additionally,

satellites spaced farther apart yield smaller triangulation error and have better geometry than satellites which are in close proximity (Moen et al. 1997).

The only non-satellite variable influencing location error was overhead canopy cover. Canopy cover influences location error by blocking available satellites and altering the resulting geometry of useable signals. This result is consistent with previous conclusions that increased location error was caused by reduced satellite availability under dense canopy (Moen et al. 1996). Similarly, Di Orio et al. (2003) reported that habitat types with high canopy closure had the largest location errors.

Fix success between manufacturers was significantly different during both seasons. This may have been caused by different fix attempt schedules. Shorter intervals between fix attempts may lead to a greater percentage of successful fixes (Cain et al. 2005). GPS receivers will use the previous location's satellite geometry to begin searching for satellites, and they have a time-out function where the GPS receiver will shut off if a location has not been successful by the set time (Cain et al. 2005). Therefore, when location attempts are closer together, the satellite geometry has less time to change, thus increasing the chance of a successful fix before time-out. This explanation is logical during the leaf-off season when Sirtrack (i.e., shorter fix attempt interval) had a higher fix success than Lotek, but not during the leaf-on season when the opposite was true. An alternative explanation to describe the fix success difference between manufacturers may be sample size. A trapping effort for lynx occurred during the same time as test collars were deployed, resulting in fewer available test collars from Sirtrack. Consequently, Sirtrack collars were tested in 49 fewer test sites than Lotek, in 1 less habitat class, during only half the duration that Lotek collars were tested, and

resulted in 122 fewer fix attempts than Lotek test collars during the leaf-on season. During the leaf-off season, Sirtrack collars were tested in 33 fewer test sites than Lotek, which may have contributed to the difference in fix success between the 2 manufacturers.

Deciduous regeneration (DR) had the lowest fix success (63%) and was significantly different from all other habitat classes, except mature conifer (83%), during the leaf-on season. Canopy cover was very high (100%) in this habitat; however, all other habitat classes, except for road (65.8%), had relatively high canopy cover (range 91-100%). The low fix success in this habitat class may be explained by leaf area or density, a vegetation variable that I did not measure. Di Orio et al. (2003) suggested that canopy density created by the different foliage characteristics of species may influence fix success more than canopy cover. One species found commonly in DR, but not in other habitat classes, was striped maple (*Acer pennsylvanicum*). This species has leaves as large as 18x18 cm (Little 1980), which may interfere more with transmissions between GPS collars and satellites, than species with smaller leaves or needles. Additionally, DR was not sampled as intensively as other habitats during the leaf-on season because of limited test collars. The smaller number of test sites, and consequently the smaller number of fix attempts in the DR habitat class may have contributed to its lowered fix success compared to the other habitat classes.

Similar studies have concluded canopy cover as a leading factor influencing fix success, but few have been in similar habitat and topography as this study (see Moen et al. 1997 and Rempel et al. 1995). Conducted in a study area with similar tree species, but in an experimental forest with evenly spaced trees, Rempel et al. (1995) reported that fix success decreased as canopy cover increased. In contrast, Dussault et al. (1999) had

similar tree species as my study, but concluded that tree height caused reduced fix success. This discrepancy may be explained by differences in canopy cover between the two study areas. Their study area had an average canopy cover in coniferous stands in the winter of 27% and 21% during the summer, whereas canopy cover in this study area during the winter in conifer dominated stands was 90% and was 95% during the summer. Similar tree species composition between study areas may lead to similar influences on fix success, but should not be assumed because of potential differences in vegetative structure that may influence fix success.

Missed locations caused by dense canopy can produce habitat-dependent bias in habitat use analyses. Habitat classes that decrease signal transmission from satellites to GPS collars may be underrepresented because of missed locations (Nams 1989, Rempel et al. 1995). For example, during the leaf-off season, the conifer habitat class had the greatest chance of missed locations because it had the lowest fix success (Table 1.5) and highest canopy cover (Table 1.8). This is a concern because the conifer habitat class includes conifer dominated clearcuts that lynx prefer during the leaf-off (Fuller et al. 2007, Vashon et al. 2008b) and leaf-on seasons (Vashon et al. 2008b), which could bias habitat selection in companion studies using GPS collars (Chapter 3). To correct for missed locations it is suggested that researchers estimate the number of missed locations in each habitat class by using observed locations (i.e., GPS collar locations) divided by known fix success values for each habitat class (Table 1.5). Following this approach, I will correct for habitat-dependent bias caused by GPS collars in Chapter 3.

Habitat selection and spatial analyses can be biased when location error exceeds the mean habitat patch size (Rettie and McLoughlin 1999). Large location errors can

cause misrepresentation of habitat use, especially when the error around a location includes more than one habitat class (Rettie and McLoughlin 1999). A common method to address this problem is to construct error polygons around each location (Nams 1989, Samuel and Kenow 1992, Rettie and McLoughlin 1999). Location errors recorded from test GPS collars (Table 1.9) can be used to construct error polygons for every season, collar manufacturer, and habitat class to reduce habitat dependent biases in companion studies (Chapter 3).

Another method to further decrease error associated with GPS collars is data screening, which can be used to increase overall accuracy of GPS collar locations. Proper data screening is effective at removing large outliers, which will increase the overall accuracy of locations, while balancing data loss (Dussault et al. 2001, D'Eon and Delparte 2005). My screening criteria for Lotek collars (2D and DOP ≥10) is in agreement with Lewis et al. (2007), who concluded the best screening criteria was to remove 2D locations at a specific DOP cutoff.

Despite testing fix success and location error for collar manufacturers, seasons, and habitat classes with fixed test collars, not all errors associated with GPS collars may be known. Lotek test collars recorded an overall fix success of 87% during the leaf-on season and 90% during the leaf-off season, but Lotek collars worn by lynx only recorded successful fixes 55% and 70% of total attempts during the leaf-on and leaf-off seasons respectively. Additionally, Sirtrack collars worn by lynx missed 32% and 34% more locations during the leaf-on season and leaf-off season, respectively, than the Sirtrack test collars. Animal activity may help explain the discrepancy between GPS collars worn by lynx and fixed test collars. Animal activity such as bedding (Moen et al. 1996, Bowman

et al. 2000, Schwartz et al. 2009, Mattisson et al. 2010) and movement (Graves and Waller 2006) have been suggested in previous studies to cause a decrease in fix success. Antenna orientation, affected by bedding and movement, may specifically be a leading cause of the decline of fix success. As antenna orientation moves from a vertical to horizontal position, fix success will decrease (D'Eon et al. 2002, Belant 2009). Thus, lynx activities such as bedding (i.e., laying on their side) or feeding (i.e., head at a downward angle) may decrease fix success. A decrease in fix success caused by low angles of collar orientation may be further exacerbated by an interaction with canopy cover (Heard et al. 2008), the leading cause of decrease in fix success in this study. Unfortunately, the scope of my study did not allow for investigation of this source of error, but future research should quantify the link between animal activity and fix success, perhaps utilizing activity sensors that record collar movement to determine a relationship with fix success.

MANAGEMENT IMPLICATIONS

Caution should be used when applying these results to other studies that are outside of the Acadian forest, or that use different habitat classes with canopy cover values outside the range in this study. Further caution should be used for areas that have more topographical relief or mountainous terrain than this study area, as previous studies have suggested it will influence fix success and location error. If canopy cover is known to be high in an area, researchers can likely expect a reduction in fix success and underrepresentation of habitat classes with high vegetative obstruction above the animal. Thus, potential bias may occur in habitat analyses that do not correct for habitat-specific differences in fix success. Additionally, researchers and users of GPS collars should be

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aware that the number of available satellites and their geometry are important in determining location error. Data screening can be used to reduce location error and a combination of 2D/3D and DOP classifications of locations should be considered as screening criteria by future researchers.

Other direct implications of this work pertain to increasing accuracy of locations and estimating missed locations for spatial and habitat analyses. Habitat selection analysis accuracy will be increased by creating error polygons using location errors recorded from test collars, as a means for accurately determining the habitat class each location represents. Additionally, underrepresentation of habitat classes by missed locations can be avoided by using known fix success values recorded by test collars to estimate missed locations. Overall accuracy of locations will benefit all habitat and spatial analysis by using the developed data screening criteria to remove outliers. However, not all potential errors influencing GPS collars in northern Maine were explained. The large difference in fix success between GPS test collars and GPS collars worn by lynx should be further evaluated.

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CHAPTER 2

SPATIAL RESPONSES OF A SOUTHERN POPULATION OF CANADA LYNX

TO A DECLINE IN SNOWSHOE HARES

ABSTRACT

Knowledge of the spatial responses of Canada lynx (*Lynx canadensis*) to changes

in densities of their primary prey, the snowshoe hare (*Lepus americanus*), has resulted

from studies within boreal forests of northwestern Canada and Alaska. Since lynx were

listed as a U.S. federally threatened species in 2000, increased emphasis has been placed

upon understanding lynx within the Acadian forests near the southeastern extent of their

range within the contiguous United States. Within northern boreal forests, lynx and

snowshoe hares share an 8-11 year population cycle and lynx have been documented to

increase their home range areas during the decline phase of hares. Further, emigration

rates of adult lynx increase after hare density drops below ~0.5 hares/ha. It is unclear

whether hares cycle in the southeastern portion of their geographic range and the

corresponding spatial responses of lynx to changing hare densities have not been studied

in southern populations. Within the coterminous U.S., spatial ecology of lynx has been

studied during an apparent high phase of the hare cycle in Maine, as well as during a

single phase of the hare cycle in Minnesota, Montana, and Washington. Thus, my

objectives were to evaluate lynx home range area and overlap between periods of high

and low hare density to evaluate how lynx in the more diverse forests and communities of

the transitional Acadian forest region respond to changes in hare densities during a

decade (2001-2010) when hare densities changed > 2-fold. I estimated 90% fixed kernel

home ranges using an ad hoc bandwidth selection for the annual and reproduction-

specific periods. I also evaluated the potential and realized extent of intrasexual and intersexual overlap among home ranges of lynx between periods of high versus low hare abundance. Home range area did not change as hare densities declined except for females during the denning period and males during the breeding period. During the high hare density period, most female lynx produced kittens and maintained smaller home range areas during the denning period. In contrast, during the low hare density period most collared female lynx were not observed with kittens and maintained larger home range areas during the denning period. Intra- and intersexual overlap among home ranges of lynx did not change as hare densities declined, except that extent of overlap among adjacent females declined during the period of low hare density. Given that reproduction was suppressed during the low hare density period, I expect that reduced overlap among females during the period of lower density may have been caused by reduced opportunities among breeding females and their surviving female offspring. Lynx may shift energy expenditures towards territory maintenance and survival and reduce reproductive investment during a period of relatively lower prey density. In my population, male and female lynx appeared to maintain residency, similar home range areas, continued to exhibit intersexual territoriality, and appeared to maintain a stable spatial structure despite a decline in hare density and reproduction. Hare densities in my study area near the southeastern extent of lynx range did not decline to the extremely low levels (<0.1 hares/ha) observed during the extreme low of cyclic northern populations, which may have prevented the drastic changes in spatial behavior associated with abandonment of home ranges, territorial breakdown, and emigration as has been observed by lynx and bobcats (*Lynx rufus*) in regions where prey declines are more drastic. Given

a strategy of reduced reproductive effort and stable spatial structure during periods of declining prey abundance, southern populations of lynx may be more sensitive to anthropogenic factors when hare populations are depressed.

INTRODUCTION

Canada lynx (*Lynx canadensis*) are considered a specialist predator of snowshoe hares, and in their northern range in the boreal forests of Canada and Alaska, their population cycle closely tracks the snowshoe hare population cycle with a 1-3 year time-lag (Nellis et al. 1972, Brand et al. 1976, Brand and Keith 1979, Mowat et al. 2000, O'Donoghue et al. 2001). Lynx population dynamics, survival, movements, and habitat selection are influenced by spatial and temporal hare abundance (Koehler 1990, Poole 1994, O'Donoghue et al. 1997, Apps 2000, Aubry et al. 2000, Mowat et al. 2000). Lynx in northern populations have been documented to increase home range area during low and declining phases of the hare cycle (Ward and Krebs 1985, Slough and Mowat 1996, O'Donoghue et al. 2001). In southwestern Yukon, lynx increased home range area from 13.2 to 39.2 km^2 as hare density declined from 14.7 to 0.2 hares/ha (Ward and Krebs 1985). Lynx studied near Whitehorse, Yukon, increased their home range areas approximately 30x for females and 7x for males as stand-scale hare density decreased from 7.5 to 1.1 hares/ha (Slough and Mowat 1996). As prey density declines, foraging may take priority over other activities such as territorial maintenance, mating, and reproduction (Parker et al. 1983, Ward and Krebs 1985). Thus, home range areas may be expanded as lynx travel farther to find food and reproduction may decline as foraging efficiency decreases during the decline phase in hare cycles.

Reduced reproduction rates and recruitment have been documented in lynx and other felids as prey density declined. Eurasian lynx (*Lynx lynx*) in Poland experienced a decline in reproduction rates during 4 years of a roe deer (*Capreolus capreolus*) decline (Okarma et al. 1997). Denning rates of bobcats (*Lynx rufus*) may decline during years of reduced prey abundance, and recruitment of kittens may also (Knick 1990, Blankenship 2000). Breeding activity of lynx, including ovulation and implantation in some cases, still occurred as hare density declined, but recruitment was reduced to zero as kittens did not survive until early winter when hare densities declined to 0.4-1.3 hares/ha in the Yukon and Northwest Territories, Canada (Poole 1994, Mowat et al. 1996).

If home range area increases as lynx travel farther to access a declining prey resource, overlap between intra- and intersexual home ranges would be predicted to increase as prey declines. Home range overlap among lynx increased and was associated with increased home range areas of lynx during a period of declining hare densities in the Yukon (O'Donoghue et al. 2001). In contrast, home range overlap did not change as hare density declined in the southwestern Yukon and the Northwest Territories (Ward and Krebs 1985, Poole 1995). Overlap is difficult to determine and compare between studies because of different methods of estimating home ranges, geographical areas, and sample sizes, and may be further complicated because genetic relationships between individuals (e.g., tolerance may be greater among adult females and their female offspring) may influence extent of home range overlap among adjacent adult lynx (Mowat et al. 2000).

Lynx spatial ecology in the southern portion of the species' geographic range has been hypothesized to resemble lynx populations at the northern extent of their range during a cyclic low in hare populations (Koehler and Aubry 1994, Aubry et al. 2000, but

see Vashon et al. 2008a). Others have hypothesized that southern populations are

sustained via immigration of lynx from the northern core of their geographic range

because hare densities may be insufficient to sustain southern populations (McKelvey et

al. 2000, Ruggiero et al. 2000, Murray et al. 2008). Consequently, researchers have

suggested that maintaining connectivity with source populations will be important to

maintain lynx populations at the southern edge of their geographic range (Walpole et al.

2012, Squires et al. 2013). Early research in Washington (Koehler 1990), Minnesota

(Mech 1980), and the southern Canadian Rocky Mountains (Apps 2000) has reported

large home ranges and low hare densities, raising questions about viability of lynx

populations in the patchier landscapes within some portions of the southern range of lynx,

especially in regards to fluctuating prey densities (Buskirk et al. 2000, Murray et al.

2008). However, habitat in Maine's Acadian forest is structurally different than the

habitat that occurs in the Rocky Mountain portions of the southern lynx range (Agee

2000), and mean hare densities in extensive areas of conifer-dominated, regenerating

forests exceeded 1.8 hares/ha (Homyack et al. 2007). Further, spatial ecology of lynx in

Maine during a period of relatively high hare density (Vashon et al. 2008a) did not

support the hypothesis that southern populations of lynx exhibit the spatial and

demographic characteristics of northern lynx populations during periods of low hare

density.

Maine likely supports the largest population of lynx in the contiguous United

States, and in 2009, 24,597 km^2 of predominately commercially owned and managed

forestland in the state was designated as critical habitat (U. S. Department of Interior

2009). Harvesting practices in the 1970s and 1980s have been credited as a reason for

current lynx abundance, as clearcuts treated with herbicide have since regenerated into extensive areas of dense, conifer-dominated saplings that support high hare density (Hoving et al. 2004, Homyack et al. 2007, Scott 2009, Simons 2009). Additionally, substantial areas of northern Maine are typically characterized by deep snow packs (Hoving et al. 2005), which lynx are physically adapted for (McCord and Cardoza 1982, Elbroch 2003), and which may provide a competitive advantage (Krohn et al. 2004, Hoving et al. 2005) over other potentially competing carnivores (e.g. fisher (*Martes pennanti*), bobcats).

Spatial ecology of lynx in Maine has been previously documented (Vashon et al. 2008a), as well as habitat selection at the landscape scale (Hoving et al. 2004, Simons-Legaard et al. 2013) and home range scale (Fuller et al. 2007, Vashon et al. 2008b). All previously published research for lynx populations in Maine was conducted during a period of high hare density (HIGH) during 1997-2006 where hare density ranged between 1.79-2.29 hares/ha in regenerating clearcuts dominated by dense conifer saplings (Fuller and Harrison 2005, Homyack et al. 2007, Scott 2009). A period of declining hare density (LOW) in these stands occurred from 2007-2012 when hare density ranged between 0.75-1.19 hares/ha (Scott 2009; D. Harrison, University of Maine, unpublished data). In comparison, hare density in northern populations can range between 1.6-9 hares/ha during peak high density periods and between 0.01-1.0 hares/ha (Poole 1994, Hodges et al. 2001) during low density periods. Location data for collared lynx was collected from 1999-2011, allowing a comparison of spatial ecology and habitat selection (see Chapter 3) between HIGH and LOW.

My goal was to increase understanding of the ecology of lynx at the southeastern extent of their geographic range by evaluating spatial responses of lynx to changing density of snowshoe hares. Specifically, my objectives were to compare home range areas of resident male and female lynx and to evaluate changes in extent of intersexual and intrasexual home range overlap between periods of relatively high (i.e., ≥ 1.8 hares/ha) and low (i.e., ≤ 1.0 hares/ha) periods of hare density in regenerating conifer stands selected by lynx.

STUDY AREA

My primary study area included 4 townships (T11 R12 WELS, T11 R11 WELS, T12 R11 WELS, T12 R12 WELS) in the Musquacook Lakes region of northwestern Maine where the lynx capture and monitoring effort was focused. Climate data collected from 1971-2000 at the nearest weather station located in T11 R14 WELS (46°37'N, 69°31'W, 304.8 m elevation, National Climatic Data Center, National Oceanic and Atmospheric Administration) indicated mean annual rainfall of 90.2 cm and mean annual snowfall of 202.95 cm. Average temperatures were 2.3°C, with the highest mean daily temperatures occurring in July (17.1°C) and the lowest mean daily temperature occurring in January (-14.2°C).

The 4 township area was privately owned and commercially managed for pulpwood and sawlogs by forest-based companies and investor organizations (Seymour and Hunter 1992, McWilliams et al. 2005). Average annual timber harvesting in Maine occurred on 286,600 acres during 1982-1989, 449,200 acres during 1990-1994, and 531,000 acres during 1995-2002 (McWilliams et al. 2005), and was predominately clearcuts and various forms of partial harvests (Smith et al. 1997). Approximately 46%

(17,562 ha) of the study area was harvested by clearcuts during the 1970's and 1980's (Vashon et al. 2008a).

A spruce budworm (*Choristoneura fumiferana*) epidemic in the 1970's and 1980's affected many spruce-fir dominated stands, which resulted in extensive areas of clearcuts (McWilliams et al. 2005). Herbicide (e.g., glyphosate) was applied 4-21 years after cutting to favor regeneration of coniferous species. The resulting stands are primarily composed of balsam fir (*Abies balsamea*) with varying representation of red spruce (*Picea rubens*), black spruce (*P. mariana*), white spruce (*P. gluca*), eastern white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*). Although these stands typically were composed of 60 – 90% saplings, deciduous species including red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), pin cherry (*Prunus pennsylvanica*), and raspberry (*Rubus* sp.) were typically present (Homyack et al. 2007). Stands that had been partially harvested primarily contained residual trees represented by sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch, yellow birch (*Betula alleghaniensis*), eastern white pine, and northern white cedar, with other species occurring less frequently that included red spruce, white pine, red maple, pin cherry, striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*) (Fuller and Harrison 2005).

METHODS

Capture and Telemetry

Lynx were captured from March 1999 - October 2011 using methodologies described by Vashon et al. (2008a). Lotek (New Market, Ontario, Canada) and

Advanced Telemetry Systems (Isanti, MN) very high frequency (VHF) collars were fitted

to lynx during 1999 to 2007 and locations were obtained to within 80 m from aircraft

(Vashon et al. 2008a). Lotek and Sirtrack (Havelock North, Hawkes Bay, New Zealand)

Global Positioning System (GPS) collars were deployed on lynx during 2004-2011.

Location data was stored onboard the collars and was recovered by either re-capture of

lynx or via an automatic drop-off mechanism on the collar. Location data from VHF and

GPS collars was separated into biological years beginning May 15 and ending the

following May 14, and was based on the approximate start of the birth and denning

period for female lynx, which occurred approximately mid-May (Slough 1999, Poole

2003, Organ et al. 2008). Additionally, snowshoe hare pellet counts for estimating winter

hare density were conducted beginning mid-May (Homyack et al. 2007) which coincides

with the leafing out of many deciduous trees in northern Maine.

I used only VHF locations during HIGH and GPS locations during LOW to

estimate home range areas and spatial overlap of lynx. Location attempt frequency

varied between VHF and GPS collars because aerial telemetry for VHF collars was

typically conducted 2-3 times per week, whereas GPS collars were set to attempt fixes as

often as every 4.5 hours for Sirtrack collars and once per day for Lotek collars. A shorter

interval between location attempts by GPS collars may yield more successful fixes (Mills

et al. 2006), but battery life of the collars used in this study was a major concern, thus

longer (≥4.5 hours) times between location attempts were used.

I subsampled GPS locations of lynx during the low period of hare density (LOW)

to match VHF location attempt frequency during the high period of hare density (HIGH).

Lynx with VHF collars averaged 8 locations per month (range = 4-14), and never had

≥121 locations in 12 months. Thus, I randomly subsampled GPS locations using Ablebits Random Generator (Homel, Belarus) for Microsoft Excel to match the average number of locations per month for VHF collars, and to match the mean number of VHF locations based on the number of months a lynx was monitored. Each recorded location, for both VHF and GPS locations, was selected >24 hours apart to ensure temporal independence based on previous studies of wide-ranging, terrestrial carnivores (Harrison and Gilbert 1985, Katnik et al. 1994).

Accuracy of GPS locations can be improved by a screening process (D'Eon and Delparte 2005, Lewis et al. 2007). First, I tested stationary Sirtrack and Lotek GPS collars in 7 habitat classes within my study area to determine appropriate screening criteria (Chapter 1). I then selected a screening criterion to remove all 2D locations with ≥10 dilution of precision (DOP) for Lotek collars and ≥10 DOP locations for Sirtrack collars (Sirtrack does not specify 2D/3D classifications; Chapter 1) and applied the screening criteria to remove locations with unacceptably large location error to increase overall accuracy.

Home Range Estimation

I estimated lynx home ranges using a fixed kernel density method (Worton 1989) with Home Range Tools Analysis Extension (HRT) in ArcGIS 9.3 (Rodgers et al. 2007). I created a subsample of 20 lynx (10 M, 10 F) from HIGH and 20 lynx (15 M, 5 F) from LOW using annual locations. Because of sample size constraints there was not an even sex distribution during LOW in the subsample. Two males during HIGH, one female during HIGH, and 4 males during LOW were represented in the subsample more than once (i.e., locations from different years) to reach a total of 20 lynx in each period. Using

that subsample of lynx, I constructed home ranges spanning isopleths from 75-95% to determine the largest isopleth that included the maximum number of locations without a sharp increase in home range area.

I evaluated multiple bandwidth selection methods with limited success. Least squares cross validation (LSCV) is a popular bandwidth selection, but failed with 5 of 10 subsampled female lynx during HIGH. Failure of LSCV approaches were likely caused by multiple, identical locations (e.g., at dens) and variation resulting from small numbers of locations (Silverman 1986, Hemson et al. 2005, Gitzen et al. 2006). Additionally, likelihood cross-validation (CV) bandwidth selection (Horne and Garton 2006) was attempted, but also failed with 3 subsampled female lynx during HIGH; again I suspect this outcome resulted from similar causes. An ad hoc bandwidth selection method was successful for all subsampled lynx and gave the best results. The ad hoc method chooses the smallest 5% increment of the reference bandwidth (h_{ref}) that results in a contiguous home range for each individual (Berger and Gese 2007, Jacques et al. 2009, Kie et al. 2010).

As many as 300 locations have been suggested to be required to accurately estimate annual home ranges using GPS telemetry and probabilistic home range estimators (Girard et al. 2002). Thus, I constructed area-observation curves to determine the minimum number of locations needed to accurately estimate home ranges for both sexes of lynx. Using methods similar to Hearn (2007), I used the subsample of 20 lynx from both HIGH and LOW, and used the bootstrap function in Animal Movements Extension (Hooge and Eichenlaub 2000) for ArcView 3.3 to create 50 random samples for each individual. I set the minimum number of locations at 5, maximum number at 89,

and sampled in intervals (step) of 2. I averaged home range areas at each step to plot the curve. The asymptote of the curve represented the lowest number of locations required to accurately estimate home range area of an individual lynx. I determined the asymptote by calculating the number of locations where the 95% confidence interval was within 5% of the overall home range estimate for at least 10 consecutive locations (Laver and Kelly 2008).

Battery life of a collar was the largest limiting factor in determining how long a lynx was monitored, especially when using GPS collars. Thus, I determined the minimum number of months needed to accurately estimate a home range for both genders. I randomly selected 4 females and 4 males from among lynx that had been monitored ca. year from each hare density time-period. I estimated cumulative home range areas, starting at the first month and progressing through the total number of months that the individual was monitored. I ran 10 iterations for each individual, starting at a different month for each iteration. The 4 lynx in each gender were averaged within HIGH and LOW periods and I plotted home range area for each month to determine the asymptote of the curve representing the smallest number of months needed to estimate an annual home range, and employed the same criteria that was used for area-observation curves.

I tested for core area use within home ranges using the same subsample of 20 lynx that I used when creating area-observation curves. I used area/probability curves to determine if lynx utilized core areas. When core areas were detected, I determined the average isopleth of the core areas. This method is preferred over an ad hoc method because it is objective and based on the spatial distribution of locations (Powell 2000). I

calculated the inflection point of the curve using methods from Bingham and Noon

(1997) and Burdett et al. (2007). I transformed the dependent variable (i.e., percent of

total home range area at each isopleth) by the natural logarithm, fit an exponential

regression function ($y = e^{bx}$) forced through the origin on the dependent variable, and

performed regressions on the area/probability curves for each lynx in each hare density

time period (HIGH: n = 20, LOW: n = 20) (Bingham and Noon 1997). The regression

coefficient (b_i) was used to solve $x = (\ln(1/ b_i))/(b_i)$ (Bingham and Noon 1997). The

point where the slope of the regression curve equals 1 was used to estimate the isopleth

level where a core area was defined (Bingham and Noon 1997).

Lynx are a territorial species (Saunders 1963, Kesterson 1988, Poole 2003) that

will follow an ideal despotic distribution (Fretwell and Lucas 1970, Fretwell 1972).

Therefore, dominant individuals may maintain higher quality habitat that may allow for a

longer lifespan and a higher probability to be monitored for >1 year. Underrepresentation

of these individuals may occur if lynx that were monitored for >1 year were pooled

across all years monitored within each hare density period. Further, conspecific density

(i.e., lynx may move into territories of deceased lynx) and home range fidelity may

change annually. Lynx home ranges previously estimated in this study area during HIGH

were not statistically stable from year to year, but exhibited minimal shifts in home range

centroids, suggesting the shifts may not have been biologically important (Vashon et al.

2008a). When evident, however, male home range instability was caused by shifts, but

female home range instability resulted from shifts, contraction, and expansion (Vashon et

al. 2008a). Thus, to reduce potential bias of underrepresentation and decrease chances of

Type II error caused by low sample size, I determined the unit of replication was each

year that a lynx was monitored. Additionally, males will actively seek out females during

the breeding period which can temporarily increase their space use (Burdett et al. 2007),

and females with kittens exhibit strong affinities to the proximity near their den site

(Kesterson 1988, Mowat and Slough 1998). Consequently, home ranges were estimated

for the periods of breeding and non-breeding for males, for denning and non-denning for

females, and annually for both sexes.

Presence of kittens with females was assessed to determine their influence on

female home ranges. Females were intensively monitored by telemetry from mid-May

through early June to determine presence of a den site (Organ et al. 2008). Maine

Department of Inland Fisheries and Wildlife (MDIFW) staff confirmed den sites by

walking to suspected den locations, searching intensively, and recording

presence/absence of kittens (Organ et al. 2008). As an additional confirmation of

successful reproduction during 2008-2009, I backtracked collared female lynx on snow

during the following January-March, 2009-2010 to document presence of kittens

traveling with their mother. Each female was backtracked on 2 different days, with each

tracking session ≥1 km. If absence of kittens was recorded during den surveys, but

presence detected during the following winter backtracking, kittens were assumed to be

missed during den surveys and consequently were counted as present at dens.

I identified non-breeding/non-denning (NB/ND) home ranges to quantify spatial

use outside of the normal reproductive periods. The NB/ND home ranges excluded the

months of March and April for males (breeding period; Tumilson 1987, Mowat et al.

1996, Mowat and Slough 1998, Poole 2003, Burdett et al. 2007) and June and July for

females (denning period; Mowat et al. 1996, Slough and Mowat 1996, Mowat and Slough

1998, Poole 2003); all other months were included. Annual home ranges included all months a lynx was monitored during a year, but also included ≥31 days of either the breeding (males) or denning (females) period. The breeding/denning (B/D) home range included the 2 months of either the breeding (males) or denning (females) period. This two month time frame was too small to estimate home range area using a fixed kernel method, so an index to home range area was estimated using the mean minimum distance between consecutive, temporally non-correlated locations as an index to home range area (MINDIST; Harrison and Gilbert 1985, Poole 1994, Phillips et al. 1998). MINDIST has been correlated with marten home ranges (Phillips et al. 1998, Payer 1999, Gosse 2005, Hearn et al. 2010), so for comparison in this study, MINDIST was also calculated for NB/ND and annual home ranges. I estimated MINDIST for lynx that were monitored for ≥31 days and for ≥9 locations during either the breeding (males) or denning period (females).

I compared changes in intrasexual annual and reproductive-season home range area between HIGH and LOW using Mann-Whitney tests with a significance level set at 0.1 to balance probability of Type I and Type II errors. I also plotted fixed kernel home range area versus MINDIST for NB/ND and annual home ranges and used linear regression to determine the reliability of MINDIST as an index of home range area during the B/D period. All statistical analyses were conducted in SYSTAT 12 (SYSTAT Software Inc., Chicago, Illinois).

Overlap Analysis

I compared intrasexual (M/M & F/F) and intersexual (M/F & F/M) overlap among NB/ND home ranges of lynx between HIGH and LOW. M/F defines the percent of a

male home range overlapped by a potentially overlapping female and F/M defines the percent of a female home range overlapped by a potentially overlapping male. Overlap may vary each year because of emigration, immigration, mortality, births, home range stability, and annual contraction/expansion of home ranges. Additionally, underrepresentation of dominant individuals may occur if they were monitored for > 1 year, but pooled across all years monitored. Thus, if lynx were monitored for multiple years during either HIGH or LOW, each year was treated as a separate replicate. It was possible there were lynx which were not collared within my study area each year; therefore, physical overlap was measured only when the home ranges were deemed potentially overlapping. Potential overlap was defined by evaluating whether the distance between the nearest edges of each potentially overlapping home range was less than the mean home range radius for the sex in question. This definition of potential overlap removed all individual home ranges from the analysis that did not have potential for overlap with other home ranges, while including all home ranges with potential for overlap based on proximity. I calculated the proportion of potentially overlapping home ranges that physically overlapped and compared between hare density time periods using a two-sample equality of proportion test. I also calculated the percent of the area of the home range that overlapped both within and between sexes and tested for differences in home range overlap between the HIGH and LOW periods using t-tests with arcsine transformed percentages (Zar 1999).

RESULTS

Determining Home Range Criteria, Sample Size, and Reproduction

Female lynx with VHF collars during HIGH had asymptotic home ranges at 45 locations and males exhibited asymptotic home ranges at 41 locations (Figure 2.1). Males and females with GPS collars during LOW exhibited asymptotic home ranges at 49 locations (Figure 2.1). The minimum number of months of monitoring required to estimate home range areas ranged from 3.5 to 4.75 for both sexes in HIGH and LOW (Figure 2.2). For consistency between sex and hare density periods, I used 4 months as the minimum monitoring interval to estimate the annual home range area of an individual lynx. Also, I chose a 90% isopleth to define home range areas of lynx based on the most noticeable inflection of home range areas for both sexes, occurring between 90% and 95% isopleths during both HIGH and LOW (Figure 2.3).

I determined there was no evidence of core areas based on isopleths of home ranges using area/probability curves. The fit of the exponential function was high during both HIGH (R^2 = 92.55%, range = 90.48 – 96.07%) and LOW (R^2 = 92.55%, range = 90.48 – 96.07%) suggesting an exponential curve fit the data well. The inflection point of the exponential curve indicated that an isopleth estimate of 83% ± 1 (range 61-100%) would define a core area for both sexes and during both hare density time periods. This core isopleth estimate was very close to the 90% isopleth level used to estimate the total home range area, and was considered unlikely to represent a biologically meaningful core area; therefore, my analyses were restricted to estimates of 90% fixed-kernel home ranges of lynx.
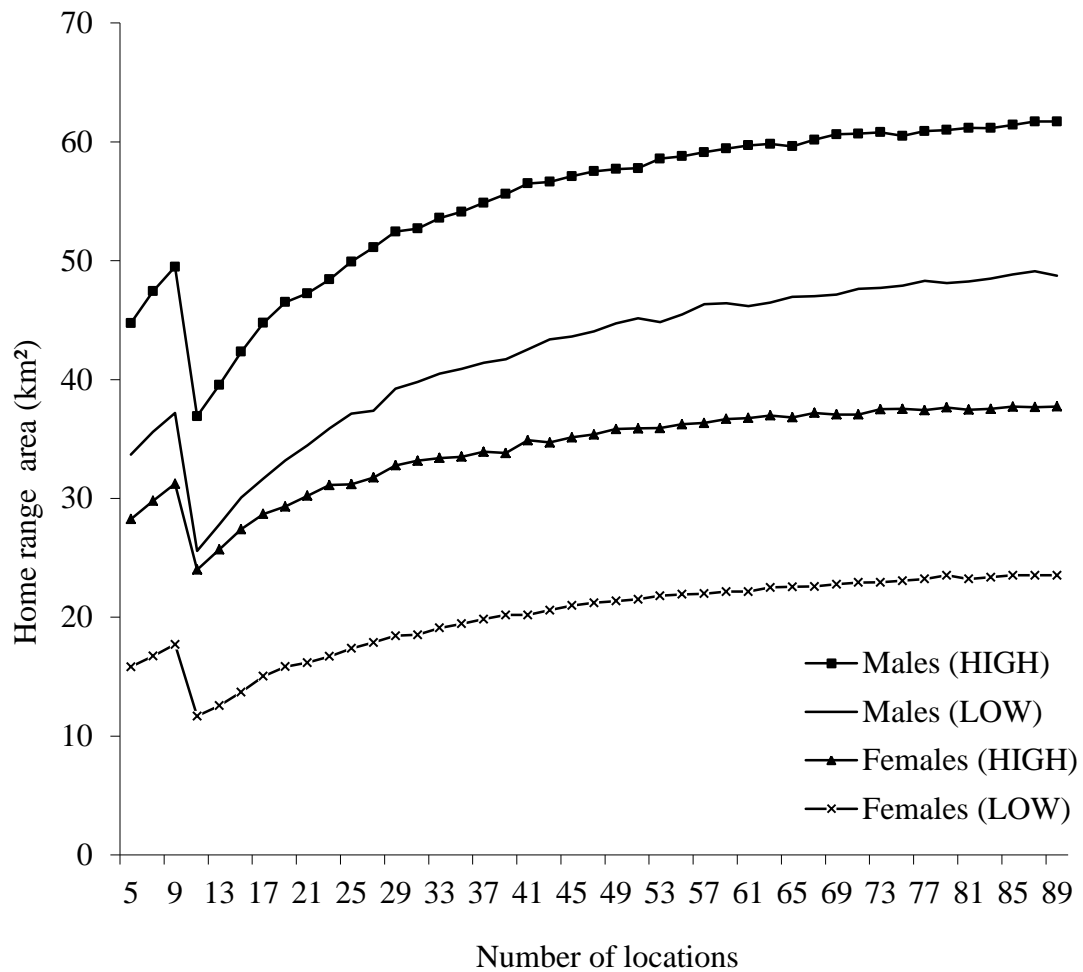
Figure 2.1. Averaged area-observation curves for 20 lynx (10 M, 10F) from HIGH (1997-2006) and LOW (2007-2012) hare density period in northern Maine, USA. Asymptote was calculated to determine the smallest number of locations needed to accurately estimate home range area based on number of locations where the 95% confidence interval was within 5% of the total home range area for at least 10 consecutive locations (Laver and Kelly 2008).
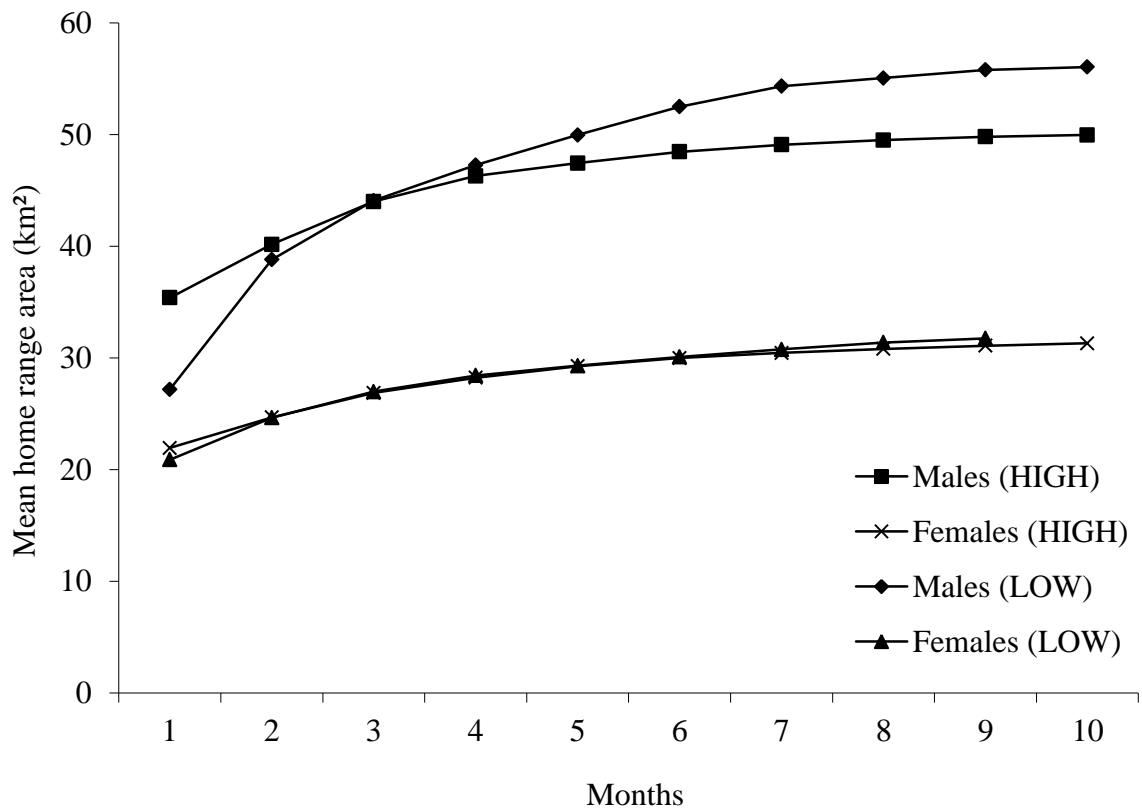
Figure 2.2. Relationship between mean 90% fixed kernel home range area and number of
months that lynx were sampled (range 1-10 months) for male and female lynx during
HIGH (1997-2006) and LOW (2007-2012) hare density periods. The asymptote was
used to determine the sampling interval required to estimate home range areas of lynx in
northern Maine, USA. Breeding months for males (March and April) and denning
months for females (June and July) were omitted from analysis. For each individual, 10
iterations were calculated and averaged for each month. Asymptote was determined by
calculating the number of locations where the 95% confidence interval is within 5% of
the overall (i.e., all locations included) home range estimate for at least 10 consecutive
locations (Laver and Kelly 2008).
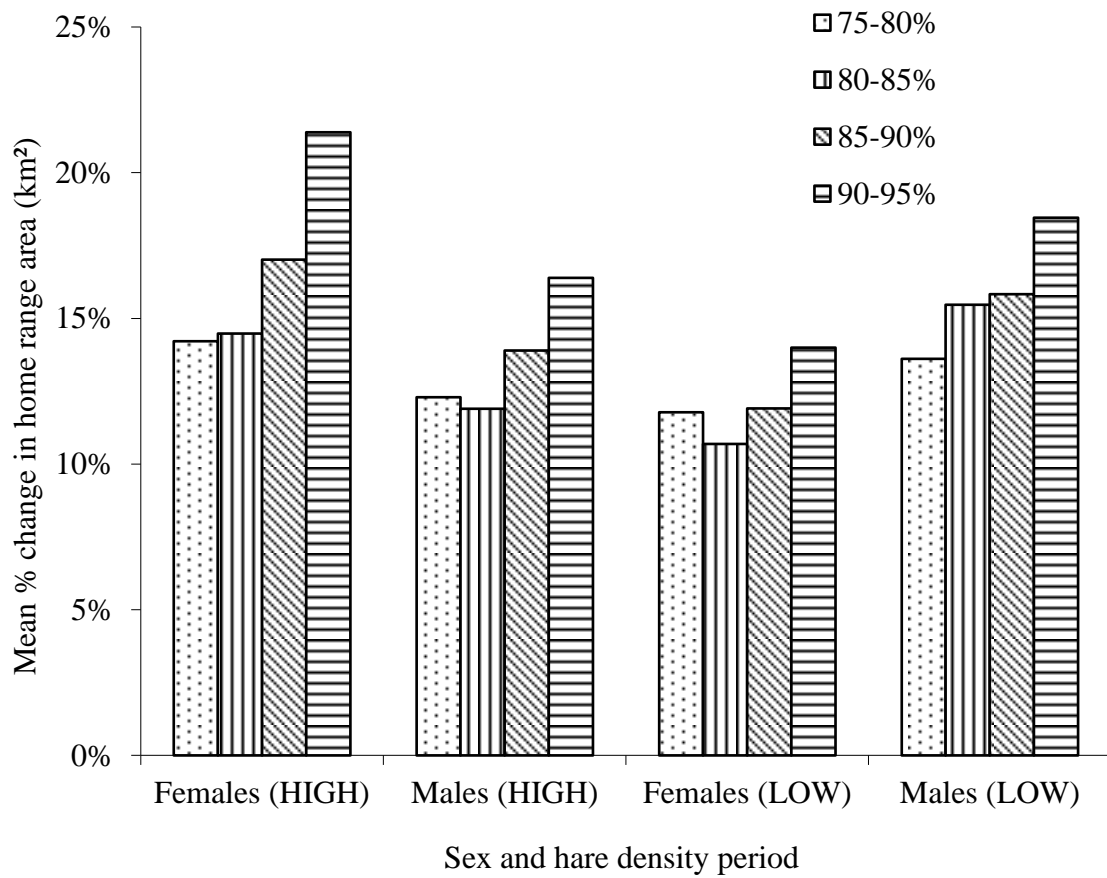
Figure 2.3. Mean percent change in isopleth levels of fixed kernel home range areas from a subsample of 20 lynx using all annual locations from each hare density time period. Home ranges were evaluated across 4 isopleth levels (75-95%) for lynx during HIGH (1997-2006) and LOW (2007-2012) period of hare density in northern Maine, USA.

MDIFW captured 85 adult and sub-adult lynx (44 M, 41 F) from March 1999 to October 2011. However, only 31 lynx (16 M, 15 F) during HIGH and 21 lynx (12 M, 9 F) during LOW were adult ($\geq$ 2 years old) residents monitored sufficiently to produce annual or reproductive season-specific home range areas and MINDIST estimates. Twenty two lynx (12 M, 10 F) during HIGH and 12 lynx (9 M, 3 F) during LOW were monitored > 1 year (Appendix A), which enhanced sample sizes (i.e., each animal monitored for $\geq$4 months within a year was considered a unit of replication, page 65) for annual and NB/ND home ranges, as well as all lynx with $\geq$9 locations during a 2 month breeding/denning period used to estimate MINDIST values (Table 2.1). Although this approach considered the importance of adults with survival across multiple years to lynx conservation, greatly increased effective sample sizes, and reduced probability of unacceptably large Type II errors, trends and statistical conclusions were unaffected relative to using each individual only once in home range calculations (see Appendix B).

Thirty three of 38 females used in the B/D comparison (i.e., met requirements for MINDIST estimation) during HIGH were attending kittens at dens, where only 3 of 13 females during LOW were attending kittens at dens. Thus, all females that were exceptions in each period (i.e., no kittens during HIGH and kittens during LOW) were omitted from statistical analysis to be able to compare spatial differences between females with kittens and without kittens. The smaller sample size of lynx during LOW may not reflect lynx density in the study area given that methodology issues caused shorter battery life of GPS collars, drop-off mechanisms on GPS collars frequently malfunctioned, and difficulty of recapturing female lynx in cage traps to recover GPS

Table 2.1. Sample sizes, mean number of locations, and mean number of months of monitored lynx used to estimate 3 types of home ranges during 2 periods of hare density. Home ranges were non-breeding/non-denning (NB/ND) 90% fixed kernel home range areas, annual 90% fixed kernel home range areas, and breeding/denning (B/D) estimates of minimum distance traveled between consecutive independent locations (MINDIST; Harrison and Gilbert 1985) during a HIGH (1997-2006) and LOW (2007-2012) hare density period in Maine, USA. Each lynx monitored in each biological year (May 15 – May 14) was treated as a replicate.

Home range type	Hare density period	Sample Size	Mean # of locations (SE)	Range of locations	Mean # of months (SE)	Range of months
Male NB/ND	HIGH	45	66.73 (1.72)	44 - 106	10.94 (0.22)	6 - 12
Male NB/ND	LOW	16	65.38 (3.23)	49 - 85	9.09 (0.47)	5 - 12
Male Annual	HIGH	37	80.19 (2.25)	53 - 119	11.19 (0.25)	7 – 12
Male Annual	LOW	10	81 (3.88)	55 - 97	9.5 (0.57)	7 - 12
Male Breeding	HIGH	36	13.22 (0.28)	9 - 16	2	N/A[a]
Male Breeding	LOW	19	14.55 (0.74)	9 - 19	2	N/A[a]
Female NB/ND	HIGH	33	67.14 (2.04)	45 - 94	10.66 (0.35)	5 - 12
Female NB/ND	LOW	7	65.57 (3.93)	52 – 80	7.86 (1)	4 - 12
Female Annual	HIGH	35	81.08 (2.93)	45 – 121	10.78 (0.31)	7 - 12

Table 2.1 continued.

Home range type	Hare density period	Sample Size	Mean # locations (SE)	Range of locations	Mean # of months	Range of months
Female Annual	LOW	4	83.25 (5.76)	68 – 96	9.25 (1.05)	7 - 12
Female Denning	HIGH	33[b]	17.13 (0.69)	11 – 29	2	N/A[a]
Female Denning	LOW	10[c]	13.54 (1/02)	10 – 19	2	N/A[a]

[a] All male Breeding and female Denning MINDIST estimates were only 2 months

[b] Thirty eight females were monitored during HIGH, but 5 females were removed from analysis because there was no presence of kittens detected during den visits

[c] Thirteen females were monitored during LOW, but 3 females were removed from analysis because presence of kittens were detected during den visits

collars (J. Vashon, Maine Department of Inland Fisheries and Wildlife, *personal communication*).

MDIFW conducted 39 total den visits during HIGH, where 32 females (82.1%) were attending kittens. In contrast, 29 dens were visited during LOW, where only 8 females (27.6%) were attending kittens, suggesting that reproduction declined during LOW ($Z = 4.513$, $P < 0.001$). In 2009, 7 backtrack surveys (individual mean total length = 1.61 km) on 3 females confirmed absence of kittens from 2008 den visits, and in 2010, 14 backtrack surveys (individual mean total length = 1.63 km) on 5 females confirmed absence of kittens determined from 2009 den visits. Consequently, it was not necessary for me to adjust determinations of female denning activity based solely on den searches.

Non-Breeding/Non-Denning Home Ranges

The median home range area of males during the non-breeding period was similar between HIGH ($\tilde{x} = 51.66$, range = $18.2 - 96.72$) and LOW ($\tilde{x} = 40.75$, range = $20.11 - 130.38$). Similarly, female NB/ND home range area during the denning period remained relatively stable from HIGH ($\tilde{x} = 34.26$, range = $17.38 - 108.25$) to LOW ($\tilde{x} = 29.74$, range $20.15 - 83.7$; Figure 2.4). There were no statistical differences in NB/ND home ranges of males ($U = 372.5$, $P = 0.838$) or females ($U = 149$, $P = 0.233$) between HIGH and LOW.

Annual Home Ranges

Annual home range areas (Methods, page 67) for males ($U = 248$, $P = 0.102$) and females ($U = 86$, $P = 0.459$) also were not different between HIGH and LOW (Figure 2.5). However, the difference between annual home ranges of males during HIGH ($\tilde{x} = 61.18$, range = $22.81 - 106$) and LOW ($\tilde{x} = 37.59$, range = $23.72 - 102.16$) was
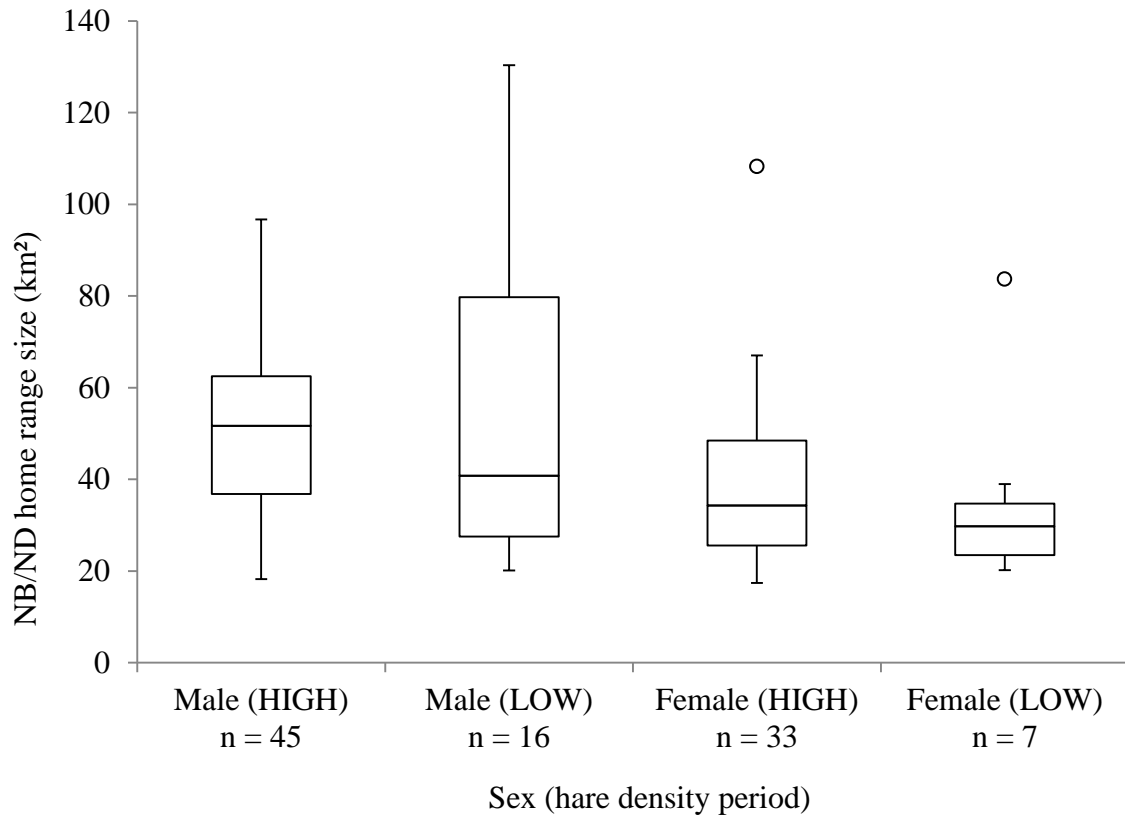
Figure 2.4. A comparison of 90% fixed kernel home range areas during the non-breeding/non-denning (NB/ND) period for male and female lynx in northern Maine, USA during periods of HIGH (1997-2006) and LOW (2007-2012) hare density. Upper boundary of each box is the 75th percentile, middle line is the median, and lower box boundary is the 25th percentile. The difference between the 75th percentile and the 25th percentile is the interquartile range (IQR). Whiskers above the box indicate the largest data point within the upper limit, where the upper limit is the 75th percentile plus 1.5*IQR. Whiskers below the box indicate the smallest data point within the lower limit, where the lower limit is the 25th percentile minus 1.5*IQR. Outliers are points 1.5 times the IQR above the 75th percentile or below the 25th percentile and are represented by circles.
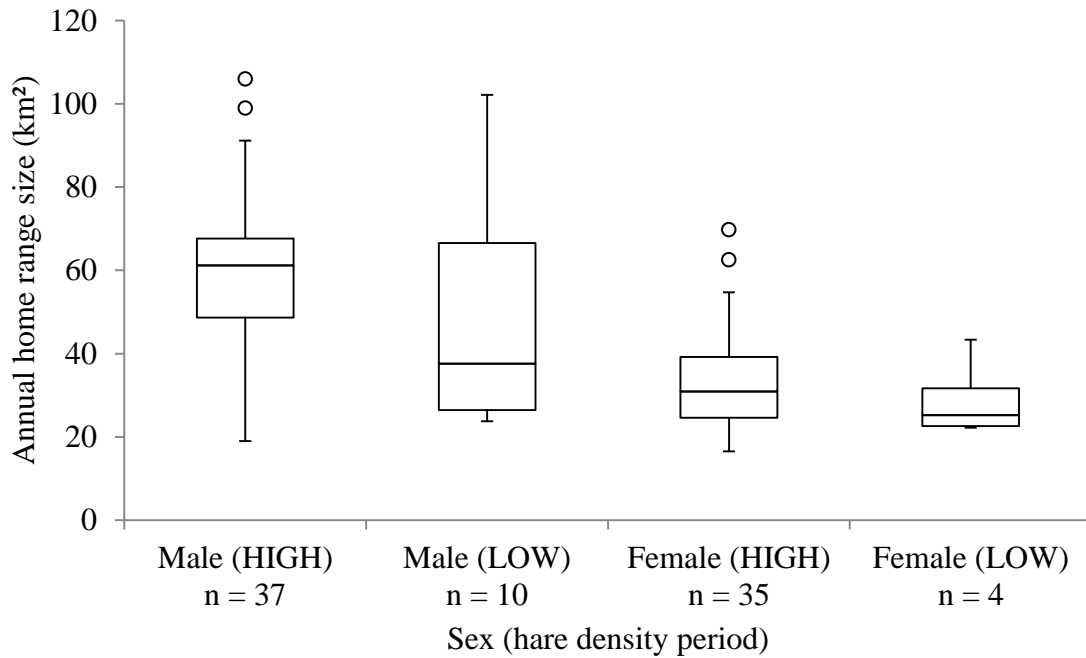
Figure 2.5. A comparison of 90% fixed kernel home range areas of male and female lynx during the annual (May 15 – May 14) period in northern Maine, USA during periods of HIGH (1997-2006) and LOW (2007-2012) hare density. Upper boundary of each box is the 75th percentile, middle line is the median, and lower box boundary is the 25th percentile. The difference between the 75th percentile and the 25th percentile is the interquartile range (IQR). Whiskers above the box indicate the largest data point within the upper limit, where the upper limit is the 75th percentile plus 1.5*IQR. Whiskers below the box indicate the smallest data point within the lower limit, where the lower limit is the 25th percentile minus 1.5*IQR. Outliers are points 1.5*IQR above the 75th percentile or below the 25th percentile and are represented by circles.

substantial and statistical comparisons were equivocal ($\alpha = 0.100$), indicating uncertainty as to whether annual home range areas of males contracted or remained stable during LOW.

Breeding/Denning Home Ranges

Home range areas of females during the non-denning and annual periods were significantly related to MINDIST (Annual: P = 0.001; ND: P < 0.001), but had a poor fit (Annual: R = 0.493; ND: R = 0.589; Figure 2.6). Conversely, non-breeding and annual home ranges of males were better predicted using MINDIST (Annual: P < 0.001, R = 0.815; NB: P < 0.001, R = 0.84; Figure 2.7). Both sexes had a significant relationship between NB/ND and annual home ranges and MINDIST, but the association was weak for females; therefore, I used MINDIST as an index, but not a predictor of home range area during the breeding and denning periods.

The MINDIST values for males were not different between breeding and non-breeding periods during either HIGH (U = 966, p = 0.138) or LOW (U = 147, p = 0.868), suggesting stable home range areas of resident male lynx throughout an annual cycle and regardless of the relative density of hares. Within the breeding period, however, males had larger MINDIST values (U = 465, P = 0.029) during HIGH ($\tilde{x}$ = 4054.54, range = 2493.7 − 8646.43) than during LOW ($\tilde{x}$ = 3155.76, range = 2308.34 − 6753.17; Figure 2.8). In contrast, females during HIGH ($\tilde{x}$ = 944.56, range = 446.12 − 4561.03) had smaller MINDIST values than females during LOW ($\tilde{x}$ = 2987.81, range = 1385.92 − 3419.15; Figure 2.8). However, the result for females is confounded by changes in reproductive status of females between HIGH and LOW. In fact, females with kittens had similar MINDIST values during both HIGH and LOW, and females without kittens
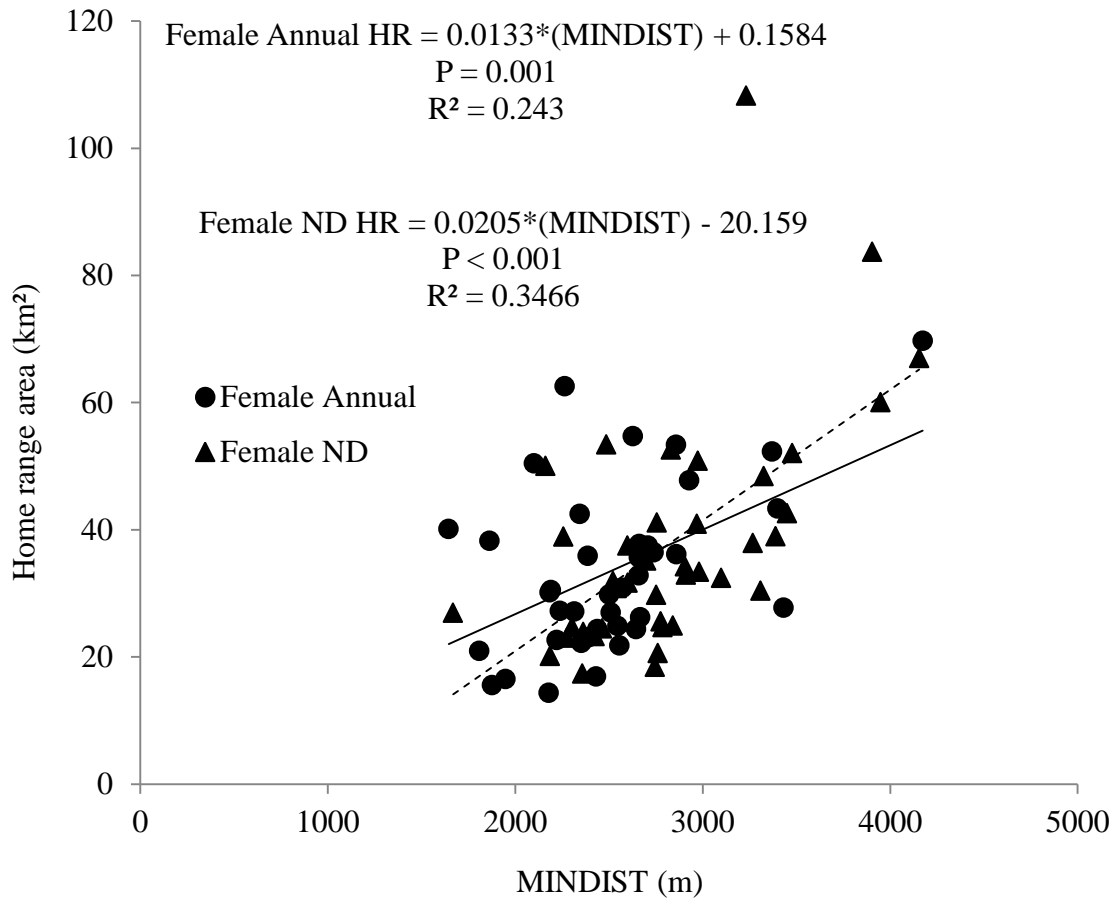
Figure 2.6. Relationship among 90% fixed kernel home range area and distance between consecutive locations separated by ≥24 hours (MINDIST; Harrison and Gilbert 1985) from annual and non-denning (ND) home ranges for female lynx in northern Maine, USA 1999-2011. The solid line represents the best-fit relationship between annual 90% fixed kernel home range area and MINDIST, whereas the dashed line depicts that relationship during the non-denning (ND) period.
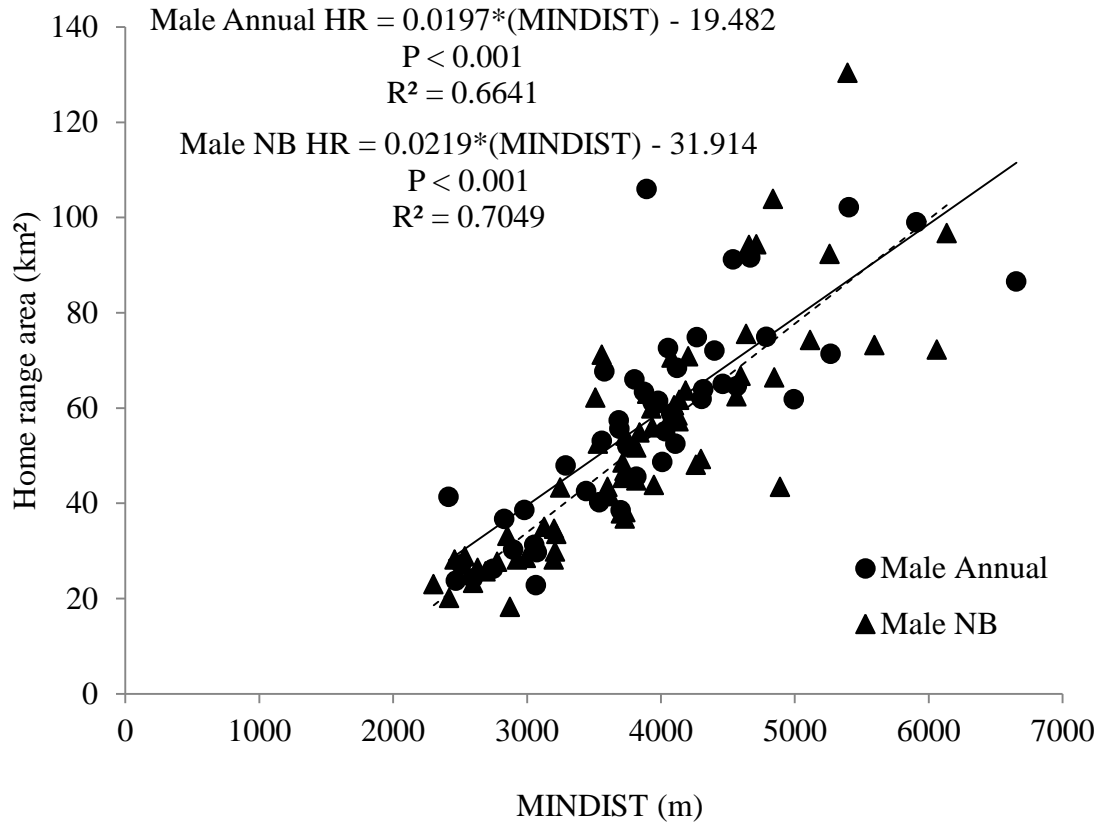
Figure 2.7. Relationship among 90% fixed kernel home range area and distance between consecutive locations separated by ≥24 hours (MINDIST; Harrison and Gilbert 1985) from annual and non-breeding (NB) home ranges for male lynx in northern Maine, USA 1999-2011. The solid line represents the best-fit relationship between annual 90% fixed kernel home range area and MINDIST, whereas the dashed line depicts that relationship during the non-breeding (NB) period.
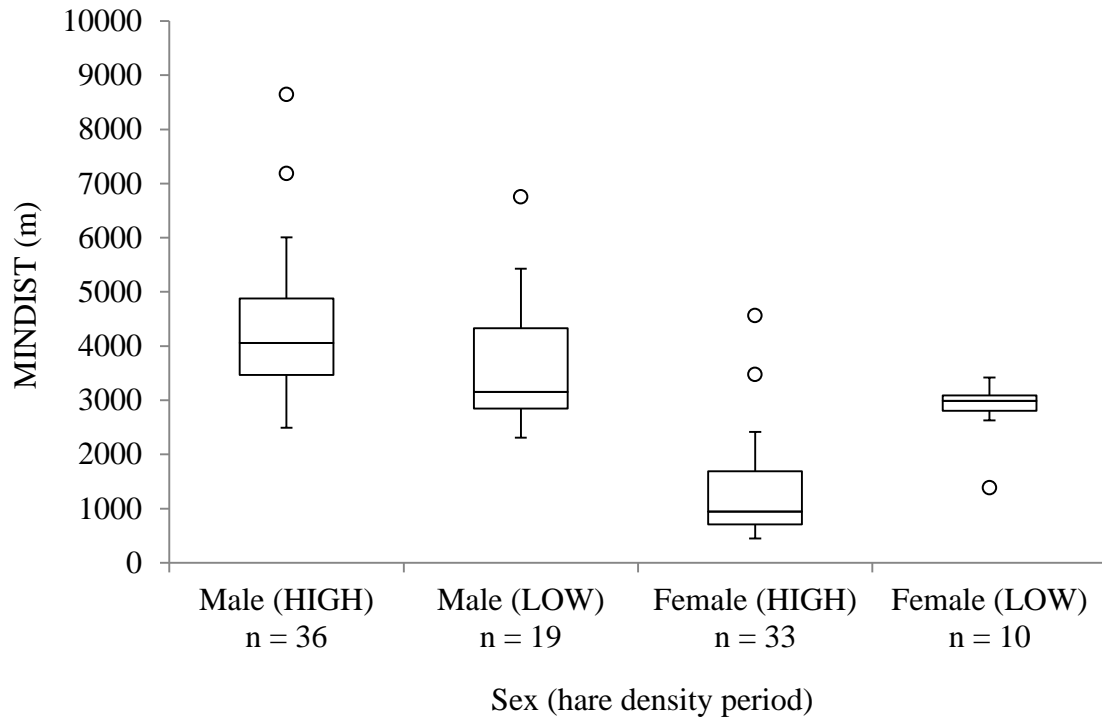
Figure 2.8. A comparison of MINDIST values of male lynx during the breeding season and females during the potential denning season between periods of HIGH (1997 – 2006) and LOW (2007 – 2012) hare density in northern Maine, USA. Upper boundary of each box is the 75th percentile, middle line is the median, and lower box boundary is the 25th percentile. The difference between the 75th percentile and the 25th percentile is the interquartile range (IQR). Whiskers above the box indicate the largest data point within the upper limit, where the upper limit is the 75th percentile plus 1.5*IQR. Whiskers below the box indicate the smallest data point within the lower limit, where the lower limit is the 25th percentile minus 1.5*IQR. Outliers are points 1.5*IQR above the 75th percentile or below the 25th percentile and are represented by circles.

also had similar MINDIST values between HIGH and LOW (Figure 2.9), suggesting that reproductive status and not hare densities most greatly influenced MINDIST values of females during the denning period (Figure 2.9).

Home Range Overlap

There was little evidence to indicate that extent of physical overlap between potentially overlapping home ranges was affected by changing hare densities. Extent of overlap did not change significantly between HIGH and LOW within sexes M/M ($Z = -1.175$, $P = 0.24$), F/F ($Z = -1.36$, $P = 0.174$), or between sexes (M/F and F/M; $Z = -1.598$, $P=0.11$); however, the raw proportion of ranges that overlapped increased 8-20% from HIGH to LOW across the 3 categories of comparison (Table 2.2). Additionally, the percent of physical overlap between shared home ranges of sympatric males ($t = -0.434$, $P = 0.665$) did not change between HIGH and LOW; however, sympatric females overlapped significantly more during HIGH than during LOW ($t = 1.932$, $P = 0.058$) (Table 2.3). Between sexes, the proportion of sympatric home ranges that overlapped was similar (M/F: $t = 0.859$, $P = 0.393$; F/M: $t = 1.188$, $P = 0.196$) between HIGH and LOW (Table 2.3).

DISCUSSION

In the boreal region, home range area increased as hare densities declined (Ward and Krebs 1985, Poole 1994, Slough and Mowat 1996). In contrast, I observed that annual, non-breeding (males), and non-denning (females) home range area did not change significantly between HIGH and LOW in the transitional Acadian Forest region. During the denning season, however, my index of home range area (MINDIST) increased for females during LOW. Declining hare density may be a factor involved with this
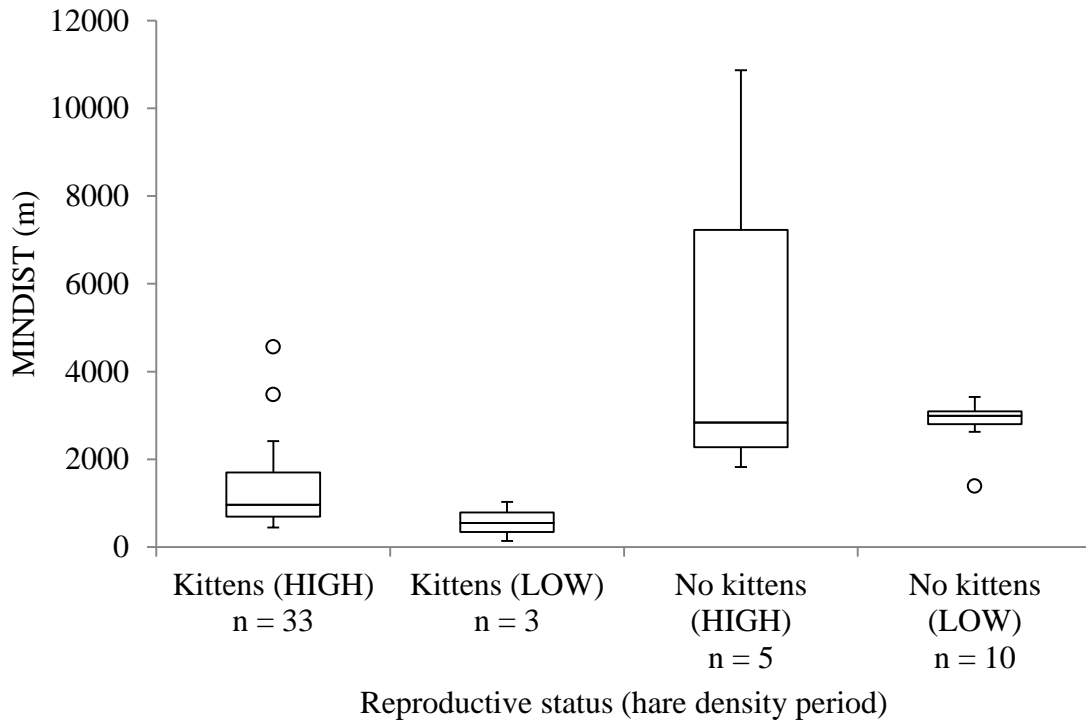
Figure 2.9. Minimum distance between consecutive independent locations $\geq$ 24 hours (MINDIST; Harrison and Gilbert 1985) for female lynx (with and without kittens) during the potential denning period (June-July) in northern Maine, USA during HIGH (2001-2006) and LOW (2007-2010) hare density periods. Upper boundary of each box is the 75th percentile, middle line is the median, and lower box boundary is the 25th percentile. The difference between the 75th percentile and the 25th percentile is the interquartile range (IQR). Whiskers above the box indicate the largest data point within the upper limit, where the upper limit is the 75th percentile plus 1.5*IQR. Whiskers below the box indicate the smallest data point within the lower limit, where the lower limit is the 25th percentile minus 1.5*IQR. Outliers are points 1.5*IQR above the 75th percentile or below the 25th percentile and are represented by circles.

Table 2.2. Proportion of potentially overlapping non-breeding/non-denning 90% fixed kernel home ranges[a] that physically overlapped among lynx during periods of HIGH (1997-2006) and LOW (2007-2012) hare density in northern Maine, USA.

Sex comparisons	Hare density period	Potential overlap	Physical overlap	Proportion	90% CI
M/M[b]	HIGH	210	94	0.448	-0.196 – 0.033
	LOW	68	36	0.529	
M/F & F/M[c]	HIGH	164	80	0.488	-0.288 – 0
	LOW	38	24	0.632	
F/F[d]	HIGH	108	50	0.463	-0.441 – 0.034
	LOW	12	8	0.667	

[a] A home range is potentially overlapped by another if the distance between them is smaller than the mean home range radius for the corresponding sex of the home range in question

[b] Male/male (M/M) is the proportion of potentially overlapping male home ranges that are physically overlapped by another male

[c] Male/female (M/F) is the proportion of potentially overlapping male home ranges that are physically overlapped by a female and female/male (F/M) is the proportion of potentially overlapping female home ranges that are physically overlapped by a male

[e] Female/female (F/F) is the proportion of potentially overlapping female home ranges that are physically overlapped by another female

Table 2.3. Percent of physical overlap of shared (i.e., > 0%) non-breeding/non-denning 90% fixed kernel home ranges of adult, resident lynx during the non-breeding period (males) and non-denning period (females) during a period of HIGH (1997-2006) and LOW (2007-2012) hare density in northern Maine, USA.

Sex comparisons	Hare density period	n	Mean ± SE	Range
M/M[a]	HIGH	94	8.3% ± 0.7	0.3–28.3%
	LOW	36	8.9% ± 1.4	0.1–42.1%
M/F[b]	HIGH	80	24.3% ± 2.7	0.1–87.1%
	LOW	24	20.1% ± 5.8	0.3–93.6%
F/M[c]	HIGH	80	37.7% ± 4.2	0.3–99.8%
	LOW	24	27.7% ± 6.4	0.3–97.3%
F/F[d]	HIGH	50	17.3% ± 3.2	0.1–87.3%
	LOW	8	3.8% ± 1.0	0.1–7.9%

[a] Male/male (M/M) is the % of a male home range overlapped by another male
[b] Male/female (M/F) is the % of a male home range overlapped by a female
[c] Female/male (F/M) is the % of a female home range overlapped by a male
[d] Female/female (F/F) is the % of a female home range overlapped by another female

change for females, but the presence of kittens may also be the cause, which seemed related to hare density. In fact, female lynx were attending kittens during 33 of 38 adult female lynx-years during HIGH, whereas females attended kittens during only 3 of 13 adult female lynx-years during LOW. Presence of kittens reduced the movement and home range area of adult female lynx in Alaska, Yukon, and Minnesota (Kesterson 1988, Slough and Mowat 1996, Burdett et al. 2007, Moen et al. 2008). Female lynx in the southern Canadian Rocky Mountains also had smaller movements around activity centers (i.e., den sites) when they were believed to be accompanied by kittens (Apps 2000). Additionally, the 5 lynx in this study without kittens during HIGH exhibited MINDIST values during the denning period that were similar to females without kittens during LOW. Further, 3 female lynx with kittens during LOW exhibited similar MINDIST values to females with kittens during HIGH. Despite limited sample sizes, these results suggest that presence of kittens, and not hare density, most greatly influenced female MINDIST values during the denning period, but that presence of kittens may be affected by hare density, as indicated by the significant difference in percent of females observed with kittens at den sites between HIGH and LOW.

During the breeding season, MINDIST values for males decreased during LOW. Males will increase distance traveled and their home ranges to seek females during the breeding period (Kesterson 1988, Mowat and Slough 1998). Additionally, Burdett et al. (2007) reported that home ranges of male lynx in Minnesota increased during the breeding period. In contrast, my data suggested that home range areas of male lynx did not increase during the breeding season. I observed no significant differences between non-breeding and breeding MINDIST values during either HIGH or LOW. Lynx in

Maine during HIGH overlapped their home ranges with ≥3 females (Vashon et al. 2008a), indicating abundant access to females and suggesting that males may have maintained stable territories to ensure access to overlapping females, rather than roaming more widely in search of uncertain breeding opportunities.

Male lynx in the Northwest Territories increased their MINDIST values by ~1.3 km in March as hare densities declined across a 3 year period (Poole 1994). Hare densities declined to 0.4-1.0 hares/ha during that study, whereas the lowest annual hare density in regenerating conifer patches was 0.75 hares/ha during my study (Scott 2009; D. Harrison, University of Maine, unpublished data). Thus, I hypothesize that hare density in Maine may not have dropped to a level low enough to require male lynx to expand their home ranges to encompass additional prey resources. Alternatively, male lynx may have decreased their MINDIST values as hare density declined as a result of prey-switching (O'Donoghue et al. 1998b, O'Donoghue et al. 2001). Consequently, this may correspond to a shift in patch-scale habitat selection (see Chapter 3) if the alternate prey is relatively more available in habitats other than those selected by lynx when foraging for hares (O'Donoghue et al. 2001).

There were only 5 lynx (3 M, 2 F) monitored sufficiently during both HIGH and LOW to estimate NB/ND home ranges and only 4 lynx (2 M, 2 F) to estimate annual home ranges. For all lynx in this study, there was no statistical change for NB/ND (Figure 2.4) and annual home ranges (Figure 2.5), but there was a decrease in median size of breeding (males) and an increase in denning (female) home ranges between HIGH and LOW (Figure 2.8). However, of the individuals monitored during both HIGH and LOW, only 1 male had NB/ND and annual home range estimates follow this trend, all other

individuals monitored in both HIGH and LOW exhibited an increase in home range

estimates. Although those individuals provide contrary results, the sample sizes for

individuals monitored in both hare density periods are too small for statistical

comparisons or strong conclusions.

Similar to what was observed in this study, home range overlap was not affected

by declining hare densities in Alberta or the Northwest Territories, Canada (Ward and

Krebs 1985, Poole 1995). In a Yukon study, however, overlap increased as hare density

declined and the authors hypothesized that territoriality may have declined as lynx

traveled further in search of prey (O'Donoghue et al. 2001). Bobcats (*Lynx rufus*) in the

western United States also exhibited spatial responses to declining prey density. Home

range area and overlap increased as lagomorph populations declined in southeastern

Idaho (Bailey 1974, Bailey 1981, Knick 1990). My results are not consistent with either

lynx responses in the Yukon or Idaho bobcats, suggesting territoriality did not break

down in Maine when hares declined to 0.75/ha in preferred hare and lynx habitat.

Female-female home range overlap was 78.1% greater during HIGH (17.3%) than

LOW (3.8%), suggesting that hare density affected social relationships among resident

adult female lynx. Mowat et al. (2000) presents evidence of matrilineal linkage in lynx

where female pair bonds develop and mothers may share territories with their offspring

(Breitenmoser et al. 1993). As hare density declines, females are less likely to reproduce

(Nellis et al. 1972, Brand et al. 1976, Parker et al. 1983), and instead focus energy on

maintaining their territory and maximizing survival. Throughout northern Maine, only

24.1% of female lynx monitored during the denning period had kittens during LOW,

whereas 82.1% of female lynx had kittens during HIGH. A decrease in reproduction

during LOW would result in less female offspring born and a subsequent reduction in female intrasexual overlap among female lynx and their female offspring.

Another potential contributing factor to the decrease of female/female overlap in LOW may have been caused by low sample sizes from collar and capture related issues. VHF collars used during HIGH had a battery life of up to 3 years, whereas GPS collars used in this study rarely exceeded 1 year of battery life, resulting in less continuous data during LOW than HIGH (Appendix A). Additionally, automatic drop-off mechanisms on some GPS collars failed and females are more difficult to recapture in cage traps, resulting in lost data from unrecovered GPS collars (J. Vashon, Maine Department of Inland Fisheries and Wildlife, *personal communication*).

I decreased the impact of small sample sizes by treating each year a lynx was monitored as the unit of replication. This increased my sample size and decreased the chance of making Type II errors. This may have increased my chances of making Type I errors (i.e., pseudoreplication), but because many of my P-values were not equivocal I do not believe this was an issue. Also, I do not believe this decision influenced my results because if I used only 1 year for each lynx as the unit of replication, results were similar to results presented herein (Appendix B).

Lynx in Maine did not exhibit spatial responses to a declining hare density, except that extent of female intrasexual overlap declined and male breeding MINDIST decreased. One reason for this may be explained by the core population hypothesis, which suggests that a portion of a lynx population will maintain stable home ranges during hare declines (Breitenmoser et al. 1993). Reproduction will increase during the increase phase of the hare cycle, male offspring will disperse, and female offspring will

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stay within their mother's home range, whereas as prey density decreases, reproduction

declines and offspring may be less likely to disperse (Breitenmoser et al. 1993).

Presumably, lynx that form this core population and remain as residents with stable home

ranges during periods of moderate hare decline would be more likely to survive a decline

in hare density than lynx that disperse and become transients. Foregoing reproduction

during the same time may also increase chances of survival as energy expenditures can be

focused on maintaining home ranges, searching for prey, and avoiding the need for

females to restrict their home range area when central-place foraging from dens.

Another possible reason for lack of spatial response of lynx during LOW in

Maine is that hare densities may not have reached levels low enough to require lynx to

respond spatially. Social structure may erode during a decline period in more northerly

areas within the boreal forest region (Poole 1995), which can cause dispersal of

individuals in search of more productive habitat (Poole 1994;1997). Similar patterns

have been observed in bobcats as lagomorph populations decline (Bailey 1981, Knick

and Bailey 1986). In the northern boreal forest, hare densities can range from as low as

0.01 hares/ha during the low period (Hodges et al. 2001) to 9 hares/ha during the high

period of the cycle (Poole 1994), but between 0.5-1.0 hare/ha may be required for lynx to

persist (Ruggiero et al. 2000). If hares decline to densities lower than 0.5 hares/ha, lynx

may abandon their home ranges and emigrate to find better habitat (Ward and Krebs

1985). At the home range-scale in Maine, average hare density in the regenerating

conifer-dominated stands preferred by hares (Fuller and Harrison 2013) and selected by

lynx (Fuller et al. 2007, Vashon et al. 2008b) was as high as 2.29 hares/ha during a period

of relatively high hare density, but never dropped below 0.75 hares/ha during the low

hare density period (Scott 2009; D. Harrison, University of Maine, unpublished data).
Thus, lynx in Maine may not have reached landscape hare densities that were low enough
to encourage dispersal, home range expansion, and abandonment of established territories
by resident adult lynx.

A third possible reason for a lack of spatial response is because lynx may have
altered their habitat selection. Lynx maintained similar home range area and extent of
overlap between HIGH and LOW, except the extent of female intrasexual overlap, but
could shift their habitat selection to other habitats within their home ranges. During the
HIGH in Maine, lynx selected for conifer-dominated, regenerating habitats (Fuller et al.
2007, Vashon et al. 2008b), but lynx selection of habitats during LOW is unknown and
may change because of a decline in hare density. Habitat responses of lynx to changing
hare densities were investigated in Chapter 3.

SUMMARY AND MANAGEMENT IMPLICATIONS

Hare density in Maine did not reach the low levels common during the nadir of
the hare cycle in the boreal forests of northern Canada and Alaska, which may be a
potential cause of the different lynx spatial responses exhibited in this study compared to
responses by lynx in more northerly boreal regions. Consequently, lynx spatial responses
to hare densities outside of the range that occurred during this study could cause different
spatial responses of lynx in Maine than I observed.

During a period of reduced hare population, we observed reduced reproduction in
our study population (see page 76): therefore, lynx populations may be more sensitive to
anthropogenic factors during extended periods of low hare density (Ward and Krebs
1985, Poole 1994, Slough and Mowat 1996, Poole 1997). Others have recommended

management directed to reduce human-caused mortality of adult lynx, particularly females during periods of depressed hare populations (Parker et al. 1983, Poole 1994, Slough and Mowat 1996).

To enhance understanding of home range overlap and extent of territoriality among lynx, genetic relatedness between individuals (e.g., offspring) should be investigated. Additionally, to further support the core population hypothesis, reproduction and recruitment, as well as territory sharing between mothers and their offspring should be studied during a period of increasing hare populations in the Acadian forest region. Additionally, studies documenting the extent of prey switching by lynx between periods of high and low hare abundance in this region are needed.

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CHAPTER 3

HABITAT RESPONSES OF A SOUTHERN POPULATION OF CANADA LYNX

TO A DECLINE IN SNOWSHOE HARE DENSITY

ABSTRACT

Canada lynx (*Lynx canadensis*) are closely associated with conifer-dominated stands that provide dense understory and high horizontal cover, supporting high abundance of their primary prey, the snowshoe hare (*Lepus americanus*). Hare populations can fluctuate dramatically and lynx may exhibit habitat switching as hares become scarce. Thus, comparisons of habitat selection by lynx between periods of high and low hare densities may enhance understanding of the complex interaction among lynx, hares, and forest habitat conditions at the southeastern extent of the geographic range of this U.S. federally threatened species. I investigated change in use of high-quality hare habitat (HQHH) at the home range scale (i.e., landscape-scale use), and change in selection of HQHH within home ranges (i.e., patch-scale) by resident lynx between periods of high and low hare density during 2000-2010. Lynx locations were obtained using VHF and GPS collars during 1999-2011 and I estimated 90% fixed kernel, non-breeding/non-denning period home ranges for 104 lynx, which included all years a lynx was monitored. For both resident adult male and female lynx, percent of HQHH within home ranges was similar during a period of high hare density (44.3%) and during a period of low hare density (44.6%). Additionally, lynx exhibited stand-scale selection for HQHH during both the high and low hare density periods. Thus, despite declines in hares, lynx continued to use and select HQHH, presumably in attempts to maximize foraging success while avoiding home range shifts and territory abandonment (see

Chapter 2). Females, however, reduced their intensity of selection for HQHH from 0.186

during the period of high hare density to 0.067 during the period of low hare density,

suggesting that they may have changed to become less specialized on hares when density

declined. Future evaluation of the lynx diet within the transitional Acadian Forest region

is needed to shed insights into potential shifts toward a more generalized diet by lynx

when hares decline. This is important, given that communities of prey and potential

competitors differ from boreal regions where lynx have been previously studied. Where

lynx conservation is a concern, particularly in intensively managed forests within their

southeastern range, forest management should focus on maintaining previously

recommended levels of HQHH on the landscape to meet minimum requirements for

available HQHH within home ranges of lynx.

INTRODUCTION

Canada lynx (*Lynx canadensis*) are listed as federally threatened under the

Endangered Species Act in the contiguous United States (United States Department of the

Interior 2000) and in March 2009, 2.45 million hectares (9,447 mi^2) of northern Maine

were designated as Critical Habitat for Canada lynx (United States Department of the

Interior 2009). Lynx are found throughout the boreal forests of Canada and Alaska, the

subalpine forests of the western United States and southwestern Canada, and the mixed

coniferous/deciduous forests of the Great Lakes region and the northeastern United States

(Agee 2000). Until recently, research of lynx habitat preferences and responses to cyclic

changes in prey density have been focused within northerly populations in the boreal

forest region; however, since being U.S. federally listed, research efforts have expanded

in the contiguous United States (Burdett et al. 2007, Fuller et al. 2007, Koehler et al.

2008, Moen et al. 2008, Vashon et al. 2008a, Vashon et al. 2008b, Squires et al. 2010).

Although habitat use by lynx in response to cyclic changes in prey densities have been

studied in the boreal region (Ward and Krebs 1985, Murray et al. 1994, Poole et al. 1996,

O'Donoghue et al. 1998a, O'Donoghue et al. 2001, Mowat and Slough 2003), no

published results have linked changes in home range-scale habitat use and stand-scale

habitat selection by lynx in response to changes in density of snowshoe hare (*Lepus*

americanus) within the sub-boreal, southeastern portion of the geographic range of lynx.

This is particularly relevant given that densities of hares near the southern extent of lynx

range have been speculated by some previous researchers to be inadequate to support

persistent lynx populations (McKelvey et al. 2000, Ruggiero et al. 2000, Murray et al.

2008).

Snowshoe hares compose up to 97% of the lynx diet (Parker et al. 1983, Squires

and Ruggiero 2007). Within the boreal forests of Canada and Alaska, hares and lynx

exhibit distinctive population cycles where lynx populations will lag 1-3 years behind

hares (Nellis et al. 1972, Brand and Keith 1979, Boutin et al. 1995, Mowat et al. 2000,

Hodges 2000a, Hodges et al. 2001, O'Donoghue et al. 2001). Although this phenomenon

is well documented in the northern portion of their range, there is uncertainty surrounding

the magnitude of fluctuations and existence of cyclicity with populations of hares within

the sub-boreal portion of their geographic range (Howell 1923, Keith 1963, Hodges

2000b, Murray et al. 2008). Recent studies in Maine have documented >2-fold changes

in hare densities over a decade, but presence of cyclicity remains uncertain (Scott 2009).

Hares select stands with dense understories of coniferous saplings (Keith et al.

1984, Litvaitis et al. 1985, Fuller and Heisey 1986, Homyack et al. 2007, Lewis et al.

2011, Fuller and Harrison 2013) during all phases of their population cycle (Hodges 2000a; but see Wolff 1980), which provides them cover from predators (Sievert and Keith 1985), thermal protection, and browse (Wolff 1980, Litvaitis et al. 1985). Lynx select habitats where hares are abundant (Mowat et al. 2000, O'Donoghue et al. 2001, Fuller and Harrison 2010, Squires et al. 2010), such as early seral, conifer-dominated stands that have high understory cover (Parker et al. 1983, Koehler 1990, Murray et al. 1995, O'Donoghue et al. 1998a, Mowat et al. 2000, Fuller et al. 2007, Homyack et al. 2007, Vashon et al. 2008b). In the boreal forest of their northern geographic range, lynx occupy conifer and mixed-wood dominated forests (Mowat et al. 2000, Poole 2003), selected regenerating pine forests in the Yukon (Mowat and Slough 2003), and selected dense coniferous and deciduous forests in the Northwest Territories at the home range-scale (Poole et al. 1996). Lynx in the southern region of their geographic range, however, have more diverse types of habitats available to them in transitional forests that may influence their habitat choices (Agee 2000).

In the northwestern United States and southwestern Canada, conifer-dominated subalpine forests dominate, whereas the Great Lakes region and northeastern United States occur within transitional zones between boreal and temperate forests that contain a variety of both deciduous and coniferous species (Agee 2000). Lynx in Montana preferred mature, multistoried conifer forests with high horizontal cover (Squires et al. 2010), similar to lynx in Washington that selected conifer forests with moderate canopy cover (Koehler et al. 2008). In Maine, hare habitat can be much denser than in the western United States, where stem density can exceed 14,000 stems/ha (Fuller et al. 2007, Scott 2009) compared to 1,500-3,200 stems/ha reported for western Wyoming

(Berg et al. 2012). This suggests that regional differences in forest conditions may provide alternative habitat structure required by hares and lynx. Lynx in Maine, during a period of high hare density (>1.8 hares/ha), have been documented to select tall, regenerating clearcuts (Fuller et al. 2007), conifer-dominated sapling forests (Vashon et al. 2008b), and established partial harvests (11-26 years postharvest) that have 7,000-11,000 stems/ha, presumably because they offer intermediate cover for hares, and high to intermediate encounter rates of hares by lynx (Fuller et al. 2007).

Lynx and hares did not change habitat selection in the boreal forest as hare density changed (Murray et al. 1994, Hodges 2000a, Mowat and Slough 2003), suggesting either lynx maintained an adequate amount of habitat to encounter hares throughout the cycle, or they opportunistically switched to alternative prey while continuing to focus on declining hare densities when making foraging decisions. Lynx that survived during a hare density decline in the Yukon changed hunting tactics and became adept at catching red squirrels (*Tamiasciurus hudsonicus*) (O'Donoghue et al. 2001), which made up 20.4 – 43.9% of the total prey biomass of lynx during a period of low hare density (O'Donoghue et al. 1998a). Voles (*Microtus* sp. and *Clethrionomys* sp.), ruffed grouse (*Bonasa umbellus*), spruce grouse (*Falcipennis canadensis*), mice (*Peromyscus* sp.), and carrion also have all been documented as alternate prey items for lynx (Saunders 1963a, van Zyll De Jong 1966, Brand et al. 1976, Parker et al. 1983) and commonly occur within the mixed coniferous-deciduous forests of the Acadian Forest region (Seymour and Hunter 1992) and the southeastern extent of the geographic range of Canada lynx. This area includes most of Maine, the northern extent of New Hampshire and Vermont, and the maritime provinces of eastern Canada.

My research was focused on understanding habitat choices of lynx as hare density declined to evaluate alternative hypotheses: 1) lynx are more generalized in habitat use and selection during a period of high hare density to maximize foraging success on hares, which are forced to occupy suboptimal habitat resulting from density-dependent habitat selection; 2) lynx are more generalized in habitat selection during a period of low hare density to take advantage of alternative prey (e.g., ruffed grouse [*Bonasa umbellus*], red squirrels, deer mice [*Peromyscus maniculatus*], southern red-backed voles [*Clethrionomys gapperi*]) which maintain higher abundances in vegetation types other than dense, regenerating conifer habitats (Martin et al. 2001, Fuller et al. 2004, Fisher and Bradbury 2006, Holloway and Malcolm 2006); and 3) lynx maintain use and selection for high-quality hare habitats (HQHH) during periods of both high and low hare density because of their extreme specialization on hares and the costs of expanding foraging activity into unfamiliar areas and reducing their maintenance of established territories which may be crucial to future survival and reproductive success. Thus, my objectives were to compare use of HQHH within lynx home ranges to evaluate home range shifts (i.e., landscape-scale) and the intensity of intrasexual selection of HQHH within home ranges (i.e., patch-scale) between periods of high hare density (i.e., mean = 2.1 hares/ha; 1997 – 2006, HIGH) and low hare density (i.e., mean = ≤1.0 hares/ha; 2007 – 2012, LOW) in the sub-boreal, Acadian forests of northern Maine.

STUDY AREA

My study area included 33 townships in northwestern Maine (T 9, R 12-15 WELS; T 10, R 10-15 WELS; T 11, R 9-15 WELS; T 12, R 9-14 WELS; T 13, R 10-14 WELS; T 14, R 11-13 WELS; Eagle Lake and Soper Mountain). Lynx capture and

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monitoring effort, however, was focused in 4 townships (T11 R12 WELS, T11 R11

WELS, T12 R11 WELS, T12 R12 WELS) within the Musquacook lakes region of

northwestern Maine. Climate data was collected at the nearest weather station located in

T11 R14 WELS (46°37'N, 69°31'W, at an elevation of 304.8 m, National Climatic Data

Center, National Oceanic and Atmospheric Administration). The lowest mean daily

temperature occurred in January (-14.2°C) and the highest mean daily temperature

occurred in July (17.1°C). Average temperatures were 2.3°C, mean annual rainfall was

90.2 cm, and mean annual snowfall was 202.95 cm.

The 33 township area was privately owned and commercially managed for

pulpwood and sawlogs by forest industry companies and investor organizations

(McWilliams et al. 2005). Across commercial forests of Maine, average annual timber

harvesting occurred on 115,983 ha during 1982-1989, 181,785 ha during 1990-1994, and

214888 ha during 1995-2002 (McWilliams et al. 2005); harvests were categorized as

clearcuts and various forms of partial harvests (Smith et al. 1997), with clearcutting

decreasing and partial harvesting increasing in relative extent from 1982-2002. By

Maine law, clearcuts are defined as a removal of a stand with residual trees over 11.4 cm

diameter at breast height (DBH) and residual basal area <6.9 cm^2/ha (Maine Forest

Service 1990). Partial harvesting is a broad term describing shelterwood, selection, and

overstory removal harvests. Shelterwood harvests target removal of overstory trees to

promote regeneration under partial shade (Smith et al. 1997), selection harvests are

multiple entries in a stand that removes single or small groups of trees to create an

uneven age stand (Smith et al. 1997), and overstory removals are re-entries into stands

previously partially harvested to remove residual overstory trees and promote

regeneration (Smith et al. 1997).

A spruce budworm (*Choristoneura fumiferana*) epidemic in the 1970s and 1980s

affected spruce-fir stands in northern Maine, which was associated with increased

clearcutting (McWilliams et al. 2005). On most regenerating clearcut stands in my study

area, herbicide (e.g., glyphosate) was typically applied 4-10 years after cutting to favor

regeneration of coniferous species. The resulting stands were primarily composed of

balsam fir (*Abies balsamea*) with red spruce (*Picea rubens*), black spruce (*P. mariana*),

white spruce (*P. gluca*), eastern white pine (*Pinus strobes*), northern white cedar (*Thuja

occidentalis*), and eastern hemlock (*Tsuga canadensis*). Although these stands were

composed of 60 – 90% conifer saplings, deciduous species including red maple (*Acer

rubrum*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), pin cherry

(*Prunus pennsylvanica*), and raspberry (*Rubus* sp.) were present (Homyack et al. 2007).

Stands that had been partially harvested primarily contained residual trees represented by

sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch, yellow

birch (*Betula alleghaniensis*), and northern white cedar (*Thuja occidentalis*). Less

frequently occurring residual tree species included, red spruce, white pine, and red maple,

whereas pin cherry, striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*)

also colonized disturbed areas where herbicides were not applied or effective (Fuller and

Harrison 2005).

METHODS

Lynx were captured from March 1999 - October 2011 using methods described by

Vashon et al. (2008a). Lynx were outfitted with either Lotek (New Market, Ontario,

Canada) or ATS (Advanced Telemetry Systems, Isanti, MN) very high frequency (VHF) collars during 1999 – 2007; whereas during 2004-2011 lynx were equipped with Global Positioning System (GPS) collars (manufactured by either Lotek or Sirtrack [Havelock North, Hawkes Bay, New Zealand]). Locations were acquired by aerial telemetry for VHF collars (see Vashon et al. 2008a) or stored onboard GPS collars for download. After collection, location data from both VHF and GPS collars were separated into biological years beginning at estimated parturition on May 15 (Slough 1999, Poole 2003, Organ et al. 2008) and ending the following May 14. The May 15 cutoff also coincided with the end of the leaf-off season period used for estimating over-winter hare density across 2 regions in northern Maine (Homyack et al. 2007, Scott 2009).

I tested Sirtrack and Lotek GPS collars within 7 habitat classes in my study area (Chapter 1) and selected a screening criterion to remove all 2D locations with ≥10 dilution of precision (DOP) for Lotek collars and locations with ≥10 DOP for Sirtrack collars (Sirtrack collars did not give a 2D/3D classification). DOP is a measure of the geometry of satellites and a 2D/3D classification refers to the number of satellites used to calculate a location (Rempel et al. 1995, Moen et al. 1996, Rodgers et al. 1996, Moen et al. 1997). Screening removes locations with unacceptably large location errors (i.e., outliers) and increases overall accuracy (D'Eon and Delparte 2005, Lewis et al. 2007).

I separated location data into lynx biological years (May 15 – May 14), which began with the approximate start of the birth and denning period (Slough 1999, Poole 2003, Organ et al. 2008). I also separated location data into HIGH and LOW based on annual, leaf-off (i.e., winter) hare densities (Homyack et al. 2007, Scott 2009; D. Harrison, University of Maine, unpublished data) estimated from pellet counts using the

regression of Homyack et al. (2006). Lynx used in this study were equipped with only VHF collars during HIGH and with only GPS collars during LOW. Thus, I subsampled the GPS collar locations (collected every 4.5 hours for Sirtrack and once per day for Lotek collars) to match the location attempt frequency of the VHF collars (2-3x/week) to avoid sampling biases when comparing habitat use and selection between HIGH and LOW. VHF collar locations were collected an average of 8 locations/month (range = 4-14) with ≤121 locations per year. I used Ablebits Random Generator for Microsoft Excel (Homel, Belarus) to randomly subsample locations from GPS collars to match the number of average monthly locations and the total number of locations of VHF collars, based on the number of months monitored.

VHF locations obtained from aircraft had associated pilot-specific telemetry error, calculated by comparing aerial coordinates of collars on mortality mode to mortality site coordinates (Vashon et al. 2008a), whereas GPS locations were subject to location errors influenced by overhead cover and the number of transmitting satellites (Chapter 1). I corrected for these errors by creating an error polygon around each location and used the bivariate-weighted method as described by Montgomery et al. (2010), to determine the most probable habitat class associated with each location. The radius for each VHF error polygon corresponded with each pilot's maximum telemetry error, and the radius for GPS error polygons corresponded to the largest location error recorded for test collars (Chapter 1). Within each error polygon, I generated points in a grid with 30m spacing to match the resolution of the LANDSAT-derived habitat maps, using Hawth's Analysis Tools for ArcGIS (Beyer 2004). I assigned a habitat-specific probability for each location based on the half-normal distribution. Points closer to the center location point

are assigned a probability approaching 1, whereas points near the boundary of the error polygon have assigned probabilities approaching 0 (Montgomery et al. 2010); probabilities for each point were added together for each of my 2 habitat classes (HQHH and non-HQHH).

Canopy cover can cause missed locations from GPS collars (Rempel et al. 1995, Moen et al. 1996, Chapter 1), which can cause bias in habitat selection analyses (D'Eon 2003, Frair et al. 2004, Hebblewhite et al. 2007). Consequently, I analyzed missed locations from test collars (Chapter 1) to determine the fix success of each collar manufacturer by season and habitat class (Table 1.4). Fix success of test collars in regenerating, conifer-dominated habitats during the leaf-on season and in all conifer-dominated habitats during the leaf-off season were used to represent fix success values for HQHH (Chapter 1). Fix success across all other habitat classes were used to represent non-HQHH. I estimated missed locations from GPS collars by dividing the observed locations from each collar by the percentage of fix success for each collar manufacturer according to season and habitat class (Table 1.4). The resulting number of estimated missed locations was then added to the observed locations for each lynx.

I created a binary habitat map of HQHH and non-HQHH for 2001, 2004, and 2008. Simons (2009) developed a model of probability of lynx occurrence that used hare densities from previous research in Maine (Litvaitis et al. 1985, Lachowski 1997, Fuller and Harrison 2005, Robinson 2006, Homyack et al. 2007) and Quebec (de Bellefeuille et al. 2001), where densities of ≥1 hare/ha were associated with HQHH. Subsequently, lynx have been documented to exhibit strong positive selection for HQHH at the landscape- (Vashon et al. 2008b, Simons-Legaard et al. 2013), patch- (Fuller et al. 2007, Vashon et

al. 2008b), and within-patch- (Fuller and Harrison 2010) scales within the Acadian forest region. Thus, HQHH was defined as conifer-dominated and mixed conifer-deciduous regenerating forest, 13-40 years after a stand-replacing disturbance and a herbicide treatment, as those were the only forest types estimated to support hare densities ≥1 /ha (Fuller and Harrison 2005, Homyack et al. 2007, Scott 2009) during companion studies in Maine. Non-HQHH was defined as all other forest and non-forest habitats estimated to support < 1 hare/ha.

I used 13 LANDSAT Thematic Mapper (TM) satellite images from 2 scenes in northern Maine, spanning 1984-1995, to create the habitat maps. Time between images ranged from 1-3 years depending on availability of cloud free images. I combined all documented lynx home ranges during both HIGH and LOW (Chapter 2) into one shapefile, and clipped all satellite images to their boundary, using a 1 km perimeter buffer. Similar to methods of Simons-Legaard et al. (2013), I used a supervised classification to detect recent (1-3 years), stand-replacing harvests (i.e., clearcuts and heavy partial harvests) in the projection of red band 3, near-infrared (NIR) band 4, and mid-infrared (MIR) band 5 of each image.

I used a satellite image from 1984 to serve as a base map and used images in future years to build a harvest history. It takes at least 13 years for a herbicided clearcut stand to grow into HQHH (Simons-Legaard et al. 2013), thus satellite images from 1984-1988 were used to develop the 2001 habitat map, 1984-1991 were used to develop the 2004 map, and 1984-1995 images were used to map HQHH in 2008. I reduced the chance of classifying non-HQHH pixels as HQHH by masking all out wetlands, roads, and deciduous dominated forests. Additionally, I used the Majority Filter function in

ArcMap 9.3 (Environmental Science Research Institute [ESRI], Inc., Redlands, California, USA) to smooth each map based on the majority of each neighboring pixel's classification.

A known map of HQHH and non-HQHH of my study area did not exist to compare and evaluate the accuracy of my mapping of HQHH. The closest available map resulted from the combination of a 2004 forest cover map (Simons-Legaard et al. 2013) and a 1970-2007 harvest detection time series (K. R. Legaard, University of Maine, unpublished data). The 2004 forest cover map had 90% agreement of HQHH with United States Forest Service Inventory Analysis spatial plot data (Simons-Legaard et al. 2013) and overlapped with 39.94% of the maps I developed. I used this combination of 2 maps and overlaid them on my maps of HQHH to assess the percent of pixels where HQHH was in agreement. Additionally, I evaluated pixel agreement of HQHH and non-HQHH within the boundaries of stands used by The University of Maine and the Maine Department of Inland Fisheries and Wildlife (MDIFW) for hare pellet sampling (Homyack 2003, Robinson 2006, Scott 2009, J. H. Vashon, Maine Department of Inland Fisheries and Wildlife, unpublished data). Those plots of approximately 15 ha were chosen to be consistent in overstory composition, were extensively ground-truthed, and were representative of either conifer-dominated, regenerating (HQHH), partial harvest (non-HQHH), or mature (non-HQHH) stands. Although the area of those pellet plots equaled 0.12% of my total map area, they totaled 1,812 different 900 m^2 pixels for comparison with my base maps.

I evaluated the difference in percentage of HQHH within 90% fixed kernel, non-breeding/non-denning (NB/ND) lynx home ranges (Chapter 2) between HIGH and LOW

(i.e., landscape-scale use). I chose to investigate use at the landscape-scale because I was

explicitly interested in HQHH as the only habitat at this scale and wanted to determine if

lynx shifted home ranges to include more HQHH as hare density declined. Home ranges

from 1999/2000-2002/2003 were overlaid onto the 2001 map, home ranges from

2003/2004-2005/2006 were overlaid onto the 2004 map, and home ranges documented

during 2006/2007-2009/2010 were overlaid onto the 2008 map of HQHH. If lynx were

monitored for multiple years within a period, each year was treated as a separate

individual. Lynx are a territorial species (Saunders 1963b, Kesterson 1988, Poole 2003)

and follow an ideal despotic distribution (Fretwell and Lucas 1970, Fretwell 1972).

Therefore, dominant, resident individuals may maintain habitat of relatively higher

quality across consecutive years to avoid losing their territory to an adjacent or

colonizing con-sexual. Thus, I was concerned HQHH that is occupied for multiple years

would be underrepresented in my analyses if individuals monitored for multiple years

were pooled into an average value. Such an approach would reduce the representation of

habitats occupied by resident lynx across multiple years to the same representation as

habitats that were only used or included in a single lynx home range during a single year

across my 12-year study.

Statistical analyses were performed in SYSTAT 12 (SYSTAT Software Inc.,

Chicago, Illinois, USA) using a generalized linear model (GLM). I set a significance

level of 0.10 for all statistical tests to balance probability of Type I and Type II errors.

Normality of data was assessed visually using boxplots and statistically by Shaprio-Wilk

tests.

I compared the difference in percentage of HQHH within home ranges between HIGH and LOW for females with and without kittens. Kitten presence was determined by den visits during June and via ≥1 km of winter backtracking of all collared females on snow. Backtracking was conducted in 2009 and 2010 during 2 different days between the months of January-March to further verify presence of kittens determined during den visits of 2008 and 2009. I compared the percentage of HQHH within female home ranges with and without kittens with a t-test. Normality of data was assessed visually using boxplots and statistically by Shaprio-Wilk tests.

I also evaluated whether the intensity of selection by lynx for patches of HQHH within their home ranges (i.e., patch-scale selection) changed from HIGH to LOW. I restricted these analyses to locations obtained during the NB/ND season and quantified selection using an index of [ln(use/availability); (Aebischer et al. 1993)] where use was the percent of locations observed in HQHH within a lynx home range, and availability was the percent of HQHH within that individual lynx's home range. If lynx were monitored for multiple years within a hare density period, each year was treated as a separate individual. Because lynx are a territorial species, habitats within home ranges of dominant lynx are controlled for multiple years, and will be underrepresented if years are pooled or averaged for lynx monitored for >1 year. Within sexes, I tested for differences in selection index between periods of HIGH and LOW hare density using two Mann-Whitney tests. I used a non-parametric test because the observed selection values were not normally distributed. Further, I used 2 sex specific Mann-Whitney tests as opposed to a single Kruskal-Wallis test because sample sizes for males were much greater than for females and I did not want to skew the results by using a global test.

RESULTS

The MDIFW captured 85 (44 M, 41 F) adult and sub-adult lynx from March 1999 to October 2011. For my analyses, I used a subsample of 46 adult, resident (≥2 years old) lynx during HIGH (16 M, 13 F) and LOW (10 M, 7 F) that were monitored for ≥4 months to produce NB/ND home ranges. Twenty one lynx (11 M, 10 F) during HIGH and 5 lynx (5 M, 0 F) during LOW were monitored > 1 year, increasing total sample size (i.e., each year a lynx was monitored was treated as a unit of replication) to 81 lynx (45 M, 36 F) during HIGH and 23 lynx (16 M, 7 F) during LOW. Additionally, I used location data of 10 female lynx that had kittens during HIGH, including 9 which were monitored for > 1 year, totaling 26 adult female-years with kittens. I used 7 females, each monitored for only 1 year, which did not have kittens during LOW.

I created 3 habitat maps (Figure 3.1), but because of the dates of the 2 existing maps of my study area, only the 2004 map was compatible to make a comparison of pixel agreement. Pixel agreement of HQHH between the 2004 map and the 2004 forest cover map (Simons 2009) and 1970-2007 harvest detection time series (K. R. Legaard, University of Maine, unpublished data) was 61%. Pixel agreement was increased to 67% by expanding all of the HQHH boundaries by 1 pixel (30 m), which was justified given that the average transition distance between preferred and non-preferred patches of habitat within lynx home ranges was estimated to be 58 m (Fuller and Harrison 2010). I believe 67 % agreement is acceptable, considering the combination of the 2004 forest cover map and the 1970-2007 harvest detection time series was not a 100% true map. The best measure of accuracy would be a comparison of my maps and known sites of HQHH and non-HQHH.

Figure 3.1. High-quality hare habitat (HQHH) and non-HQHH maps in northern Maine for the years a) 2001, b) 2004, and c) 2008. Maps were created from 13 LANDSAT TM images during the years 1984-1995 and were clipped to the extent of all 90% fixed kernel non-breeding/non-denning home ranges (plus 1 km buffer).

a)
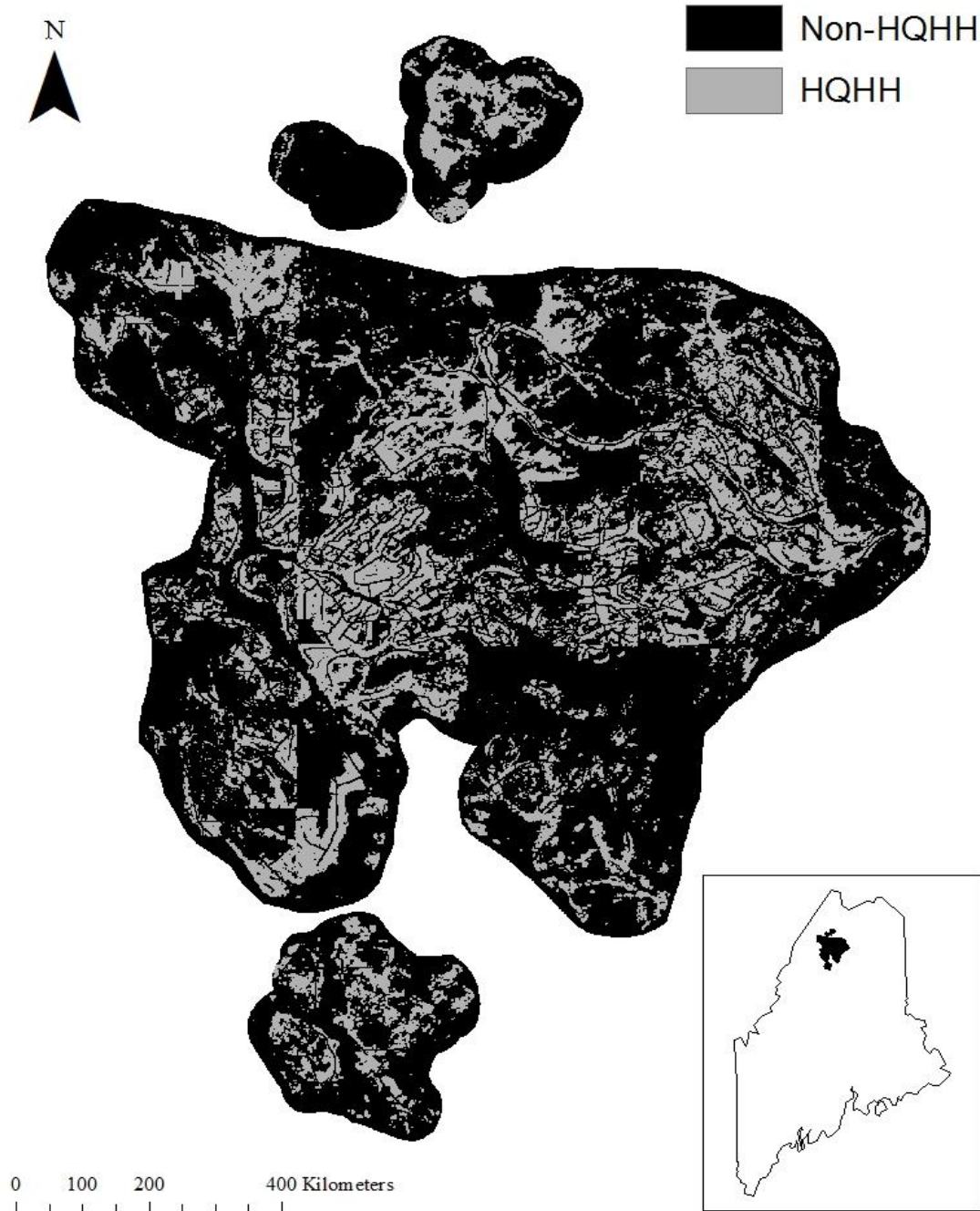
b)
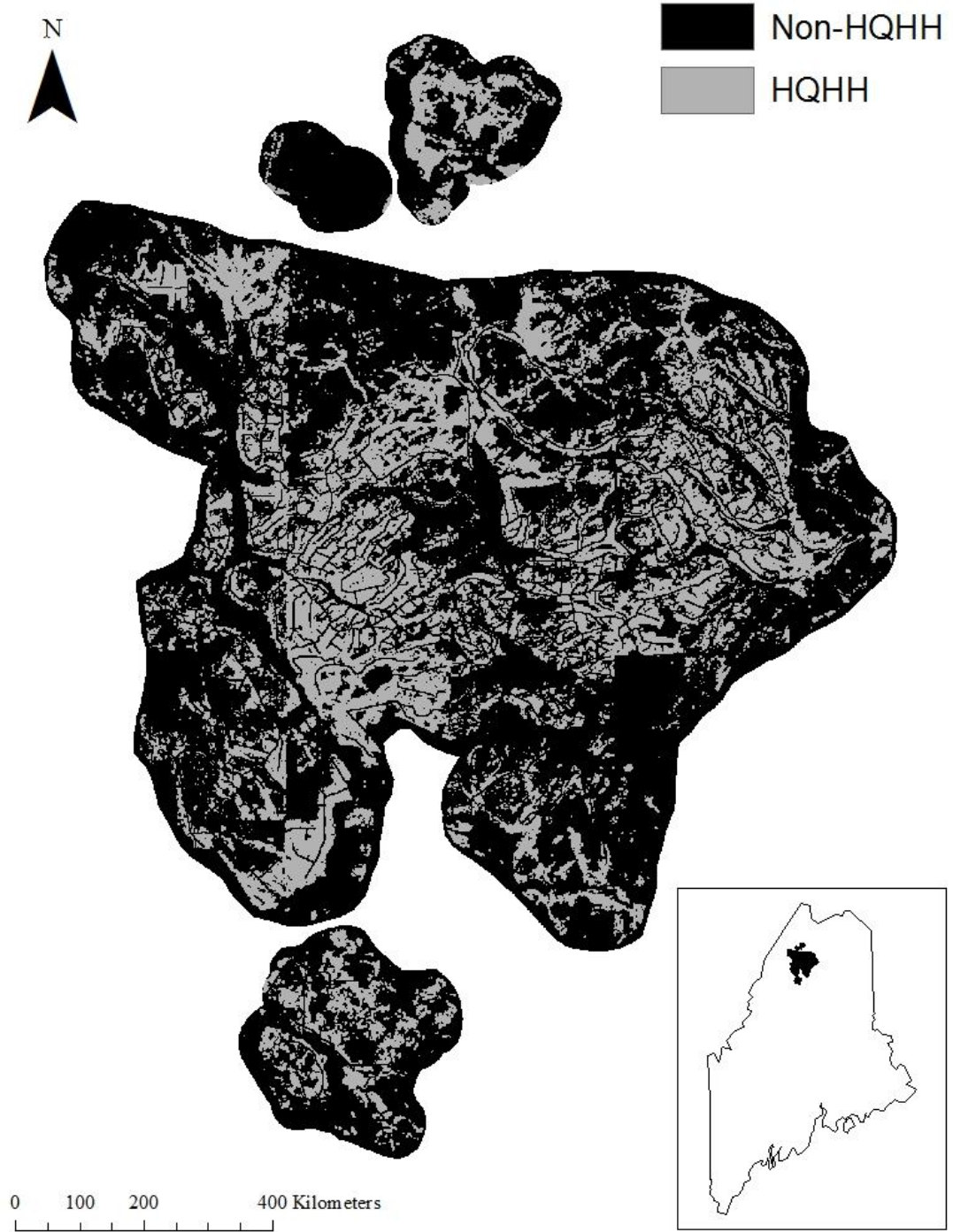
c)
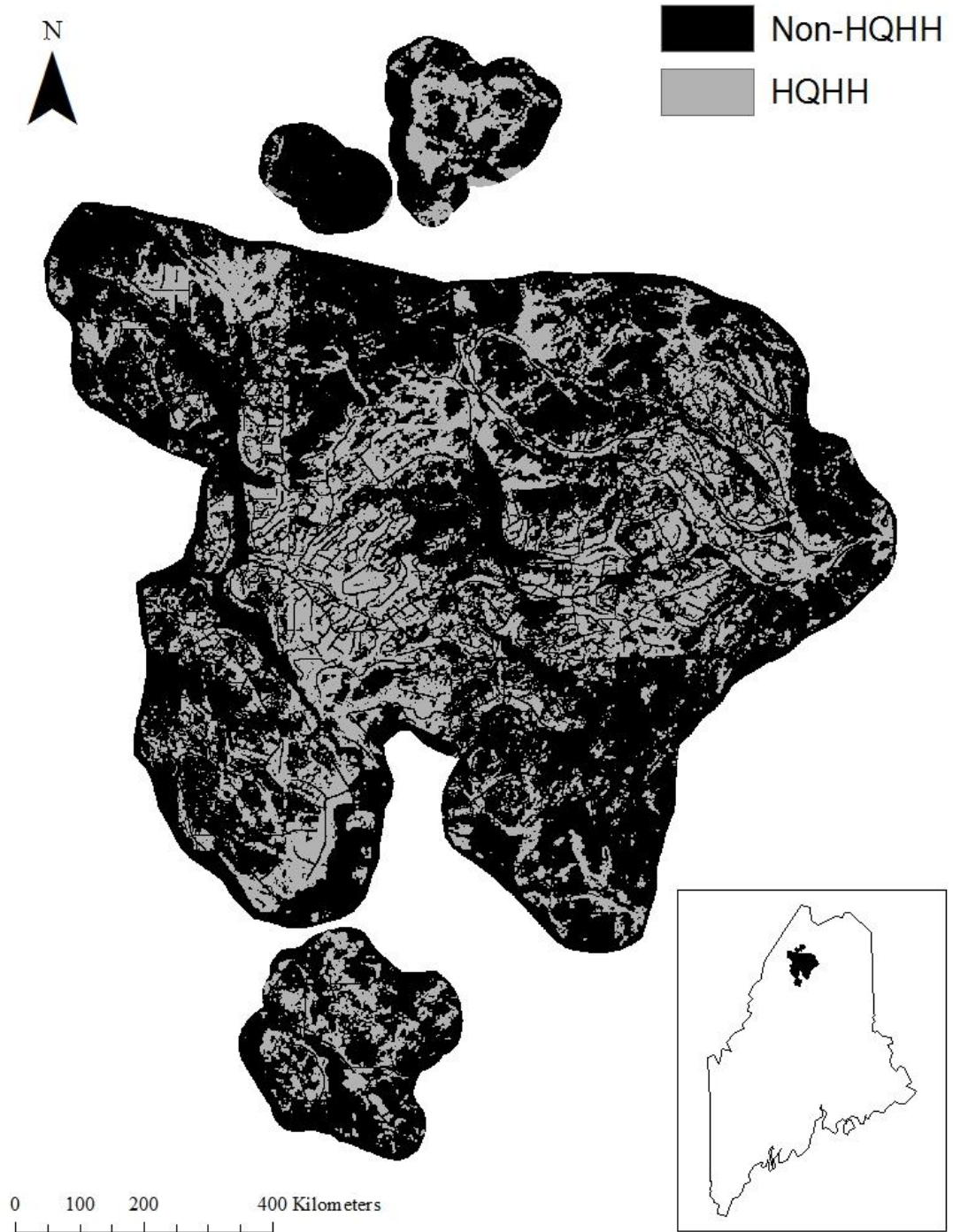
HQHH pixel agreement for each of the 3 maps of HQHH that I developed (2001, 2004, and 2008) was higher when compared to stands of known forest types that were established and extensively ground-truthed during companion studies conducted by personnel at The University of Maine and MDIFW (Table 3.1). HQHH had higher percentages of pixel agreement during all years than non-HQHH (Table 3.1). The lower pixel agreement for non-HQHH may be caused by underrepresentation of heavy partial harvests, which have similar spectral signatures to clearcuts, and may be erroneously classified as HQHH in my maps.

Use of HQHH by lynx at the landscape scale was not different between the HIGH and LOW periods (F = 0.014, P = 0.906) or sexes (F = 0.827, P = 0.365). Further, there was no evidence of a strong interaction between sex and period (F = 2.078, P = 0.153), indicating that both sexes behaved similarly and occupied ranges that were composed of 42-47% HQHH during both the HIGH and LOW (Table 3.2). Additionally, percent of home range in HQHH was not different (t = -0.998, P = 0.329) between females with kittens (44%) and females without kittens (47%).

Lynx of both sexes exhibited selection for HQHH, as evidenced by selection indices > 0 across both the HIGH and LOW periods (Figure 3.2). Males exhibited similar intensity of selection across both periods (U = 367.5, P = 0.902). Females, however, reduced their intensity of selection for HQHH as hare densities declined (U = 187, P = 0.045).

DISCUSSION

The percentage of HQHH within home ranges did not change between HIGH and LOW for either sex, and companion analyses (Chapter 2) also indicated that lynx did not

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Table 3.1. Pixel-level agreement (%) between 3 maps of high-quality hare habitat (HQHH) and non-HQHH (2001, 2004, and 2008) and stands selected and ground-truthed by personnel of The University of Maine and Maine Department of Inland Fisheries and Wildlife in northern Maine, USA. HQHH was defined as conifer-dominated regenerating forest (13-40 years old) where hare densities were documented to be ≥ 1.0 hares/ha. Non-HQHH included mature ($\geq$40 years since last harvest), selection harvest, and shelterwood harvest stands where hare densities were documented to be < 1.0 hares/ha.

Habitat maps	HQHH (n=8)			Non-HQHH (n=17)		
	Pixels in agreement	Total pixels	%	Pixels in agreement	Total pixels	%
2001	573	676	84.8	856	1136	75.4
2004	635	676	93.9	789	1136	66.5
2008	646	677	95.4	808	1136	71.1

Table 3.2. Percent of the home range composed of high-quality hare habitat (HQHH) of a) males and females in HIGH (1997-2006) and LOW (2007-2012) hare density periods and b) females with kittens (HIGH) and without kittens (LOW) in northern Maine, USA.

a)

Sex (Period)	n	Mean ± SE	Range
M (HIGH)	45	44.9 ± 1.4	20.3 – 62.2
M (LOW)	16	41.9 ± 2.4	21.6 – 55.9
F (HIGH)	36	43.7 ± 1.3	32.4 – 59.6
F (LOW)	7	47.2 ± 3.2	38.3 – 59.6

b)

Females	n	Mean ± SE	Range
With kittens	26	43.5 ± 1.6	32.4 – 59.6
Without kittens	7	47.2 ± 3.2	38.3 – 59.6
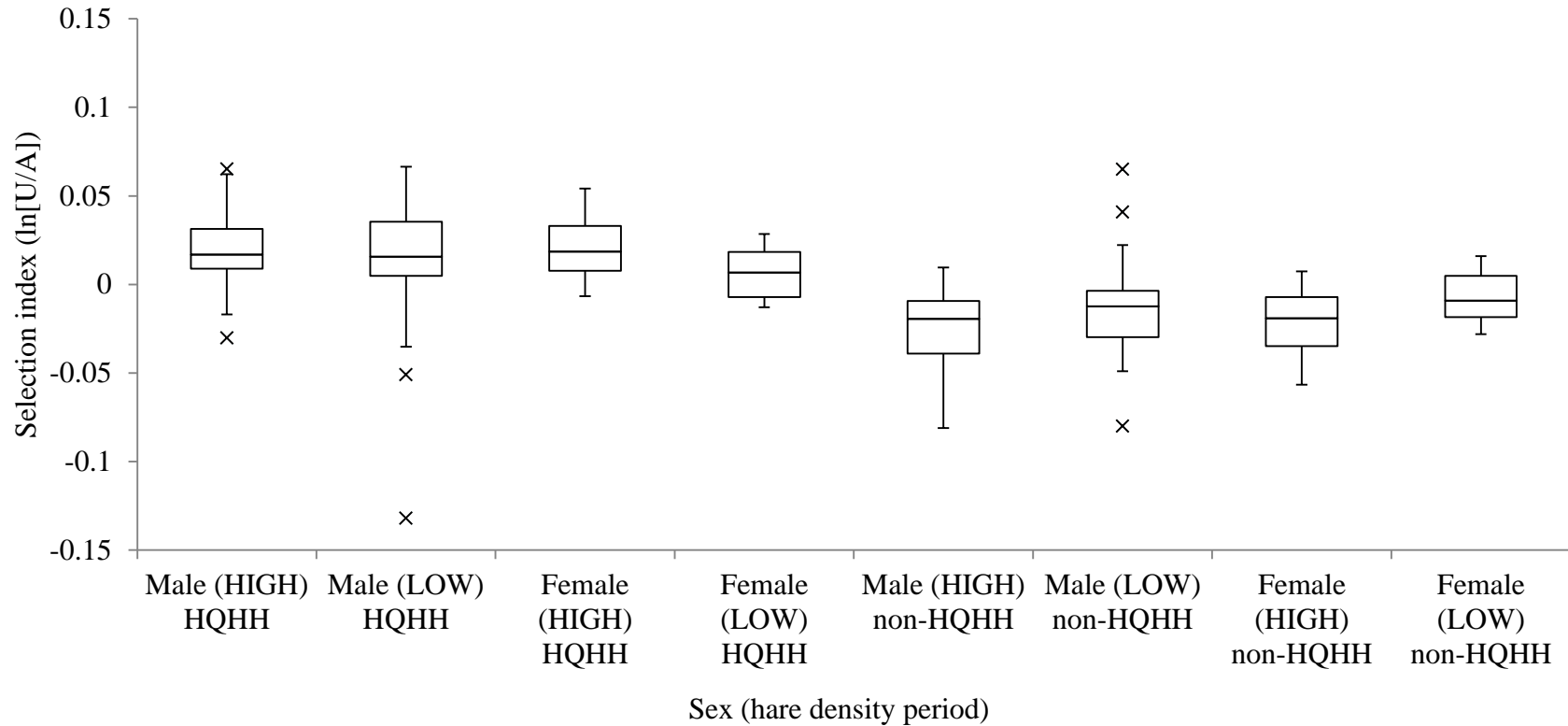
Figure 3.2. Habitat selection [ln(use/availability)] indices of high-quality hare habitat (HQHH) of male and female lynx during HIGH (1997-2006) (n = 45 M, 36 F) and LOW (2007-2012) (n = 16 M, 7 F) hare density periods in northern Maine, USA. Selection indices > 0 indicate positive selection, whereas negative indices indicate selection against. The upper box boundary is the 75th percentile, middle line is the median, and lower box boundary is the 25th percentile. The difference between the 75th and 25th percentile is the interquartile range (IQR). Whiskers above the box indicate the largest data point within the upper limit, where the upper limit is the 75th percentile plus 1.5*IQR. Whiskers below the box indicate the smallest data point within the lower limit, where the lower limit is the 25th percentile minus 1.5*IQR. The symbol "X" represents outliers.

change the area of their home ranges as hare densities declined. These results suggest

that lynx maintained their territories when densities of prey fluctuated ~2.5 fold in

optimal habitats, and that lynx continued to exhibit high landscape-scale use of areas with

optimal habitat for snowshoe hares. In contrast, this response to changing hare densities

is different from lynx in the boreal regions of Canada and Alaska where hare densities

have been documented to fluctuate 5-25 fold (Hodges 2000a, Hodges et al. 2001).

Further, hare densities may decline to <0.1 hares/ha (Hodges 2000a) at the nadir of the

cycle in boreal regions, whereas densities in HQHH during the low in this study were

~0.8 hares/ha (Scott 2009, D. Harrison, University of Maine, unpublished data). Where

hare densities fluctuated more widely in northern boreal regions, lynx responded by

increasing home range area or by abandoning their territory and dispersing to new areas

(Ward and Krebs 1985, Poole 1994, Poole 1995, Poole 1997, O'Donoghue et al. 2001).

Those responses may not have been required by lynx in my study because they had

substantial amounts of HQHH within their home ranges and may have been able to

continue to focus on hares during the period of relatively low hare density. Regional

differences in hare population dynamics are important to consider when evaluating lynx

responses to changing prey populations.

The amount of HQHH previously recommended to promote landscape-scale

densities of >0.5 hares/ha and home range-scale occurrence of lynx was 27% (Simons-

Legaard et al. 2013). I documented that home ranges of lynx, regardless of sex or

reproductive status, were composed of ≥42% HQHH during both HIGH and LOW (Table

3.2). This suggests that landscape-scale availability of HQHH in my study area greatly

exceeded minimum requirements for occupancy at the scale of the individual lynx home

range as suggested by Simons-Legaard et al. (2013). The abundance of HQHH on my study area may have reduced the need for lynx to shift or expand home ranges as hare density declined. The levels of HQHH within lynx home ranges that I observed may exceed landscape-scale requirements for lynx in the Acadian forest region.

Two other explanations for the high levels of HQHH could be: 1) mapping inaccuracies; or 2) temporal increases in HQHH resulting from succession of newly clearcut areas into regenerating patches of HQHH. The 3 maps ranged in HQHH accuracy from 85-95% (Table 3.1), allowing some room for inaccuracy to influence results, but likely did not affect overall conclusions. Additionally, there was no decrease of HQHH (i.e., outgrowth) during the duration of the study because no stands of HQHH reached ages ≥40 years (Simons-Legaard et al. 2013). In fact, the amount of HQHH in the study area increased 4.5% from 2004 to 2008 as additional clearcut stands were recruited into HQHH. Overall, lynx had slightly more HQHH available to them during LOW, but incorporated a similar amount of HQHH in their home ranges during both HIGH and LOW.

At the patch-scale, lynx selected for dense, regenerating conifer forests (i.e., HQHH) during both the LOW and HIGH periods. This is in contrast to what has been observed in the Yukon, Canada, where as hare densities decline, both lynx and hares increased their use of the densest habitats (O'Donoghue et al. 1998a). This is consistent with the theory that hares seek refuge in denser habitats as their density declines (Wolff 1980, Hik 1995). However, a review of habitat use patterns by hares suggested that evidence is lacking to support the hare refuge theory (Hodges 2000a), and concluded there is no shift in habitat use throughout the cycle within the northern boreal portion of

the geographic range of hares. In the southeastern portion of the snowshoe hare's range, their habitat use is similar to the north (Hodges 2000b); early seral forests, dense understory cover, and high stem density are important (Wolff 1980, Litvaitis et al. 1985, Hik 1995, O'Donoghue et al. 1998a, Berg et al. 2012, Fuller and Harrison 2013). Additionally, a 16 year study in the southern range documented no cyclic change in hare habitat use (Fuller and Heisey 1986). In the mixed Acadian forests near the southeastern extent of the geographic range of hares, it appears that early-seral, conifer forests that support HQHH are selected strongly by lynx at the scale of the home range (Vashon et al. 2008b, Simons-Legaard et al. 2013), and that this selection is maintained across the range of hare densities (0.8 – 2.1 hares/ha) that occurred in HQHH during my study. At the patch scale, hares maintained highest densities in HQHH across the range of forest types occurring in the region (Fuller and Harrison 2005, D. Harrison, University of Maine, unpublished data), and lynx consistently exhibited selection for HQHH during both HIGH and LOW. This suggests that in the southeastern portion of the range of Canada lynx, early regenerating conifer forests may be the most critical habitat component to maintain regardless of changing hare densities where management and recovery of this U.S. federally threatened species is a priority. In the Rocky Mountain region, lynx and hares have shown affinities for multi-storied conifer forests; thus, regional differences in habitat conditions that provide the dense horizontal cover required by hares and lynx should also be considered.

Lynx exhibited positive selection for HQHH during both HIGH and LOW, similar to previous research in Maine during HIGH, where lynx selected for conifer-dominated, regenerating stands at the patch-scale (Fuller et al. 2007, Vashon et al. 2008b) and for

habitats that support high hare density at the landscape-scale (Simons-Legaard et al. 2013). However, the intensity of this positive selection decreased for females as hare density declined, although the ability to detect differences between HIGH and LOW may have been affected by the small sample size of females during LOW. I believe the effect of a small number of monitored females during LOW, however, was mitigated by my choice of unit of replication and non-parametric statistical tests.

I hypothesize that the decrease in intensity of female selection of HQHH from HIGH to LOW may indicate that females spent more time foraging in non-HQHH during LOW to encounter alternative prey. Fuller et al. (2007) documented lynx selection for established partial harvests (11-26 years post-harvest) during HIGH because they offered intermediate hare encounter rates and a lower stem density than conifer-dominated, regenerating stands, thus enhancing higher hunting success. Established partial harvest stands, and other habitats that offer higher hunting success, may have more importance during LOW, as lynx may use habitats with high prey use, but not habitats that hares prefer to be in (i.e., dense stands that reduce hunting success for predators) (Keim et al. 2011). Established partial harvest stands would have been represented as non-HQHH in my analyses, thus if lynx showed a strong selection for it during LOW, as an alternative to HQHH, my analysis would not have detected that shift.

Female lynx may have decreased their selection of HQHH as hare density declined because of shifts to alternate prey. During hare density declines in the northern range of lynx, they have been documented to consume red squirrels, grouse, small mammals, and carrion (Saunders 1963a, van Zyll De Jong 1966, Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1998a). Although red squirrels may only be

equivalent to 0.2 hares for dietary requirements (Nellis and Keith 1968), they are an important alternative prey species across the lynx range (Roth et al. 2007). In Yukon, Canada, red squirrels were 20-44% biomass of a lynx diet during a low period of hare density compared to 0-4% biomass during a high period (O'Donoghue et al. 1998b). Further, in Washington, squirrels occurred in 24% of lynx scats (Koehler 1990). Red squirrels and other potential alternate prey are present in Maine, but diets of lynx have not yet been evaluated.

Red squirrels rely on conifer seed production, thus they are found in habitats with large densities of mature conifer trees (Fisher and Bradbury 2006, Holloway and Malcolm 2006). Another alternate prey item for lynx are ruffed grouse (van Zyll De Jong 1966, Parker et al. 1983), which prefer habitats with a large deciduous component, especially *Betula* and *Populus* species (Martin et al. 2001), where aspen (*Populus tremuloides*) is an important year round food in Maine (Brown 1946). Mature habitat (>40 years postharvest, 62% conifer composition) supporting red squirrels and partial harvest habitat (11.5 m^2/ha deciduous basal area) supporting grouse, were classified in a similar study, composing 8% and 14% of the area, respectively, within 2 townships of my study area during HIGH (Fuller et al. 2007). Additionally, 17% and 14% of available habitat within 4 townships in my study area were classified during HIGH as conifer dominated mature (>12.2 m) and deciduous dominated sapling (<7.3 m) habitats (Vashon et al. 2008b). Thus, habitats preferred by red squirrels and ruffed grouse were available in my study area and may have provided lynx with substantial access to alternative prey.

Females with kittens and without kittens did not alter the percentage of HQHH within home ranges between HIGH and LOW. Lynx exhibited a strategy of focusing reproductive effort during periods when prey were abundant and decreased reproduction when prey are scarce. If lynx consumed alternate prey (e.g., red squirrels) during LOW, lynx may decrease reproduction and could experience kitten mortality because of difficultly of female lynx to meet energy requirements of kittens when central-place foraging from dens. Assuming red squirrels are approximately 1/5 the energy equivalent of hares (Nellis and Keith 1968), female lynx would require high capture success of squirrels to meet daily energetic requirements for provisioning kittens, if dependent on switching to alternate prey (Koehler 1990). The percentage of biomass of alternate prey species increased compared to hare biomass in lynx stomachs as hare density declined in Alberta, coinciding with a decrease in pregnancy rates and litter sizes (Brand and Keith 1979). Additionally, lower recruitment rates during a decline of hare density, coincided with an increase of red squirrels as a food source of lynx, composing 58-72% of total prey biomass (O'Donoghue et al. 1997). In Maine, reproduction, as determined by den visits, declined from HIGH to LOW where 82.1% of females surveyed during denning season in HIGH were attending kittens, whereas 27.6% of females during LOW were attending kittens (Chapter 2). Additionally, backtracking of female lynx in the winters of 2 years during LOW, who were not attending kittens during den visits the previous year, confirmed the absence of kittens being recruited into the population (Chapter 2). This suggests energetic requirements of female lynx to support reproduction during a hare density decline may not have been met during the period of reduced hare density.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Hare density in Maine did not reach the low levels common in the boreal forests of northern Canada and Alaska, thus lynx in Maine did not exhibit similar responses to declining hare density as has been previously reported for lynx in their northern range. Consequently, regional differences in magnitude and duration of hare population fluctuations will influence lynx responses and are important considerations for future management of lynx. Additionally, hare densities outside of the ranges presented here (0.75 – 2.3 hares/ha), may elicit different responses of lynx in Maine. If hare densities decline to levels observed in their boreal northern range (≤0.5 hares/ha), lynx responses in Maine may more closely resemble responses in their northern range (i.e., territory and social structure breakdown, prey switching) that were not directly observed during this study. Future research should consider evaluating lynx responses to hare density outside of the levels observed herein.

Lynx in Maine maintained their territories (Chapter 2) and similar amounts of HQHH within their home ranges during LOW to maintain access to hares as hare density declined. My findings provide further support for the recommendations of Simons-Legaard et al. (2013), who recommended that forest management should favor silvicultural treatments that provide adequate amounts of HQHH (>27% HQHH within 100-km^2) at the landscape scale in areas prioritized for home range-scale occupancy by lynx. Further, my results indicate that these recommendations are relevant during periods of both high and low hare density.

Lynx demonstrated selection for HQHH during both HIGH and LOW, but the intensity of selection for HQHH weakened for females during LOW. As hare density

declined, females spent relatively more time in non-HQHH, presumably hunting for alternate prey. Alternate prey species important to lynx in their northern range are available to lynx in Maine, but lynx diets in Maine are currently unknown. Additionally, alternate prey may not provide the energetic requirements needed for reproduction, which may have contributed to the reduced reproduction during LOW reported during companion studies (Chapter 2). Consequently, future management and research of lynx should focus on conservation of breeding females during LOW and should attempt to evaluate the diets of lynx during both HIGH and LOW. Also, more information on the extent of prey switching and use of alternate prey by lynx in the Acadian Forest region is needed.

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APPENDICES

Appendix A

NUMBER OF LYNX MONITORED FOR MULTIPLE YEARS

Table A.1. Description of the number of lynx monitored for consecutive biological years (May 15 – May 14) during 7 years in a period of high hare density (1999/2000 – 2005/2006; HIGH) that wore VHF collars and during 5 years in a period of low hare density (2006/2007-2010/2011; LOW) that wore GPS collars. The numbers of lynx presented are lynx who met minimum requirements for at least 1 of 3 types of home ranges (non-breeding/non-denning, annual, and breeding/denning).

Years monitored	HIGH		LOW	
	Male	Female	Male	Female
Lynx monitored 1 year	5	4	3	6
Lynx monitored 2 years	5	2	7	1
Lynx monitored 3 years	1	1	1	2
Lynx monitored 4 years	2	4	1	0
Lynx monitored 5 years	2	2	0	0
Lynx monitored 6 years	2	1	0	0

Appendix B

HOME RANGE ANALYSIS RESULTS FROM TREATING INDIVIDUAL LYNX

AS UNIT OF REPLICATION

Lynx home ranges were analyzed using the individual lynx as the unit of

replication, different than presented in Chapter 2 that used each year a lynx was

monitored as the unit of replication. In this appendix, if lynx were monitored for >1 year,

only the year with the greatest number of locations was used to estimate home ranges.

Sample sizes using individual lynx as the unit of replication were smaller (Table A.1)

than sample sizes that used each year a lynx was monitored as the unit of replication

(Table A.2). However, statistical test results were similar between the 2 methods. Using

the individual lynx as the unit of replication, I compared intrasexual differences between

a period of high hare density (HIGH) and low hare density (LOW) for 3 types of home

ranges using Mann-Whitney tests. The 3 types of home ranges were 90% fixed kernel

non-breeding/non-denning (NB/ND) and annual home ranges, as well as an index of

home range area during the breeding/denning (B/D) period of the mean minimum

distance between independent, consecutive locations (MINDIST; Harrison and Gilbert

1985). The only methodological and statistical difference between this analysis and the

analysis presented in Chapter 2 was the unit of replication (see Methods, page 65). Male

NB/ND home range area did not change between HIGH and LOW (U = 62, P = 0.895).

Further, female NB/ND home range area also did not change significantly (U = 24, P =

0.189). Similarly, male and female home range area did not change between HIGH and

LOW (Males: U = 48, P = 0.612; Females: U = 29, P = 0.361). Male breeding MINDIST

values did not change between HIGH and LOW (U = 53, P = 0.353), but female denning

MINDIST values increased from HIGH to LOW (U = 39, P = 0.026). The only change

in statistical interpretations that occurred when the unit of replication was switched to the

individual lynx was that the significant decrease of male breeding MINDIST value (same

trends but more statistical power) observed when the unit of replication was each year a

lynx was monitored (Chapter 2 Results, page 79), was not statistically significant (same

trends but likely Type II error) when the unit of replication was switched to the individual

lynx.

Table B.1. Home range area (km^2) for non-breeding/non-denning (NB/ND) 90% fixed kernel home range areas, annual 90% fixed kernel home range areas, and breeding/denning (B/D) estimates of minimum distance traveled (m) between consecutive independent locations (MINDIST; Harrison and Gilbert 1985) during a HIGH (1997-2006) and LOW (2007-2012) hare density period in Maine, USA. If lynx were monitored for >1 year during either hare density period, the biological year (May 15 - May 14) with the greatest number of locations, was the only year used for home range and MINDIST analysis.

Sex (Period)	NB/ND			Annual			B/D		
	n	Median	Range	n	Median	Range	n	Median	Range
M (High)	12	52.52	27.72 – 96.72	12	59.5	30.28 – 68.69	12	3959.56	3,312.81 – 6,004.17
M (Low)	10	56.81	23.26 – 130.38	7	38.51	24.19 – 102.16	7	3509.18	2,508.29 – 6,753.17
F (High)	11	38.92	18.42 – 67	11	32.96	16.92 – 69.73	9	706.99	4,46.12 – 1,022.11
F (Low)	7	29.74	20.15 – 83.7	4	25.2	22.23 – 43.35	4	2987.81	1,385.92 – 3,419.15

Table B.2. Home range area (km^2) for non-breeding/non-denning (NB/ND) 90% fixed kernel home range areas, annual 90% fixed kernel home range areas, and breeding/denning (B/D) estimates of minimum distance traveled (m) between consecutive independent locations (MINDIST; Harrison and Gilbert 1985) during a HIGH (1997-2006) and LOW (2007-2012) hare density period in Maine, USA. Each lynx monitored in each biological year (May 15 – May 14) was treated as a replicate.

Sex (Period)	NB/ND			Annual			B/D		
	n	Median	Range	n	Median	Range	n	Median	Range
M (High)	45	51.66	18.2 – 96.72	37	61.18	22.81 – 106	36	4054.54	2493.7 – 8646.43
M (Low)	16	40.75	20.11 – 130.38	10	37.59	23.72 – 102.16	19	3155.76	2308.34 – 6753.17
F (High)	33	34.26	17.38 – 108.25	35	30.86	14.37 – 69.73	33	944.55	446.12 – 4561.03
F (Low)	7	29.74	20.15 – 83.7	4	25.2	22.23 – 43.35	10	2987.81	1,385.92 – 3,419.15

BIOGRAPHY OF THE AUTHOR

David Glenn Mallett was born in Smithville, Missouri on December 16, 1983. He remained there until completing his high school education in May 2002. He then attended the University of Missouri in Columbia, MO where he received a B.S. in Fisheries & Wildlife, a B.S. in Forestry, and a Minor in Business in 2007. He was voted the Outstanding Senior in Forestry in 2007. After completing his undergraduate education, he began work in a series of field related jobs that took him through Colorado, South Dakota, and Wyoming, where he performed a variety of research related tasks working with species such as coyotes, pronghorn, bison, and moose. David moved to Maine in April 2008 where he began pursuit of a Master of Science degree. In recognition of his research efforts, he received the Fred Griffee Graduate Research Award in 2010. In 2011, David left Maine to move to Iowa to get married and start a new life. He continued to work on his thesis long distance, but returned in early 2014 to complete his research and degree. He is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in May 2014.