Evaluating the Effects of Habitat Loss and Fragmentation on
Canada Lynx (*Lynx canadensis*)

A Dissertation Submitted to the Committee on Graduate Studies in
Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy in the Faculty of Arts and Science

TRENT UNIVERSITY
Peterborough, Ontario, Canada

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Environmental and Life Sciences Ph.D. Graduate Program
September 2014
ABSTRACT

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Megan L. Hornseth

Current major issues in conservation biology include habitat loss, fragmentation and population over-exploitation. Animals can respond to landscape change through behavioural flexibility, allowing individuals to persist in disturbed landscapes. Individual behaviour has only recently been explicitly included in spatial population models. Carnivores may be sensitive to changing landscapes due to their wide-ranging behaviour, low densities and reproductive rates. Canada lynx (Lynx canadensis) is a primary predator of snowshoe hares (Lepus americanus). Both species range throughout the boreal forests of North America, however lynx are declining in the southern range periphery. In this dissertation, I developed new insights into the effects of habitat loss and fragmentation on lynx. In Chapter 2, I created a habitat suitability model for lynx in Ontario and examined occurrence patterns across 2 regions to determine if habitat selection is flexible when different amounts of habitat are available. Although lynx avoided areas with <30% suitable habitat where suitable land cover is abundant, I found that they have flexible habitat selection patterns where suitable land cover is rare and occurred in low habitat areas. In Chapter 3, I investigated the effects of dispersal plasticity on occupancy patterns using a spatially explicit individual-based model. I showed that flexible dispersers, capable of crossing inhospitable matrix, had higher densities and a lower risk of patch extinction. In contrast, inflexible dispersers (unable to cross
inhospitable matrix), were most limited by landscape connectivity, resulting in a high extinction risk in isolated patches. I developed three predictions to be explored with empirical data; (1) dispersal plasticity affects estimates of functional connectivity; (2) variation in dispersal behaviour increases the resilience of patchy populations; and (3) dispersal behaviour promotes non-random distribution of phenotypes. In Chapter 4, I examined the consequences of anthropogenic harvest on naturally cycling populations. I found that harvest mortality can exacerbate the effects of habitat fragmentation, especially when lynx densities are low. Dynamic harvest regimes maintained lynx densities and cycle dynamics while reducing the risk of population extinction. These results suggest that lynx display some flexibility to changing landscapes and that the metapopulation structure is more resilient to increasing habitat loss and fragmentation than previously understood. Future studies should focus on determining a threshold of connectivity necessary for population persistence and examining the effects of habitat loss on the fecundity of lynx.

**Keywords:** Canada lynx; fluctuating populations; connectivity; habitat loss; habitat fragmentation; occupancy dynamics; spatially explicit individual-based models
**Preface**

This dissertation is written in article format. For chapters of which I am not the sole author, the co-authors are noted on the title page. These chapters are either submitted or in preparation for peer-reviewed journals (Chapters 2-4).

Experimental design, analyses, and manuscript preparation were all carried out by the Ph.D. candidate. Co-authors of chapters contributed conceptual discussions, expertise in analysis, and critiquing of written materials. The journal style of each manuscript is listed on the title page.
Acknowledgements

I am indebted to so many who have provided me with assistance and support throughout this endeavour. First of all, I would like to thank my supervisor, Dennis Murray, for providing me with this opportunity and for his academic and financial contributions. I would like to thank my supervisory committee, Jeff Bowman, Justina Ray, and Marie-Josée Fortin, for supporting me through thick and thin, and providing valuable feedback and advice along the way. Many thanks go to my unofficial committee member, Lyle Walton, who kept me afloat while I was in the field. I would also like to thank Bruce Pond, for providing continued guidance and support throughout my years at Trent. Thanks to my funders listed on the following page, along with the many field assistants for their incredible hard work over the years. Hopefully the hundreds of kilometers of snow tracking data will be put to use in the future.

I would like to thank my mom, for her endless support, advice, patience, and understanding over the last 7 years, and Joe for reminding me to always listen to my heart. A huge thank you to Kevin Downing: your support and advice – in the field and in the years since – has been truly invaluable. Thanks to Linda Cardwell for convincing me to stick with it, always being a listening ear, and providing helpful advice. I would like to thank my office mates - K’moose and Aaron Walpole in the early years, and more recently, Kristen and Morgan, for putting up with my rants, providing advice, and sharing a laugh. I also want to thank the Happy PhD Club – Eunice, Glynis, Andrea: it’s been a long haul, but we’re making it through! To Kamila Baranowska, Laura Finnegan, Erin Koen, Natalie Rosso and Lindsay Spenceley – I
wouldn't have made it through without the bonfires, long walks, nights in, nights out, good laughs (and hugs), and always being able to find a voice of reason in at least one of you! Thank you to those at CNFER, especially Rob Rempel, for supporting me in finishing my thesis while working full time - it wasn't easy, but definitely forced me to use my time wisely.

There are countless others to thank: Alyssa, Kelly and Vicki, for understanding the trials and tribulations of grad school, or at least trying to. Thanks to Mike Reaume for our endless discussions – they are truly motivating and have helped me in countless ways, John Marris for opening my eyes to a world beyond science and always lending an ear to my rants, and to Erin Koen for always lending a listening ear (and sending baked goods when necessary!). Thanks to the physiotherapists and massage therapists helped me through my recovery, the ultimate community and the climbing crew for providing hours of stress release and allowing me to focus on something other than my thesis. Finally, a huge thank you to my loyal companion, Hudson, without our long walks I wouldn't have made it through these last 5 years.
**Funders**

NSERC
Wildlife Conservation Society
Ontario Ministry of Natural Resources
Wildlife Conservation Society Canada
Canadian National Sportsman Show
Trent University
Panthera
CFI

**Field Assistance**

Guillermo Alba
Jesse Archer
Dave Ballak
Daniel Brubaker
Todd Copeland
Maria Diebolt
Kevin Downing
Alex Howard
Eric Huskinson
Erin Koen
Jason Moulard
Eric Newkirk
Andrew Orton
Kirk Sobey
Lyle Walton

Thanks to Everyone!
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Chapter 1: General Introduction

Habitat loss and fragmentation are among the most important threats to global biodiversity and population persistence (Saunders et al. 1991; Debinski et al. 2000). Habitat fragmentation implies a loss of habitat, a reduction in patch size, and an increase in patch isolation (Andren 1994), which can result in increased mortality risk and reduced fecundity, leading to population decline, range loss, and altered metapopulation structure (Hanski 1999; Moilanen and Hanski 1998). Landscape ecology focuses on how the spatial configuration of the landscape influences populations and community dynamics of organisms. Spatial patterns are the result of disturbance and the interplay between abiotic and biotic factors; these patterns are crucial in understanding broad-scale processes that are integral to species distributions, population dynamics, dispersal patterns, and predator-prey interactions (Turner et al. 2001; Tilman et al. 1997). Resource distribution is ever-changing due to land-use disturbance and is therefore a critical issue for conservation biology and ecosystem management (Fahrig and Merriam 1994). Strategies to mediate the effects of landscape change may be formulated by merging the understanding of broad-scale habitat disturbance with the responses of organisms and populations (Collinge 2001). Large carnivores may be particularly sensitive to habitat loss and fragmentation because of their low densities, wide-ranging behaviour requiring broad spatial extents, and low reproductive output (Weaver et al. 1996; Clark et al. 1996; Noss et al. 1996).

A landscape-scale focus is required to identify how to manage populations over large areas while mitigating the effects of habitat loss and fragmentation, as well as
planning human settlement (Turner et al. 2001). These principles have become key components of ecosystem management (Agee and Johnson 1988; Slocombe 1993; Christensen et al. 1996; DeFries et al. 2004). Each of these challenges demands an understanding of the processes occurring at broad spatial and temporal scales, and therefore requires management solutions that operate at appropriately broad scales often crossing regional or jurisdictional boundaries. Landscape models provide a means to represent a system or process, permitting the development of predictions and testing of hypotheses, and therefore are an essential tool in landscape ecology (Turner et al. 2001). Broad spatial scales are inherently difficult and expensive to study. Although it is nearly impossible to create large scale disturbances in the field, it is important to understand what the implications of these disturbances might be (Dale et al. 1998). The use of spatial models provides a means to extrapolate knowledge from smaller studies and apply the concepts at the appropriate scale for the system, permitting the exploration of ecological consequences and mitigation techniques for broad-scale disturbances by relaxing empirical constraints (Turner et al. 2001). Spatial models are required when the amount and arrangement of spatial attributes are important to the question of interest as they can simulate changes in the pattern through time to evaluate alternative hypotheses (Turner 1987; Turner et al. 2001). Habitat loss and fragmentation can create a metapopulation structure where a population distributed over habitat fragments (or subpopulations) is interconnected by dispersing individuals (Hanski 1999; Moilanen and Hanski 1998). The likelihood of a metapopulation persisting over time is dependent upon the ability of individuals to disperse from one subpopulation to
another and is subject to the turnover rate within each patch (Hanski 1999; Fahrig 2002). However, the earliest metapopulation model, described by Levins (1969), is a “patch-occupancy model” in that it considers immigration and emigration among patches of equal quality at an equal distance; however, it does not factor in births and deaths within a single patch or the cost of dispersing across the matrix. Since Levins’ work, there have been several advancements in classic metapopulation theory to include population dynamics within a patch, so that patch occupancy is a function of births, deaths, immigration and emigration, as well as dispersal behaviour and landscape heterogeneity. Collectively, these changes make many contemporary models more realistic and applicable to natural systems (Fahrig 2002).

Landscape ecologists typically use spatially explicit population models, such as spatially explicit individual-based models, which specify the spatial arrangement of habitat patches and include other landscape features such as patch size, shape, and quality (Dunning et al. 1995). These models can be used to address issues regarding habitat loss and fragmentation, isolation, and patch size, on the population of interest (Turner et al. 2001). Spatially explicit models address the limitations of other metapopulation models as they explicitly include landscape pattern, population dynamics within a patch, dispersal mortality risk, as well as stochasticity (Fahrig 2002). These models can be used to incorporate animal behaviour, population dynamics, and habitat quality into a landscape mosaic, providing a context to investigate broad-scale processes such as metapopulation dynamics resulting from habitat fragmentation. This approach can facilitate comparisons of
mitigation solutions and policy options in ecosystem management (Turner et al. 1995).

**Lynx-Hare Dynamics**

Canada lynx (*Lynx canadensis*) is a mesocarnivore and specialist predator of snowshoe hare (*Lepus americanus*); their ranges are largely coincident across North America (Koehler 1990, Aubry et al. 2000; Poole 2003). These species display a classic predator-prey relationship. Throughout most of their range across the boreal forest, both species exhibit an 8-11 year cycle in abundance, with a slight time lag, where the rise and fall of lynx is 1-2 years after that of snowshoe hares (Elton and Nicholson 1942; Keith 1963; Koehler 1990; Hodges 2000; Murray 2000). Lynx densities can be as high as 30 adult lynx/100 km² in their northern range (Poole 1994), whereas densities in the southern extent tend to be substantially lower (2.3 adult lynx/100 km² (Koehler 1990); 15.5 lynx/100 km² (Vashon et al. 2008a)). This discrepancy likely is due to landscape heterogeneity in the southern range and attendant reduced densities of snowshoe hares (Murray et al. 2008), which may also result in prey-switching by lynx (Roth et al. 2007). Although hares cycle with 26- to 100-fold amplitudes in the northern part of their range (Krebs et al. 1986; Boutin et al. 1995), in the southern part of their range hares may cycle with lower amplitudes (<15-fold, Marshall 1954; Brooks 1955) or may fluctuate irregularly (Keith 1990).

Lynx prefer conifer-dominated sapling stands (20-40 years of age) but avoid very young stands (<20 years; Mowat and Slough 2003; Vashon et al. 2008b). While stand-level selection of lynx closely follows that of hares, hares prefer areas dense understory cover to provide thermal shelter and visual cover from predators (Wolff...
where lynx have difficulty hunting (Mowat et al. 2000). Hares have much smaller spatial requirements than lynx, with home ranges that vary from approximately five to 10 ha (Wolff 1980; Murray 2003) and can occupy patchy, fragmented areas (Wirsing et al. 2002). In contrast, lynx have relatively large spatial requirements with home ranges varying in size from 25 km$^2$ to 100 km$^2$ (or 25 000 ha to 100 000 ha) (Mowat et al. 2000; Vashon et al. 2008a). While fragmentation has not yet been explicitly examined in lynx, several other wild felid populations are sensitive to fragmentation (e.g. Iberian lynx ($Lynx pardinus$) (Ferreras 2001), bobcat ($Lynx rufus$) and cougar ($Puma concolor$) (Crooks 2002)). As a result, habitat loss and fragmentation could differentially affect lynx and hares.

Reduced hare densities, combined with increased anthropogenic and natural disturbance in the southern portion of the lynx range has subsequently fragmented the population distribution (Hodges 2000; Aubry et al. 2000), resulting in a metapopulation (Schwartz et al. 2002, Rueness et al. 2003). While there is currently no evidence that this is causing genetic isolation, maintaining connectivity between southern populations and larger core populations is a significant factor in the maintenance of peripheral populations (Schwartz et al. 2002). This required connectivity, as well as reduced densities at the southern range edge, led to the listing of Canada lynx as threatened under the Endangered Species Act in the contiguous United States (USFWS 2006). In Canada, lynx are abundant in most provinces and are still trapped across much of their range, including southern Canada. These populations at the southern range edge are currently in decline and
the range is contracting due to habitat loss and changes in environmental conditions (Poole 2003; Koen et al. 2014).

**Objectives**

My approach with this research project was to understand the broad-scale implications of habitat loss and fragmentation on lynx. Landscape models require a definition of habitat suitability for the population of interest as a precursor to examining metapopulation dynamics (Hansi and Simberloff 1997), so my first objective was to create a habitat suitability model for Canada lynx and quantify the effects of habitat loss and fragmentation on occurrence patterns on landscapes varying in levels of suitable land cover to determine if there was a threshold at which selection patterns changed, and whether lynx became more or less sensitive to fragmentation when habitat was limiting (Chapter 2). My next objective was to use a simplified spatially explicit individual-based model to understand the implications of fragmentation on occupancy patterns in experimental landscapes with different amounts of habitat fragmentation (Chapter 3). My final objective was to expand upon the landscape model used in Chapter 3 and apply it to a real landscape in northeastern Ontario to examine how human-induced harvest mortality on a forestry-dominated landscape affects natural population cycles (Chapter 4).
References


Chapter 2: Impacts of habitat loss on the occurrence patterns of Canada lynx at the southern range edge


Contributions: MLH and DLM conceived of the study; MLH designed the study, analyzed the data and wrote the paper; MLH, AAW and LRW collected data; AAW, LRW, JB, JCR, M-JF and DLM critically reviewed the chapter.

Submitted to PLoS ONE

Abstract

Peripheral populations often experience more extreme environmental conditions than those in the centre of a species’ range, including increased fragmentation of habitat. Habitat fragmentation involves a loss of habitat, reduction in patch size, and increased distance between remaining patches. The ‘threshold hypothesis’ predicts when the proportion of habitat is low, the number of small and isolated patches increases, so habitat fragmentation may compound the effects of habitat loss, but when habitat is abundant, effects on populations are due to only habitat loss. Alternatively, the ‘flexibility hypothesis’ individuals may respond to increased habitat disturbance by altering their selection patterns and becoming less sensitive to habitat loss and fragmentation. While the range of Canada lynx (Lynx canadensis) has contracted due to habitat loss, the combined effects of habitat loss and fragmentation are only beginning to be understood. We used a habitat suitability model to delineate suitable land cover and contrasted lynx occupancy patterns across 2 regions in Ontario, each with 3 landscapes differing in the amount of suitable land cover, to determine if there is support for the ‘threshold hypothesis’ or if lynx have more flexibility in response to habitat fragmentation than previously
understood. When suitable land cover was widely available, lynx avoided areas with less than 30% habitat and were unaffected by habitat fragmentation. However, on the landscapes with minimal suitable land cover, lynx occurrence was not related to either process, indicating flexibility in habitat selection patterns instead of support for the ‘threshold hypothesis’. We conclude that although lynx are affected by habitat loss and not habitat fragmentation, occurrence patterns are flexible depending on landscape condition. We suggest that lynx may alter their selection patterns more than previously considered, thereby allowing them to be less sensitive to anthropogenically-driven habitat alteration.

Introduction

Populations occurring at the periphery of a species’ geographic range often occupy habitats that are of lower overall quality, leading to reduced survival, reproduction and population density, compared to populations in the core of the range [1]. In addition, peripheral populations tend to be more sensitive to environmental variability than those in the core, which can promote increased demographic stochasticity and lower resiliency [2-4]. As a result, individuals in the range periphery may be more sensitive to the processes of habitat loss and fragmentation. Alternatively, animals may respond with more flexible habitat selection patterns, enabling them to move among variable environments to enhance their fitness [5]. This flexibility should increase species’ persistence in landscapes experiencing anthropogenic change, such as in areas subject to high habitat fragmentation. However, much of our perception of how wide-ranging species respond to these landscape-scale processes is speculative, especially in peripheral populations where
occurrences are often limited. This shortcoming is especially relevant because as landscapes continue to be altered by anthropogenic disturbance, many species are faced with declines in range size [6]. An improved understanding of the effects of habitat fragmentation on species occurrence patterns will enhance our understanding of how these processes may impact species distributions.

Habitat fragmentation consists of three main components, loss of habitat, reduction in patch size, and increased patch isolation, where these latter two processes are often considered together as habitat configuration [7]. Highly fragmented landscapes have smaller habitat patches that are farther apart, reducing connectivity, potentially limiting dispersal ability, and affecting predator-prey dynamics [8]. The ‘threshold hypothesis’ predicts that when habitat is abundant, the effect of habitat fragmentation on populations would be limited to habitat loss and not due to the effects of habitat configuration; however, when the proportion of habitat declines at a landscape level, small and isolated patches become more abundant on the landscape, and the effects of habitat configuration can complement those of habitat loss [7,9]. Habitat fragmentation may therefore have a greater effect at the range edge, where habitat is often limiting [2]. The ‘threshold hypothesis’ has been supported by several studies examining the population size and presence of birds and small mammals [8, 10, 11]. In contrast, the ‘flexibility hypothesis’ suggests that individuals may alter their habitat selection patterns to permitting them to inhabit variable environments that would otherwise be unsuitable due to habitat fragmentation [5,12].
Canada lynx (*Lynx canadensis*) occur across the boreal forest of North America, where their primary prey is snowshoe hare (*Lepus americanus*). Lynx select forested habitat where hares are most abundant or easily depredated [13-15], whereas hares select young coniferous forests where both food and cover are adequate [16,17]. In the southern periphery of the species’ range, forest composition is more heterogeneous and hare densities are naturally lower, leading to reduced abundance and restricted distribution of lynx [18]. Because habitat for both lynx and hare has been reduced and fragmented due to anthropogenic activities in their southern range peripheries, the distribution and abundance of both species is now restricted [19,20]. The southern range of lynx in Ontario has contracted by over 175 km since 1970 [21]. Although the mechanisms ultimately limiting lynx populations at the southern range periphery remain to be fully understood, there may be sensitivity due to habitat fragmentation [22], with habitat loss and climate change as other important factors [21]. Several other felid species are reported to be sensitive to habitat fragmentation (e.g. Iberian lynx (*Lynx pardinus*) [23], bobcat (*Lynx rufus*) and cougar (*Puma concolor*) [24]). However, whether these species express any flexibility in relation to the amount of habitat on a landscape has not yet been explored.

We examined the occurrence patterns of Canada lynx across the 2 regions in the southern geographic range of the species in Ontario to assess patterns of occurrence in relation to habitat fragmentation. Given that lynx are prey specialists, requiring areas within a narrow range of suitable conditions to meet prey and habitat requirements [25] as well as connectivity requirements [26], we predicted
that they would be sensitive to habitat loss when habitat was widely available, and sensitive to both habitat loss and fragmentation when suitable habitat was less than 30% supporting the ‘threshold hypothesis’[7,9]. These patterns may be expressed more strongly along the southern range periphery, due to increased levels of habitat loss and reduced habitat quality [21], leading us to speculate that any sensitivity to habitat fragmentation would be most apparent here. Alternatively, the ‘flexibility hypothesis’ suggests that lynx will have greater tolerance to both habitat loss and fragmentation than previously thought, such that their occurrence patterns may not correlate with either process, indicating flexibility in habitat selection. We developed a habitat suitability model for lynx and tested the above predictions using patterns of track occurrence across the species’ southern range edge. We compared two regions each with three comparable levels of suitable land cover as determined by the habitat suitability model to examine if occurrence patterns differ across landscapes with varying amounts of suitable land cover. Observations of lynx tracks in areas with limited suitable land cover and increased fragmentation would imply that lynx are not sensitive to habitat fragmentation, or that the importance of suitable habitat on occurrence patterns at the range periphery are less critical than previously understood.

Methods

ETHICS STATEMENT

The Trent University Research Ethics Board fully approved the study (reference #21083). In the introduction of the study, participants were explicitly told that informed consent was implied if they submitted their survey data. The field
component consisted of non-invasive track surveys conducted on public land, so no access permits or animal care protocols were required. Canada lynx are considered not at risk under provincial and federal guidelines.

STUDY AREA

The study area encompassed 200,000 km\(^2\) in central Ontario (Figure 2.1A), across the southern boreal forest and the Great Lakes St. Lawrence forest, a transition zone from boreal to deciduous forest, encompassing the southern range limit of lynx occurrence in the region [27]. The area is largely comprised of boreal forest, with spruce (*Picea glauca, P. mariana*), balsam fir (*Abies balsamea*), trembling poplar (*Populus tremuloides*) and white birch (*Betula papyrifera*) as dominant tree species. The southerly portions of the study area in the Great Lakes St. Lawrence region include pines (*Pinus resinosa, P. strobus*), eastern hemlock (*Tsuga canadensis*), yellow birch (*B. alleghaniensis*) and maples (*Acer saccharum, A. rubrum*). Habitat fragmentation throughout the study area is caused primarily by forestry and associated road construction; historically 1% of the entire region (approximately 2000 km\(^2\)) was harvested annually [27], current levels are 0.04% or 800 km\(^2\) (2000-2010 average; [28]). Other sources of habitat loss include populated areas, agriculture, and natural disturbance such as forest fire and disease.

HABITAT SUITABILITY MODEL

In order to quantify lynx habitat suitability, we used the analytic hierarchy process, which is a decision-making procedure that is useful in the development of habitat suitability models for wide-ranging mammals (see [29,30] for description of methodology). We developed the survey design based on a literature review
identifying important ecological factors affecting lynx occurrence, with an emphasis on factors affecting lynx occurrence in the southern range. The primary habitat characteristics were land cover attributes (e.g., [14,15]), forest age class (e.g., [15,31]), annual snowfall (e.g., [32]) and road density (e.g., [33]). We developed two separate models of habitat suitability, one based on expert-opinion, where we received 11 solicited responses from lynx researchers across North America, and the other using a literature-based approach with four ‘naïve’ participants with no previous knowledge of lynx ecology. Both experts and naïve participants received the same survey and the naïve participants also received four research papers providing a detailed description of the basic habitat requirements of lynx from across its range [14,15,33,34]. The survey consisted of five separate pair-wise comparison matrices based on each of the features of interest (land cover, forest development stage, snowfall, and road density) and an overall comparison of the relative importance among all features. The overall ranking of features was used to weight parameters within the model and estimate the relative importance of factors affecting lynx habitat suitability, whereas weights within a feature determined the ranking for its attributes.

We used the Ontario Forest Resource Inventory to characterize land cover; these data provide a detailed description of species composition and forest stand age as determined by aerial photo interpretation. The study area included 41 provincial forest management units, and each unit was updated with forest fire and harvest information up to and including 2008. Standardized forest units were combined to create six generalized land cover types (coniferous forest, deciduous
forest, mixedwood forest, developed land, wetland, and open areas) and five forest development stages (presapling, sapling, immature, mature and old; [35]), which improved the accuracy of the dataset [36]. We converted the land cover map to a geospatial raster for analysis; all GIS analyses were conducted in ArcGIS 9.2 (ESRI, Redlands, CA, USA).

We evaluated the lynx habitat model in a portion of the study area near the North Bay - Temagami region of northeastern Ontario, Canada (47.01°N, 79.97°W; see Figure 2.1A). The Temagami region is approximately 8,000 km² and was selected because it is located within the southern range of lynx in Ontario and the transition zone of boreal forest with the northern Great Lakes-St. Lawrence forest. Between January and March 2009, we surveyed lynx occurrence at 48 randomly selected sites that represented a gradient in available land cover types [33]. We assessed lynx presence by snowtracking triangular transects around the centroid of the cell (dimensions 0.5 km per side, [33]). Additional lynx tracks that were encountered opportunistically while travelling within the landscape were also considered as lynx presence. We calculated habitat suitability at the centre of each transect and each opportunistic track, using both models. We used receiver operating characteristic plots as an independent measure of model accuracy via the program ROC/AUC [37]. We selected $P_{fair}$, the value where specificity and sensitivity are equal, as the threshold habitat suitable for lynx occurrence.

**QUANTIFICATION OF HABITAT FRAGMENTATION**

Landscape connectivity can be considered across a variety of spatial and ecological scales, and for our analysis the metrics of interest included estimates of: (i)
structural connectivity, which represents the spatial configuration of suitable patches; and (ii) functional connectivity, which includes animal response to patches [38]. We used PatchMorph [39] to create a binary landscape using the literature-based habitat suitability model; we estimated a ‘functionally’ connected landscape for lynx using: (1) a critical threshold of habitat suitability value of 52 (threshold tuned by balancing the error rate between false positives and false negatives [36]), (2) a minimum patch size of 5 ha (the minimum mappable forest stand (Ontario Ministry of Natural Resources, unpublished data)), and (3) a crossing distance of 200 m (M. Hornseth, unpublished data). Note that the crossing distance is defined as the distance that lynx will travel in unsuitable habitat; the minimum for this is two raster pixels and that parameters were set conservatively as per published observations of lynx habitat use patterns (see [14,40]). Although we acknowledge that actual functional connectivity requirements for lynx are just beginning to be understood (see [41]), we consider our selected values as being within the range of those that are plausible, with minor deviations likely affecting our results only qualitatively. Additionally, we did a sensitivity analysis with crossing distances of 200 to 1000m in 400m increments to determine the effect of this parameter on our estimates of connectivity.

We calculated habitat fragmentation as effective mesh size ($M_{eff}$) in ArcMap 10.1 [42]. $M_{eff}$ is calculated by:

$$M_{eff} = \frac{1}{A_e} \sum_{i=1}^{n} A_i^2,$$
where \( A \) is the area of a single patch and \( A_t \), can be either the total area of the polygon or the total amount of suitable habitat (i.e., the sum of all patch areas). In order to remove correlation between habitat amount and effective mesh size, we used the total amount of suitable habitat as the denominator (L. Fahrig, pers. comm.). Effective mesh size can be defined as the average area potentially accessed by an animal on a given landscape without having to cross defined borders or low quality habitat, so larger values indicate that the landscape is more connected and smaller values indicate the landscape is more fragmented [39,43]. For both lynx and pseudo-absence locations, we used effective mesh size within each area (see [44]) on the PatchMorph output to estimate habitat fragmentation, and calculated the percentage of suitable lynx habitat using the habitat suitability model to quantify habitat loss. To avoid confusion of working at multiple scales, we used the term suitable land cover to describe the output of the habitat suitability model at a landscape-level and suitable habitat to describe this output at a finer spatial scale (home range scale).

LYNX OCCURRENCE SAMPLING

Two regions were selected to document lynx occurrence (estimated by track identification) in landscapes across a gradient of habitat fragmentation. Each region fell within the larger study site which encompassed the southern boreal forest and Great Lakes-St. Lawrence Forest, and was divided into three landscapes based on the amount of suitable land cover (high, moderate, and low) as determined by the habitat suitability model (Figure 2.1B). The Chapleau region was 12 900 km\(^2\), located primarily in the boreal forest; the western portion of the region had the
highest amount of suitable land cover and is the least fragmented landscape in this region. The central area of the Chapleau region is highly fragmented with the most habitat loss due to forestry, roads, and human settlements; the easternmost portion has a moderate amount of suitable land cover and a moderate level of fragmentation due to forestry roads (Table 2.1). The Mississagi region was 12 800 km$^2$ located primarily in the Great Lakes St. Lawrence forest. The northern portion of this region had moderate amounts of suitable land cover, but was fragmented due to forestry roads; the central portion had the highest amount of suitable land cover and was least fragmented, and the southernmost landscape had the least amount of suitable land cover in this region, with habitat loss due to forestry, human settlements and roads. These regions were surveyed for lynx tracks from January to March 2010, each identified track was recorded as a lynx occurrence point. All forest access roads, trails, hydro-electric line corridors, cutovers and riparian areas were sampled via snowmobile, totalling 9 320 km of survey lines in both landscapes. All lynx track locations were documented; Chapleau had 104 track points and Mississagi had 89 points.

Roads in these two regions were limited to 1 or 2 highways, <20 secondary roads, and forestry roads. To test whether there was any bias arising from track proximity to surveyed roads, we randomly selected 100 points from roads (including highways, primary, secondary and tertiary roads, and snowmobile trails) and the surrounding landscape (not bisected by roads) and compared them at five spatial scales (10 km$^2$, 25 km$^2$, 50 km$^2$, 75 km$^2$, and 100 km$^2$) to assess any differences in habitat quality in each region. We found that there was no difference
in the amount of lynx habitat (as defined by the suitability model) in any landscape, regardless of spatial scale and distance to roads (M. Hornseth, unpublished data, but see [33]). Accordingly, we deemed that proximity of locations to roads was not relevant to our particular analysis.

We randomly selected points (equal to the number of lynx locations) from survey logs to represent pseudo-absences in Chapleau and Mississagi. These locations were at least 1 km apart and at least 1 km from the nearest lynx location. To examine the effect of spatial scale, and to encompass overall selection patterns, we buffered both observed lynx tracks and pseudo-absences with radii of 2.82 km and 5.61 km to simulate home ranges of 25 km$^2$ and 100 km$^2$ (from published estimates), to assess the role of spatial scale on occurrence patterns (see [15,34]).

**DATA ANALYSIS**

We aimed to determine whether lynx are limited by habitat amount, habitat fragmentation, or both processes, by contrasting patterns on landscapes with different amounts of suitable land cover. We hypothesized that lynx habitat requirements would restrict their occurrence to highly-connected areas in each landscape. We used one-sided unpaired $t$-tests to examine whether habitat amount and effective mesh size ($M_{\text{eff}}$) was greater in presence areas than pseudo-absence areas at each spatial scale among landscapes with high, moderate, and low amounts of habitat amount in each region. We examined any correlations between these two within each region and landscape. Finally, we used logistic regression and model selection to determine if habitat fragmentation ($M_{\text{eff}}$), habitat amount (percent habitat), or both measures best explained lynx occurrence in landscapes across the
levels of suitable land cover. We tested 3 *a priori* hypotheses to explain lynx occurrence; i) lynx are limited by habitat fragmentation, ii) lynx are limited only by habitat loss, and iii) lynx occurrence is limited by both habitat amount and habitat fragmentation. We used Akaike's information criterion and standard model selection procedures to evaluate the candidate models for each simulated home range size and landscape within each region. We considered ΔAIC > 2 to indicate a significant difference in model likelihood [49]. AIC does not assess model performance, and only models that performed well were considered plausible models for the AIC model selection, so we used the Logistic Regression $\chi^2$ model likelihood ratio test to determine model fit.

**Results**

**HABITAT SUITABILITY MODEL**

Both the expert-opinion and literature-based models suggested that coniferous forest land cover, and forest in a sapling developmental stage, provided the most suitable habitat for lynx. However, models differed with respect to the relative importance of overall features, with the literature-based model suggesting that land cover was only slightly (1.04 times) more important than development stage whereas expert opinion suggesting that development stage was substantially (1.20 times) more important than land cover type. We omitted annual snowfall and road density from the final habitat suitability models due to low overall importance in both models (see Table S2.1).

We detected lynx at 19% ($n=48$) of the sites within the Temagami landscape; we also included 14 more lynx track occurrences that we encountered
opportunistically within the study site, increasing the total number of validation locations to 62. The literature-based model had a good overall fit (AUC: 0.912, \( p<0.001 \)) and correctly predicted 83.9\% of all sites (\( n=62 \)) and 82.6\% of lynx occurrences (\( n=23 \)). The expert opinion model had a comparable fit (AUC: 0.855 \( p<0.001 \)), correctly classifying 82.3\% of all sites and 78.2\% of lynx occurrences. Although both models performed well, the literature-based model surpassed the expert-opinion model in every comparison (see Table S2.1) and was selected for the remaining analyses (see Table S2.2).

LANDSCAPE CHARACTERISTICS

The landscapes within both regions had similar amounts of suitable land cover (Table 2.1), but different levels of habitat fragmentation. The landscape with the highest amount of suitable land cover in Chapleau consisted of 41.9\% suitable land cover with an effective mesh size of 87.3 km\(^2\). In Mississagi the matched landscape approximately the same amount of suitable land cover (42.8\%), but a much larger mesh size of 258.6 km\(^2\). The landscapes with a moderate amount of suitable land cover in the Chapleau and Mississagi regions had similar amounts of suitable land cover (35.0\% and 31.9\%, respectively) and mesh sizes (22.4 km\(^2\) and 23.1 km\(^2\), respectively). The landscapes with a low suitable land cover had similar amounts (20.6 \% in Chapleau, 25.5\% in Mississagi), however this landscape in the Chapleau region was substantially more fragmented (\( M_{\text{eff}} \) 5.7 km\(^2\)) in comparison to the matched landscape in the Mississagi region (\( M_{\text{eff}} \) 18.6 km\(^2\)). This indicated that although the two landscapes had similar amounts of suitable land cover, generally the Mississagi landscape was more connected.
LYNX OCCURRENCE

Where possible, lynx selected areas with higher amounts of high quality habitat (structural connectivity) at the 25 km$^2$ simulated home range size (Table 2.2). There was a positive correlation between the amount of suitable habitat and lynx occurrence areas in both high- and moderate-levels of suitable land cover in the Chapleau region, and in the landscape with a moderate-level of suitable land cover in the Mississagi region when the simulated home range was 25 km$^2$ (Figure 2.2). In both regions, on landscapes with high- and moderate-levels of land cover, lynx consistently occurred in areas with at least 50% habitat and avoided areas with <30% habitat (Figure 2.3). However, in the landscapes where the amount of suitable land cover was the lowest, approximately half lynx occurrences had less than 30% habitat at a spatial scale of 25 km$^2$. These trends were consistent across regions. At a spatial scale of 100 km$^2$, there were no correlations between the amount of suitable habitat and lynx occurrence at any level of suitable land cover (Table 2.3).

There was a correlation between habitat fragmentation ($M_{eff}$) and habitat amount at all levels of suitable land cover on both regions. This correlation was positive and ranged from 0.63 to 0.77 on landscapes in the Chapleau region and 0.76 to 0.83 on the Mississagi region landscapes. However, even on the landscape with the highest mesh size of 258.9 km$^2$ (high suitable land cover landscape in Mississagi), lynx occurrence areas contained mesh sizes ranging from 0.46 km$^2$ to 19.49 km$^2$. While the average mesh size increased as the amount of habitat increased in each landscape, overall the ranges of mesh size were consistent across each landscape and region (Table 2.2).
Lynx occurrence patterns differed across landscapes, but the trends were consistent across regions. In the landscapes with moderate levels of suitable land cover, model selection determined that the top model included both the proportion of suitable habitat and effective mesh size explained lynx occurrence; however, only the proportion of suitable habitat had a positive association on lynx occurrence (Figure 2.4; Table 2.3). In single variable models, both effective mesh size and the proportion of habitat had positive associations with lynx occurrence, but the model with only effective mesh size was not significant. In landscapes where suitable land cover was high or low, there was no significant correlation between lynx occurrence patterns and proportion of suitable habitat or effective mesh size (Table 2.3).

SENSITIVITY ANALYSIS

We examined 3 crossing distances in the PatchMorph output to determine if crossing distance was underestimated or had a significant effect on lynx occurrence. We tested crossing distances of 200 m, 600 m, and 1000 m, and used standardized regression coefficients from single variable logistic regressions to determine its influence. Effective mesh size coefficient estimates ranged from -0.02 to 0.04, with no visible trend; none of the coefficients were significant (p values ranged from 0.228-0.589). Increasing the estimated crossing distance did not affect model fit.

Discussion

Our results confirm that lynx are not sensitive to habitat fragmentation at low levels of suitable habitat, and also suggest that they display considerable flexibility in habitat selection patterns, supporting the ‘flexibility hypothesis’. We showed that in landscapes with moderate and high amounts of suitable land cover (30-35% and
>40%, respectively), lynx occurred in areas with at least 30% available habitat and largely avoided areas below that threshold, while being unaffected by habitat fragmentation. While this is consistent with the ‘threshold hypothesis’, this hypothesis also predicts that lynx would be more sensitive to habitat fragmentation on landscapes where suitable land cover was low. However, our results showed that on landscapes where suitable land cover was limited (<25%), lynx did not select areas with concentrated habitat and lynx occurrence patterns were not well correlated with either habitat amount or habitat fragmentation, supporting the ‘flexibility hypothesis’ instead. Overall, we did detect a threshold at which lynx occurrence patterns changed, but instead of being more sensitive of habitat fragmentation at low levels of suitable habitat, lynx displayed more flexibility in habitat selection on these landscapes. This indicates that lynx habitat choices are complex and either involve factors beyond mere resource preference or selection of different land cover types in these areas.

**PATTERNS OF OCCURRENCE**

As predicted by the literature-based habitat suitability model, lynx were most likely to occur in sapling-stage coniferous forest. These results are consistent with other literature on lynx habitat ecology [14,15]. Road density and annual snowfall were not important for occurrence in Ontario. This finding contrasts with previous work (e.g., [32,33]) but is consistent with a companion occupancy model within our study area [41], suggesting that these factors differentially affect lynx occurrence across their range and may be threshold dependent. We surmise that low variation in snowfall patterns and low abundance of major highways as well as low road density
in our study site may have accounted for the disparate results. Lynx occurrence as determined by snow tracks across the study area also supported this model, signifying that our model is generally robust. We recommend the use of this habitat suitability model as a tool to evaluate future forest condition on resource availability for Canada lynx in Ontario.

FLEXIBILITY IN RESPONSE TO HABITAT LOSS

Our results suggest that when approximately 30-35% of the landscape consists of suitable land cover, there is a strong correlation between the amount of suitable habitat and lynx occurrence. While this trend was not significant at higher levels of land cover at a landscape scale, in landscapes with both high and moderate amounts of suitable land cover, lynx occurrence patterns suggest that lynx preferred for areas with at least 50% suitable land cover. While lynx will occur in some areas with less available than 50% suitable land cover, lynx consistently avoided areas with less than 30% suitable habitat when suitable land cover was abundant at a landscape level. This is consistent with previous work on small mammals and birds showing that habitat occupancy dynamics are determined by species-specific tolerance thresholds [7,11,45].

When suitable land cover comprised only 20-25% of the landscape, our results showed that there was no correlation between lynx occurrence and habitat amount, indicating some flexibility in habitat requirements on these landscapes. In contrast, when suitable habitat was limited, lynx did not avoid areas with less than 30% land cover and were not associated with areas with more than 50% suitable habitat, despite the local presence of areas with more than 50% suitable habitat. It
is possible that when suitable habitat is scarce, lynx can survive provided that hares remain available. This speculation is supported by observations of resident snowshoe hares occupying small patches < 10 ha in fragmented landscapes [46,47]. While it is unknown whether lynx are capable of successfully reproducing when suitable habitat is so low, evidence suggests that they are capable of prey switching in some areas across their range [48], which could improve their likelihood of persistence at the southern range periphery [26]. This pattern of labile specialization has been recently documented in bird species, whereby the most specialized species tend to generalize their habitat selection pattern following disturbance [49]. However, the results of our study contrasts previous work by Swihart et al. [5,50], who showed that some species have greater sensitivity to habitat change at range margins. This suggests that there is a wide range of responses to habitat degradation and that further work is necessary to clarify this relationship.

HABITAT FRAGMENTATION

Our results show that there is a weak correlation between lynx occurrence patterns and habitat fragmentation; mesh size is a measure of habitat connectivity, so a negative coefficient indicates a positive relationship with habitat fragmentation, which is the opposite of what we predicted. In addition, the results from our sensitivity analysis suggest that increasing crossing distance does not improve the measure of habitat fragmentation for lynx. While some studies have suggested that fragmentation may only be important when habitat amount is below 30% [7,9,51], our results do not support this hypothesis. The mesh size and habitat amount
variables where strongly correlated, which explains why the single variable models contained positive coefficients while in the regression models that contained both variables, mesh size had a negative coefficient. At low levels of suitable land cover there was no relationship between fragmentation and lynx occurrence, consistent with other studies where the effects of habitat loss are generally far greater than the effects of fragmentation [7,9,52]. However, results may differ if the landscape matrix is low quality and presents a higher risk to lynx persistence, for example in highly urbanized areas that did not exist in our study regions. We recommend that future studies try to disentangle the effects of habitat loss and habitat fragmentation by removing the effects of habitat loss from measures of habitat fragmentation [52]. Only by separating these effects can we fully understand the implications of habitat loss and habitat fragmentation, improving conservation priorities and increasing population persistence.

Acknowledgements

We thank B. Pond, E. Koen, K. Middel, L. Fahrig, and K. Downing for valuable input and feedback. We also thank all those who participated in the expert-opinion and literature-based surveys. Also thanks to T. Copeland, N. Woodhouse, E. Smith, A. Wilson, D. Ballak, and many volunteers for field support.
References


Table 2.1 Summary of the amount of suitable land cover and habitat fragmentation across two regions in the southern boreal forest in Ontario, Canada.

<table>
<thead>
<tr>
<th>Region</th>
<th>Land Cover&lt;sup&gt;a&lt;/sup&gt; Level</th>
<th>Area (km²)</th>
<th>Proportion of Suitable Land Cover</th>
<th>$M_{\text{eff}}$ (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapleau</td>
<td>High</td>
<td>5 085.7</td>
<td>41.88</td>
<td>87.31</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>3 162.8</td>
<td>34.95</td>
<td>22.41</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>4 639.7</td>
<td>20.64</td>
<td>5.68</td>
</tr>
<tr>
<td>Mississagi</td>
<td>High</td>
<td>7 873.2</td>
<td>42.84</td>
<td>258.61</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>3 016.8</td>
<td>31.85</td>
<td>23.14</td>
</tr>
<tr>
<td></td>
<td>Low</td>
<td>2 356.4</td>
<td>25.5</td>
<td>18.55</td>
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</table>

<sup>a</sup> Land cover is the amount of suitable land cover measured at the landscape level as determined by the habitat suitability model.
Table 2.2. Summary of the differences in connectivity measures of Canada lynx occurrence and pseudo-absences in Ontario, Canada; all t-tests were one-sided with p-values <0.05 in bold and p-values <0.1 in italics.

<table>
<thead>
<tr>
<th>Region</th>
<th>Home Range size (km²)</th>
<th>Land Cover</th>
<th>Variable</th>
<th>Present</th>
<th>Pseudo-absent</th>
<th>t-test</th>
<th>p-value</th>
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</thead>
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<tr>
<td>Mississagi</td>
<td>25</td>
<td>High</td>
<td>Habitat</td>
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<td>54.90</td>
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<td>0.300</td>
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<td>M eff</td>
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<td>5.67</td>
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<td>0.187</td>
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<td></td>
<td></td>
<td>Low</td>
<td>Habitat</td>
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<td>-0.76</td>
<td>0.772</td>
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<td></td>
<td></td>
<td></td>
<td>M eff</td>
<td>1.48</td>
<td>2.04</td>
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<td>0.908</td>
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<td></td>
<td>100</td>
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<td></td>
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<td>M eff</td>
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<td>Habitat</td>
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<td>31.11</td>
<td>1.33</td>
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<td></td>
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<td>M eff</td>
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<td>4.35</td>
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<td></td>
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<td>Habitat</td>
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<td>M eff</td>
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<tr>
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<td>High</td>
<td>Habitat</td>
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<td>46.39</td>
<td>1.96</td>
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<td></td>
<td></td>
<td></td>
<td>M eff</td>
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<tr>
<td></td>
<td></td>
<td>Moderate</td>
<td>Habitat</td>
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<td>3.01</td>
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<td>M eff</td>
<td>2.92</td>
<td>2.73</td>
<td>0.33</td>
<td>0.368</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>Habitat</td>
<td>29.87</td>
<td>29.88</td>
<td>-0.01</td>
<td>0.502</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M eff</td>
<td>1.29</td>
<td>1.23</td>
<td>0.23</td>
<td>0.408</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>High</td>
<td>Habitat</td>
<td>41.16</td>
<td>39.88</td>
<td>0.52</td>
<td>0.300</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M eff</td>
<td>5.45</td>
<td>6.19</td>
<td>-0.52</td>
<td>0.696</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Moderate</td>
<td>Habitat</td>
<td>39.78</td>
<td>34.75</td>
<td>2.33</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M eff</td>
<td>2.71</td>
<td>2.77</td>
<td>-0.16</td>
<td>0.564</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>Habitat</td>
<td>22.22</td>
<td>21.89</td>
<td>0.14</td>
<td>0.442</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>M eff</td>
<td>1.56</td>
<td>1.71</td>
<td>-1.03</td>
<td>0.845</td>
</tr>
</tbody>
</table>

aLand cover is the amount of suitable land cover measured at the landscape level as determined by the habitat suitability model.
bHabitat is the proportion of suitable habitat within home ranges and pseudo-absences based on the habitat suitability model.
c\(M_{\text{eff}}\) is the mesh size (km²; see text), a measure of functional connectivity, within the home ranges and pseudo-absences.
Table 2.3 Model selection of 3 *a priori* hypotheses proposed to explain lynx occurrence patterns across 3 landscapes differing in the amount of suitable landscape-level land cover in 2 regions (Chapleau and Mississagi) within an area of 25 km$^2$ for each lynx track and pseudo-absence.

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Chapleau</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>High Land Cover</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>0.031*</td>
<td>107.2</td>
<td>0.00</td>
<td>0.57</td>
<td>3.61</td>
<td>0.057</td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>-0.079</td>
<td>0.049*</td>
<td>108.6</td>
<td>1.41</td>
<td>0.28</td>
<td>4.36</td>
<td>0.113</td>
</tr>
<tr>
<td>$M_{eff}$ Only</td>
<td>0.054</td>
<td>-</td>
<td>109.9</td>
<td>2.72</td>
<td>0.15</td>
<td>0.90</td>
<td>0.344</td>
</tr>
<tr>
<td><strong>Moderate Land Cover</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>-0.253*</td>
<td>0.086*</td>
<td>108.7</td>
<td>0.00</td>
<td>0.74</td>
<td>13.00</td>
<td>0.002</td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>0.053*</td>
<td>110.8</td>
<td>2.15</td>
<td>0.25</td>
<td>8.85</td>
<td>0.003</td>
</tr>
<tr>
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<td>0.031</td>
<td>-</td>
<td>119.1</td>
<td>10.42</td>
<td>0.01</td>
<td>0.12</td>
<td>0.73</td>
</tr>
<tr>
<td><strong>Low Land Cover</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{eff}$ Only</td>
<td>0.055</td>
<td>-</td>
<td>100.3</td>
<td>0.00</td>
<td>0.43</td>
<td>0.06</td>
<td>0.802</td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>0.0001</td>
<td>100.4</td>
<td>0.11</td>
<td>0.41</td>
<td>0.00</td>
<td>0.996</td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>0.098</td>
<td>-0.006</td>
<td>102.4</td>
<td>2.11</td>
<td>0.15</td>
<td>0.11</td>
<td>0.945</td>
</tr>
<tr>
<td><strong>Mississagi</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>High Land Cover</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{eff}$ Only</td>
<td>0.039</td>
<td>-</td>
<td>166.4</td>
<td>0.00</td>
<td>0.47</td>
<td>0.79</td>
<td>0.373</td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>0.006</td>
<td>166.9</td>
<td>0.49</td>
<td>0.36</td>
<td>0.28</td>
<td>0.596</td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>0.098</td>
<td>-0.006</td>
<td>168.4</td>
<td>2.03</td>
<td>0.17</td>
<td>0.87</td>
<td>0.646</td>
</tr>
<tr>
<td><strong>Moderate Land Cover</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>-0.388*</td>
<td>0.147*</td>
<td>63.6</td>
<td>0.00</td>
<td>0.89</td>
<td>17.50</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>0.063*</td>
<td>67.8</td>
<td>4.22</td>
<td>0.11</td>
<td>11.27</td>
<td>0.008</td>
</tr>
<tr>
<td>$M_{eff}$ Only</td>
<td>0.117</td>
<td>-</td>
<td>76.8</td>
<td>13.27</td>
<td>0.00</td>
<td>2.43</td>
<td>0.119</td>
</tr>
<tr>
<td><strong>Low Land Cover</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{eff}$ Only</td>
<td>-0.203</td>
<td>-</td>
<td>100.3</td>
<td>0.00</td>
<td>0.47</td>
<td>0.85</td>
<td>0.356</td>
</tr>
<tr>
<td>Habitat Only</td>
<td>-</td>
<td>-0.016</td>
<td>100.4</td>
<td>0.39</td>
<td>0.39</td>
<td>0.45</td>
<td>0.511</td>
</tr>
<tr>
<td>Habitat + $M_{eff}$</td>
<td>-0.234</td>
<td>0.004</td>
<td>102.4</td>
<td>2.35</td>
<td>0.14</td>
<td>0.86</td>
<td>0.651</td>
</tr>
</tbody>
</table>

$M_{eff}$ is the mesh size (km$^2$; see text), a measure of functional connectivity, within the home ranges and pseudo-absences.

Habitat is the proportion of suitable habitat within home ranges and pseudo-absences based on the habitat suitability model.
**Figure Legend**

**Figure 2.1.** Habitat suitability map for Canada lynx in (A) central Ontario with Regions outlined and (B) suitable land cover levels within each region, as determined by the literature-based habitat suitability model.

**Figure 2.2.** Mean percentage of suitable habitat (with standard errors) for lynx presences compared to pseudo-absences at the 25 km² scale in the regions of Chapleau and Mississagi with three levels of suitable land cover.

**Figure 2.3** Distribution of lynx occurrences and pseudo-absences in relation to the amount of suitable habitat at the 25 km² scale in the regions of Chapleau and Mississagi with three levels of suitable land cover.

**Figure 2.4.** Regression plots for logistic models of Canada lynx occurrence in relation to the proportion of suitable habitat at the 25 km² spatial scale on (A) Mississagi and (B) Chapleau with moderate levels of fragmentation. The shaded area indicates the standard error.
Figure 2.1
Figure 2.2
Figure 2.3
Figure 2.4
Appendix 2.1: Comparison of expert option and literature-based models

**Table S2.1.** Performance metrics for the expert-opinion and literature based habitat suitability models for Canada lynx occurrence in Ontario, Canada. Receiver operating characteristic was based on 62 presence/absence locations near Temagami, Ontario. Bold text indicates better model performance.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Expert-opinion model</th>
<th>Literature based model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Critical threshold ($P_{fair}$)</td>
<td>62</td>
<td>52</td>
</tr>
<tr>
<td>AUC (SE)</td>
<td>0.855 (0.046)</td>
<td>0.912 (0.037)</td>
</tr>
<tr>
<td>p-value (AUC)</td>
<td>0.0008</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Correct classification rate ($n=62$)</td>
<td>82.3%</td>
<td>83.4%</td>
</tr>
<tr>
<td>Sensitivity (True Positive Rate) ($n=23$)</td>
<td>78.3%</td>
<td>82.6%</td>
</tr>
<tr>
<td>Kappa</td>
<td>0.623</td>
<td>0.661</td>
</tr>
</tbody>
</table>
Table S2.2. Expert-opinion and literature based model weights for all variables used in the development of the habitat suitability model for Canada lynx in Ontario, Canada. Models were based on a survey using the analytic hierarchy decision-making process to rate the importance of different variables. The expert-opinion model is based on the replies of nine lynx researchers; the literature based model is based on the responses of 4 unbiased observers after having reviewed four research papers on lynx habitat selection.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Expert-opinion model</th>
<th>Literature based model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Weight (SE)</td>
<td>Percent importance from top variable</td>
</tr>
<tr>
<td>Land cover</td>
<td>1.30 (0.02)</td>
<td>85</td>
</tr>
<tr>
<td>Forest Development Stage</td>
<td>1.53 (0.02)</td>
<td>100</td>
</tr>
<tr>
<td>Annual snowfall</td>
<td>0.54 (0.02)</td>
<td>35</td>
</tr>
<tr>
<td>Road density</td>
<td>0.62 (0.02)</td>
<td>41</td>
</tr>
</tbody>
</table>

a Annual snowfall and road density were removed from the final model due to their relative low importance to lynx habitat suitability.
Chapter 3: Behavioural plasticity of dispersal affects occupancy patterns: assessing landscape connectivity for Canada lynx

Authorship: Megan L. Hornseth and Dennis L. Murray

Contributions: MLH and DLM conceived of the study; MLH designed the study, ran the simulations, analyzed the data, and wrote the chapter; DLM critically reviewed the chapter

Prepared for submission to Ecological Modelling

Abstract

Behavioural plasticity is an animal's first response to landscape change, allowing individuals to adapt and persist in disturbed landscapes. We evaluated effects of dispersal plasticity on occupancy and population density across simulated source-sink landscapes with differing levels of fragmentation, using a spatially explicit individual-based model. Given the difficulty in gaining empirical dispersal data for wide-ranging species, theoretical modeling is a cost-effective approach to studying the effects of dispersal on population dynamics. Our focus was on Canada lynx (Lynx canadensis), a useful model species because of its long-distance dispersal abilities, habitat use patterns, and close association with prey (snowshoe hares, Lepus americanus). We parameterized two dispersal phenotypes using estimates derived from free-ranging lynx to explore the impacts of behavioural plasticity on functional connectivity of lynx habitat, and determine the importance of landscape structure on occupancy dynamics. Populations with only flexible dispersers (capable of crossing the matrix) had densities 2-5 times higher than populations with only inflexible dispersers (incapable of crossing the matrix), resulting in 96%
fewer habitat patch extinctions. Landscape structure had different impacts on each phenotype; inflexible dispersers were largely limited by connectivity, whereas flexible dispersers were most limited by high perimeter-to-area patch ratios. We found that dispersal corridors were important only for inflexible dispersers because these individuals were unable to travel between patches via non-corridor habitat. Our results lead to 3 predictions to be further explored with empirical data: (1) dispersal plasticity affects estimates of functional habitat connectivity across the landscape; (2) variation in dispersal behaviour increases the stability and resilience of patchy population distributions; and (3) dispersal behaviour promotes non-random distribution of phenotypes across a landscape.

**Introduction**

Behavioural landscape ecology seeks to provide a thorough basis for examining the influence of behavioural decisions of an individual on a population or species, when faced with heterogeneous or temporally dynamic landscapes (Zollner and Lima, 1996; Morales and Ellner, 2002; Heinz and Strand, 2006). Despite the importance of integrating behavioural aspects into landscape analysis, behavioural phenotypes are difficult to quantify as they are reversible and capable of rapid change (Ghalambor et al., 2010). However, spatially explicit individual-based models provide a basis for integrating behaviourally-based parameters into landscape-level analysis for the purposes of providing broad-scale insight into the consequences of landscape change and exploring the long-term effects of various approaches to mitigate impacts of such change (Knowlton and Graham, 2010). Behavioural plasticity in dispersal movements plays a large role in metapopulation
biology, range dynamics, and population dynamics. However, knowledge of the consequences of environmentally-induced phenotypic plasticity within a single species is limited.

Research on phenotypic plasticity has focused on morphological, physiological, and life history traits, but until recently has largely overlooked behaviour owing to inherent difficulties in rigorously quantifying such responses (Ghalambor et al., 2010). Behavioural plasticity is one of the first ways to facilitate a species’ response to contemporary landscape disturbance (Hewison et al., 2001; Magle and Angeloni, 2011), specifically by permitting animals to survive and persist in disturbed or novel landscapes (e.g., Price et al., 2003; Hendry et al., 2008). Plasticity may be adaptive, maladaptive or neutral for an animal’s overall fitness; however, animals displaying rigidity to changing circumstances may be limited in dynamic landscapes. In contrast, animals with increased flexibility may be more adept at reacting to changes, thus increasing individual fitness and population persistence (Ghalambor et al. 2007). Adaptive behavioural plasticity can be environmentally-induced when several phenotypes exist within a population and populations are exposed to variable environments, but no single phenotype has high fitness across all environments (Ghalambor et al., 2010). Often in source-sink scenarios, selection for a single phenotype may be obscured in the sinks if dispersal rates are high or selection is weak, leading to maladjusted dispersers from the source population predominating in sink habitat (Holt and Barfield, 2011).

Functional landscape connectivity is based on a species’ ability to move and disperse across landscapes with different configurations, and it follows that
movement and dispersal is a key element in spatial population viability models and source-sink dynamics (Bowler and Benton, 2005; Stevens and Baguette, 2008). Most population distributions are patchy, so an animal’s inability to disperse through unfavourable habitat types can prevent the occupancy of potentially viable habitat patches (Holt and Barfield, 2011). Dispersing animals may move through various land cover types, including unsuitable habitat, when good habitat is limited in availability (With and King, 1999; Baguette and Van Dyck, 2007; Schtickzelle et al., 2007). Several types of dispersers can occur within a landscape or population at any given time (Baguette and Van Dyck 2007; Cote et al., 2010; Holt and Barfield, 2011), and these differences may or may not have a genetic underpinning. The interaction between individual behaviour and environmental or landscape conditions can determine whether a dispersal behaviour type is adaptive (Meylan et al., 2009; Cote et al., 2010). Given the difficulties associated with examining dispersal, theoretical studies are important to predict the population level effects of dispersal (Bowler and Benton, 2005). Henein et al. (1998) used a simulation study to show that connectivity was the best predictor of population persistence for eastern chipmunks (Tamias striatus), a habitat specialist that was unable to cross hostile matrix; in contrast, generalist white-footed mice (Peromyscus leucopus) were more flexible in their habitat requirements and better able to persist in fragmented landscapes. However, this study focused on smaller scales, and daily movements, not dispersal, while contrasting two species with different reproductive and survival rates. Only the empirical work of Holt and Barfield (2011) has described demographic consequences of dispersal types in source-sink situations. This work focused on
Daphnia species in discrete habitats, so the broader landscape conditions that may favour one phenotype over another for behaviourally plastic animals remain largely unknown.

We examined the implications of dispersal flexibility on source-sink occupancy patterns using the wide-ranging carnivore, Canada lynx (Lynx canadensis), as a model species. Lynx are a suitable candidate for such work because of their well-established habitat relationships (Murray et al., 1994; Mowat and Slough, 2003; Hoving et al., 2005) and close reliance upon snowshoe hares (Lepus americanus), resulting in a 9–11 year population cycle of both species (O'Donoghue et al., 1997; Krebs et al., 2001). Lynx demographics may be characterized by a dispersal pulse, which occurs after the cyclic decline of snowshoe hare populations (Poole, 1997; Schwartz et al., 2002; Murray et al., 2008), often resulting in long distance dispersal movements (Mech, 1980; Poole, 1997). Their persistence in disturbed areas that characterize their southern distribution likely is owing to dispersal among spatially discontinuous patches, where lynx populations have been declining in recent years (Poole, 2003; Squires et al. 2013; USFWS, 2006). While the southern range edge has receded in recent years due to habitat loss and environmental conditions (Koen et al. 2014), there is new evidence that lynx display flexibility in habitat selection in response to habitat loss, allowing occurrence in more disturbed landscapes (Chapter 2). This led us to predict that lynx may have flexibility in dispersal decisions as a response to habitat loss and fragmentation. We used a spatially explicit individual-based model on landscapes with differing levels of fragmentation to assess how landscape structure affects occupancy patterns of
different dispersal phenotypes. We used simulations to develop predictions regarding the effects of dispersal plasticity on occupancy patterns in landscapes with differing structures, where risk of crossing the matrix is high and a number of suitable patches remain unoccupied. We also explored the use of corridors to increase population size for rigid dispersers that would otherwise be unable to cross an inhospitable matrix.

**Methods**

*Landscape Structure*

To integrate parameters of lynx population demography into a spatially explicit model, we used the program Hexsim 2.2 (Schumaker, 2011). HexSim is a modelling system which uses hexagons to facilitate movement to and from cells in six directions instead of the standard four, creating more realistic movement across landscapes. Since the spatial scale of the model is user-defined, the model can be scaled to the species of interest; we selected a hexagon size of 1 km².

We used SELES (Fall and Fall, 2001) to create three landscapes differing in spatial configuration, patch aggregation and patch size. A patch was defined as the minimum area to sustain at least 2 lynx, estimated at 25 km², comparable in size to the smallest reported home range for lynx (Vashon et al., 2008a; Burdett et al., 2007). A core patch was defined as an area large enough to serve as a population ‘source’, set at 1000 km². Each landscape consisted of an inhospitable matrix, a hospitable matrix, and habitat in varying relative proportions. Landscapes A and B consisted of a central core surrounded by smaller peripheral patches and had approximately the same amount of habitat (34%), however, landscape B was more
fragmented than landscape A (Table 3.1; Figure 3.1). Landscape C lacked a central core but contained 2 large patches to serve as population sources; it was the most fragmented, reflective of landscapes at the southern range periphery for lynx, with less available habitat (25%) (Chapter 2).

Rarely are landscapes composed only of habitat patches and non-habitat matrix, instead, they usually are a mosaic of habitat types; habitat suitability maps aim to quantify landscape mosaics on a relative, species-specific scale (With et al. 1997). We randomly assigned habitat quality values to each hexagon, ranging from 85 to 100 for suitable habitat. Hospitable matrix had a value of 50 and inhospitable matrix had a value of 1. These parameter estimates were reflective of field conditions where hospitable matrix would be used for dispersal movement, but unsuitable for foraging or reproduction needs, such as deciduous forest for lynx. Individuals in inhospitable matrix had a high risk of mortality, equivalent to frozen lakes in winter, developed agricultural land or recently clear cut forests, as in the habitat suitability model developed in Chapter 2.

Each patch within the landscape was connected to a nearby patch using 1 km wide corridors, which is generally comparable to the size of corridors identified for lynx in Ontario (Walpole et al., 2012). Corridors had a suitability value of 70, so they were more favourable than the matrix, but not suitable for home ranges. This controlled for the effect of corridors on patch shape and size as well as population size (Haddad and Baum, 1999). Corridors were placed in the shortest distance between patches and routed through hospitable matrix or stepping stones of habitat, wherever possible (sometimes extending corridor length). Corridors ranged
in length from 1 to 20 km (mean: 5.01 km), which is well within the dispersal capabilities of lynx (Poole et al., 1993) and is reflective of the dispersal distances that might characterize a metapopulation of lynx in North America.

Model Structure

Demographic rates (survival, productivity) for lynx were taken from the review by Steury and Murray (2004), who reported a strong correspondence between annual demographic rates and absolute density or change in density of snowshoe hares. Therefore, we created a baseline snowshoe hare population cycle to guide variation in lynx dynamics, using historical abundance data for this species. Perhaps the most reliable long-term hare abundance dataset is derived from hunter surveys: MacLulich (1937) estimated hare abundance during 1906-1936 from questionnaires sent to trappers across Canada. Snowshoe hare abundance was ln-transformed and centered on the mean to create a null cycle. Each value in the cycle was multiplied by 0.691, the reported average density of hares (per ha) at the cycle low (Steury and Murray, 2004). Accordingly, the questionnaire dataset characterized density changes in a ‘typical’ snowshoe hare population. The dataset was broken into 5 distinct cycles that were randomly selected to create a 50-year cycle of hare density. We added stochasticity to this cycle before inputting values into the population viability model. Since Steury and Murray (2004) showed that lynx demographic rates are closely related to annual hare density and the change in hare density, we used our ‘typical’ snowshoe hare cycle to determine the predicted reproductive and survival inputs for lynx. Survival rates ranged from 0-0.70 (mean: 0.33) for kittens and 0.37 to 0.95 (mean: 0.90) for juveniles and adults.
Reproductive rates ranged from 0.019 to 0.82 (mean: 0.12) for juveniles and 0.24 to 1.7 (mean: 0.72) for adults. Because the objective of our model was to characterize lynx habitat occupancy through space and time, we assumed that individuals who were not able to establish a home range had a reduced survival rate (0.25) and were unable to reproduce. In accordance with empirical research, dispersers that were unable to find a suitable new home range or habitat patch experienced a higher mortality rate due to the risks of crossing the matrix and energetic demands of dispersal (Kramer-Schadt et al., 2005). The model structure is outlined in Figure 3.2; each model was run for 150 time steps, with the first 50 serving as a 'burn in' period, and 100 replicates.

Since lynx may have flexibility in habitat selection patterns, including a greater propensity to use smaller patches when suitable land cover on the landscape is rare (Chapter 2) we used two repulsion factors to invoke differences in dispersal propensity in the lynx population, as some individuals may have a greater propensity to cross the matrix than others (see also Baguette and Van Dyck, 2007 and Kramer-Schadt et al., 2005). Inflexible dispersers (repulsion value: 1) were unable to cross inhospitable matrix and could only travel in patches that had values greater than 1, including hospitable matrix, corridors and habitat. In contrast, flexible dispersers (repulsion value: 0.9) while having a strong preference for remaining in hexagons with higher values, were able to cross inhospitable matrix, which is consistent with research on Eurasian lynx (Lynx lynx) (Kramer-Schadt et al., 2005). We assessed lower repulsion values in a sensitivity analysis; although there were small qualitative changes in the propensity to cross the matrix, there were no
quantitative differences in the results. We created two scenarios to examine the effects of landscape factors on both types of dispersers. We created additional scenarios to characterize the dispersal pulse occurring after the decline of hare populations. These scenarios had two types of baseline dispersers (25% short- and 75% long-distance dispersers) as well as “pulse dispersers” which are capable of dispersing long distances (see Mech, 1980, Poole et al., 1997) to represent this change in behaviour. Additionally, we created scenarios where inflexible pulse dispersers co-existed with flexible baseline dispersers. In all scenarios, dispersal behaviour was randomly assigned to individuals and not under genetic selection.

The spatial parameters associated with each type of disperser were estimated from the literature (e.g., Poole 1997; Burdett et al., 2007; Vashon et al., 2008a) and included home range size, dispersal path length, and proportion of total population (Table 3.2). Nevertheless, it was essential to evaluate the sensitivity of our model to variability in parameter estimates. Steury and Murray (2004) reported that lynx require a minimum of density 1.5 hares/ha to persist in a landscape: pulse dispersers were created when accumulated hare density (estimated with habitat suitability) fell below 80% of this threshold. Given that there is some controversy in the number of hares required for lynx persistence (0.5 – 1.5 hares/ha; see Ruggiero et al., 2000; Steury and Murray 2004; Vashon et al., 2008b), we assessed threshold in the sensitivity analysis outlined below.

Data Analysis

Each landscape consisted of 85-128 habitat patches ranging in size from 25 to 2,509 km²; a patch on the smallest end of this scale was only capable of
supporting 2 individuals, whereas a 250 km² patch might support on average 20 individuals. In contrast, a large core patch (>1000 km²) could support over 100 lynx (Vashon et al., 2008a; Burdett et al., 2008). We calculated the nearest neighbour, area, and effective mesh size (including high-quality matrix and corridors, where applicable) using Vector-based Analysis Tools Extension for ArcMap 10.0 (Lang et al., 2004). Effective mesh size can be defined as the average area potentially accessed by an animal on a given landscape without having to cross defined borders or low quality habitat (Girvetz and Greco, 2007). The mesh sizes for landscapes A and B are consistent with those from fragmented landscapes in the range periphery for lynx (Chapter 2); landscape C is highly fragmented but representative of the higher fragmentation levels at the southern range boundary for lynx. We also measured the Euclidean distance to the edge of the nearest core patch, number of patches connected within a network, perimeter-area ratio, and corridor length, to assess which factors are most important for increasing lynx density within a patch.

We used generalized linear modeling, using the patch as the sampling unit, to assess the impact of patch-based metrics on patch density on the landscapes without corridors, the change in density after the addition of corridors, and with an additional dispersal pulse. We created 14 a priori models for each scenario to assess the relative impact of landscape structure on patch density; these models included the following variables: area, mesh size (including high-quality matrix habitat), Δ mesh size (for corridor simulation only), distance to medium (>500 km²) and large (>1000 km²) core patches, nearest neighbour distance, perimeter-area ratio and a blocking landscape variable to account for variability among landscapes. We used
Akaike’s Information Criterion to select models; variables from top models (ΔAIC <2) were model-averaged using the package AICcmodavg (Mazerolle, 2006). We then used a generalized linear model in R 2.14.0 (R Core team 2011) to determine the importance of each factor on density within a patch (scaled to 100 km²) or difference in density (corridor simulation only).

Sensitivity analysis

To assess the reliability of our conclusions, spatial and demographic parameters were evaluated in a sensitivity analysis for both flexible and inflexible dispersers. Because we were interested in the difference in minimum and maximum lynx density within a patch rather than patch extinction risk, we used standardized regression coefficients in our sensitivity analysis to determine the importance of our estimated spatial parameters on the global model assessing patch density determinants. We assessed initial population size, male-biased sex-dispersal, relative proportion of dispersers, cycle stochasticity and initial cycle phase in the preliminary analysis; the model was robust to these factors. We conducted a separate sensitivity analysis of the spatial parameters including dispersal path length specified as a log-normal distribution mean (range: 60-160 km), minimum home range size (20-50 km²), autocorrelation of movement (0.6 to 0.9) and minimum accumulated hare density threshold for pulse-dispersers.

Results

Landscape A was the least fragmented with 85 patches and an overall mesh size of 2204 km². Landscape B contained 102 patches and a mesh size of 1320 km². Landscape C was further fragmented and had less habitat than the other landscapes,
with 127 patches and a mesh size of 352 km². There were 61 corridors on landscape A, 73 on landscape B, and 93 corridors on landscape C. Corridors improved connectivity on each landscape, effectively quadrupling the effective mesh size of a network. Landscape C lacked large source patches, so large networks (over 3000 km²) were absent from the landscape. There were differences across landscapes with respect to both minimum and maximum density for both inflexible and flexible dispersers (Table 3.3). Lynx populations with only inflexible dispersers had the lowest density across all scenarios; Landscapes A and C had similar minimum density (0.4 and 0.2 lynx/100 km², respectively) and maximum density (1.3 and 1.0 lynx/100 km², respectively). However, Landscape B had higher minimum and maximum density (0.6 and 2.4 lynx/100 km², respectively). Although the overall connectivity was greater for Landscape A than Landscape B, Landscape B had 10 networks (connected patches) >1000 km², totalling 18 641 km², whereas Landscape A had 3 networks of this size totalling 12 971 km², which would account for the increased densities caused by more movement on the landscape. Corridors increased both minimum and maximum density by 2 to 3 times across all landscapes; Landscapes A and C had the largest increases (Table 3.3). Overall, lynx density was slightly higher for flexible dispersers, minimum density was consistent across landscapes (1.3 ± 0.05 lynx/100 km²), but maximum density was higher in Landscape B than Landscapes A and C (6.7 lynx/100 km² vs. 5.1 and 4.5 lynx/100 km², Table 3.3). For flexible dispersers, corridors had a negligible impact on both minimum and maximum density (<0.1 lynx/100 km²).

*Occupancy Patterns*
Extinction dynamics differed substantially between populations comprised of flexible and inflexible dispersers. For flexible dispersers, only 5 (<2%) patches suffered extinction. In contrast, extinction occurred in 40% of the patches (124 of 312 patches) across all landscapes for inflexible dispersers. In both scenarios, patches that suffered extinction were small (flexible: <30 km², inflexible <60 km²) and had low connectivity, with mesh sizes averaging 67 km² for flexible dispersers compared to 89 km² for inflexible dispersers. The mean patch size of all patches was 236 km² and the average mesh size was 426 km². Not surprisingly, creation of corridors increased the average mesh size to 891 km² and prevented extinction for inflexible dispersers in all but 8 patches, however had relatively little effect on the dynamics of flexible dispersers.

Population Density

Our generalized linear models assessing patch density dynamics revealed that the relationship between explanatory variables and the minimum density were amplified at maximum density for both inflexible and flexible dispersers. We restricted our discussion to the results of the more relevant minimum population density. Overall, landscape structure better explained patterns of population density for inflexible than flexible dispersers.

Landscape structure effectively described patterns of population density across all landscapes for inflexible dispersers. Without corridors, the minimum density was closely related to mesh size, which explained the majority of the variation of the data (Figure 3.3). The Euclidean distance to medium core patches was also important, but less so than mesh size (Table 3.3). With the addition of
corridors, minimum density was best explained by mesh size, the perimeter-area ratio of the patch and distance to medium-sized core patches (Table 3.4). The difference in minimum density within a patch was largely explained by the increase in mesh size created by corridors (Figure 3.4) and the perimeter-area ratio of the patch (Table 3.5). Patches that benefited the most from a corridor were small, with low perimeter to area ratio (e.g., minimal edge exposed to the matrix) and connected to a large patch, resulting in a large mesh size within the network. Corridor length had no effect on its usefulness. Overall, corridors increased the mean population size of inflexible dispersers in all landscapes by an average 10% of the population. At a patch scale, corridors increased the population density of inflexible dispersers in 93% of all patches and on average doubled the minimum population density (Table 3.3). The average minimum density of flexible dispersers was 3.89 times that of inflexible dispersers. In contrast to inflexible dispersers, corridors had relatively little effect on patch density for flexible dispersers, reducing densities by 20%. Although approximately one-third of patches experienced an increase in population density, these increases were typically small (mean: 0.5 lynx per 100 km²; range: 0.02 - 2.25). Overall, patterns of patch density were less well explained by landscape structure for flexible dispersers in contrast to inflexible dispersers. Minimum density without corridors was negatively related to the Euclidean distance to large core patches and the perimeter-area ratio of each patch (Table 3.4). However, these relationships with landscape variables were weaker with flexible dispersers than inflexible dispersers (Figure 3.3, ii vs v and iii vs vi).
Because the overall difference in population density was minimal with the addition of corridors for flexible dispersers, we did not model these patterns explicitly.

**Dispersal Pulse**

We created two types of dispersal pulses, one with dispersers having the same plasticity (i.e. flexible pulse dispersers into flexible disperser scenario) and one with dispersers having alternate plasticity (i.e. flexible pulse dispersers into inflexible disperser scenario) to represent the occurrence of multiple phenotypes in a natural population. When the plasticity was the same for all types of dispersers, the population size increased moderately (on average by 50%). Patterns of patch occupancy in relation to landscape structure were almost identical to the scenarios without pulse dispersers, so we did not include these. However, when flexible pulse dispersers entered a landscape with only inflexible dispersers, minimum population size tripled and maximum population size increased by 4-fold. Consequently, even without corridors on the landscape, only 5 patches went extinct; minimum density within a patch increased on average by 1.3 lynx per 100 km$^2$ (range: 0-3.77). We also examined inflexible dispersers into a flexible disperser scenario, but there was no effect on any parameter. Patterns of minimum density were best related to mesh size and perimeter-area ratio (Table 3.4). Including corridors in the landscape structure resulted in only moderate increases in patch density, whereby density within a patch increased on average by 0.39 lynx per 100 km$^2$.

**Sensitivity analysis**

Our sensitivity analysis revealed that only home range size had an effect on standardized regression coefficients for inflexible dispersers (Figure A3.1f). Changes
in dispersal distance, autocorrelation of movement and hare scaling factor all had relatively minor effects on coefficient estimates. For flexible dispersers, autocorrelation of the movement path, dispersal distance, and hare scaling factor had a minimal effect on most parameters in the global generalized linear model, however there was some variation in the distance to core patch coefficients. In contrast, changes in home range size led to higher variability in standardized regression coefficients (Figure A3.1ii). Overall, there was little variation in the range of home range sizes within each scenario. Although these variations affected population densities across the landscapes, qualitatively the model results with respect to landscape variables were consistent across all analyses.

We also examined how the dispersal parameters, median dispersal distance and autocorrelation of movement path affected the average displacement of individuals in scenario 1. Displacement is the straight-line distance from birth hexagon to death hexagon, for all individuals in the simulation. Autocorrelation rates varied from 0.60 to 0.90 (0.75 used in scenarios), which reduced mean displacement distance by 35% and increased by 65% respectively. In contrast, median dispersal distance had a less severe effect on displacement; mean displacement was reduced by 13% at an average dispersal distance of 60 km and increased by 15% when the average dispersal distance was 160 km. For the pulse-disperser scenarios, we examined how the threshold of hare density necessary to create pulse-dispersers affected the results. There was little effect of this threshold on standardized regression coefficient for minimum and maximum hare density, indicating that although the addition of a dispersal pulse had a large effect on
saturating the landscape, the model was robust to the effects of landscape structure on lynx density within a patch (Table A1). Thus, to summarize our model results were reasonably insensitive to realistic variability in model parameters.

**Discussion**

By modeling the contrast between flexible and inflexible dispersers, we examined the interaction between this behavioural trait and landscape structure, as well as the extent to which source-sink occupancy patterns are governed by dispersal type. Our results from the spatially explicit scenarios indicated that plastic behaviour was most beneficial in more fragmented landscapes, where a number of suitable habitat patches remain unoccupied. Our models suggest that this difference in behaviour can have a large effect on occupancy patterns across landscapes with variation in habitat fragmentation. As a result, we infer that there is a need to quantify the effects of behavioural plasticity to further our understanding of metapopulation dynamics. Consequently, this interaction between behaviour and environmental conditions can lead to differences in the estimated functional connectivity of a landscape. It is important to note that, although we did not examine the upper threshold for fragmentation as a limiting factor in lynx populations, we recommend that further modeling explore this concern. Our results suggest that patches with a high perimeter-area ratio have the greatest risk of extinction. Dispersal behaviour is difficult to assess empirically, especially for wide-ranging species. However, our model provides a suitable alternative to assess population-level implications of dispersal plasticity. As a result of our modeling efforts we developed three predictions, outlined below, to summarize our results.
Prediction 1: Dispersal behaviour affects estimates of functional connectivity

Functional connectivity has been defined as a species-specific behavioural response to the structural arrangement of habitat patches and boundaries (Collinge and Forman, 1998; Tischendorf and Fahrig, 2000). As decision making processes and the resulting behavioural responses of a species are difficult to quantify, estimating the functional connectivity of a landscape has proven to be difficult. Our modeling efforts suggest that functional connectivity is not just species-specific, but also phenotype-dependent, whereby considerable variation in behavioural syndromes may lead to significant differences in the definition of functional connectivity within a single species (Pe’er et al., 2011). This can lead to large discrepancies in the efficiency of corridor design, whereby corridors may be necessary for some, but not all individuals of a species, depending on both the existing structural connectivity and the variation in behavioural traits within a population. Our models indicated that corridors should be most beneficial when individuals are shy and refuse to cross into low-quality matrix. Corridors may be relatively ineffective for bold individuals who are not limited by the arrangement of habitat patches as they are more likely to cross the matrix (Haddad, 1999; Sih et al., 2012). Our modeling efforts revealed that even if crossings by dispersers are infrequent, they create adequate movement on a landscape to negate the effectiveness of corridors, possibly due to the difficulty of dispersing animals locating corridors on a landscape. Measures of connectivity will be substantially improved by considering the behavioural responses of the animal. This is especially necessary if the species’ response to environment is variable or adaptive as it may
have substantial consequences on the functional connectivity of a landscape. For example, the movement ability of Natterjack toads (*Bufo calamita*) is strongly affected by habitat type and subject to individual differences that are distinct from body size or relatedness, resulting in different land cover types presenting different viscosity for dispersers (Stevens et al., 2004). Adjusting estimates for these differences in behaviour may refine metapopulation projections and result in a shift in the perceived overall functional connectivity of a landscape.

*Prediction 2: Dispersal variation stabilizes populations*

Dispersal types can stabilize populations in a stochastic environment, reduce extinction risk and increase population density through variation in the behavioural traits of the dispersing individuals. A species with both bold and shy individuals can do well in a variety of ecological conditions. Bold individuals are best adapted to low-risk landscapes and shy individuals succeed in high-risk environments (Sih et al., 2012). Conversely, if there is disparity or variability between the landscape conditions and the dominant dispersal behaviour, this could destabilize the population (Clobert et al., 2009; Cote et al., 2010). In our modeling exercise, inflexible individuals were highly dependent on structural connectivity whereas flexible individuals were more capable of moving through the low-quality matrix. In a real landscapes, there would be trade-offs associated with this difference in behaviour, whereby flexible individuals may have a greater risk to survival (or lower productivity) within the inhospitable matrix. There may be other behavioural traits associated with disperser type, such as aggression, activity level and sociality (Cote et al., 2010), which may further confound an individual's fitness and
persistence in a new habitat patch. For example, western bluebirds (*Sialia mexicana*) have distinct dispersal phenotypes, whereby males who are long distance dispersers are also more aggressive than non-dispersers (Duckworth 2008). Our modeling set the foundation for assessing the effects of dispersal plasticity across a range of modeled scenarios. However, given the high mobility and notable variability in dispersal patterns of mid-sized and large carnivores, more empirical studies regarding the impacts of dispersal plasticity are necessary.

*Prediction 3: Dispersal plasticity can result in non-random distribution*

Dispersal behaviour affects the distribution of individuals within a patch and across a landscape, leading to a non-random distribution of individual behaviours (Duckworth, 2008). This is especially true in a patchy landscape where bold dispersers are more likely to end up in habitat sinks, and shy individuals will remain within a patch (Holt and Barfield, 2011). Our model results revealed that variation in dispersal type within a population increased persistence in patchy landscapes by reducing the patch extinction rate. This modeling scenarios established a basis for empirical work to test this prediction, as there may be repercussions, especially at species range limits, where distributions are often limited by dispersal and landscapes are patchy (Gaston, 2009). For example, it is understood that there are different dispersal syndromes for western bluebird populations at the edge of their expanding range leading to peripheral populations that are more aggressive than core populations (Duckworth, 2008).

Our models show that behavioural plasticity in dispersal can have significant effects on population dynamics and occupancy patterns. Our results offer specific
predictions that can be evaluated through more extensive investigation of the interactions between landscape structure and dispersal plasticity, as this variation may be an important mechanistic response to rapid landscape change and thus reflect particular adaptation to novel environments. As a result, this variation in plasticity may allow species to be more resilient to disturbance, increase population density, and improve stability in dynamic landscapes. Since behavioural traits can be adaptive, differences in behaviour often are rapid and constitute the first response to landscape change and novel conditions. It follows that these differences can have a large effect on the evolution of other traits, regardless of whether the traits are genetically determined (Sih et al., 2010). Further understanding of these dynamics on a broader scale for large, long-lived species is necessary, especially in light of the current rates of anthropogenic landscape change and the important role of habitat fragmentation on metapopulation ecology.

Acknowledgements

This research received financial support from Natural Science and Engineering Research Council (NSERC) Strategic and IPS grants, the Panthera Foundation, the Ontario Ministry of Natural Resources and Wildlife Conservation Society Canada. We thank N. Schumaker for invaluable assistance in learning HexSim, and J. Bowman, M.J. Fortin, J. Ray and L. Walton for valuable input and feedback.
References


Table 3.1: Summary of each simulated landscape; landscapes A and B have a central core whereas landscape C is highly fragmented without a central core.

<table>
<thead>
<tr>
<th>Landscape</th>
<th>Number of patches</th>
<th>Mean patch size (min-max)</th>
<th>Percent Habitat</th>
<th>Landscape mesh size (km²)</th>
<th>Mean Corridor length (range, km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>85</td>
<td>312 (26 – 4975)</td>
<td>33.6</td>
<td>2022.1</td>
<td>4.9 (0.6 – 17.4)</td>
</tr>
<tr>
<td>B</td>
<td>102</td>
<td>277 (28 – 2509)</td>
<td>33.9</td>
<td>843.7</td>
<td>4.4 (0.6 – 13.1)</td>
</tr>
<tr>
<td>C</td>
<td>128</td>
<td>155 (26 – 1354)</td>
<td>24.6</td>
<td>403.3</td>
<td>5.6 (0.7 – 19.9)</td>
</tr>
</tbody>
</table>
Table 3.2: Summary of parameters used in modelling scenarios for each type of disperser; each scenario consists of both short-distance and long-distance dispersers, however pulse dispersers are only in the dispersal pulse scenario. Parameters were the same for flexible and inflexible dispersers, except flexible dispersers had a repulsion of 0.9 and could cross inhospitable matrix occasionally, whereas inflexible dispersers had a repulsion of 1.0 so could not cross matrix.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Short-distance dispersers</th>
<th>Long-distance dispersers</th>
<th>Pulse dispersers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autocorrelation coefficient</td>
<td>0.50</td>
<td>0.75</td>
<td>0.75</td>
</tr>
<tr>
<td>Median dispersal length (s.d.)</td>
<td>20 (5)</td>
<td>100 (10)</td>
<td>300 (20)</td>
</tr>
<tr>
<td>Proportion of population</td>
<td>0.25</td>
<td>0.75</td>
<td>Based on snowshoe hare density, accumulated at each time step</td>
</tr>
</tbody>
</table>

1Typically, animals move more quickly and with a higher degree of correlation through the matrix and on longer distance movements (Zollner and Lima, 1996; Kramer-Schadt et al., 2004; Revilla et al., 2004; Schtickzelle et al., 2007).

2Dispersal distances taken from a log-normal distribution and parameters estimated from Poole et al., 1993.
Table 3.3: The estimated minimum and maximum density of lynx on the simulated landscape, using different types of dispersal behaviour. Flexible dispersers are able to cross inhospitable matrix, whereas inflexible dispersers are restricted to movement through high-quality habitat, high quality matrix or corridors. Pulse dispersers are triggered by a decline in the hare population cycle. Landscapes increase in fragmentation whereby landscape A is the most connected and landscape C is the most fragmented.

<table>
<thead>
<tr>
<th>Disperser type</th>
<th>Landscape</th>
<th>Density (lynx/100 km²)</th>
<th>Minimum (SE)</th>
<th>Maximum (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflexible dispersers</td>
<td>A</td>
<td>0.35 (0.06)</td>
<td>1.31 (0.21)</td>
<td></td>
</tr>
<tr>
<td>No Corridors</td>
<td>B</td>
<td>0.60 (0.07)</td>
<td>2.36 (0.26)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.24 (0.03)</td>
<td>1.02 (0.10)</td>
<td></td>
</tr>
<tr>
<td>Inflexible dispersers</td>
<td>A</td>
<td>0.83 (0.08)</td>
<td>3.06 (0.26)</td>
<td></td>
</tr>
<tr>
<td>Corridors</td>
<td>B</td>
<td>1.23 (0.09)</td>
<td>4.60 (0.31)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.68 (0.05)</td>
<td>2.54 (0.14)</td>
<td></td>
</tr>
<tr>
<td>Inflexible dispersers</td>
<td>A</td>
<td>1.18 (0.07)</td>
<td>6.43 (0.29)</td>
<td></td>
</tr>
<tr>
<td>Pulse (flexible dispersers)</td>
<td>B</td>
<td>1.87 (0.07)</td>
<td>8.83 (0.20)</td>
<td></td>
</tr>
<tr>
<td>No Corridors</td>
<td>C</td>
<td>1.86 (0.06)</td>
<td>7.07 (0.14)</td>
<td></td>
</tr>
<tr>
<td>Flexible Dispersers</td>
<td>A</td>
<td>1.22 (0.06)</td>
<td>5.08 (0.24)</td>
<td></td>
</tr>
<tr>
<td>No Corridors</td>
<td>B</td>
<td>1.31 (0.06)</td>
<td>6.67 (0.20)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1.28 (0.04)</td>
<td>4.45 (0.10)</td>
<td></td>
</tr>
</tbody>
</table>
**Table 3.4:** Generalized linear regression models of the minimum patch density in relation to landscape metrics. We present the coefficient estimate, standard error (SE), lower and upper confidence intervals (CI) and the importance of each parameter (using AIC weights) for simulations with inflexible and flexible dispersers. Distance to core refers to the Euclidean distance to the closest patch larger than 500 km$^2$ (medium) and 1000 km$^2$ (large). Mesh size refers to the area of the patch plus any surrounding high-quality matrix and any patches connected by high-quality matrix. (Landscape coefficients are based on using landscape A as a reference.) Italics indicate significant parameters (not overlapping 0).

<table>
<thead>
<tr>
<th>Disperser/Landscape Type</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flexible/No corridors</td>
<td><strong>Intercept</strong></td>
<td>2.25</td>
<td>0.14</td>
<td>1.97</td>
<td>2.52</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Distance to Large Core</em></td>
<td>-0.14</td>
<td>0.02</td>
<td>-0.19</td>
<td>-0.10</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td><em>Perimeter:Area Ratio</em></td>
<td>-0.47</td>
<td>0.14</td>
<td>-0.74</td>
<td>-0.20</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td><em>Nearest Neighbour</em></td>
<td>0.07</td>
<td>0.04</td>
<td>-0.02</td>
<td>0.15</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Landscape B</td>
<td>0.31</td>
<td>0.08</td>
<td>0.22</td>
<td>0.55</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Landscape C</td>
<td>0.31</td>
<td>0.08</td>
<td>0.31</td>
<td>0.63</td>
<td>0.74</td>
</tr>
<tr>
<td>Inflexible/No corridors</td>
<td><strong>Intercept</strong></td>
<td>-1.90</td>
<td>0.14</td>
<td>-2.18</td>
<td>-1.63</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Distance to Large Core</em></td>
<td>-0.03</td>
<td>0.02</td>
<td>-0.06</td>
<td>0.01</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td><em>Distance to Medium Core</em></td>
<td>-0.09</td>
<td>0.02</td>
<td>-0.12</td>
<td>-0.05</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td><em>Perimeter:Area Ratio</em></td>
<td>0.05</td>
<td>1.08</td>
<td>-2.07</td>
<td>2.17</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td><em>Mesh</em></td>
<td>0.50</td>
<td>0.20</td>
<td>0.11</td>
<td>0.88</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Landscape B</td>
<td>0.00</td>
<td>0.05</td>
<td>-0.10</td>
<td>0.11</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Landscape C</td>
<td>0.07</td>
<td>0.05</td>
<td>-0.04</td>
<td>0.17</td>
<td>0.81</td>
</tr>
<tr>
<td>Inflexible/With corridors</td>
<td><strong>Intercept</strong></td>
<td>-3.08</td>
<td>0.28</td>
<td>-3.63</td>
<td>-2.54</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Distance to Large Core</em></td>
<td>-0.02</td>
<td>0.03</td>
<td>-0.06</td>
<td>0.03</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td><em>Distance to Medium Core</em></td>
<td>-0.06</td>
<td>0.02</td>
<td>-0.11</td>
<td>-0.01</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td><em>Perimeter:Area Ratio</em></td>
<td>-0.50</td>
<td>0.12</td>
<td>-0.74</td>
<td>-0.27</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td><em>Mesh</em></td>
<td>0.70</td>
<td>0.03</td>
<td>0.64</td>
<td>0.76</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Landscape B</td>
<td>-0.01</td>
<td>0.07</td>
<td>-0.16</td>
<td>0.13</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Landscape C</td>
<td>0.30</td>
<td>0.07</td>
<td>0.16</td>
<td>0.45</td>
<td>0.81</td>
</tr>
<tr>
<td>Inflexible, with Dispersal pulse/No Corridors</td>
<td><strong>Intercept</strong></td>
<td>1.45</td>
<td>0.33</td>
<td>0.81</td>
<td>2.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Distance to Large Core</em></td>
<td>-0.10</td>
<td>0.03</td>
<td>-0.16</td>
<td>-0.05</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td><em>Distance to Medium Core</em></td>
<td>-0.02</td>
<td>0.03</td>
<td>-0.08</td>
<td>0.04</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td><em>Perimeter:Area Ratio</em></td>
<td>-0.63</td>
<td>0.14</td>
<td>-0.90</td>
<td>-0.36</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td><em>Nearest Neighbour</em></td>
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<td>0.04</td>
<td>-0.08</td>
<td>0.10</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td><em>Mesh</em></td>
<td>0.16</td>
<td>0.04</td>
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</tr>
<tr>
<td></td>
<td>Landscape B</td>
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<td>0.03</td>
<td>0.36</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>Landscape C</td>
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<td>0.08</td>
<td>0.31</td>
<td>0.63</td>
<td>0.89</td>
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Table 3.5: Generalized linear regression models of the change in minimum density by the addition of corridors for inflexible dispersers in relation to landscape metrics as determined by AIC and model averaging. We present the coefficient estimate, standard error (SE), lower and upper confidence intervals (CI) and the weight of each parameter as determined by AIC. Δ mesh size refers to the increase in mesh size resulting from the addition of corridors. Italics indicate that the parameter is significant (does not overlap 0). Landscape coefficients are based on using landscape A as a reference.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>SE</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Weight</th>
</tr>
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<tr>
<td>(Intercept)</td>
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<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
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</tr>
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<td>Δ Mesh size</td>
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<td>0.43</td>
<td>0.51</td>
<td>0.95</td>
</tr>
<tr>
<td>Perimeter:Area ratio</td>
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<td>-0.81</td>
<td>-0.38</td>
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</tr>
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<td>-0.06</td>
<td>0.01</td>
<td>0.27</td>
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<tr>
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<td>-0.11</td>
<td>0.02</td>
<td>0.63</td>
</tr>
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<td>Landscape B</td>
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<td>0.25</td>
<td>0.95</td>
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<tr>
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<td>0.06</td>
<td>-0.14</td>
<td>0.10</td>
<td>0.95</td>
</tr>
</tbody>
</table>
Figure Legend

**Figure 3.1**: Configurations of Landscapes A-C. Dark grey depicts habitat, light grey shows hospitable matrix, and white shows inhospitable matrix.

**Figure 3.2**: Conceptual diagram summarizing the Canada lynx population cycle as implemented in HexSim. Solid lines indicate the model pathway, hashed lines indicate the influence of phenotypic plasticity. Hare density influences survival and reproduction at each life stages. Specific equations regarding survival and fecundity are shown in Appendix 3.1.

**Figure 3.3**: Minimum density of lynx across all landscapes in relation to mesh size, distance from core patches and perimeter:area ratio (i-iii) without corridors, and (iv-vi) with corridors. Flexible dispersers are represented by open circles and dotted lines; inflexible dispersers are closed circles and solid lines.

**Figure 3.4**: The change in minimum density within a patch by the addition of corridors in relation to Δ mesh size across all landscapes for inflexible dispersers. Δ mesh size refers to the increase in mesh size by the inclusion of corridors.
Figure 3.1
Figure 3.2
Figure 3.3
Figure 3.1
Appendix 3.1

Results of the sensitivity analysis on spatial parameters (dispersal distance, autocorrelation of movement paths and home range size)

Table A3.1. Parameter and its range for each spatial factor assessed in the sensitivity analysis and the resultant mean patch density.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter range</th>
<th>Mean Patch density range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dispersal Path Length</td>
<td>60 km – 160 km</td>
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</tr>
<tr>
<td>Autocorrelation of Movement</td>
<td>0.6 - 0.9</td>
<td>8.08-9.92</td>
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<tr>
<td>Home Range Size</td>
<td>20 km² – 50 km²</td>
<td>8.27-16.38</td>
</tr>
<tr>
<td>Hare Pulse Threshold¹</td>
<td>0.5-1.5 hares/ha</td>
<td>13.24-15.13</td>
</tr>
</tbody>
</table>

¹Used in the dispersal pulse simulations only
**Figure A3.1:** Standardized regression coefficients resulting from the sensitivity analysis of home range size on the minimum density within a patch for (i) flexible and (ii) inflexible dispersers. The solid line represents distance to core patches, the long dashed line is for perimeter-area ratio, the dotted line is for mesh size and the dashed line is for nearest neighbour.
Chapter 4 Conserving natural population cycles in harvested species and forestry-dominated landscapes: A case study using Canada lynx

Authorship: Megan L. Hornseth, Jeff Bowman, Dennis L. Murray

Contributions: MLH, JB and DLM conceived of the study; MLH designed the study, ran the simulations, analyzed the data, and wrote the chapter; JB and DLM critically reviewed the chapter

Prepared for submission to Biological Conservation

Abstract

Habitat fragmentation and exploitation of wildlife populations are key issues influencing population sustainability, ecosystem structure, and conservation biology. In this context, naturally fluctuating populations present a particularly vexing conservation challenge, due to the potentially compounding influence of anthropogenic stressors such as habitat fragmentation and wildlife harvest. Both processes can reduce numbers and increase extinction risk when population size varies naturally and dramatically through time. We examined the role of harvest strategy [fixed-proportion harvest (constant rate) versus punctuated harvest (variable rate according to cycle phase)] on Canada lynx (*Lynx canadensis*), a furbearer with broadly fluctuating populations. We used habitat suitability model developed for lynx in a forestry-dominated landscape in Ontario, Canada, combined with a spatially explicit population viability model. We found that punctuated harvest regimes effectively maintained high lynx population density and cyclic dynamics, while reducing the risk of population extinction in fragmented landscapes. In contrast, fixed-proportion harvest regimes reduced population size,
increased extinction risk, and promoted cyclic attenuation. In addition, despite the periodic harvest closures, punctuated regimes permitted more individuals to be harvested across a cycle than fixed-proportion regimes. Our simulation results suggest that effects of anthropogenic harvest mortality likely are additive to those from habitat fragmentation, however the magnitude of this effect is variable depending on population density and harvest pressure. Due to the complexity associated with anthropogenic stressors and their combined influence on cyclic populations, we recommend that harvest strategies be tailored conservatively to mitigate potentially strong additive effects of harvest on population size and cyclic propensity.

**Introduction**

Some of the most important global concerns in conservation biology include the effects of harvest, habitat loss and fragmentation on the sustainability of wildlife populations (Fahrig, 2003; Milner-Gulland et al., 2003; Fischer and Lindenmayer, 2007). These are especially relevant for species that experience large fluctuations in population size, because even modest changes in landscape structure can lead to dampened oscillations (Ecke et al., 2009) and harvesting when populations are already at low density can greatly increase extinction risk (Lande et al., 1997; Hutchings 2000). However, the combined effects of landscape fragmentation and harvest on population size and variability have not been fully considered in either a theoretical or empirical context, even though such interactions may be synergistic and particularly influential to conservation efforts. This shortcoming is especially relevant to carnivore conservation because many species have: (i) substantive
natural fluctuations in abundance (Kendall et al., 1998; Post et al., 2002); (ii) large spatial requirements and attendant susceptibility to habitat loss and fragmentation (Woodroffe and Ginsberg, 1998); and (iii) economic value as a harvestable resource (Milner et al., 2007). Yet, since habitat fragmentation due to forestry and harvest mortality are direct results of anthropogenic activity, it may be possible to adjust such human-induced changes to mitigate their effects on carnivores and other wildlife. It follows that to reach this point, it is necessary to better understand how anthropogenic stressors may act alone or in tandem to influence carnivore population size, variability, and cycle propensity.

Anthropogenic activities such as agriculture, forestry, and urban expansion can alter the structure, composition, and function of ecosystems (Saunders et al., 1991). This human modification of landscapes has led to increased rates of habitat loss and fragmentation; habitat loss reduces patch size while fragmentation increases patch isolation (Fahrig, 2003). In turn, such changes reduce diversity within a patch and lower inter-patch connectivity (Andrén, 1994; Fahrig, 2003). Fragmentation can directly affect carnivores by limiting dispersal ability through suitable habitat (Kramer-Schadt et al. 2005), although there may also be an indirect consequence involving the role of fragmentation on population decline or cyclic attenuation of prey species (Dalkvist et al., 2011). Dampened population cycles have been reported for keystone herbivores such as lemmings and voles across Europe, where populations have experienced periods of low and declining amplitude spanning the last 20 to 30 years (Ims et al., 2008; Cornulier et al., 2013). Similar attenuation is evident in North American grouse population cycles (Williams et al.,
Although approximately 30% of all populations are naturally cyclic (Kendall et al., 1998), factors leading to cycle attenuation are poorly understood but may relate to climatic drivers (Ims et al., 2008; Cornulier et al., 2013) or habitat fragmentation (Ecke et al., 2010; Dalkvist et al., 2011).

Dampened population oscillations can have cascading impacts on trophic levels, where a decline in cyclic prey numbers may cause substantial decline in primary predators (Schmidt et al., 2012), meaning that attendant cycle attenuation of predators relying on formerly cyclic prey populations is a possibility. When this scenario is coupled with population exploitation of carnivores, the population’s capacity to recover from stochastic events is reduced and the risk of extinction is heightened (see Beddington and May, 1997). Overall, there is general uncertainty regarding the consequences of fragmentation on cyclic populations and whether its effects are additive with other stressors, including anthropogenic harvest. Indeed, because both rates of removal as well as the actual identity of individuals removed do not necessarily conform to losses owing to natural processes, harvest may play a compounding role to that of landscape fragmentation in affecting the dynamics and viability of populations.

Canada lynx (Lynx canadensis) populations cycle with those of their primary prey, snowshoe hares (Lepus americanus), alongside numerous other mammals and birds in the boreal forest of North America (Boutin et al., 1995; Krebs, 2011). Lynx are an important species in the wild fur industry (Quinn and Parker, 1987); approximately 4,500 to 12,000 lynx are harvested annually across Canada (Statistics Canada, 2012), except in the provinces of Prince Edward Island (where they have
been extirpated), Nova Scotia and New Brunswick, where they are at risk (Poole, 2003). Recently, lynx experienced population declines and range loss across the southern range edge of their distribution, largely due to the effects of habitat loss (Poole, 2003; USFWS, 2006) and climate change (Koen et al. 2014). Similarly, habitat fragmentation may contribute to declines in snowshoe hare densities (Hodges, 2000; Lewis et al., 2011), and perhaps to reductions in their cyclic amplitude (Strohm and Tyson, 2009). There is a well-established relationship between hare density and lynx density (Steury and Murray, 2004; Figure A4.1), so we used this relationship to compare the impacts of declines in hare population density or cyclic attenuation as a result of habitat fragmentation, on lynx population dynamics and assess alternative management regimes. Our prediction was that habitat fragmentation (through forestry practices) interacts with harvest mortality by further reducing both lynx population size and cycle amplitude, thus compounding the role of either stressor on its own. To explore the potential relevance of harvest strategy on lynx populations, we modeled the role of fixed versus punctuated harvest on an oscillating lynx population, using a spatially explicit individual-based approach applied to a real, dynamic landscape with a habitat suitability map developed specifically for lynx (Chapter 2).

**Methods**

*Study Site and Spatial data*

The study area was a large landscape located in northeastern Ontario spanning the southern extent of the boreal forest and the northern extent of the Great Lakes-St. Lawrence forest (see Figure 4.1A); this region coincides with the
southern range periphery of lynx in Ontario (Walpole et al., 2012; Koen et al., 2014). The region is dominated by coniferous and mixedwood forests with some deciduous stands, combined with agricultural development towards the eastern portion and forestry activities interspersed throughout the area. In 2009/10, the boreal forest zone across Ontario contained 852 clearcuts having an average size of 60 ha (maximum: 1422 ha) and in the Great Lakes-St. Lawrence forest there were 654 clearcuts (average: 40 ha, maximum: 754; OMNR, 2011). Within the study area we selected a large focal study area (49,149 km²) that allowed us to avoid boundary effects (see Koen et al., 2010). The study region included 310 lynx harvest areas (traplines) ranging from 11 km² to 382 km² (mean: 140 km²), and 8 untrapped refugia ranging from 15 to 2888 km². Using Forest Resource Inventory data (1994-2009) and maps for allocated silvicultural harvest blocks for the region (2010-2020; OMNR unpublished data), we determined the extent of current and predicted future forest harvest in the region to assess how projected fragmentation may affect lynx population dynamics.

Although landscape pattern often is categorized based on the presence of one or more land cover types (e.g., Brückmann et al., 2010), for species such as lynx that inhabit a variety of habitat types, a species-specific approach in quantifying habitat pattern is more appropriate (Wiegand et al., 1998). Our habitat suitability model for lynx (Chapter 2) served as a basis for the present analysis and used general forest types (e.g., conifer, mixedwood and deciduous forest) and development stage (Holloway et al., 2004) to elicit lynx patterns of habitat suitability across a broad landscape; suitability ranged from 1 (developed agricultural land) to 100 (sapling
stage coniferous forest). As hexagon size increased, there were more inclusions of non-preferred habitat, which may have obscured the dominant cover type within a hexagon and the overall suitability value, especially on a heterogeneous landscape. Based on a subjective comparison of the habitat suitability hexagons with the original habitat suitability map, we reduced the threshold from 52 (Chapter 2), to 40 to reflect the 10-fold increase in the scale over which suitability was averaged. This was necessary because the map hexagons do not follow the original stand boundaries, so hexagons around the edge of a patch would have inclusions of non-preferred habitat, thereby reducing the overall suitability value. However, from a lynx perspective, this would not eliminate the patch as being preferred habitat. We applied the habitat suitability model to the forest resource inventory data and forest management plans to create land cover suitability maps for lynx in the study region, for the time periods 1994-2008, 2009-2019 and 2020-2040.

Management practices

Harvest mortality can be additive or compensatory to natural mortality rates depending on the actual identity and potential demographic contribution of individuals removed from the population and the numerical responses of remaining individuals to such removal. Additive mortality results in an increase in the total mortality rate that is proportional to the harvest rate, whereas compensatory harvest causes no decline in total mortality by promoting increased reproductive success or survival (Burnham and Anderson, 1984). However, for many species harvest mortality is not dichotomous; increase in total mortality owing to harvest is not in direct proportion to harvest mortality (i.e., partial compensation, see Boyce et
al., 1999). Depending on where a population is located on the additive vs. compensatory mortality continuum can directly affect the ability to mitigate harvest effects and the likelihood of success of long-term conservation efforts (Burnham and Anderson, 1984).

In most Canadian jurisdictions (British Columbia, Manitoba, Saskatchewan, Newfoundland and Labrador, Yukon, Nunavut, the Northwest Territories, parts of Ontario and Quebec), lynx are harvested using an open-quota system, such that trappers self-regulate their harvest according to the local abundance of lynx in a given year (Government of British Columbia, 2012; Government of Newfoundland and Labrador, 2012; Saskatchewan Ministry of Environment, 2012). In contrast, Alberta, parts of Quebec and parts of Ontario limit lynx trapping via area-based quota systems (Government of Alberta, 2012; Ministère des Ressources Naturelles et de la Faune, 2011; Statutes of Ontario, 1997). In northern Ontario, there are 2380 registered traplines with the annual harvest averaging 1053 lynx (range: 637 to 1846 between 1993 and 2009; OMNR unpublished data). Two styles of management are used across the region. In much of northwestern Ontario there are no annual limits on the number of lynx trapped, in contrast managers in northeastern Ontario set lynx harvest limits at the level of the individual trapline, with harvest being set at approximately 1 lynx per 25 km², regardless of cycle phase (Figure 4.2). We examined two different types of harvest strategies; fixed-proportion harvest, where a constant proportion of individuals was harvested each year regardless of population size (consistent with lynx harvest strategy for many jurisdictions), and punctuated harvest, where no individuals were harvested at the low phase,
intermediate numbers were harvested at the increase phase, and a larger percentage harvested at the peak phase (e.g., Brand and Keith, 1979; Lande et al., 1997).

**Population Model Structure**

We modeled lynx population dynamics across a single landscape with three land cover maps to determine: (i) lynx harvest rates that can reliably sustain their characteristic population dynamics (i.e., typical patterns in abundance and cyclicity); and (ii) if anthropogenic harvest is additive to the effects of habitat fragmentation. We used HexSim (Schumaker 2011), a spatially explicit individually-based program to apply the model described by Hornseth and Murray (Chapter 3) to a real landscape. HexSim is useful for relating population demography and habitat quality (e.g., Heinrichs et al., 2010). In the present context, we considered that lynx density should be directly related to habitat quality and snowshoe hare density (Figure 4.3), given that hares are the primary prey of lynx and densities of the two species are highly correlated (Figure A4.1; Krebs et al., 2001; Steury and Murray, 2004). Habitat quality determines lynx distribution across the landscape, so home range size and movement parameters were related to the habitat suitability score as an index of habitat quality. Home range size was determined as a function of habitat quality as lynx in lower quality habitats establish larger home ranges (Ward and Krebs, 1985). Lynx home range sizes vary greatly across their range, with smallest home ranges being observed in the north during peak snowshoe hare density years (range: 13-48 km², all home ranges estimated as 95% maximum annual convex polygons). Home ranges increase in size in the north during periods of hare paucity.
(range: 23-266 km²) and are also large across the southern range extent (range: 36-277 km²; Aubry et al., 2000), so it seems likely that this variability is caused, at least in part, by differences in habitat quality and prey abundance. In addition, we used habitat suitability as a determinant of lynx movement paths whereby we predicted that individuals would more likely move through habitats with higher suitability and avoid moving through areas with poor habitat suitability (Walpole et al., 2012). The model was designed to emulate natural conditions, so reproduction occurred in the spring and harvest was programmed to remove individuals during the winter, after juveniles have dispersed (in Ontario, the harvest season runs from October 25 to February 28 (Statutes of Ontario, 1997)).

We established four scenarios regarding posited effects of fragmentation on hare population dynamics: (i) cyclic (hereafter: CYC), which serves as a reference scenario and proposes that there is no effect of fragmentation on hare populations (i.e. cyclic oscillations characteristic of northern populations); (ii) low density (LD), where habitat fragmentation results in reduced density; however, populations maintain cyclic fluctuations (Hodges, 2000; Keith 1990); (iii) reduced amplitude (RA), where fragmentation results in a reduced amplitude of the cycle but has no effect on the average hare density across years (Strohm and Tyson, 2009); and (iv) low density and reduced amplitude (LDRA), where habitat fragmentation results in lower hare numbers and dampened oscillations (Murray, 2000). There is no long-term snowshoe hare density dataset for Ontario that has been validated with hare density estimates from live-trapping, so we used hare density estimates from southwest Yukon as a basis for simulations (Krebs, 2012). These data are the most
robust data of snowshoe hare population density in the boreal forest (see Krebs et al., 2001, 1987), to which we generated 4 different fluctuations in hare density based on the hypothesized effects that fragmentation can have on hare distribution and abundance (see Table 4.1). For each scenario we replicated the hare data and added stochasticity to create a 50-year time series. At southern latitudes and when hares are scarce, lynx consume 10-50% alternate prey items (e.g., red squirrel *Tamiasciurus hudsonicus*; Murray et al., 2008; Roth et al., 2007), so we used a scaling factor to account for the differential use of hares as prey between Yukon (92%) and Ontario (64%; from Roth et al., 2007). The CYC scenario included three relatively consistent cycles to serve as a reference scenario. To represent the LD scenario, we selected years of the Kluane cycle where hare density was uncharacteristically low (Krebs 2012). For the RA scenario, we used years 1977-1999, but limited the peaks and the lows, to reduce the cyclic amplitude without a reduction in average density. We considered peaks to be local maxima with at least a 2-fold increase in hare density over a 1- to 2-year period and we defined lows as hare densities with ≤0.50 hares/ha. For the LDRA scenario, we used years the same years and the same average density as the low density scenario, but limited the peaks and lows to reduce the overall amplitude. Appendix 4.1 details the hare input (hares/ha) range and average for each cycle. The scaled densities were used as the input data to the lynx population viability model created by Steury and Murray (2004), which found that survival for kittens is dependent upon hare density, survival of juveniles and adults is dependent upon the change in hare density from year_{t-1} to year_{t}, and
fecundity of juvenile and adult females is dependent on the hare density (equations in Appendix 4.2).

In addition, lynx were subjected to density-dependent mortality whereby individuals that were unable to establish a home range had an increased mortality risk due to the high energetic demands of dispersal (Kramer-Schadt et al., 2005). Each scenario was run for 120 time steps with 100 simulations, with the first 50 serving as a ‘burn in’ period using the CYC hare dataset to stabilize population dynamics and allow the lynx to move across the landscape, after which the harvest scheme and hare dynamics were applied. We averaged output of the 100 simulations and used time steps 75-120 as the period of analysis, which corresponded to years 1995 to 2040 on the Ontario landscape. This procedure stabilized populations which were subjected to harvest historically, as preliminary results showed that the first few years of proportional harvest are artificially inflated (M. Hornseth, unpublished data). In our modeled scenarios, lynx dispersal distances ranged from 1-208 km, consistent with those observed by Poole (1997). The model contained the following parameter estimates: (i) average lynx home range size of 40 km² (Aubry et al., 2000); (ii) dispersal mean path length of 100 km (taken from a log-normal distribution; Poole 1997); (iii) hare scaling factor of 1.35, which was a multiplier of the hare density data to account for differential use of hares across their range (Roth et al., 2007); and iv) a critical suitability threshold of 40. Dispersal path length was estimated using a log-normal distribution with a mean of 100 km, minimum and maximum bounds of 20 and 500 km. While dispersal
distances >500 km exist, they are rare (Poole 1997) and would cross the entire landscape.

Using fixed-proportion and punctuated harvest strategies, we examined 3 levels of harvest based on preliminary analysis; (i) Conservative (fixed-proportion harvest: 2%, punctuated harvest: 1% at the increase, 5% at the peak, with no harvest at the low); (ii) Moderate (fixed-proportion harvest: 5%, punctuated harvest: 2% at the increase, 8% at the peak, with no harvest at the low); and (iii) Liberal harvest (fixed-proportion harvest: 8%, punctuated harvest: 5% at the increase, 12% at the peak, with no harvest at the low). Although there are limited reported estimates of the proportion of the lynx population that are harvested annually across Canada, our estimates are in line with proportional harvest reported for lynx in Alberta in the late 1960s (Brand and Keith, 1979) and comparable to reported rates for other large furbearers (wolves; Robichaud and Boyce, 2010). To examine the effects of habitat fragmentation alone, we included a null-model with no harvest in each scenario.

Data Analysis and Sensitivity Analysis

We measured connectivity for each of the habitat suitability maps as mesh size, defined as the average area potentially accessed by an animal on a given landscape without having to cross defined borders or low quality habitat (Girvetz and Greco, 2007). For each population scenario (CYC, RA, LD, and LDRA) we measured the average population density within each time period (1995-2007; 2008-2019; and 2020-2040) under each harvest regime. We also quantified the number of lynx harvested from 1995 to 2040. We compared the population density
under each harvest regime to the null harvest scenario to determine the overall effect of each regime on population density.

Harvest theory predicts that if harvest is: (i) additive, population oscillations should be dampened with an overall decline in population density often resulting in unsustainable harvest; (ii) fully compensatory, there should be only negligible changes in density with no effects on cycle propensity, permitting sustainable harvest (Burnham and Anderson, 1984); or (iii) partially compensatory, there should be no decline in population cyclicity with a moderate decline in density and resulting in sustainable harvest (Table 4.2) (Boyce, 1999). Sustainable use has been defined as a harvest rate that does not lead to the long-term decline of biological diversity, therefore maintaining populations to meet the needs of future generations (Convention on Biological Diversity 1993). However, these limits have been better researched for aquatic than terrestrial ecosystems (Wienbaum et al., 2013). Both cyclic propensity (the frequency of peaks, reflected in spectral power of the population time series) and cyclic amplitude are important components of lynx population dynamics (Roth et al., 2007). We analyzed natural log-transformed time series generated by our model using spectral analysis based on the Lomb-Scargle algorithm (LombScargle package in R 2.15.1, Glynn et al., 2006). Specifically, we determined whether populations retained their cyclic dynamics under harvest pressure; (i.e., if \( P < 0.05 \), where \( P = 1 - (1 - e^{-z})^n \), and \( z \) is the corresponding spectral peak and \( n \) is the sample size, see Kendall et al., 1998). We measured the variability in fluctuations as the s-index, calculated as the standard deviation of log-density, to assess stability in abundance across time series (Stenseth and Framstad, 1980; Roth
et al., 2007), where a smaller s-index indicates less variability in population size. Period was calculated as 1/spectral frequency.

We examined a number of the input spatial parameters in a sensitivity analysis, including home range size, median dispersal distance, proportion of long distance dispersers, hare density scaling factor, and the critical suitability threshold value. We examined 3 average home range sizes (30 km², 40 km², and 50 km²; Aubry et al., 2000; Vashon et al., 2008), 3 proportions of long distance dispersers (35%, 50% and 65%, where the remaining population is a short-distance disperser), and 3 median dispersal path lengths (75 km, 100 km and 125 km; Poole 1997, 2003). We also used a range of scalars (from 1.25 to 1.45) applied to the Kluane hare density data to reflect the lynx’s ability to utilize alternative prey species at southern latitudes and at cyclic lows (Roth et al., 2007). We also examined the influence of the critical habitat suitability threshold on lynx population trajectories by analyzing the results of 5 alternative thresholds at 5-point increments from suitability values from 30 to 50, the 25th and 75th percentiles distribution of the non-zero habitat suitability values. We compared the relative influence of each variable by examining the effect on the population size in the CYC scenario with no harvest pressure.

Results

Landscape Structure

We assessed landscape structure over three consecutive time periods 1995-2008, 2009-2019, and 2020-2040. Each landscape was comprised of 1 or 2 large patches of lynx habitat (>1000 km²) and hundreds of smaller patches (range: 1-85
The total amount of suitable habitat for lynx was consistent across time periods at an average of 39,232 km² (±/− 2%). However, the number of habitat patches declined slightly from 1108 habitat patches in time period 1 to 1010 patches in time period 2. Although there was little change in the overall amount of suitable habitat across the study time period, mesh size decreased by 44% from 1995 to 2020 (Figure 4.1B), owing to the increase in number of habitat patches while the average patch size decreased. The fragmentation of a single, large patch (Figure 4.1C) resulted in a loss of connectivity. In 1995, the largest habitat patch was 26,839 km², this patch was split into 134 smaller patches in 2008, the largest of which was 24,773 km². The original patch was further fragmented into 173 smaller patches by 2020, the largest of which was 16,477 km².

**Fragmentation and Population Dynamics**

We examined the population size of each of the four scenarios (CYC, LD, RA and LDRA) with no harvest pressure across the 3 time periods, to isolate the effects of fragmentation on lynx densities. On average, lynx density varied by less than 10% in each scenario (range: 0.01-0.31 lynx per 100 km²). Hare densities varied by an average of 7% (0.26 hares per ha; Table A4.2). The scenarios with reduced cycle amplitudes had higher lynx density, regardless of input hare density (Table 4.3A). Lynx density is not well known for populations in northeastern Ontario, but trapline harvest records show that between 1993 and 2009, on average 0.63 lynx per 100km² were harvested annually on our study site (range: 0.27 lynx per 100 km² (2008/09) to 1.26 lynx harvested per 100 km² (2007/08) (OMNR unpublished data)). The cyclic scenario (CYC) had the most variable cycle with an S-index of
0.179 (S.E. 0.004), indicating a high cycle propensity, which was substantially higher than other scenarios where the s-index ranged from 0.071-0.110 (Table 4.3A).

*Sustainable harvest: additive vs. compensatory effects*

Harvest mortality was additive to habitat fragmentation at low population densities (under both low density and cyclic scenarios). In the CYC and LDRA scenarios, implementation of the punctuated harvest regime reduced the impact of harvest mortality by restricting harvest at low density periods. For example, in the CYC scenario, moderate levels of harvest pressure with the fixed harvest regime resulted in a 56.2% decline in population size, in contrast to a 34.3% decline with the punctuated harvest regime. In addition, there was minimal change in the frequency of cycle peaks or the s-index under moderate harvest pressure (0.003 to 0.007), but there was an increase in the s-index with liberal harvest pressure (0.015 to 0.022 Table 4.3B), so moderate harvest under a punctuated regime was most stable in the CYC scenarios. Under the LDRA scenario with moderate harvest pressure, fixed proportion harvesting reduced lynx densities by 37.3% (+/- 5.7), whereas punctuated regimes reduced densities by only half that magnitude, while increasing the total number of lynx harvested by 10% (Table 4.4A&B). Neither regime had an effect on s-index at this level of harvest pressure. In contrast, when population declines due to habitat fragmentation were minimal (<10% RA scenario; Table 4.4A), harvest was completely compensatory and there was no change in cycle propensity (Table 4.3B&C). Under these conditions, both harvest regimes were sustainable, but as harvest pressure increased, punctuated harvest regimes had a lesser impact on population size than fixed-proportion harvest (16.0 vs. 23.9%
reduction in population size, respectively). Under the LD scenario, harvest was unsustainable with additive mortality effects under all harvest regimes, including substantial declines in population density (decrease of 36%-87%) and a decrease in cycle frequency by 0.6 to 0.9 years.

Sensitivity Analysis

Our sensitivity analysis revealed that home range size and critical habitat threshold had the largest impact on population size. We measured the effects of average home range size (ranging from 30 to 50 km\(^2\)) on mean population size compared to the 40 km\(^2\) home range in the scenarios. At a home range size of 30 km\(^2\), the mean population size increased by 36%. When home range size was increased to 50 km\(^2\), the mean population size declined by 26%; importantly, propensity for cyclic dynamics was unaltered by these scenarios. We measured the effects of the critical habitat suitability threshold (set at 40 in scenarios) on population size (range: 30-50). Average population size correlated with the amount of available habitat at each threshold. When the threshold was set at 30, 71% of the landscape was available as habitat, 25% more than in the base model where the threshold was set at 40; as a result the average population size increased by 75%. At a threshold of 35, 12% more hexagons were available in comparison to the base model and population size increased by 44%. When we increased the critical threshold to 45, the amount of available habitat declined by 8%, to a total of 42% of the landscape; the corresponding reduction in population size was 43%. At a threshold of 50, only 31% of the landscape was available habitat, so population size decreased by 85%. The threshold for suitable habitat had a direct effect on
landscape connectivity and thus population size, however, these variables had a minimal effect on the time series trends; the s-index varied by less than 0.01 for these permutations. The hare scaling factor had a moderate effect on population size; when the factor was increased from 1.35 in the model scenarios to 1.45 in the sensitivity analysis, population sizes increased by 9%. However, when the scaling factor was reduced to 1.25, population sizes declined by 22%. Median dispersal distance and the proportion of dispersers had a minimal effect on population size (<3% change).

Discussion

Our results showed that whether habitat fragmentation affects the density and/or cycle amplitude of hare populations (Hodges 2000; Strohm and Tyson 2009), there are vastly different implications on lynx cycle dynamics which amplify the interaction with anthropogenic harvest. Our simulations suggest that the effects of anthropogenic harvest exacerbate the impacts of habitat fragmentation, especially when both harvest pressure is high and hare densities decline as a result of fragmentation. However, when harvest pressure is low and population density is high, the harvest effects are partially compensatory and population cycle dynamics are sustained. Increased harvest pressure heightens the risk of dampening oscillations, but punctuated harvest can be used to mitigate this risk, if harvest is within sustainable limits, and cycle amplitude and population density are not low. Our findings suggest that current management practices for cyclic furbearers across the boreal forest, where levels of forest fragmentation are increasing at the southern extent in particular and high fur harvest rates exist, should be synchronized to
population dynamics of the furbearers themselves, lest management activities contribute to cycle attenuation and increased extinction risk (Fryxell et al., 2010).

While our results involve theoretical modeling on a real landscape, they build on empirical studies showing the importance of limiting trapping mortality during cyclic lows (Brand and Keith 1979). While fluctuations in pelt value are known to have an effect on trapper effort (Brand and Keith, 1979; Poole, 2003), we demonstrate that quotas should be reflective of population dynamics especially for populations with high-amplitude fluctuations or dampening oscillations resulting in a loss of abundance. The results from our reference scenario demonstrates that without fragmentation impacting population dynamics, harvest mortality can have partially compensatory effects during the increase and peak phases. This demonstrates that lynx were not directly limited by connectivity, but instead were affected by the hypothesized impacts of fragmentation on the hare cycle. However, our results also reveal that harvest is always an additive source of mortality when lynx densities are low, therefore most lynx populations would benefit from harvest closure during cyclic lows to allow the population to recover (Lande et al., 1997). In addition, areas with low densities of lynx and hares should highly regulate lynx trapping to avoid augmenting extinction risk (Fryxell et al., 2010). Harvest records show that over the last 40 years, the southern range edge of lynx in Ontario has contracted by >175 km due to habitat loss and changes in environmental conditions (Koen et al., 2014). We caution that continued harvest in this region may amplify the effects of habitat loss and fragmentation and thus further contribute to the decline of southern lynx populations by reducing connectivity and increasing isolation.
(Squires et al., 2013). We recommend frequent reassessment of lynx harvest levels and trends to ensure that trapper quotas are reflective of current population dynamics, which can reduce the impact of harvest on the population as a whole (Anderson et al. 2008; Botsfield et al. 1997). Currently, such activities seem to be uncommon across most jurisdictions where lynx are harvested. In particular, our sensitivity analysis highlighted the need for robust estimates of hare population size, dispersal capacity through unsuitable habitat, and overall landscape connectivity. For land-use planning, it is necessary to consider connectivity measures in conjunction with the amount of available habitat, as plans including only habitat amount will lead to small and disconnected habitat patches that fail to provide enough resources to support lynx.

Our study is among the first to examine the interplay between habitat fragmentation and population oscillations in a harvested population. Because habitat fragmentation seems to be one of the leading candidate causes of cyclic attenuation (Ecke et al., 2010; Dalkvist et al., 2011), harvested populations may have reduced capacity to recover from perturbations resulting from environmental stochasticity, landscape modification, or overharvesting events (Beddington and May, 1977; Peron, 2013). Additionally, habitat fragmentation is of particular concern to carnivores due to their large spatial requirements (Woodroffe and Ginsberg 1998), as with reduced connectivity, harvest mortality can further amplify extinction risk and dampen cyclic oscillations. At higher levels of fragmentation, the risks of cycle attenuation could be much greater for primary predators (Schmidt et al., 2012). However, some predators may be better adapted to prolonged periods of
low prey density by compensating through dispersal to neighbouring populations, if a large number of non-breeding adults are on the landscape (Barraquand et al., 2014). While adult lynx have a relatively high natural survival rate, even in low hare density years, long periods of low prey density can greatly reduce the reproductive capacity of lynx (Steury and Murray 2004), so anthropogenic harvest in these low density years greatly increases extinction risk. Our results suggest that when harvest mortality is low, lynx populations are better able to compensate for the indirect effects of habitat fragmentation (due to changes in hare dynamics) than when anthropogenic mortality is high. This result is consistent with studies addressing the variations in anthropogenic mortality on the additive-compensatory continuum for wolves (Canis lupus, Murray et al., 2010), waterfowl (Peron, 2013), and fish (Reynolds et al., 2005). In addition, research has shown that species with long-lived, low fecundity life-histories are less capable of compensating for mortality resulting from environmental fluctuations and anthropogenic harvest than species with short lifespans and high fecundity (Reynolds et al., 2005, Peron, 2013).

Our study suggests that habitat fragmentation and anthropogenic harvest mortality have additive effects on naturally cycling populations and thus, we recommend that both land-use planners and conservation biologists consider the ecosystem-level effects of this interaction to ensure that management strategies promote sustainable resource use. Our spatial population viability model can be used to examine the effects of landscape scenario models and management strategies on lynx population dynamics, identifying the conditions where
anthropogenic harvest could lead to population collapse. Sustainable resource management is especially important for lynx populations at the southern range margin where functional connectivity is low (Walpole et al., 2012; Squires et al., 2013), the range is receding, and subsequently, genetic diversity is in decline (Koen et al., 2014). Further understanding of the interplay between fragmentation and harvest and their roles in shaping population dynamics in both cycling and non-cycling populations is necessary, especially given the current rates of human-caused landscape change and the important roles of both habitat fragmentation and anthropogenic harvest on population ecology.

Acknowledgements

This research received financial support from Natural Science and Engineering Research Council (NSERC) Strategic and IPS grants, the Panthera Foundation, the Ontario Ministry of Natural Resources and Wildlife Conservation Society Canada. We thank the Ontario Ministry of Natural Resources for contributing trapline and silvicultural data and N. Schumaker for invaluable assistance with HexSim. Thanks to M.J. Fortin, J. Ray, R. Rempel, and L. Walton for helpful input and feedback.
References


**Table 4.1**: Different snowshoe hare cycle scenarios generated from Kluane Monitoring dataset (Krebs 2012) and the resulting range in hare densities. Additional information is in Appendix 4.1. CYC refers to the cyclic scenario, RA is the reduced amplitude scenario, LD is the low density scenario, and LDRA refers to the low density, reduced amplitude scenario.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Kluane Dataset Years</th>
<th>Adjustments</th>
<th>Hare Density (hares/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CYC</td>
<td>1977-1999</td>
<td>Stochasticity</td>
<td>0.21-4.13</td>
</tr>
<tr>
<td>LD</td>
<td>2000-2011</td>
<td>Stochasticity</td>
<td>0.49-3.00</td>
</tr>
<tr>
<td>RA</td>
<td>1977-1999</td>
<td>Limited peaks/lows, stochasticity</td>
<td>0.17-2.51</td>
</tr>
<tr>
<td>LDRA</td>
<td>1977-2011</td>
<td>Limited peaks, stochasticity</td>
<td>0.42-2.15</td>
</tr>
</tbody>
</table>
Table 4.2: Summary of the predicted effects of additive, compensatory and partially compensatory mortality on population density and cycle propensity.

<table>
<thead>
<tr>
<th>Mortality effects</th>
<th>Effect on population density</th>
<th>Effect on cycle propensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) Additive</td>
<td>Decline</td>
<td>Decline(^a)</td>
</tr>
<tr>
<td>(ii) Compensatory</td>
<td>No effect</td>
<td>No effect</td>
</tr>
<tr>
<td>(iii) Partially compensatory</td>
<td>Small decline</td>
<td>No effect</td>
</tr>
</tbody>
</table>

\(^a\) Frequency of cyclic peaks changes by >0.5 years (measured by peak spectral density) or a ≥0.01 decrease in fluctuation variability, as measured by S-index
Table 4.3: Summarized results of A. no harvest scenarios, B. spectral analysis\textsuperscript{a}, and C. S-index\textsuperscript{b} for populations with fixed-proportion and punctuated harvest strategies over a 45-year time period (1995-2040). CYC refers to the cyclic scenario, RA is the reduced amplitude scenario, LD refers to the low density scenario, and LDRA is the low density, reduced amplitude scenario.

A. Summary parameters for no harvest scenarios

<table>
<thead>
<tr>
<th>Parameter</th>
<th>CYC</th>
<th>RA</th>
<th>LD</th>
<th>LDA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Hare Density (hares/ha)</td>
<td>1.60</td>
<td>1.60</td>
<td>0.95</td>
<td>0.95</td>
</tr>
<tr>
<td>Average Lynx Density (lynx per 100 km\textsuperscript{2})</td>
<td>0.77</td>
<td>1.61</td>
<td>0.53</td>
<td>1.22</td>
</tr>
<tr>
<td>Peak Spectral Density\textsuperscript{a}</td>
<td>13.3**</td>
<td>11.9**</td>
<td>6.5</td>
<td>3.7</td>
</tr>
<tr>
<td>S-index\textsuperscript{b}</td>
<td>0.179</td>
<td>0.087</td>
<td>0.110</td>
<td>0.071</td>
</tr>
</tbody>
</table>

B. Peak Spectral Density\textsuperscript{a}

<table>
<thead>
<tr>
<th>Harvest Pressure</th>
<th>Regime</th>
<th>CYC</th>
<th>RA</th>
<th>LD</th>
<th>LDRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservative</td>
<td>Fixed</td>
<td>13.6**</td>
<td>11.2**</td>
<td>5.9</td>
<td>4.1</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>13.7**</td>
<td>11.4**</td>
<td>5.6</td>
<td>3.9</td>
</tr>
<tr>
<td>Moderate</td>
<td>Fixed</td>
<td>13.6**</td>
<td>11.0**</td>
<td>4.7</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>13.8**</td>
<td>11.0*</td>
<td>5.9</td>
<td>4.2</td>
</tr>
<tr>
<td>Liberal</td>
<td>Fixed</td>
<td>12.4**</td>
<td>10.2**</td>
<td>4.0</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>13.9**</td>
<td>10.7*</td>
<td>4.9</td>
<td>4.5</td>
</tr>
</tbody>
</table>

C. S-index\textsuperscript{b}

<table>
<thead>
<tr>
<th>Harvest Pressure</th>
<th>Regime</th>
<th>CYC</th>
<th>RA</th>
<th>LD</th>
<th>LDRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservative</td>
<td>Fixed</td>
<td>0.179</td>
<td>0.087</td>
<td>0.103</td>
<td>0.075</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>0.171</td>
<td>0.086</td>
<td>0.105</td>
<td>0.074</td>
</tr>
<tr>
<td>Moderate</td>
<td>Fixed</td>
<td>0.183</td>
<td>0.088</td>
<td>0.123</td>
<td>0.074</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>0.174</td>
<td>0.086</td>
<td>0.112</td>
<td>0.076</td>
</tr>
<tr>
<td>Liberal</td>
<td>Fixed</td>
<td>0.198</td>
<td>0.091</td>
<td>0.140</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>0.175</td>
<td>0.091</td>
<td>0.139</td>
<td>0.066</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Spectral analysis was completed on a natural log transformed time series. Populations were considered cyclic if $p < 0.1$, where $P = 1 - (1 - e^{-z})^n$, and $z$ is the corresponding spectral peak and $n$ is the sample size (Kendall et al. 1998).

\textsuperscript{b} s-index calculated as the standard deviation of log-density (Stenseth and Framstad 1980)

** Significance level: $p < 0.001$

* Significance level: $p < 0.01$
Table 4.4: Average (A) change in population size (as a percent), and (B) total number of lynx harvested under different harvest regimes over a 45-year window from 1995 to 2040 for 4 types of scenarios. CYC refers to the cyclic scenario, RA is the reduced amplitude scenario, LD refers to the low density scenario, and LDRA is the low density, reduced amplitude scenario.

A. Change in Population Size

<table>
<thead>
<tr>
<th>Harvest Pressure</th>
<th>Regime</th>
<th>CYC</th>
<th>RA</th>
<th>LD</th>
<th>LDRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservative</td>
<td>Fixed</td>
<td>-22.8</td>
<td>-5.0</td>
<td>-42.1</td>
<td>-11.9</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>-24.5</td>
<td>-5.7</td>
<td>-35.8</td>
<td>-9.6</td>
</tr>
<tr>
<td>Moderate</td>
<td>Fixed</td>
<td>-56.2</td>
<td>-13.8</td>
<td>-75.5</td>
<td>-37.3</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>-34.3</td>
<td>-9.0</td>
<td>-54.6</td>
<td>-18.5</td>
</tr>
<tr>
<td>Liberal</td>
<td>Fixed</td>
<td>-75.8</td>
<td>-23.9</td>
<td>-87.2</td>
<td>-62.0</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>-57.2</td>
<td>-16.0</td>
<td>-75.6</td>
<td>-38.7</td>
</tr>
</tbody>
</table>

B. Total Number of Lynx Harvested

<table>
<thead>
<tr>
<th>Harvest Pressure</th>
<th>Regime</th>
<th>CYC</th>
<th>RA</th>
<th>LD</th>
<th>LDRA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservative</td>
<td>Fixed</td>
<td>380</td>
<td>1019</td>
<td>224</td>
<td>704</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>525</td>
<td>804</td>
<td>245</td>
<td>756</td>
</tr>
<tr>
<td>Moderate</td>
<td>Fixed</td>
<td>537</td>
<td>2301</td>
<td>209</td>
<td>1138</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>589</td>
<td>1315</td>
<td>285</td>
<td>1246</td>
</tr>
<tr>
<td>Liberal</td>
<td>Fixed</td>
<td>463</td>
<td>3211</td>
<td>169</td>
<td>1174</td>
</tr>
<tr>
<td></td>
<td>Punctuated</td>
<td>649</td>
<td>2166</td>
<td>275</td>
<td>1458</td>
</tr>
</tbody>
</table>
Figure Legend

**Figure 4.1:** Mapped location of the study area in northeastern Ontario (A) where the black line shows the border of the southern boreal forest and the northern border of the Great Lakes St. Lawrence forest; (B) describes the decline in estimated mesh size over the 45 year study period; and (C) shows the fragmentation of a large habitat patch from 1995 to 2009 to 2020. All shades of grey represent habitat patches in the landscape; the darkest grey represents the intact large patch from 1995, the medium grey represents remnants of the 1995 patch in that were fragmented in subsequent years, and the lightest grey depicts smaller patches on the landscape.

**Figure 4.2:** Harvest returns of Canada lynx over an area of 250 traplines in northeastern Ontario from 1993 to 2009. Peak harvest was in 2006/07 at 465 lynx and the low was in 2008; data courtesy of the Ontario Ministry of Natural Resources.

**Figure 4.3:** Conceptual diagram summarizing the Canada lynx population cycle as implemented in HexSim. Solid lines indicate the model pathway, hashed lines indicate the influence of habitat suitability score, and the dot-dash line indicates the influence of hare density on survival and reproduction at different life stages. Specific equations regarding survival and fecundity are shown in Appendix 4.1.

**Figure 4.4:** Time series of lynx populations under the moderate fixed-proportion and punctuated harvest regimes across three fragmentation scenarios with fragmentation increasing at years 2008 and 2020 under each scenario; i) reference scenario (average input hare density: 1.60 hares/ha, range: 0.21-4.13), ii) reduced amplitude where the density of hares was equivalent to the reference scenario and the cycle amplitude was reduced (average 1.60 hares/ha range: 0.49 – 3.00), iii) low density (0.95 hares/ha, range: 0.17-2.51) and iv) low density/low amplitude (0.95 hares/ha, range: 0.45-2.15) [Moderate fixed-proportion harvest: 2% across all cycle phases. Moderate punctuated harvest strategy: 0% harvest at low, 2% harvest at increase and 8% harvest at peak.]
Figure 4.1
Figure 4.2
Figure 4.3
Figure 4.4
Appendix 4.1: Snowshoe hare input data and scenario descriptions

For the CYC scenario, we used hare population estimates spanning years 1977-1999, which include 3 relatively consistent cycles, as a reference scenario. Scaled hare densities ranged from 0.21-4.13 hares/ha (average: 1.60), which correspond with snowshoe hare density estimates from the core of the boreal forest (Poole, 1994, Slough and Mowat, 1996; Brand and Keith, 1979). To represent the LD scenario, we used years 2000-2011 of the Kluane dataset, where hare density was uncharacteristically low (Krebs 2012). Scaled hare density ranged from 0.49 to 3.00 hares/ha (average: 0.95, characteristic of more southern populations; Litvaitis et al., 1985; Keith et al., 1993; Murray, 2000). For the RA scenario, we used years 1977-1999, but limited the peaks and the lows, to reduce the cyclic amplitude without a reduction in average density. We considered peaks to be local maxima with at least a 2-fold increase in hare density over a 1- to 2- year period and we defined lows as hare densities local minima where ≤0.50 hares/ha. The resulting dataset had the same average hare density as the CYC dataset (1.60 hares/ha) with a range of scaled densities from 0.17-2.51 hares/ha. For the LDRA scenario, we used years 2001-2011 of the Kluane dataset and maintained the same average density as the low density scenario (0.95 hares/ha), but limited the peaks and lows to reduce the overall amplitude, resulting in a range of 0.42-2.15 hares/ha.
Table S4.1 Input hare densities (per hectare) and output lynx densities (per 100 km²) for each scenario and time period. CYC refers to the cyclic scenario, RA is the reduced amplitude scenario, LD is the low density scenario, and LDRA refers to the low density, reduced amplitude scenario.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>CYC Hares</th>
<th>Lynx (SE)</th>
<th>RA Hares</th>
<th>Lynx (SE)</th>
<th>LD Hares</th>
<th>Lynx (SE)</th>
<th>LDRA Hares</th>
<th>Lynx (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.20</td>
<td>0.69 (0.07)</td>
<td>1.40</td>
<td>1.39 (0.08)</td>
<td>0.86</td>
<td>0.47 (0.02)</td>
<td>0.84</td>
<td>1.04 (0.05)</td>
</tr>
<tr>
<td>2</td>
<td>1.20</td>
<td>0.75 (0.10)</td>
<td>1.86</td>
<td>1.65 (0.09)</td>
<td>0.96</td>
<td>0.48 (0.05)</td>
<td>0.93</td>
<td>1.21 (0.04)</td>
</tr>
<tr>
<td>3</td>
<td>1.84</td>
<td>0.78 (0.05)</td>
<td>1.63</td>
<td>1.72 (0.06)</td>
<td>0.96</td>
<td>0.60 (0.03)</td>
<td>0.93</td>
<td>1.35 (0.03)</td>
</tr>
</tbody>
</table>
Appendix 4.2: Equations for population viability model

Equations used to estimate lynx survival and reproduction (reproduced from Steury and Murray, 2004)

Survival of kittens is given by:

\[ S_t = \frac{0.6984}{1 + 2.63 \times 10^{10} e^{-14.5421 h}} \]

where \( h \) is hare density in year \( t \).

Survival of juveniles and adults is given by:

\[ S_t = \frac{0.9487}{1 + 0.0021 e^{-8.0086 \frac{(h_t - h_{t-1})}{h_{t-1}}}} \]

where \( h \) is hare density in year \( t \) and \( h_{t-1} \) is hare density in year \( t-1 \).

Fecundity of juvenile females is given by:

\[ F_t = \frac{3.3059}{1 + 142.8867 e^{-1.0361 h}} \]

where \( h \) is hare density in year \( t \).

Fecundity of adult females is given by:

\[ F_t = \frac{3.3121}{1 + 11.1641 e^{-1.087 h}} \]

where \( h \) is hare density in year \( t \).
**Table S4.2** Mean and range of survival and fecundity rates for each scenario using the equations from Appendix 4.2.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Survival</th>
<th></th>
<th>Fecundity</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kitten</td>
<td>Juvenile/Adult</td>
<td>Juvenile</td>
<td>Adult</td>
</tr>
<tr>
<td>CYC</td>
<td>0.295 (0-0.698)</td>
<td>0.867 (0.270-0.959)</td>
<td>0.098 (0.014-0.419)</td>
<td>0.645 (0.179-1.519)</td>
</tr>
<tr>
<td>RA</td>
<td>0.242 (0-0.698)</td>
<td>0.920 (0.602-0.949)</td>
<td>0.052 (0.017-0.131)</td>
<td>0.522 (0.211-1.001)</td>
</tr>
<tr>
<td>LD</td>
<td>0.128 (0-0.698)</td>
<td>0.879 (0.460-0.949)</td>
<td>0.042 (0.014-0.143)</td>
<td>0.430 (0.175-1.049)</td>
</tr>
<tr>
<td>LDRA</td>
<td>0.043 (0-0.436)</td>
<td>0.922 (0.628-0.949)</td>
<td>0.032 (0.017-0.064)</td>
<td>0.366 (0.219-0.650)</td>
</tr>
</tbody>
</table>
Figure A4.1 Relationship of hare density to lynx density with a one year time lag.

Values from Appendix A of Steury and Murray (2004) were log-transformed and used in a linear regression $R^2$ is 0.55; we corrected for bias (Sprugel 1983).
Chapter 5: Synthesis

In this dissertation, I developed insights into the direct effects of habitat loss and the indirect effects of habitat fragmentation on Canada lynx (*Lynx canadensis*). I demonstrated, through the use of a habitat suitability model and occurrence patterns, that on landscapes where suitable land cover is abundant, lynx are limited by habitat loss, not fragmentation. However, I also demonstrated that lynx have flexibility in their habitat selection, whereby they are not limited by habitat loss on landscapes where suitable land cover is rare in northeastern Ontario (Chapter 2). I used a spatially-explicit individual-based model to show that plasticity in dispersal behaviour affects occupancy patterns in fragmented experimental landscapes, connectivity corridors are most beneficial for inflexible dispersers, and dispersal behaviour can promote non-random distribution of phenotypes across a landscape (Chapter 3). I applied both models to a landscape in northeastern Ontario and determined that, although this landscape is becoming more fragmented over time, the landscape structure was not limiting for lynx. I also showed that anthropogenic harvest amplifies the effects of habitat fragmentation on lynx (Chapter 4).

Lynx have flexibility in their habitat selection patterns; they prefer areas with abundant suitable habitat when possible, but when suitable land cover is rare, occur throughout the landscape and are not limited by the lack of habitat (Chapter 2). These results suggest that lynx are flexible and likely less affected by disturbance than previously predicted (Koehler et al. 2008). This flexibility could be due to changes in diet (Roth et al. 2007; Peers et al. 2014), but the fecundity of individuals in these disturbed areas is still unknown and the southern range edge for lynx in
Ontario has contracted by >175 km over the last 40 years due to habitat loss and changes in environmental conditions (Koen et al. 2014).

Although lynx are considered primarily predators of snowshoe hare, there is increasing evidence that lynx are capable of expanding their diet at the southern extent of their range to include red squirrels (Tamiasciurus hudsonicus; Roth et al. 2007) and ruffed (Bonasa umbellus) and spruce grouse (Fasipennis canadensis; personal observation). The binary categories of “specialization” and “generalization” are prolific in ecology (e.g., habitat specialists, prey specialists), but, in practice the phenomena are much more continuous, as individuals can exhibit various degrees of behavioural plasticity (Colles et al. 2009). This permits individuals to occupy variable environments (Holt and Barfield 2008) and be resilient to recent disturbance (Boydston et al. 2003, Réale et al. 2003), thus leading to long-term persistence in a changing landscape (Hendry et al. 2008). Dispersal plasticity can promote stability in spatially-structured metapopulations, and the consequences of behavioural plasticity therefore may have a large impact on a species’ ability to adjust to broad-scale processes, such as habitat fragmentation (Chapter 3). This indicates that humans can be an important driver of phenotypic divergence (Hendry et al. 2008). Conservation biologists should further examine how phenotypic plasticity may lead to behavioural changes resulting in increased fitness as this may have important implications in population persistence.

Functional connectivity is dependent on spatial and structural features of the landscape as well as species’ interactions within that spatial structure and is an essential element of landscape connectivity (Wiens et al. 1997). The ability of
animals to move between patches through a landscape is crucial to the functioning of a metapopulation (Hansson 1991). Lynx are characteristically long-distance dispersers, capable of long dispersal distances on rare occasions (up to 900 km (Poole 1997; Mech 1980)). Using a landscape model (Chapter 3), I developed the following predictions regarding plasticity in dispersal behaviour: 1) dispersal plasticity affects estimates of functional connectivity across the landscape; (2) variation in dispersal behaviour increases the stability and resilience of patchy population distributions; and (3) dispersal behaviour promotes non-random distribution of phenotypes across a landscape. Dispersal behaviour is an important component in metapopulation dynamics and is a key parameter in spatially explicit individual-based modelling. Recent work has shown that dispersal may promote stability and synchrony in spatially-structured metapopulations (Abbott 2011), so further understanding of the implications of this process are essential to management of metapopulations.

Ecosystem management is a paradigm focussed on the sustainability of natural resources and ecosystem functions by providing an integrative and adaptive framework for management decisions (Franklin 1997). An essential element for population managers is determining whether harvest mortality is an additive or a compensatory process (Lessard et al. 2005). I showed that this spectrum can be dynamic, but that harvest mortality is additive to the effects of habitat fragmentation. I demonstrated that dynamic harvest regimes with minimal harvest at cyclic lows promote the persistence of natural cycles (in fluctuating populations) and reduce extinction risk. This is congruent with the recommendations of Brand
and Keith (1979) for lynx harvest and Bischof et al. (2012) for wolverines (*Gulo gulo*) and European lynx (*Lynx lynx*), but requires more intensive monitoring of populations than is currently in place. Understanding the variability in mortality processes is an essential component of ecosystem management, especially for maintaining the metapopulation functions that are essential for persistence of subpopulations located in the United States. I recommend further exploration of the implications of fragmentation on both lynx and snowshoe hares to uncover the mechanisms driving dynamics at the southern range edge.

These results suggest that the lynx metapopulation structure, characteristic of populations across the southern extent of their range, is more resilient to increasing habitat loss and fragmentation than previously understood. However, this does not explain recent range contractions (Koen et al. 2014) suggesting that we need to improve our understanding of *i)* the reproductive capacity of lynx in disturbed landscapes and *ii)* the dispersal behaviour of lynx that is essential to the persistence of subpopulations. These two processes are not independent, as there are trade-offs between reproduction and dispersal (at a cost to fecundity; King and Roff 2010). Dispersal requires high energetic output, may not be successful, and, especially in disturbed landscapes, there is a high cost associated with crossing unsuitable habitat (Bonte et al. 2012; Kramer-Schadt et al. 2005). Recent advances in modelling have provided a mechanistic framework to explicitly integrate the three processes of dispersal (emigration, movement, and settlement) and the costs associated with each (Travis et al. 2012). However, there are challenges in applying this framework to real populations as the costs associated with each stage are difficult to estimate.
realistically. Further examination of plasticity in dispersal behaviour, predictors of dispersal success, and fecundity rates in populations on disturbed landscapes would improve our understanding of metapopulation dynamics in anthropogenically disturbed landscapes.
References


