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Metapopulation Dynamics and Multi-Scale Habitat Selection of a Montane Forest Songbird

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METAPOPULATION DYNAMICS AND MULTI-SCALE HABITAT SELECTION OF
A MONTANE FOREST SONGBIRD

A Thesis Presented

by

Sarah Jean Kiuama Frey

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Wildlife Biology

May, 2008
Accepted by the Faculty of the Graduate College, The University of Vermont, in partial fulfillment of the requirements for the degree of Master of Science, specializing in Wildlife Biology.

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ABSTRACT

Variations in species occurrence and distribution across the landscape over time provide fundamental information concerning population dynamics. How this relates to habitat characteristics at multiple scales can elucidate the process of habitat selection. I evaluated these processes for a montane fir (Abies) forest specialist, Bicknell’s Thrush (Catharus bicknelli) in Vermont. This species is threatened by a suite of anthropogenic disturbances on its breeding grounds and quantifying the effects of environmental change at the population level for this songbird has not been addressed. The naturally fragmented breeding habitat of varying size, quality, and connectivity warranted a metapopulation approach and a robust occupancy analysis.

Detection/non-detection data was collected for Bicknell’s Thrush across 88 sites during the breeding seasons in 2006 and 2007. Local habitat characteristics were measured for each site and landscape-level features were calculated using a predictive habitat model. The six local habitat variables were combined using a principal component analysis. Principal component 1 (PC1) described a gradient of increasing coniferous shrub density and proportion of coniferous dominated forest with decreasing canopy height. The landscape covariate was calculated by dividing patch size by patch isolation creating a continuum of small, isolated patches to large, less isolated patches. Thus each site was characterized by a single local habitat (PC1) and landscape metric.

From these data, 67 models considering all combinations of landscape and local habitat scores (univariate, additive and interaction) were evaluated for individual estimates of the following parameters: (1) probability of detection, (2) probability of initial site occupancy, (3) probability of site colonization, and (4) probability of local site extinction. AIC model selection techniques were used to rank the models, which represented ecologically plausible hypotheses that compared the strength of local habitat characteristics to large-scale landscape features. Models within 4 AICc points of the top model were considered plausible. The top eight models were all plausible. Landscape characteristics alone were not significant in driving population dynamics. The relative importance of landscape + local habitat was highest for both probability of initial occupancy and local site extinction. Probability of occupancy increased and extinction decreased with the combination of increased patch size and decreased patch isolation (landscape) and increased coniferous shrub density, proportion of coniferous dominated forest and decreased canopy height (local habitat). Probability of site colonization was driven mainly by local habitat features and increased with increasing habitat quality.

These results indicate a complex system with intricate links between landscape and local scales. Preserving large tracts of habitat may not be sufficient in assuring future species persistence, but could minimize local extinction risk. Careful consideration should be given to local habitat features within habitat fragments, particularly to maintain adequate colonization rates. Because important features from both scales are correlated, in intact montane forest patches, landscape-scale attributes alone may serve as a surrogate for identifying quality breeding habitat, assuming processes of natural disturbance can be maintained.
DEDICATION

To Erika, whose friendship and love will forever be a source of light in my life. I strive to be the role model that you were to me.
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I am grateful to my committee members, A. Strong, T. Donovan, and S. Helms-Cahan. Their insight and support enhanced the quality of my research and thesis by making it more comprehensive and meaningful. My advisor, A. Strong was a constant source of creativity and guidance and always helped me see the bigger ecological picture when my view had narrowed to the inter-workings of occupancy modeling. I admire his sense of humor, even after being sprayed in the face with poop by a European Starling with really good aim. His work ethic and lack of fear impressed me when he was determined to finish a vegetation plot on the top of Dewey Mountain in the middle of a thunder and lightning storm and I was more than ready to start running down the mountain. I attribute my deeper understanding of population modeling to T. Donovan, who made learning it accessible and even fun at times. I thank my fellow lab mates for their friendship, encouragement, and advice. Funding for my research was provided through the McIntire-Stennis Cooperative Forestry Program.

My research would not have been possible without collaboration with the biologists from the Vermont Center for Ecostudies. I am very thankful to D. Lambert and J. Hart for granting me access to the Mountain Birdwatch database. I learned a lot from the many conversations I shared with K. McFarland throughout the different stages of my research and I appreciate his patience for my unending requests for advice. I am thankful to C. Rimmer for making sure my husband was out of the country working with Bicknell’s Thrush on their wintering grounds during the key stages of my graduate career: comprehensive exams and thesis writing.

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# TABLE OF CONTENTS

DEDICATION ................................................................................................................. ii

ACKNOWLEDGEMENTS ............................................................................................. iii

TABLE OF CONTENTS ................................................................................................ iv

LIST OF TABLES .......................................................................................................... vi

LIST OF FIGURES ....................................................................................................... vii

LIST OF APPENDICES ................................................................................................. ix

CHAPTER 1: COMPREHENSIVE LITERATURE REVIEW ........................................... 1

POPULATION DYNAMICS ............................................................................................ 1
  Occupancy modeling as a tool for understanding population dynamics ............... 3

HABITAT SELECTION ................................................................................................. 6
  Ultimate and proximate factors ............................................................................. 6
  Scale ....................................................................................................................... 7

STUDY SPECIES: BICKNELL’S THRUSH ................................................................. 8
  Distribution and habitat ....................................................................................... 8
  Mating system and connectivity ......................................................................... 9
  Population limitation .......................................................................................... 10
  Population status and threats ........................................................................... 11
  Applying population modeling to Bicknell’s Thrush ....................................... 14

LITERATURE CITED ................................................................................................. 17
CHAPTER 2: THE IMPORTANCE OF SCALE IN DETERMINING HABITAT SELECTION AND CHANGES IN PATCH OCCUPANCY FOR BICKNELL’S THRUSH IN VERMONT ......................................................................................................................... 21

INTRODUCTION ............................................................................................................ 21

METHODS .................................................................................................................... 23
Field surveys ............................................................................................................. 23
Local-scale habitat measurements ............................................................................ 25
Landscape-scale habitat features .............................................................................. 26
Data preparation ........................................................................................................ 27
Site occupancy modeling and parameter estimation ................................................. 28

RESULTS ...................................................................................................................... 31
Model selection ......................................................................................................... 33
Detection probability (p) ........................................................................................... 34
Probability of initial occupancy (ψ) .......................................................................... 34
Probability of colonization (γ) .................................................................................. 34
Probability of local extinction (ε) ............................................................................. 35
Model averaging ....................................................................................................... 35

DISCUSSION ................................................................................................................. 36
Probability of initial site occupancy and local site extinction .............................. 36
Probability of site colonization and habitat selection ............................................. 38
Further considerations ............................................................................................... 43
Conservation and management implications ............................................................ 44

LITERATURE CITED...................................................................................................... 46

APPENDICES ................................................................................................................ 65

COMPREHENSIVE BIBLIOGRAPHY ............................................................................. 74
LIST OF TABLES

Chapter 2

Table 1: Abbreviations for local- and landscape-scale habitat variables used in this study. ........................................................................................................................................... 51

Table 2: Correlations between all variables considered in this study (see Table 1 for abbreviations). The cells in the upper right half of the table contain the $r$ values and in the lower left are the $P$ values ($\alpha < 0.05$ in bold). All $P$ values are Bonferroni corrected. ........................................................................................................................................... 52

Table 3: Factor coefficients and % variance explained by three principal components derived from six local habitat variables (see Table 1). .....................................................53

Table 4: AIC model selection results for determining the effects of landscape and local-scale habitat covariates on initial occupancy ($\psi$), colonization ($\gamma$), and local extinction ($\epsilon$). Detection probability ($p$) was modeled as survey number + patch size for all models. $K$ is the number of parameters estimated in the model. $L$ is the log likelihood. Each model is ranked by its AICc score, which represents how well the model fits the data. A lower $\Delta$AICc value is indicative of a better model. Only models within 4 AICc points of the top model were considered plausible and are displayed. The probability that the model (of the models tested) would best explain the data is indicated by AICc$\omega_i$. Model likelihood is the ratio of each model’s AICc$\omega_i$ to the top model’s AICc$\omega_i$. ......................................54

Table 5: Beta ($\beta$) estimates, standard errors (SE) and 95% confidence intervals (lower = LCI and upper = UCI) for the following parameters: probability of initial site occupancy ($\psi$), site colonization ($\gamma$), local site extinction ($\epsilon$) and detection probability ($p$) in the most supported model: $\psi_{\text{LANDSCAPE}+\text{LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LANDSCAPE}+\text{LOCAL}}$. ................................................ 55

Table 6: Model averaged parameter estimates, standard errors (SE), and 95% confidence intervals (lower = LCI and upper = UCI) using average landscape and local habitat covariate values................................................................. 56
LIST OF FIGURES

Chapter 1

Figure 1: Bicknell’s Thrush breeding and wintering distribution and probable migration routes (Map created by Dan Busby, Canadian Wildlife Service).........................................................16

Chapter 2

Figure 1: Area of study and survey sites in Vermont located within a Bicknell's Thrush (BITH) predicted habitat model (Lambert et al. 2005)............................................................... 57

Figure 2: Box plots for local habitat (a-f), landscape features (g-h), and local and landscape habitat scores (i) compared by sites where Bicknell’s Thrush were detected (1, \( N = 60 \)) and not detected (0, \( N = 28 \)) in 2006 and 2007. The upper (75\(^{th}\)) and lower (25\(^{th}\)) quartile limits are delineated by the upper and lower limits of the box, respectively. The line dissecting the box is the median. The smallest and largest non-outliers are represented by the lower and upper edges of the lines extending from the boxes (a.k.a. whiskers), respectively. Mild and extreme outliers are displayed using the symbols * and °, respectively................................................................. 58

Figure 3: (a) The number of sites and (b) box plots comparing landscape (standardized patch size/patch isolation) and local habitat (PC1) scores by sites that that remained vacant (00), were colonized (01), went extinct (10), and stayed occupied (11) of the sites surveyed during the 2006 and 2007 Bicknell’s Thrush breeding seasons........................ 59

Figure 4: Relative variable importance determined by summing the AIC\(_c\) for the models in which each covariate was present for probability of initial occupancy (\( \psi \)), site colonization (\( \gamma \)), and local site extinction (\( \epsilon \)).................................................. 60

Figure 5: Estimate of detection probability (\( p \)) by survey number as a function of patch size (ha) from the top ranked model: \( \psi_{\text{LANDSCAPE}+\text{LOCAL}}\gamma_{\text{LOCAL}}\epsilon_{\text{LANDSCAPE}+\text{LOCAL}} \) .................... 61

Figure 6: (a) Estimated probability of initial occupancy (\( \psi \)) as a function of local habitat (PC1 score) from the top ranked model: \( \psi_{\text{LANDSCAPE}+\text{LOCAL}}\gamma_{\text{LOCAL}}\epsilon_{\text{LANDSCAPE}+\text{LOCAL}} \). (b) The isolated effect of local habitat on \( \psi \), expressed as the PC1 score. (c) The isolated effect of landscape patch features on \( \psi \) expressed as patch size/patch isolation. Gray lines represent plus and minus one standard error............................................. 62

Figure 7: Estimated probability of colonization (\( \gamma \)) as a function of local habitat (PC1 score) from the top ranked model: \( \psi_{\text{LANDSCAPE}+\text{LOCAL}}\gamma_{\text{LOCAL}}\epsilon_{\text{LANDSCAPE}+\text{LOCAL}} \). Gray lines represent plus and minus one standard error............................................. 63
Figure 8: (a) Estimated probability of local extinction ($\epsilon$) as a function of landscape + local habitat from the top ranked model: $\psi_{\text{LANDSCAPE+LOCAL}}, \gamma_{\text{LOCAL}}, \epsilon_{\text{LANDSCAPE+LOCAL}}$. (b) The isolated effect of local habitat on $\epsilon$, expressed as a PC1 score. (c) The isolated effect of landscape on $\epsilon$, expressed as patch size/patch isolation (PS/PI). Note difference in scale of y-axis compared with (a) and (b). Gray lines represent plus and minus one standard error.
LIST OF APPENDICES

Chapter 2

Appendix 1: AIC model selection results from complete model set (67 models). Detection probability ($p$) was modeled as survey number + patch size for all models, except for the lowest ranked model ($\psi, \gamma, \epsilon, p.$) where $p$ was constant. $K$ is the number of parameters estimated in the model. $L$ is the log likelihood. Each model is ranked by its AICc score, which represents how well the model fits the data. A lower $\Delta$AICc value is indicative of a better model. The probability that the model (of the models tested) would best explain the data is indicated by the model weight (AICc$\omega_i$). Model likelihood is the ratio of each model’s AICc$\omega_i$ to the top model’s AICc$\omega_i$. 65

Appendix 2: Beta ($\beta$) estimates and standard errors (SE) from the complete set of candidate models. Detection probability ($p$) was modeled at survey number + patch size for all of the models with exception of the least supported model ($\psi, \gamma, \epsilon, p.$) in which $p$ was constant. The $\beta$s for detection probability are not included because the estimates and SE varied little among models. The probability that the model (of the models tested) would best explain the data is indicated by the model weight (AICc$\omega_i$). For each of the three parameters presented ($\psi$, $\gamma$, and $\epsilon$) a maximum of four $\beta$s could be estimated for each model. $\beta_0$ is the intercept, $\beta_1$ is the landscape covariate effect, $\beta_2$ is the local habitat covariate effect, and $\beta_3$ is the effect of the interaction of landscape and local habitat. If a $\beta$ was not estimated for a model, no estimate and SE is specified for that $\beta$. A * indicates that the $\beta$ (SE) for that parameter/model could not be properly estimated. 69
CHAPTER 1: COMPREHENSIVE LITERATURE REVIEW

Population Dynamics

Population-level studies offer information important for assessing species’ conservation status and trends. A population (a group of individuals of the same species) is an entity that can be defined in physical space, but loosens when considering migratory species. Changes in total population size are a direct consequence of differences between births and deaths, whereas immigration and emigration occur between sub-populations (Allen and Hoekstra 1992). Variation in the occurrence and distribution of a species in space and time can offer insight into these underlying population dynamics (Holmes 2006). Prioritizing conservation measures to promote population persistence requires understanding of population-level processes and can be gained from modeling them over a large portion of species’ ranges.

Incorporation of spatial structure into population dynamics is a central concept of metapopulation models (Hanski 1994). A metapopulation is defined as a network of sub-populations that are linked by migration. Changes in occupancy state, through sub-population extinction and colonization, may depend on the size and isolation of the habitat patch (Levins 1969, Hanski and Simberloff 1997). This idea is concurrent with that of island biogeography (MacArthur and Wilson 1967) which states that larger, less isolated patches have a smaller chance of extinction and a higher chance of colonization than small, isolated patches. However, this can be an oversimplification in many cases (Hastings and Harrison 1994), especially in dynamic ecosystems.
Modeling populations can be accomplished in different ways. Population studies range from assessment of birth and survival rates with marked individuals to relative abundance (individual counts) to species occurrence (presence-absence). Quantifying these processes over large areas is a daunting task, especially for rare and elusive species. The choice of which parameter to track over time will depend on the grain and extent of the study and the management objectives (MacKenzie et al. 2006).

Further, monitoring migratory bird populations is often complicated by their high dispersal capabilities and the multi-stage nature of their life cycles. They spend time in a variety of different locations (breeding grounds, wintering areas and migratory stop-over sites) which represent a multitude of habitat types and associated threats.

Understanding what limits a population throughout its annual cycle can provide insight into potential responses to a changing environment (Runge and Marra 2006). Many species are faced with a broad array of habitat threats, which include but are not limited to fragmentation, development, contamination and global climate change. These typically result in habitat loss and decreased habitat quality. It is the combination of population and habitat dynamics that will determine how a species will react to natural and human-induced environmental alterations and in turn their risk of decline or extinction (Akçakaya et al. 2004). A population model as a conservation tool provides a framework with which to identify the factors that drive system dynamics (Bessinger et al. 2006).
Occupancy modeling as a tool for understanding population dynamics

Occupancy, or the proportion of area, patches or sampling units occupied, is a commonly used state variable to determine the distribution and status of populations (MacKenzie et al. 2006). Using species occurrence (presence-absence) to monitor populations over large areas, as opposed to abundance, is generally simpler and is often used as a surrogate for abundance (Royle and Nichols 2003, MacKenzie et al. 2006). Though it is more coarse, the probability of site occupancy is a more accessible parameter to estimate because it does not require much more than visiting a site and recording whether or not the species of interest was detected. However, most species will not be perfectly detectable in the field, which can be accounted for by conducting multiple surveys at each site. These data can then be used to estimate detection probability and in turn adjust the parameters of interest, like the probability of site occupancy, accordingly. This concept is relatively new to population modeling and offers the ability to avoid parameter overestimation that results from assuming perfect detection (MacKenzie et al. 2002).

Multi-season (M.S.) occupancy models (MacKenzie et al. 2003) can be used not only to estimate the probability that a site will be occupied, but also colonization (the probability that an unoccupied site will become colonized) and extinction (the probability that an occupied site will go extinct). The parameters estimated by M.S. occupancy models are: 1) probability of species detection, given that the site is occupied ($p$), 2) the probability of initial patch occupancy ($\psi$), 3) probability of site colonization ($\gamma$) and 4) probability of local extinction ($\epsilon$). Of these four parameters, interest is usually focused
on the last three, although the inclusion of species detection probability is crucial in obtaining unbiased and precise parameter estimates (Wintle et al. 2005, MacKenzie et al. 2006). In assessing a population over a large spatial and temporal scale, the use of occupancy data may yield more meaningful and realistic inferences regarding extinction and colonization rates of a species among habitat patches across a metapopulation. More complex individually-based population models require large amounts of data for parameterization. These types of data may not always be available and moreover require extensive extrapolation to un-sampled sites.

The M.S. design involves multiple visits per site per season across multiple seasons. Surveys conducted within a season assume that the population is closed (no immigration or emigration) between surveys. Surveys conducted between seasons relax the closure assumption. Each site is given an encounter history within and among seasons which consists of detections (1) and non-detections (0) or no survey conducted (\(\cdot\)). An example of an encounter history for three surveys/season over three years may look like this: year one: 1\(\cdot\)\(\cdot\), year two: 000, year three: 001, such that in year one, the species was detected on the first survey and no further surveys were conducted, in year two it was not detected and in year three it was solely detected on the third survey. The across-years interpretation would be in year one and three the site was occupied, and was either unoccupied in year two (meaning it went extinct between year one and two and then was re-colonized in year three) or was occupied and not detected in year two. These encounter histories are expressed as probabilities using the four parameters mentioned above. Maximum likelihood procedures are then used to estimate the parameters given
the data. For example, the history probability in year one would be written as follows: $\psi p_1$. If you were to write out the entire encounter history (1..00001) throughout the years and surveys it would look like this: $\psi p_1 (1-\varepsilon)(1-p_4)(1-p_5)(1-p_6)(1-\varepsilon)(1-p_7)(1-p_8)p_9 + \psi p_1 \varepsilon(1-p_4)(1-p_5)(1-p_6)\gamma(1-p_7)(1-p_8)p_9$. This translates to: the site was occupied and the species was detected during the first survey and the site was not revisited in year one. Then it failed to go extinct and was missed on the next three surveys in year two, failed to go extinct again between year two and three and then missed on the first two surveys of the third year, but was detected on the ninth overall survey (the third in year three). Or (denoted by the + sign) the site was occupied and the species was detected during the first survey in the first year and then that site was not re-visited that year. Then the site went extinct and the species was not detected on the next three surveys in year two. The site was then re-colonized between year two and three and the species was not detected until the third survey in the third year (survey nine).

Occupancy modeling can be used to address an array of questions about ecological systems through inclusion of survey- and site-specific covariates to explain variability in parameters. These include comparing the importance of population processes to habitat features in driving species occurrence (Schmidt and Pellet 2005), comparing species’ responses to habitat fragmentation (Moore and Swihart 2005), and interspecific competition (Olson et al. 2005). Additional uses include community-level (biodiversity) studies (Manley et al. 2005), species distribution expansion or contraction over time (MacKenzie et al. 2006), and testing the effectiveness of sampling designs (Bailey et al. 2004). The most common uses seem to be for assessing species interactions
(e.g., MacKenzie et al. 2006), detecting patterns from long-term, large-scale monitoring programs (MacKenzie et al. 2006), and for identifying species-habitat relationships (Bailey et al. 2004).

**Habitat Selection**

Animals use habitat to fulfill basic life-history requirements such as foraging, nesting, and roosting (Block and Brennan 1993). Habitat selection theory states that there are factors in the environment that stimulate an individual to choose one site over another (Hildén 1965). Habitat selection is thought to occur over a short time frame for migratory birds whose window for breeding is limited (Gordon and Wittenberger 1991). Site selection is realized through assessment of physical cues that in the end determine survival and breeding success of the selecting individual through availability of resources, such as food, nest sites, and mates (Hildén 1965). Vegetation structure, competition and food resources have all been shown to be important for habitat selection in birds (Cody 1981). Our understanding of what environmental factors are important for habitat selection in birds can aid in implementation of the appropriate conservation actions.

**Ultimate and proximate factors**

Food resources, nest sites, and shelter are considered ultimate factors and are what is ultimately of importance to the survival and breeding success of the selecting individual (Hildén 1965). Proximate cues, on the other hand, are the environmental stimuli that represent presence of ultimate factors. They range from landscape characteristics and local habitat features to conspecifics and other species (Svärdson
1949, Cody 1981). There may exist a threshold in which certain conditions of the habitat must be met before triggering the “release” of the territorial response of an individual (Hildén 1965). This threshold is thought to be under selection pressure as the habitat a bird chooses to breed in most likely affects its fitness (Cody 1985), although Jones (2001) points out that it is rarely taken into account in habitat selection studies or been shown with empirical data.

**Scale**

The existence of habitat variation at multiple scales necessitates examination of ecological processes in relation to the spatial and temporal scales applicable to the organisms and processes of interest (Wiens 1989, Allen and Hoekstra 1992, Saab 1999). Ecological processes can be driven by patterns at the landscape or local habitat scale or both. Johnson (1980) proposed the recognition of a hierarchical nature to the selection process and outlined four distinct scales: 1) physical or geographical range, 2) home range of individual or group, 3) habitat components within the home range and 4) feeding site. Habitat selection is generally considered a multi-step process in which the individual first chooses the general habitat type and then selects among the patches created by variation in local-scale characteristics (Gordon and Wittenberger 1991).
“... only a freak ornithologist would think of leaving the trails for more than a few feet. The
discouragingly dense tangles in which Bicknell’s Thrushes dwell have kept their habits long wrapped in
mystery.”

- Wallace 1939

Bicknell’s Thrush (*Catharus bicknelli*) was formerly considered a subspecies of Grey-cheeked Thrush (*C. miniumus*) however, in 1995 it was separated on the basis of 1) divergent morphological characters, 2) allopatric breeding and wintering ranges, 3) discrete differences in song and 4) habitat preferences and 5) no evidence of hybridization between the two species (Ouellet 1993, American Ornithologists' Union 1995). Furthermore, genetic analyses have shown that Bicknell’s is more closely related to Veery (*C. fuscescens*) than Grey-cheeked Thrush (Outlaw et al. 2003).

**Distribution and habitat**

Bicknell’s Thrush is unique in that it is the only Nearctic - Neotropical migratory songbird that breeds solely in the northeastern U.S. and southeastern Canada (Lambert et al. 2005, Fig. 1). In the U.S., Bicknell’s Thrush breeds in the spruce-fir (*Picea-Abies*) forests atop the mountains in New England and New York. This encompasses the
Catskill and Adirondack Mountains of New York, the Green and Taconic Mountains of Vermont and the White Mountains of New Hampshire and Maine (Atwood et al. 1996).

The U.S. alone contains approximately 90% of the breeding habitat available to Bicknell’s Thrush in the world (Rimmer et al. 2001). In Canada, they inhabit stunted high-elevation forests, extending their range from southern Québec north to the gulf of the St. Laurence River and east into Nova Scotia (Ouellet 1993). They largely winter on the island of Hispaniola, but they are also found on Cuba and Jamaica (Rimmer et al. 2001, Fig. 1).

On the breeding grounds, Bicknell’s Thrush generally prefer thick regenerating balsam fir (\textit{A. balsamea}) and red spruce (\textit{P. rubens}) patches that are naturally created through disturbance events such as fir-waves (Sprugel 1976) and wind throws. As a result, their habitat is ephemeral in time and space. Bicknell’s Thrush’s local distribution within habitat patches tends to shift over time as they respond to changes in local forest composition (Rimmer et al. 2005a). Recently, they have also been found in regenerating forest patches created through man-made disturbances, such as ski area development, logging and communication/wind tower development (Nixon et al. 2001, Rimmer et al. 2004).

\textit{Mating system and connectivity}

The mating system of Bicknell’s Thrush has recently been identified as polygynandrous which entails females mating with multiple males and vice versa and multiple males providing parental care at a single nest (Goetz et al. 2003). This is
suspected to be partially correlated with a highly male-biased sex ratio and food limitation (Rimmer et al. 2001, Strong et al. 2004).

Dispersal capabilities appear to be high, characteristic of most migratory bird species, on the basis of a genetic analysis by Ellison (2001) who showed 1-18.18 individuals were exchanged between mountain ranges per generation. The Green Mountain population was estimated to receive one immigrant/generation from the Catskills, while providing 1.99, 1.0 and 1.18 emigrants/generation to the Adirondacks, White Mountains and Catskills, respectively. Hobson et al. (2001) interpreted high variation in deuterium levels in feathers within collection sites as evidence for high natal dispersal and connectivity among subpopulations.

Population limitation

Evidence exists that Bicknell’s Thrush population is limited by both food availability and high levels of biennial nest predation. Mating strategies appear to reflect resource abundance at the territory level. Strong et al. (2004) found that prey biomass on a female’s home range was significantly positively correlated with number of chicks fledged per nest and significantly negatively correlated with number of males per nest. Additionally, McFarland et al. (2008) detected a prominent biennial pattern of fall fir cone masts. Balsam fir cones are a significant food source for red squirrels (Tamiasciurus hudsonicus), thus in years following a cone mast, increased relative red squirrel abundance led to decreased productivity for Bicknell’s Thrush due to high nest predation.
Population status and threats

Bicknell’s Thrush is listed as the Neotropical migrant most at risk of extinction in the northeastern U.S. (Rich et al. 2004) with a global status of vulnerable (BirdLife International 2000, 2008). It is ranked as the top conservation priority among Neotropical migrants in the northeastern U.S. (Rosenberg and Wells 2000, Donovan et al. 2002, Rich et al. 2004). Currently the breeding population is estimated between 25,000 and 50,000 birds. These figures were derived through use of remote sensing data and mean home range size in Vermont. They assume that territories do not overlap and that the habitat is saturated (Rimmer and McFarland 2001). Survey results from a U.S. range-wide monitoring program called Mountain Birdwatch (MBW) between 2000-2004 from 47 sites showed a 9.0% annual decline for Bicknell’s Thrush (Rimmer et al. 2005a). This is comparable to the 8.3% annual decline detected (1993-2000) in the White Mountains, the largest patch of habitat available in the U.S. Continued declines at these rapid rates could reduce the global population by half in less than 10 years (Lambert 2005).

On the breeding grounds, ski area expansion, logging and wind tower development are the primary causes of habitat loss and disturbance. Although analysis of annual survival and reproductive success between ski areas and natural areas revealed no significant differences, they did suggest that on ski areas, Bicknell’s Thrush preferred smaller trail widths and larger habitat patches (Rimmer et al. 2004). The study was designed to assess the effects of existing ski areas, rather than ski area expansion and development and consequently had little power in predicting future impacts of continued ski area development on Bicknell’s Thrush. Ski resorts may appear somewhat benign
and fairly contained when compared to other human activities, however fragmentation is maximized in the relatively small concentrated area of montane forest they occupy. Studies on the effects of mountain resorts are not well known and increased degradation of these relatively fragile high elevation ecosystems could have compounding effects over a large scale or when coupled with other environmental disturbances like acid deposition and global climate change (Strong et al. 2002).

Widespread habitat loss has occurred along the Caribbean Island chain leaving less than 10% of the original broad leaf mesic forest preferred by Bicknell’s Thrush. This poses a large threat to the future viability of the population (Rimmer et al. 2001). Research in Haiti and the Dominican Republic have revealed sex, and potentially age, segregation by habitat. The majority of individuals captured (83-90%) in high quality habitat on Haiti were males whereas 72% captured in relatively disturbed, lower quality habitat were females (Rimmer et al. 2005c). Continued decline of Bicknell’s Thrush habitat on the wintering grounds combined with sexual habitat segregation could have serious implications for future population persistence.

More recently, noticeable levels of methyl mercury have been detected in the blood and feathers of Bicknell’s Thrush, previously thought to have been an occurrence only in animals inhabiting aquatic ecosystems. Further research revealed that montane forests may provide suitable conditions for absorption and movement of mercury along the food chain (Rimmer et al. 2005b). Long-term effects of mercury exposure on an insectivorous passerine like Bicknell’s Thrush are not known, warranting concern and further investigation.
Habitat alteration as a function of global climate change also poses a threat to populations of Bicknell’s Thrush. Recent declines and local extirpations that have taken place at low elevations and the southern edge of their range (Atwood et al. 1996) are cause for attention as they suggest that Bicknell’s Thrush is potentially already being affected by climate change (Lambert and McFarland 2003). A closer look at how climate change may directly affect Bicknell’s Thrush habitat reveals no foreseeable benefits for the species (Rodenhouse et al. 2007). By identifying the mean July temperature (MJT) associated with the current distribution of Bicknell’s Thrush habitat (9.3 - 15.5 °C), Rodenhouse et al. (2007) increased the MJT in increments of 1 °C, quantifying the amount of Bicknell’s Thrush habitat (number of pixels with MJT range of 9.3 - 15.5 °C) that remained after each temperature increase. After an increase of 1 °C, nearly half of the Bicknell’s Thrush habitat was eliminated in the northeast and after 2 °C, essentially all of the habitat will disappear from the Catskills of New York and the Green Mountain of Vermont. A 3 °C increase may be enough to nearly eliminate the entire available breeding habitat in the northeastern U.S. It is unclear exactly how the montane forests of the northeastern U.S. will respond to a rapidly warming climate, but Beckage et al. (2008) noted an increase in the basal area of northern hardwood species and a decrease in coniferous species in the boreal-northern hardwood ecotone over the past 40 years. Iverson and Prasad (2002) predict a large impact on habitat availability for balsam fir persistence, allowing encroachment of lower elevation hardwoods into mountain forests. Due to the dynamic nature of the habitat occupied by Bicknell’s Thrush (Rimmer et al. 2001), the potential exists for decreased recolonization by spruce and fir habitat after
local disturbances. Competitive interactions may be altered with future habitat conditions more conducive to occupation by Swainson’s Thrush (C. ustulatus), a species occupying the closest elevational niche (Noon 1981).

**Applying population modeling to Bicknell’s Thrush**

Currently, an accurate population status and the capability to reliably quantify the effects of environmental change and disturbance at the population level is lacking for Bicknell’s Thrush (Rimmer and McFarland 2001), despite ongoing long-term demographic research and region-wide monitoring efforts (Rimmer et al. 2004, Lambert 2005). The logistics of obtaining individual-level processes (birth, death, immigration, emigration) for a large number of subpopulations is unrealistic without a substantial increase in effort and resources. The need for a more accurate estimation of population size, identification of population sources and sinks, factors affecting occupancy patterns and within-patch habitat suitability are all crucial next steps for improving conservation efforts and management strategies for this species (Rimmer et al. 2005a). Occupancy modeling can use detection/non-detection data over a large area for estimating the population parameters occupancy, colonization, and local extinction at the site level (MacKenzie et al. 2003). Through incorporation of covariates, these data can be used to investigate the relationship between population dynamics and habitat features at the landscape and local scales.

The naturally fragmented breeding range of Bicknell’s Thrush results in a network of habitat patches of varying size, quality, and degrees of connectivity. This suggests that a metapopulation approach would be most appropriate for modeling
population dynamics. Although there is evidence of genetically effective mixing between mountain ranges (defined as one individual successfully exchanging genetic material with a different population each generation, Ellison 2001), lower observed genetic diversity in Vermont (Ellison 2001) indicates that panmictic mixing is not occurring within the Green Mountains.

An existing habitat model for Bicknell’s Thrush (Lambert et al. 2005) delineates potential areas where Bicknell’s Thrush could occur on a broad landscape scale. Little is known about how landscape-scale features or within patch local habitat characteristics may influence their occurrence. This may change how we manage for this species. The inextricable link between population viability and habitat quality warrants the investigation of both landscape- and fine-scale habitat characteristics and associated patch network metapopulation dynamics. This will also elucidate habitat selection tendencies for this species and test whether they are hierarchical in nature.
Figure 1: Bicknell’s Thrush breeding and wintering distribution and probable migration routes (Map created by Dan Busby, Canadian Wildlife Service).
LITERATURE CITED


Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5-26 in Metapopulation biology:


CHAPTER 2: THE IMPORTANCE OF SCALE IN DETERMINING HABITAT
SELECTION AND CHANGES IN PATCH OCCUPANCY FOR BICKNELL’S
THRUSH IN VERMONT

INTRODUCTION

Species occurrence and distribution can provide important insight into processes such as habitat selection, colonization and local extinction (MacKenzie et al. 2006). By linking these processes to habitat characteristics, both at the local- and landscape-scale, we can begin to understand the ecological factors that motivate habitat selection processes and drive changes in species occupancy. Although traditional mark-recapture methods combined with intensive studies of birth rates can provide estimates of critical population parameters, these techniques are expensive, and frequently intractable over spatial scales. By contrast, occupancy modeling provides a more logistically feasible framework in which hypotheses can be tested concerning the connection between habitat and species occurrence. Conducting such analyses for rare or declining species can be used to quantify site occupancy, a practical surrogate for population processes, over large areas with minimal effort and aid in making critical management decisions within a short time period.

Here I used occupancy modeling (MacKenzie et al. 2003) and AIC model selection techniques (Burnham and Anderson 2002) to test whether local habitat characteristics or landscape-scale features are more important in determining whether Bicknell’s Thrush (Catharus bicknelli) occupies a site and whether that site remains
occupied through time or goes locally extinct. I focused on the metapopulation of the Green, Taconic and White mountains of Vermont, where sub-populations are defined by high elevation habitat islands.

Bicknell’s Thrush is a montane fir (*Abies*) and spruce (*Picea*) forest specialist that inhabits a naturally fragmented breeding range in the northeastern United States, southeastern Quebec and Maritime Canada (Atwood et al. 1996, Rimmer et al. 2001, Lambert et al. 2005). It occupies disturbance-driven ephemeral mid-succession forest within montane regions. It winters primarily in mesic and wet broadleaf forest in the Greater Antilles from sea level to >2000m (Rimmer et al. 2001). Previously deemed a subspecies of Gray-cheeked Thrush (*C. minimus*), Bicknell’s Thrush received full species status in 1995 (Ouellet 1993, American Ornithologists' Union 1995). It is currently considered one of the rarest and most threatened passerines in eastern North America, and is ranked as the top conservation priority among Nearctic-Neotropical migrants in the Northeast (Rosenberg and Wells 2000, Rich et al. 2004) with a global status of vulnerable (BirdLife International 2000). Until now, population-level analyses over a large geographic extent had been forestalled by the species' furtive behavior and difficult-to-access habitats.

Detection/non-detection data were collected during the breeding seasons of 2006 and 2007 at 88 sites throughout the state of Vermont, USA. Local habitat characteristics and landscape-scale features deemed important for Bicknell’s Thrush were included as covariates. Using a multi-season occupancy model framework, I estimated the following four parameters: 1) detection probability (*p*), 2) probability of initial site occupancy (*ψ*),
3) probability of site colonization ($\gamma$) and 4) probability of local site extinction ($\epsilon$). I compared all possible combinations of landscape and local habitat characteristics (univariate, additive, and interaction) for the three parameters of interest ($\psi, \gamma, \epsilon$) through AIC model selection and determined relative variable importance (Burnham and Anderson 2002). I used this analysis to a) assess metapopulation processes within the existing predicted habitat model (Lambert et al. 2005) in Vermont and b) determine how they relate to habitat features at multiple scales.

**METHODS**

*Field surveys*

Detection/non-detection (presence/presumed absence) data were collected over a two-year period from 2006-2007 in the Bicknell’s Thrush breeding range within the state of Vermont, USA. A total of 88 sites were surveyed between 733 and 1236 m elevation (Fig. 1). Surveys were conducted by both myself and field technicians (29 sites) as well as through a trained volunteer-based program called Mountain Birdwatch (MBW, 59 sites, Hart and Lambert 2007). MBW was initiated in 2000, but here I used data from 2006-07 which coincides with the years of surveys conducted at additional sites (from now on referred to as SJF sites). Each site consisted of a 1-km transect of five points separated by 200-250m (some transects contained only 3 or 4 points due to logistical constraints).

MBW transect locations were placed through random prioritization of high-elevation habitat units (montane areas above 823m), although volunteer availability and
trail locations ultimately determined which sites were surveyed and placement of transects (Lambert et al. 2001, Hart and Lambert 2007). SJF sites were chosen from the remaining un-surveyed sites (mountains) in Vermont that fell within the area of the model of potential habitat for Bicknell’s Thrush in the northeastern U.S. (Lambert et al. 2005). SJF sites were generally on smaller mountains with more marginal habitat and many did not have trails. Transects were placed using ArcGIS software (ESRI 2005) before going into the field. The 1-km transects were fit into the habitat polygons defined by Lambert et al. (2005), following a straight line wherever possible. Often times transects followed a ridgeline and were placed along a trail when one was available.

A maximum of three surveys were conducted at each site each year. The survey protocol for MBW was as follows. The first survey period occurred between 04:30 and 06:30 and consisted of a 10-minute point count at each point along the transect. The second survey period consisted of a 1-minute playback of Bicknell’ Thrush songs and calls followed by a 2-minute silent listening period at each point if no Bicknell’s Thrush were detected during the first survey period. The second survey period directly followed the first survey period. The third survey period, like the second, also only occurred if no Bicknell’s Thrush were detected on both the first and second surveys, but took place on a different date within two weeks following the first two surveys (or before 15 July). It occurred between either 04:30 and 06:30 or 20:00 and 21:00 and was done by broadcasting the 1-minute playback and listening for two minutes every 100 meters along the transect.
For the SJF sites the protocol differed mainly in that all three surveys were almost always conducted within one visit to the site, weather permitting. This was achieved by conducting an evening survey before the morning point count. Both morning surveys followed the same protocol as MBW, but during the evening survey a 5-minute point count was conducted followed by broadcasting the 1-minute playback tape and listening for two minutes. For each survey at each site, a 1 (detection) or 0 (non-detection) was recorded based on whether a Bicknell’s Thrush was heard or seen at or between any of the five points along the transect.

**Local-scale habitat measurements**

Local habitat conditions were quantified in either 2006 or 2007 and were assumed to be constant within this time period. If the point was on a trail, the measurements were taken 5-10m from the trail. Local habitat measurement values were averaged across all of the points to obtain a single site value. Bird surveys and local habitat measurements covered a rectangular area of approximately 10ha (1km by 100m), which is at the scale of an average Bicknell’s Thrush breeding territory size (6.43-10.39ha, Collins 2007).

To assess shrub density at each point, I used the quarter point method (Cottam and Curtis 1956). In each of the cardinal directions from the survey point, the distance to the closest coniferous, deciduous, and dead shrub was measured with a maximum 10-meter radius. A shrub was defined as any woody plant that was >1 m in height with a diameter at breast height (DBH) ≤8cm. The basal area of both live and dead standing trees was measured using a wedge prism (2-factor metric or 10-factor English). Canopy species composition was determined by species and percentage. If one tree species
composed more than 60% of the canopy, it was considered dominant. If there was no clear dominant species apparent, a 60/40 or 50/50 mix was recorded. Each assessment of dominant canopy species was classified as coniferous, deciduous, or mixed. I calculated the dominant canopy species for the site by taking the proportion of sites along the transect for each category (coniferous, deciduous, and mixed). Average canopy height and percent canopy cover were also measured at each point.

**Landscape-scale habitat features**

Large-scale landscape features were quantified using GIS software (ESRI 2005). The two variables included in this analysis were patch size and isolation. High elevation land units delineated by an elevational-latitudinal threshold (-81.63 m/1° latitude) based on Bicknell’s Thrush breeding season presence-absence data, contained varying proportions of coniferous-dominated forest (based on forest composition from National Land Cover Data [Vogelmann et al. 2001]), which was considered potential habitat (Lambert et al. 2005). I defined patch size by the total area of coniferous dominated forest (30x30m pixels) within a given high elevation land unit.

Patch isolation was defined as the distance to the nearest patch of high elevation habitat, regardless of size. A center point for each polygon (or high elevation land unit) was created using the ‘Feature to point’ tool in ArcMAP (ESRI 2005). Using the ‘Near’ tool for point layers in ArcMAP (ESRI 2005), I calculated the distance from the center point of each polygon to the center point of the closest polygon. Each site was assigned the two metrics for the polygon in which it was located, thus, sites that shared the same polygon received identical patch size and isolation values.
I created one *landscape* variable by dividing patch size by patch isolation and then standardized this value (z-score = $x_i - \bar{x}/sd$). Smaller values represented smaller and more isolated patches whereas larger values reflected larger and less isolated patches. The disadvantage of this simplification was that the variances of both variables were made equal through standardization and that small, clumped patches may be indistinguishable from large isolated patches based on this metric.

**Data preparation**

Correlation analyses were performed on the eight site-specific covariates included in the analysis using Bonferroni corrected $P$-values. I included a subset of variables measured in the field that could be important in explaining metapopulation dynamics for Bicknell’s Thrush based on the species’ natural history. Of the three categories of shrub density measured (coniferous, deciduous, and dead), I considered coniferous shrub density the most important for Bicknell’s Thrush. I only included basal area of dead standing trees, or snags, as these are an indicator of the two main causes of natural disturbance in montane ecosystems in the northeastern U.S.: harsh weather and fir waves (Sprugel 1976). In the wake of the “wave”, mature (and senescing) trees are killed by high winds and ice, leaving dead standing trees which allows for significant fir regeneration. Bicknell’s Thrush tend to select these thick regenerating patches for nesting sites (Rimmer et al. 2001) and standing dead basal area is a useful structural indicator.

Due to the complexity inherent in incorporating six local habitat covariates in the modeling process, I simplified them into a single variable using a principle component
analysis (PCA, Table 1). I used PC1 only in the analysis, which explained a plurality of the variability in the data. This value was termed *local* in the modeling process and is the sum of the products of each variable’s factor coefficient and z-score. The drawbacks of this simplification of the local habitat data were that it did not allow me to directly assess the effects of each individual variable on population parameters, the variances for each variable are made equal through standardization and I only incorporated a portion of the variability in the dataset by including only PC1 in the models.

Site histories were created by compiling the detections (1) and non-detections (0) from surveys conducted in 2006 and 2007. Missed surveys were accounted for, but did not affect the analysis as the parameters associated with the missed surveys were simply not estimated (MacKenzie et al. 2006). Site histories also included the local vegetation score (PC1) and the landscape score (standardized patch size/patch isolation).

*Site occupancy modeling and parameter estimation*

A multi-season (M.S.) robust occupancy model framework was used following MacKenzie et al. (2003). The M.S. model examines the state variable, occupancy and changes in occupancy over time at the site level. Sites that were occupied in year $t$ could go locally extinct in year $t+1$ or remain occupied. Sites that were vacant in year $t$ could become colonized in year $t+1$ or could remain vacant. The four parameters estimated in this model are probability of detection ($p$), probability of initial site occupancy ($\psi$), probability of site (re)colonization ($\gamma$) and probability of local site extinction ($\varepsilon$).

In a M.S. occupancy model, there are two types of time periods, primary and secondary. In this study, the primary sampling period was defined as a Bicknell’s Thrush
breeding season, between which movement can occur in and out of the population that can cause local extinction and colonization events. This determines the occupancy status of a site the following year. Within a primary sampling period are surveys, or secondary sampling periods. Between surveys (or within a season), the population is assumed to be closed. The other two model assumptions are: 1) a species is not falsely detected and 2) detections from one site are independent of another (MacKenzie et al. 2003).

I conducted the modeling analyses using the programs Presence (Hines 2006) and MARK (White and Burnham 1999). Here, the covariates relating to site-specific characteristics, at the local and landscape scale (mentioned above in Data preparation) were included to test the strength of their relationship to $\psi$, $\gamma$ and $\epsilon$. Although it is not the primary parameter of interest, detection probability ($p$) was included to correct for imperfect detection of Bicknell’s Thrush in the field. Covariates used in the analysis to explain the variability in $p$ were survey number and patch size, based on previous analyses of Bicknell’s Thrush that used similar data, but with more survey sites and a longer time period (McFarland et al. 2008). Maximum likelihood techniques were used to estimate the four parameters (given the data) with the following likelihood equation from MacKenzie et al. (2003):

$$L(\psi_1, \epsilon, \gamma, p \mid X_1, \ldots, X_n) = \prod_{i=1}^{N} \Pr(X_i)$$

Here, $\psi_1$ refers to the initial occupancy in the first primary period, where thereafter $\epsilon$ and $\gamma$ determine $\psi_t$ in the following seasons. $X_i$ are the data in the form of detection histories.
A total of 67 models were compared using AIC model selection procedures (Burnham and Anderson 2002). Models were ranked based on their AICc score (a small sample size adjustment of AIC) and models with $\Delta$AICc of $\leq 4$ were considered plausible. The models consisted of all of the possible combinations of 1) landscape 2) local 3) landscape + local, and 4) landscape*local across $\psi$, $\gamma$, and $\varepsilon$ in addition to two null models (see Appendix 1 for full model set). Univariate models (landscape or local) estimated the parameters ($\psi$, $\gamma$ or $\varepsilon$) as a function of either landscape or local habitat features alone. Additive models estimated the parameters ($\psi$, $\gamma$ or $\varepsilon$) as a function of the summed effects (landscape + local). By adding an interaction term (landscape*local) to the summed effect, the model signified a relationship between a parameter ($\psi$, $\gamma$ or $\varepsilon$) and landscape features changed based on local habitat and vice versa. The two null models included one in which detection probability was a function of survey number and patch size and the other parameters ($\psi$, $\gamma$ and $\varepsilon$) were constant and one where all of the parameters were modeled as constant. A test for model goodness-of-fit was not performed because no such test exists for M.S. occupancy models or models that have missing surveys (D. MacKenzie, pers. comm.).

Once model selection procedures were completed, the beta ($\beta$) estimates for the most supported model were used to graph the relationships between the parameters and the covariates. The magnitude and nature of the effect of the covariates on the parameters are manifested by the $\beta$ s. The $\beta$s represent the intercept and slope(s) for each linear model which are converted to a probability (the parameter) using the logit link (Burnham and Anderson 2002).
I calculated relative variable importance for 1) landscape, 2) local, 3) landscape + local, and 4) landscape*local for $\psi$, $\gamma$ and $\varepsilon$ by summing the weights (AICc$\omega_i$) of the models in which they appeared for the particular parameter in question (Burnham and Anderson 2002) in each of the three types of relationships between the habitat variables (univariate, additive, and interaction).

**RESULTS**

Sites where Bicknell’s Thrush were detected tended to have steeper slopes, higher coniferous shrub density, higher basal area of snags, less percent canopy cover, higher proportion of coniferous dominated forest, shorter canopy height and be situated in larger, but more isolated, montane forest patches. Fig. 2 displays box plots comparing landscape and local habitat variables between sites where Bicknell’s Thrush were and were not detected during the study period. This represents the naïve estimate of occupancy (0.68; proportion of sites where Bicknell’s Thrush was detected/total sites surveyed) as some of the sites where Bicknell’s Thrush were not detected could have been occupied, but not detected.

Nine sites were colonized (10.2%) and six sites showed local extinction (6.8%), whereas 66 sites either remained vacant (31.8%) or occupied (43.2%) over the two years of the study (Fig. 3a). Seven sites were surveyed in only one of the two years of the study (8.0%) and therefore colonization or extinction could not be determined. Local habitat characteristics varied between sites, but were similar between sites that remained unoccupied or went extinct as well as between sites that remained occupied or became
colonized (Fig. 3b). Landscape features on the other hand were relatively similar between sites that stayed unoccupied, went extinct or became colonized, but differed from sites that remained occupied.

Of a total 28 correlation tests performed between eight variables, six resulted in significant correlations and are marked in bold in Table 2. The three variables showing the strongest separation between sites where Bicknell’s Thrush were and were not detected (coniferous shrub density, proportion of coniferous forest and patch size) were all significantly correlated. Average canopy height was significantly correlated with coniferous shrub density and proportion of coniferous forest. The landscape and local habitat scores were significantly positively correlated ($r = 0.51, P < 0.001$).

Principal component 1 (PC1), which explained 37.64% of the total variance in the local habitat data, was the only one included in the model selection procedures in order to minimize complexity (Table 3). The factor coefficient and whether it is negative or positive reflect the size and nature of the effect of that particular variable on the principal component. Positive factor coefficients indicate that as the variable increased, its influence on the PC value increased. Conversely, negative factor coefficients signify that as a variable increased, it decreased the overall PC value. Both coniferous shrub density (CSD) and proportion coniferous dominated forest (PCD) had higher positive coefficients in PC1 relative to the other five variables, whereas average canopy height (ACH) had a stronger negative coefficient. Although less influential, dead basal area (DBA) and slope (SLP) increased/decreased and percent canopy cover (PCC) decreased/increased along with the above mentioned gradient.
**Model selection**

The top eight models ($\leq 4 \Delta$AICc) showed support for both local habitat characteristics and landscape factors to influence occupancy patterns (Table 4, for full model set see Appendix 1). The combination of local and landscape habitat characteristics (additive) was consistently more important for both probability of initial site occupancy ($\psi$) and local extinction ($\epsilon$) than either covariate alone. Conversely, local site habitat characteristics alone more strongly influenced the probability of site colonization ($\gamma$). The relative importance of each covariate by parameter (considering all models, Fig. 4) showed a similar pattern. Landscape characteristics on their own had little support in the model selection results and also showed the lowest relative variable importance for all parameters. The interaction between landscape and habitat showed a lower relative importance for initial occupancy ($\psi$) and local extinction ($\epsilon$), compared to an additive relationship, but more than either of the landscape or local habitat variables alone.

All of the parameter estimations displayed in Figs. 5-8 are derived from the most supported model: $\psi_{\text{LANDSCAPE + LOCAL}} \gamma_{\text{LOCAL}} \varepsilon_{\text{LANDSCAPE + LOCAL}}$ (Table 4). Positive $\beta$ estimates indicated that the effect of landscape and local habitat was positive for initial site occupancy ($\psi$) and site colonization ($\gamma$, only local habitat), whereas negative $\beta$ estimates for probability of local extinction ($\epsilon$) indicated a strong negative effect of landscape and local habitat (Table 5, see Appendix 2 for $\beta$ estimates from complete model set).
Detection probability ($p$)

Probability of detection ($p$) decreased with survey number and increased with patch size (Fig. 5). Patch size had an equal positive effect on detection probability across all surveys (see Table 5). In the first two surveys, usually done during the same visit to the site, detection probability varied little (0.7 to nearly 1.0) and in large patches (>850 ha), probability of detection was greater than 0.75, regardless of the survey number. The third survey was generally done either at a later date in the breeding season or later in the morning (after an earlier survey), which would explain why detection probability is lower for that survey. Essentially, if a Bicknell’s Thrush occupies a site, the chances of detecting it on the first survey are 80% or greater, regardless of patch size.

Probability of initial occupancy ($\psi$)

Probability of initial site occupancy ($\psi$) was influenced by landscape and local habitat to the same degree (Fig. 6). The effects of both were positive and strong (see Table 5). The probability that a site will be occupied by Bicknell’s Thrush was positively influenced by increasing shrub density and proportion of coniferous dominated forest and decreasing canopy height (local habitat). Considering landscape-scale patch characteristics, the probability of initial occupancy increased with increasing patch size and decreasing patch isolation. The second most supported model included the interaction term for $\psi$, but its effect was minimal ($\beta \pm SE = 0.58 \pm 0.61$).

Probability of colonization ($\gamma$)

The model selection results (Table 4) and relative variable importance (Fig. 4) showed clearly that local habitat characteristics were the main force in driving
colonization of empty patches. Local habitat conditions had a strong positive effect on colonization probability \( (\gamma, \text{ Fig. 7 and Table 5}) \). Increasing coniferous shrub density and proportion of coniferous dominated forest and decreasing average canopy height positively influenced \( \gamma \). The influence of landscape-scale features was only evident in the third most supported model, but in that model the effect was weak \( (\beta \pm \text{SE} = 0.59 \pm 0.92) \), yet positive, when compared to that of local habitat characteristics.

**Probability of local extinction \( (\varepsilon) \)**

Both landscape and local habitat had a strong negative effect on probability of local extinction \( (\varepsilon, \text{ Fig. 8 and Table 5}) \). The local habitat effect was slightly stronger, but not by much. Compared to the other three parameters, the effect of landscape and local habitat on \( \varepsilon \) was more dramatic. Increasing coniferous shrub density and proportion of coniferous dominated forest and decreasing canopy height (local habitat) negatively influenced \( \varepsilon \). Probability of extinction \( (\varepsilon) \) was similarly negatively influenced by increasing patch size and decreasing patch isolation (landscape). Sites with poor landscape and local habitat conditions went extinct (or were never occupied), sites with favorable landscape and local habitat remained occupied, and sites with mixed landscape and local habitat conditions fell somewhere in between. There was a small range of covariate values in which the probability of extinction changed from zero to one.

**Model averaging**

Because there was no single model that was strongly supported, I used AIC\( \omega_i \)-based averaging (Table 6) of the parameter estimates to allow for more confident inferences to be made about the results (Burnham and Anderson 2002). The model
averaged parameter estimates are based on average covariate values. When averaging the
effect sizes alone (β), the results were very similar to those of the most supported model.
I do not present these results here because standard errors for the βs cannot be averaged
in the same manner as the βs themselves.

**DISCUSSION**

No single factor emerged as being the most influential in determining whether
Bicknell’s Thrush occurred at a site or the probability of local extinction and colonization
events. When in combination, local habitat and landscape-scale features both played
important roles in determining Bicknell’s Thrush occupancy patterns. When considered
separately, local site conditions surfaced as the most important driver for colonization
followed by an additive effect of landscape and local habitat. There was little support for
landscape features by themselves driving population processes. These results imply that
it is a complex interaction of factors at different scales acting on occupancy patterns and
driving habitat selection for Bicknell’s Thrush.

**Probability of initial site occupancy and local site extinction**

The interrelation of habitat and landscape characteristics in determining both the
probability of initial occupancy and local site extinction emphasizes the link between the
two scales. Inclusion of the interaction term ranks second in importance for occupancy
and extinction indicating that in some instances, the relationship of the parameters to
local habitat conditions can change depending on the landscape and vice versa. Neither
landscape nor local habitat was important on their own for either parameter (Fig. 4).
Bicknell’s Thrush habitat varied considerably at the two scales considered in this study
and although variables from the two scales are correlated, maintaining within patch variability appeared to be vital. Disturbance regimes that produce local variation (Brawn et al. 2001) within montane habitat patches are essential to preserve the local habitat conditions required by Bicknell’s Thrush.

Extinction probability was highly influenced by the combination of the two scales considered, suggesting that both need to be present to ensure that a patch remain occupied through time. Assuming that a smaller patch will contain fewer individuals (Connor et al. 2000), population size will be more variable and hence more vulnerable to probability of extinction. Similarly, if the proportion of suitable breeding habitat increases within the montane forest patch, there would exist the potential for more young to be produced and therefore increase the chance of population persistence in that patch.

Results from other studies that have compared how habitats at more than one scale influence bird occurrence, abundance or community composition are highly variable. Cornell (2007) compared the strength of habitat characteristics at two scales to the presence of conspecifics in predicting colonization and extinction of sites for Black-throated Blue Warblers (Dendroica caerulescens) in west-central Vermont. The interaction of the habitat variables at both scales (landscape and local) was more important in driving site selection than the presence of conspecifics. An assessment of multi-scale habitat associations for cavity nesting birds in Wyoming (Gutzwiller and Anderson 1987) found that habitat characteristics at multiple scales (three) were important for habitat use and community structure. Conversely, Saab (1999) discovered that the surrounding landscape composition, compared to micro- and macro-habitat
characteristics was the most important predictor of species occurrence in a cottonwood riparian forest in Idaho. In a managed forest in South Carolina, Mitchell et al. (2001) concluded that combining landscape and habitat did not perform better than either on its own for predicting species occurrences. Also, models fit better for habitat specialists than for generalists. The differences at which scale was important in predicting species-habitat relationships mark the importance of using the appropriate scale for the species and ecosystem of interest (Wiens et al. 1987, Hagan and Meehan 2002) and that landscape or local features may be defined differently among investigators.

**Probability of site colonization and habitat selection**

Given that site colonization is primarily influenced by local vegetation structure and composition, Bicknell’s Thrush may be able to find good breeding habitat, regardless of the patch size and connectivity. In other words, small and/or isolated patches that provide the local-scale habitat conditions necessary for Bicknell’s Thrush to breed could be colonized. Conversely, a large patch that is dominated by conifers, but that has a very open understory and tall canopy may not be sufficient to elicit a settling response by Bicknell’s Thrush for breeding. The results emphasize the importance of the dynamic processes of disturbance and subsequent regrowth by spruce and fir in these high-elevation habitat patches. Although, the addition of landscape features does rank second in importance for this parameter (Fig. 4) and appears in the third most supported model (Table 4), these results present little support for the existence of hierarchical habitat selection. However, colonization was only considered for previously unoccupied sites and therefore does not provide insight about selection of already occupied sites. As only
10.2% of the sites were unoccupied in 2006 and occupied 2007, my dataset may not have the power to provide strong inferences about colonization, although 31.8% of sites were unoccupied in both years. Considering their polygynandrous breeding system (Goetz et al. 2003), presence of conspecifics may be very important for site selection and the lack thereof may actually deter individuals from colonizing empty sites even if suitable habitat exists.

Assuming perfect detection, I found little difference existed in patch isolation between sites where Bicknell’s Thrush were and were not detected throughout the course of the study (Fig. 2). The degree of patch isolation may be inconsequential to a certain degree for a migratory songbird with strong dispersal capabilities (With et al. 2006) and that inhabits a naturally fragmented range (Hastings and Harrison 1994). In dynamic landscapes, like the montane forests of the northeastern U.S., species that show greater dispersal distances generally have a better chance of metapopulation persistence (Johst et al. 2002).

A genetic analysis by Ellison (2001) which found that 1-18.18 individuals were exchanged per year between mountain ranges suggests that Bicknell’s Thrush possess these high dispersal capabilities. In addition, a stable isotope analysis of Bicknell’s Thrush feathers (Hobson et al. 2001) interpreted high variation in deuterium levels within sampling sites as evidence for high natal dispersal and connectivity among subpopulations. Given this, can we assume that Bicknell’s Thrush could maintain connectivity between subpopulations (in this case mountains, not mountain ranges) in the event that montane patches shrink and become more isolated as is expected with global
warming (Rodenhouse et al. 2007)? Investigating metapopulation patch dynamics at the edge of Bickell’s Thrush’s range, where patches become smaller and sparser, could elucidate an important threshold in which immigration rates are no longer sufficient to maintain connectivity (Turner 1989, Holt and Keitt 2005). There could exist a point at which landscape-scale features become more important and that the fine-scale habitat characteristics will be secondary to landscape configuration (Smith et al. 2008). It is possible that the strength of landscape scale factors, specifically patch isolation could differ depending on where the study area lies within Bicknell’s Thrush’s breeding range. My dataset included only one site located in a patch that was drastically more isolated than the other patches (24.4 km). The lack of variability in the patch isolation metric coupled with the combining of patch size and isolation into one variable may have inhibited my ability to detect its effect on the population parameters.

High adult site fidelity for Bicknell’s Thrush (Rimmer et al. 2001) suggests that colonization is primarily young birds returning from the wintering grounds to breed for the first time or potentially adults that were unsuccessful breeders the previous year. Considering the male-biased sex ratio (Rimmer et al. 2001) and polygynandrous mating system (Goetz et al. 2003), colonization rates may differ by sex. Un-mated males may be the primary colonizers of small patches and female presence (or conspecifics) may largely influence or limit where a male settles.

Other habitat selection studies have found that local habitat conditions are more important than landscape features. Ball et al. (2005) used occupancy modeling to test a predictive habitat model for the Palm Springs ground squirrel (Spermophilus tereticaudus
chlorus) in California. Similar to my findings, they determined that the variation in vegetation and substrate was important in determining squirrel occurrence within the habitat model and suggest more attention be directed at the local scale. Using breeding bird atlas and habitat data at multiple scales, Brennan and Schnell (2005) found that birds responded to the habitat at the local scale. Hagan and Meehan (2002) concluded that the scale at which habitat features are important will vary by bird species, although for the majority of the species they included in their study in an industrial forest in Maine, the local scale habitat characteristics were more important. An assessment of bird-habitat relationships in New Hampshire (MacFadden and Capen 2002) similarly found that microhabitat was important for most of the species considered, but for many, multiple scales were important. Others concluded that nest site and territory selection occur at the local level (Sodhi et al. 1999, Snall et al. 2003). Direct comparison of these investigations may not be appropriate to the current results because they were conducted in different landscapes and for many of them there was little variation at the landscape scale. Also important to consider is what comprises the matrix habitat and how abrupt the transition is between the patch and the surrounding matrix habitat. Many studies assessing the effect of forest patch size and isolation on bird population processes consider landscapes subject to anthropogenic fragmentation (Lynch and Whigham 1984, Bolger et al. 1997, Donovan and Flather 2002), which may render landscape scale features much more important because they have been altered in a more abbreviated time frame. In these landscapes, connectivity may be much more significant for population persistence or occupancy of small patches (Donovan et al. 1995) because species that
occupy these areas have been recently separated by habitat fragmentation and may not have the capabilities to migrate between fragmented habitat patches or persist in small fragments. In a fragmentation study in the mid-Atlantic states (Robbins et al. 1989), patch isolation was the most important predictor of bird abundance and Neotropical migrants required the highest amount of contiguous forest to attain their highest probability of occurrence, highlighting the importance of landscape features in this system. A more comparable investigation in a naturally fragmented montane forest found that neither species richness nor abundance was positively correlated to patch size for old-growth bird species (Schieck et al. 1995). They proposed that species that inhabit naturally fragmented heterogeneous montane areas may be able to adapt better to anthropogenic habitat fragmentation and therefore introducing more heterogeneity, in the form of logging within forest patches may not have such adverse effects. Based on a mark-recapture study, Bicknell’s Thrush does not appear to be adversely affected by ski areas that fragment and introduce added heterogeneity (Rimmer et al. 2004), and in Canada they occupy regenerating areas formed by logging (Nixon et al. 2001) suggesting that they may have the capacity to adapt to within patch anthropogenic disturbance to a certain degree. On the other hand, ski areas do represent a net loss of montane forest habitat and maximize fragmentation within a small area (Strong et al. 2002). Creating glades, forested areas with an open understory, ski areas also directly remove habitat favored by Bicknell’s Thrush. A similar result occurs when pre-commercial thinning is conducted in managed forests.
Further considerations

Generally, habitat models for specialists tend to perform better than for habitat generalists (Dettmers et al. 2002). Although not the main focus of this research, the analysis served as a test of the Bicknell’s Thrush predicted habitat model (Lambert et al. 2005) as all of the surveyed sites were located within the areas delineated by the model. According to model validation done by Lambert et al. (2005), this model performed well, accurately predicting Bicknell’s Thrush presence at 84.7% of new sites, although it lacks the ability to assign a probability of occurrence at any given site. Of the 88 sites surveyed in this study, Bicknell’ Thrush was detected at 60 (68.2%) of the sites in 2006 and 2007. The incorporation of local habitat data served to refine the predictive ability of the current model. By conducting simple vegetation surveys at sites within the model the probability that the site would be occupied by Bicknell’s Thrush and how it may change through time can be known.

It is possible that my models failed to include factors or scales that might be more influential in determining Bicknell’s Thrush occurrence in Vermont. The on-site vegetation assessment was not exhaustive, but appeared to have captured the variability among sites. A small data set limited my ability to incorporate more variability by only being able to run models with one local habitat and one landscape covariate. Non-vegetation or structural aspects of the habitat, such as conspecifics, other species with similar habitat preferences or nest predators were not considered here and most likely also influence habitat selection and population processes for Bicknell’s Thrush. These factors are not easily quantifiable over a large extent and within a short time frame and
are more suited for smaller-scale studies. Additionally, because this study focused on the breeding ecology of Bicknell’s Thrush, a Neotropical migrant songbird, it is important to keep in mind the connections to and influences of/on the non-breeding stages (Rappole 1995).

This study was conducted in a short time frame and at a relatively small number of sites in a portion of the breeding range. As a result, there were few site-level colonization or extinction events between the two breeding seasons resulting in a small sample size for estimating probability of local extinction and colonization. The majority of the sites either remained occupied or vacant for the duration of the study. The pool of sites that did change occupy state between 2006 and 2007 possessed similar landscape features, resulting in little variability for that covariate, although local habitat characteristics were variable among these sites. Probability of site colonization and extinction were estimated based on one cycle between breeding seasons, which did not allow for detection of time dependent changes in these parameters.

**Conservation and management implications**

The ability of Bicknell’s Thrush to colonize and persist in small montane patches, given that they contain the necessary local habitat conditions, may have important management implications. By maintaining or even creating disturbance-driven diverse habitat conditions within small patches, the probability of colonization could be increased. This could provide potential breeding sites for Bicknell’s Thrush. However, even if a site may contain habitat conditions necessary for colonization, we cannot infer that successful breeding will follow (Oriens and Whittenberger 1991, Lawler and
Schumaker 2004). Strong et al. (2004) found a significant positive and negative
correlation between total prey biomass on Bicknell’s Thrush territories and the number of
chicks fledged per nest and the number of males that helped per nest, respectively.
Currently the relationship between habitat characteristics and prey biomass is not known,
but this relationship could connect breeding success to habitat characteristics and
elucidate potential source-sink dynamics (Pulliam 1988).

As is widespread in conservation research, time and funding are frequently
limited and quantifying fine-scale habitat characteristics can be a time-consuming and
costly endeavor when conducted at multiple sites over a large spatial extent. In an effort
to make vegetation sampling more accessible, I created a set of measurements that could
address factors that have been shown to be important to Bicknell’s Thrush based on long-
term research in the region (e.g., Rimmer et al. 2001) with relatively minor investments
in field time. Regardless, assessment of large-scale habitat features using GIS technology
can often be quicker and allows coverage of very large areas. Using GIS, my population
model has the potential for connecting on-site habitat characteristics with satellite
imagery in an attempt to better estimate population size (Hale 2006).

Detection probability for Bicknell’s Thrush in the field on the first two surveys
was relatively high (>0.7) and could reduce the need to re-visit a site more than two times
to determine its occupancy status. This could minimize the time and effort necessary for
surveying for this species over a large area as most breeding sites are isolated and
sometimes difficult to access.
The correlations between the influential habitat variables in the PCA and patch size further attest to the tie between scales. For example, as patch size increased, both coniferous shrub density and proportion of coniferous dominated forest increased. Given the correlations between the two scales of habitat characteristics considered here, and what we know about the habitat preferences of Bicknell’s Thrush (Rimmer et al. 2001), it may be safe to assume that preserving large tracts of high-elevation habitat would be sufficient in providing the necessary site-specific breeding habitat characteristics required by this species and ensure long-term persistence. That may be the case when considering undisturbed (by humans) high elevation patches, but may break down when habitat perturbation exists in the form of ski areas, wind tower development, timber harvesting (more common in Canada and Maine, U.S.), acid rain (spruce dieback) or global climate change. All of these are known to (Beckage et al. 2008) or are predicted to (Iverson and Prasad 2002) alter the vegetation structure of these high elevation forests at the local scale. This may be particularly important for maintaining colonization rates, which appear to be primarily driven by the local habitat features. In order to ensure persistence for Bicknell’s Thrush, it is imperative that local habitat is considered, but in undisturbed montane forest patches, assessment of landscape-scale features may serve as a surrogate for identifying quality breeding habitat, assuming in-patch disturbance-driven habitat dynamics are preserved.

**LITERATURE CITED**


concern; Strategies for bird conservation: The Partners in Flight planning process in Proceedings of the 3rd Partners in Flight Workshop, Cape May, NJ.


Table 1: Abbreviations for local- and landscape-scale habitat variables used in this study.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Variable</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOCAL</td>
<td>Slope (degrees)</td>
<td>SLP</td>
</tr>
<tr>
<td>LOCAL</td>
<td>Coniferous shrub density (stems/m²)</td>
<td>CSD</td>
</tr>
<tr>
<td>LOCAL</td>
<td>Dead basal area (m²/ha)</td>
<td>DBA</td>
</tr>
<tr>
<td>LOCAL</td>
<td>Percent canopy cover</td>
<td>PCC</td>
</tr>
<tr>
<td>LOCAL</td>
<td>Proportion of coniferous dominated forest points along the transect</td>
<td>PCD</td>
</tr>
<tr>
<td>LOCAL</td>
<td>Average canopy height (m)</td>
<td>ACH</td>
</tr>
<tr>
<td>LAND-SCAPE</td>
<td>Patch size (ha)</td>
<td>PS</td>
</tr>
<tr>
<td>LAND-SCAPE</td>
<td>Patch isolation (km)</td>
<td>PI</td>
</tr>
</tbody>
</table>
Table 2: Correlations between all variables considered in this study (see Table 1 for abbreviations). The cells in the upper right half of the table contain the $r$ values and in the lower left are the $P$ values ($\alpha < 0.05$ in bold). All $P$ values are Bonferroni corrected.

<table>
<thead>
<tr>
<th>Variable</th>
<th>SLP</th>
<th>CSD</th>
<th>DBA</th>
<th>PCC</th>
<th>PCD</th>
<th>ACH</th>
<th>PS</th>
<th>PI</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLP</td>
<td></td>
<td>0.04</td>
<td>0.039</td>
<td>0.07</td>
<td>0.15</td>
<td>-0.272</td>
<td>0.209</td>
<td>0.143</td>
</tr>
<tr>
<td>CSD</td>
<td>1</td>
<td></td>
<td>0.317</td>
<td>0.02</td>
<td>0.587</td>
<td>-0.402</td>
<td>0.413</td>
<td>0.105</td>
</tr>
<tr>
<td>DBA</td>
<td>1</td>
<td>0.075</td>
<td></td>
<td>0.122</td>
<td>0.409</td>
<td>-0.055</td>
<td>0.172</td>
<td>0.124</td>
</tr>
<tr>
<td>PCC</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td>-0.123</td>
<td>0.22</td>
<td>-0.14</td>
<td>0.121</td>
</tr>
<tr>
<td>PCD</td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
<td>-0.526</td>
<td>0.467</td>
<td></td>
<td>0.22</td>
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<tr>
<td>ACH</td>
<td>0.187</td>
<td>0.017</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>-0.356</td>
<td></td>
<td>-0.15</td>
</tr>
<tr>
<td>PS</td>
<td>1</td>
<td>0.005</td>
<td>1</td>
<td>1</td>
<td>0.001</td>
<td>0.119</td>
<td></td>
<td>0.185</td>
</tr>
<tr>
<td>PI</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
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Table 3: Factor coefficients and % variance explained by three principal components derived from six local habitat variables (see Table 1).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Factor coefficients</th>
<th>% Total Variance Explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLP</td>
<td>0.13</td>
<td>0.127</td>
</tr>
<tr>
<td>CSD</td>
<td>0.344</td>
<td>0.147</td>
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<tr>
<td>DBA</td>
<td>0.225</td>
<td>0.504</td>
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<td>PCC</td>
<td>-0.06</td>
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</tr>
<tr>
<td>PCD</td>
<td>0.389</td>
<td>0.019</td>
</tr>
<tr>
<td>ACH</td>
<td>-0.32</td>
<td>0.365</td>
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</table>
Table 4: AIC model selection results for determining the effects of landscape and local-scale habitat covariates on initial occupancy ($\psi$), colonization ($\gamma$), and local extinction ($\epsilon$). Detection probability ($p$) was modeled as survey number + patch size for all models. $K$ is the number of parameters estimated in the model. $L$ is the log likelihood. Each model is ranked by its AICc score, which represents how well the model fits the data. A lower $\Delta$AICc value is indicative of a better model. Only models within 4 AICc points of the top model were considered plausible and are displayed. The probability that the model (of the models tested) would best explain the data is indicated by AICc$\omega_i$. Model likelihood is the ratio of each model’s AICc$\omega_i$ to the top model’s AICc$\omega_i$.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>$-2(L)$</th>
<th>AICc</th>
<th>AICc</th>
<th>$\omega_i$</th>
<th>Likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\psi_{\text{LAND+LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LAND+LOCAL}}$</td>
<td>12</td>
<td>275.77</td>
<td>301.77</td>
<td>0.26</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>$\psi_{\text{LAND*LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LAND+LOCAL}}$</td>
<td>13</td>
<td>274.75</td>
<td>303.1</td>
<td>1.33</td>
<td>0.13</td>
<td>0.52</td>
</tr>
<tr>
<td>$\psi_{\text{LAND+LOCAL}} \gamma_{\text{LAND+LOCAL}} \epsilon_{\text{LAND+LOCAL}}$</td>
<td>13</td>
<td>275.35</td>
<td>303.7</td>
<td>1.93</td>
<td>0.1</td>
<td>0.38</td>
</tr>
<tr>
<td>$\psi_{\text{LAND+LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LOCAL}}$</td>
<td>11</td>
<td>280.38</td>
<td>304.06</td>
<td>2.28</td>
<td>0.08</td>
<td>0.32</td>
</tr>
<tr>
<td>$\psi_{\text{LAND+LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LAND*LOCAL}}$</td>
<td>13</td>
<td>275.77</td>
<td>304.12</td>
<td>2.35</td>
<td>0.08</td>
<td>0.31</td>
</tr>
<tr>
<td>$\psi_{\text{LAND*LOCAL}} \gamma_{\text{LAND+LOCAL}} \epsilon_{\text{LAND+LOCAL}}$</td>
<td>14</td>
<td>274.32</td>
<td>305.05</td>
<td>3.28</td>
<td>0.05</td>
<td>0.19</td>
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<tr>
<td>$\psi_{\text{LAND*LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LOCAL}}$</td>
<td>12</td>
<td>279.37</td>
<td>305.37</td>
<td>3.6</td>
<td>0.04</td>
<td>0.17</td>
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<tr>
<td>$\psi_{\text{LAND<em>LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LAND</em>LOCAL}}$</td>
<td>14</td>
<td>274.75</td>
<td>305.48</td>
<td>3.7</td>
<td>0.04</td>
<td>0.16</td>
</tr>
</tbody>
</table>
Table 5: Beta (β) estimates, standard errors (SE) and 95% confidence intervals (lower = LCI and upper = UCI) for the following parameters: probability of initial site occupancy (ψ), site colonization (γ), local site extinction (ε) and detection probability (p) in the most supported model: \( \psi_{\text{LANDSCAPE}+\text{LOCAL}} \gamma_{\text{LOCAL}} \varepsilon_{\text{LANDSCAPE}+\text{LOCAL}} \).

<table>
<thead>
<tr>
<th>Beta (β)</th>
<th>Estimate</th>
<th>SE</th>
<th>LCI</th>
<th>UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_0 - \psi ) intercept</td>
<td>0.766</td>
<td>0.355</td>
<td>0.071</td>
<td>1.461</td>
</tr>
<tr>
<td>( \beta_1 - \psi ) landscape effect</td>
<td>1.357</td>
<td>0.480</td>
<td>0.415</td>
<td>2.298</td>
</tr>
<tr>
<td>( \beta_2 - \psi ) local habitat effect</td>
<td>1.080</td>
<td>0.369</td>
<td>0.357</td>
<td>1.803</td>
</tr>
<tr>
<td>( \beta_0 - \gamma ) intercept</td>
<td>-0.195</td>
<td>0.555</td>
<td>-1.283</td>
<td>0.893</td>
</tr>
<tr>
<td>( \beta_1 - \gamma ) local habitat effect</td>
<td>2.139</td>
<td>0.821</td>
<td>0.530</td>
<td>3.748</td>
</tr>
<tr>
<td>( \beta_0 - \varepsilon ) intercept</td>
<td>-4.001</td>
<td>1.752</td>
<td>-7.434</td>
<td>-0.567</td>
</tr>
<tr>
<td>( \beta_1 - \varepsilon ) landscape effect</td>
<td>-3.372</td>
<td>2.072</td>
<td>-7.434</td>
<td>0.690</td>
</tr>
<tr>
<td>( \beta_2 - \varepsilon ) local habitat effect</td>
<td>-3.594</td>
<td>1.605</td>
<td>-6.740</td>
<td>-0.449</td>
</tr>
<tr>
<td>( \beta_0 - p ) survey 1 intercept</td>
<td>1.753</td>
<td>0.315</td>
<td>1.136</td>
<td>2.370</td>
</tr>
<tr>
<td>( \beta_1 - p ) survey 2 intercept</td>
<td>1.358</td>
<td>0.355</td>
<td>0.663</td>
<td>2.053</td>
</tr>
<tr>
<td>( \beta_2 - p ) survey 3 intercept</td>
<td>0.253</td>
<td>0.400</td>
<td>-0.531</td>
<td>1.036</td>
</tr>
<tr>
<td>( \beta_3 - p ) patch size effect</td>
<td>0.497</td>
<td>0.261</td>
<td>-0.014</td>
<td>1.008</td>
</tr>
</tbody>
</table>
Table 6: Model averaged parameter estimates, standard errors (SE), and 95% confidence intervals (lower = LCI and upper = UCI) using average landscape and local habitat covariate values.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>LCI</th>
<th>UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability of initial occupancy ($\psi$)</td>
<td>0.705</td>
<td>0.096</td>
<td>0.493</td>
<td>0.855</td>
</tr>
<tr>
<td>Probability of local extinction ($\varepsilon$)</td>
<td>0.026</td>
<td>0.049</td>
<td>0.001</td>
<td>0.547</td>
</tr>
<tr>
<td>Probability of recolonization ($\gamma$)</td>
<td>0.473</td>
<td>0.179</td>
<td>0.180</td>
<td>0.786</td>
</tr>
<tr>
<td>Detection probability ($p$): survey 1</td>
<td>0.852</td>
<td>0.040</td>
<td>0.755</td>
<td>0.914</td>
</tr>
<tr>
<td>Detection probability ($p$): survey 2</td>
<td>0.794</td>
<td>0.058</td>
<td>0.657</td>
<td>0.886</td>
</tr>
<tr>
<td>Detection probability ($p$): survey 3</td>
<td>0.563</td>
<td>0.099</td>
<td>0.370</td>
<td>0.738</td>
</tr>
</tbody>
</table>
Figure 1: Area of study and survey sites in Vermont located within a Bicknell's Thrush (BITH) predicted habitat model (Lambert et al. 2005).
Figure 2: Box plots for local habitat (a-f), landscape features (g-h), and local and landscape habitat scores (i) compared by sites where Bicknell’s Thrush were detected (1, \( N = 60 \)) and not detected (0, \( N = 28 \)) in 2006 and 2007. The upper (75\textsuperscript{th}) and lower (25\textsuperscript{th}) quartile limits are delineated by the upper and lower limits of the box, respectively. The line dissecting the box is the median. The smallest and largest non-outliers are represented by the lower and upper edges of the lines extending from the boxes (a.k.a. whiskers), respectively. Mild and extreme outliers are displayed using the symbols * and °, respectively.
Figure 3: (a) The number of sites and (b) box plots comparing landscape (standardized patch size/patch isolation) and local habitat (PC1) scores by sites that remained vacant (00), were colonized (01), went extinct (10), and stayed occupied (11) of the sites surveyed during the 2006 and 2007 Bicknell’s Thrush breeding seasons.
Figure 4: Relative variable importance determined by summing the AICc$\omega_i$ for the models in which each covariate was present for probability of initial occupancy ($\psi$), site colonization ($\gamma$), and local site extinction ($\varepsilon$).
Figure 5: Estimate of detection probability ($p$) by survey number as a function of patch size (ha) from the top ranked model: $\psi_{\text{LANDSCAPE+LOCAL}} \gamma_{\text{LOCAL}} \varepsilon_{\text{LANDSCAPE+LOCAL}}$. 

![Graph showing the relationship between detection probability ($p$) and patch size (ha) for Survey 1, Survey 2, and Survey 3. The graph includes a y-axis labeled $p$ ranging from 0 to 1 and an x-axis labeled Patch size (ha) ranging from 0 to 1200. Each survey is represented by a different line style: dotted for Survey 1, solid for Survey 2, and dashed for Survey 3.](image-url)
Figure 6: (a) Estimated probability of initial occupancy ($\psi$) as a function of landscape + local habitat from the top ranked model: $\psi_{\text{LANDSCAPE}+\text{LOCAL}} \gamma_{\text{LOCAL}} \varepsilon_{\text{LANDSCAPE}+\text{LOCAL}}$. (b) The isolated effect of local habitat on $\psi$, expressed as the PC1 score. (c) The isolated effect of landscape patch features on $\psi$ expressed as patch size/patch isolation. Gray lines represent plus and minus one standard error.
Figure 7: Estimated probability of colonization ($\gamma$) as a function of local habitat (PC1 score) from the top ranked model: $\psi_{\text{LANDSCAPE+LOCAL}} \gamma_{\text{LOCAL}} \epsilon_{\text{LANDSCAPE+LOCAL}}$. Gray lines represent plus and minus one standard error.
Figure 8: (a) Estimated probability of local extinction \( (\varepsilon) \) as a function of landscape + local habitat from the top ranked model: \( \psi_{\text{LANDSCAPE+LOCAL}} \). (b) The isolated effect of local habitat on \( \varepsilon \), expressed as a PC1 score. (c) The isolated effect of landscape on \( \varepsilon \), expressed as patch size/patch isolation (PS/PI). Note difference in scale of y-axis compared with (a) and (b). Gray lines represent plus and minus one standard error.
APPENDICES

Appendix 1: AIC model selection results from complete model set (67 models). Detection probability ($p$) was modeled as survey number + patch size for all models, except for the lowest ranked model ($\psi \gamma e p$) where $p$ was constant. $K$ is the number of parameters estimated in the model. $L$ is the log likelihood. Each model is ranked by its AICc score, which represents how well the model fits the data. A lower $\Delta$AICc value is indicative of a better model. The probability that the model (of the models tested) would best explain the data is indicated by the model weight (AICc$\omega_i$). Model likelihood is the ratio of each model’s AICc$\omega_i$ to the top model’s AICc$\omega_i$.

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Appendix 2: Beta ($\beta$) estimates and standard errors (SE) from the complete set of candidate models. Detection probability ($p$) was modeled at survey number + patch size for all of the models with exception of the least supported model ($\psi$, $\gamma$, $\epsilon$, $p$) in which $p$ was constant. The $\beta$s for detection probability are not included because the estimates and SE varied little among models. The probability that the model (of the models tested) would best explain the data is indicated by the model weight (AICc). For each of the three parameters presented ($\psi$, $\gamma$, and $\epsilon$) a maximum of four $\beta$s could be estimated for each model. $\beta_0$ is the intercept, $\beta_1$ is the landscape covariate effect, $\beta_2$ is the local habitat covariate effect, and $\beta_3$ is the effect of the interaction of landscape and local habitat. If a $\beta$ was not estimated for a model, no estimate and SE is specified for that $\beta$. A * indicates that the $\beta$(SE) for that parameter/model could not be properly estimated.

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<td>1.08 (0.37)</td>
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<td>0.17 (0.93)</td>
<td>2.2 (1.75)</td>
<td>-3.99 (2.07)</td>
<td>-3.35 (1.6)</td>
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## Appendix 2 continued.

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<th>AICc</th>
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<th>( \beta_1 ) est. (SE)</th>
<th>( \beta_2 ) est. (SE)</th>
<th>( \beta_3 ) est. (SE)</th>
<th>Prob. of initial site occupancy (( \psi ))</th>
<th>Prob. of site colonization (( \gamma ))</th>
<th>Prob. of local site extinction (( \epsilon ))</th>
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<td>-2.83 (1.05)</td>
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<td>$\psi$ LOCAL</td>
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### Appendix 2 continued.

<table>
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<th>Model</th>
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<td></td>
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<td>β₂ est. (SE)</td>
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**Note:** SE values are in parentheses.
COMPREHENSIVE BIBLIOGRAPHY


