

SCALE-DEPENDENT MECHANISMS OF HABITAT SELECTION AND
DEMOGRAPHY FOR A FOREST SONGBIRD IN A HETEROGENEOUS
LANDSCAPE

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ABSTRACT

The process of habitat selection involves discriminating among alternative habitats that differ in quality in terms of survival and reproduction. Thus, although habitat selection has important ecological and evolutionary consequences for individual organisms and species, the mechanisms that drive habitat selection decisions remain poorly understood. Further, human alteration of habitats that are critical for survival and reproduction currently poses a significant threat to wildlife populations worldwide and may interfere with habitat selection decisions. Understanding the factors that drive habitat selection and the demographic consequences of those decisions is important for understanding population dynamics and can provide critical information about species habitat requirements to conservation planners.

I studied the process of habitat selection and fitness consequences for a Nearctic-Neotropical migratory forest songbird, the black-throated blue warbler (*Dendroica caerulescens*) in a heterogeneous landscape in west-central Vermont. My research had three parts. First, I investigated the relative effects of habitat features at three spatial extents on four different demographic parameters including abundance, age ratio, pairing success, and annual fecundity. I used a model selection analysis framework to determine which habitat levels were most important for each demographic parameter. I found that the distribution of warblers across the landscape in Vermont matches patterns described for this species in intact landscapes, suggesting that warblers use specific proximate cues for territory selection. However, reproductive success was negatively affected by the degree of fragmentation. These results suggest that proximate habitat cues used for territory selection may be decoupled from realized fitness in this system.

Second, I conducted a conspecific playback experiment to evaluate whether conspecific attraction is important for determining abundance and occupancy patterns in high and low quality habitats by playing warbler vocalizations in previously unoccupied habitats in Vermont, USA. I used multi-season occupancy models in Program MARK to identify whether territory-level shrub density, landscape-level habitat patterns, or the attraction by conspecifics were most important for predicting territory occupancy and abundance. I found that habitat features were more important for determining both abundance and occupancy than conspecifics.

Finally, I assessed relationships between multiple demographic variables to determine whether warbler abundance can be used as a surrogate indicator of habitat quality. I found that warbler abundance is significantly positively related to both reproductive success and survival for this species in Vermont indicating that count data may be sufficient for long-term population monitoring for black-throated blue warblers.

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TABLE OF CONTENTS

	Page
Acknowledgements.....	ii
List of Tables	vii
List of Figures.....	ix
List of Appendices	xi
CHAPTER 1. INTRODUCTION.....	1
HABITAT SELECTION IN BIRDS.....	1
Ecological significance and definitions.....	1
Historical overview	2
Niche theory	3
Ultimate and proximate factors.....	4
THE LANDSCAPE ECOLOGY PARADIGM AND HIERARCHY THEORY	10
The landscape paradigm.....	10
Birds and landscapes	11
Hierarchy theory.....	15
Habitat selection as a complex hierarchical process	16
INFORMATION GAPS	16
STUDY APPROACHES.....	17
Model selection and inference.....	17
Mark-recapture analysis	19
STUDY SPECIES: A PARULINE WARBLER	22
Distribution and appearance.....	22
Population status	23
Habitat preferences for nesting and foraging	24
Breeding behaviors and demography	25
Population limitation and regulation.....	27
Response to forest management and fragmentation.....	28
DISSERTATION OBJECTIVES	29
LITERATURE CITED	31
CHAPTER 2. EFFECTS OF SPATIAL HABITAT HETEROGENEITY ON HABITAT SELECTION AND DEMOGRAPHY FOR A FOREST SONGBIRD... 45	
Abstract	45
INTRODUCTION	46
METHODS	50
Study species.....	50
Study Sites.....	51
Field Methods.....	52
Statistical Analysis: An information-theoretic approach	56

Statistical Analysis: Individual Demographic Variables	58
RESULTS	60
Habitat structure at three spatial extents	60
Demographic results.....	60
DISCUSSION	62
Territory-level shrub cover as a proximate cue of habitat selection	64
Ecological determinants of reproductive output	65
Conclusions	67
LITERATURE CITED.....	69
APPENDICES.....	89

**CHAPTER 3. SCALE-DEPENDENT MECHANISMS OF HABITAT
SELECTION FOR A MIGRATORY PASSERINE: AN EXPERIMENTAL
APPROACH..... 94**

Abstract	94
INTRODUCTION	95
METHODS	99
Study species	99
Study sites	100
Experimental design.....	101
The conspecific cue: song playbacks	102
Field Methods: abundance and occupancy surveys	102
Field methods: Quantifying habitat at each sampling point.....	103
Statistical Analyses	105
RESULTS.....	109
Abundance.....	109
Occupancy, extinction, and colonization	110
DISCUSSION.....	111
LITERATURE CITED	116
TABLES	120
APPENDICES	129

**CHAPTER 4. LANDSCAPE FRAGMENTATION DECOUPLES
ABUNDANCE AND BREEDING PERFORMANCE IN A MIGRATORY
SONGBIRD..... 135**

Abstract	135
INTRODUCTION	136
METHODS	138
Study species	138
Study Sites.....	139
Field Methods.....	140
Statistical analyses.....	143
RESULTS	146

Objective 1: abundance, daily nest survival, and annual fecundity	146
Objective 2: relationships among abundance, daily nest survival, and annual fecundity.....	147
Objective 3: mechanisms shaping reproductive success.....	148
DISCUSSION	150
LITERATURE CITED	155
COMPREHENSIVE BIBLIOGRAPHY	174

LIST OF TABLES

<p>Table 2.1. Principle component loadings for the four forest arrangement metrics. PC1 explained 91% of the total variation and PC 2 explained 96% of the total residual variation. Sites with high LANDSCAPE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e., they were more contiguous).....</p>	75
<p>Table 2.2. A priori model set. Univariate, additive, and interactive combinations of three habitat variables: TERRITORY_SHRUB, PATCH_SHRUB, and LANDSCAPE with number of estimable parameters (K).</p>	76
<p>Table 2.3. Models of black-throated blue warbler detection on counts in Vermont, USA, number of parameters (K), scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).</p>	77
<p>Table 2.4. Mean and standard deviation of territory- and patch-level habitat metrics and principle component scores for the landscape-level habitat metric.</p>	78
<p>Table 2.5. Models of mean annual abundance, male and female age ratios, pairing success, and annual fecundity of black-throated blue warblers in Vermont, USA, scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Statistics for best fit models are in bold.....</p>	80
<p>Table 3.1 Principle component loadings for the two shrub metrics and six landscape metrics. For shrubs, PC1 explained 56.8% and PC2 explained 100%. Sites with SHRUB PC1 score had high leaf densities in the understory and an overall high amount of shrub cover of species used by warblers. For landscape, PC1 explained 91% of the total variation and PC 2 explained 96% of the total variation. Sites with high LANDSCAPE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e. they were more contiguous).</p>	120
<p>Table 3.2. Models of abundance of black-throated blue warblers in Vermont, USA, scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).</p>	121
<p>Table 3.3. A 95% confidence set of models of site occupancy for black-throated blue warblers in Vermont, USA, number of model parameters (K), deviance, scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c). In all models, ψ was modeled as a function of SHRUB* LANDSCAPE and capture probability, p, was modeled as a</p>	

function of the additive effects of wind intensity, average daily temperature, date of survey, and time of day.	122
Table 3.4. Models of black-throated blue warbler detection on counts in Vermont, USA, number of parameters (K), scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).	124
Table 3.5. Summary of sampling points that went extinct or were colonized in each of the two experiment categories for each of the two time periods of the study.	125
Table 4.1. Principle component loadings for five landscape metrics describing forest composition and configuration. PC1 explained 91% of the total variation and PC 2 explained 4% of the total residual variation. PC1 was used as an explanatory variable in 1abundance, daily nest survival, and annual fecundity analyses. Sites with high LANDSCAPE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e., they were more contiguous).	159
Table 4.2. Models of mean annual abundance, daily nest survival, and annual fecundity of black-throated blue warblers in Vermont, USA, number of estimable parameters (K), scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Statistics for best fit models are in bold. A year effect was included in all models.	160
Table 4.3. Spearman correlation coefficients of relationships between model averaged abundance, model averaged daily nest success, and model averaged annual fecundity.	161
Table 4.4. Models of annual fecundity, intercept with standard error, beta coefficient with standard error, and ANOVA summary statistics.	162
Table 4.5. Logistic models of three mechanisms affecting annual fecundity (predation, parasitism, and double-brooding) as a function of landscape- and territory-level habitat features, model intercept with standard error, beta coefficient with standard error, Wald chi-square estimates, and significance value.	163

LIST OF FIGURES

Figure 1.1. A schematic of the hierarchical decision-making process involved in selection of non-breeding habitats by a migratory bird (Hutto 1985). 43

Figure 1.2. Breeding range of the black-throated blue warbler (Gough et al. 1998). 44

Figure 2.1. Overview of study design. Objective 1: use an information-theoretic analysis approach to evaluate and compare twelve models representing univariate, additive, and two-way interactive combinations of territory-, patch-, and landscape-level habitat patterns for four demographic parameters, including 1) abundance, 2) age ratios, 3) pairing success, and 4) annual fecundity. Objective 2: identify the most important spatial extent(s) affecting each parameter. 82

Figure 2.2. Twenty study sites in Chittenden and Addison Counties, Vermont, USA. Location of study region in Vermont is indicated on insert map. Black areas represent water; gray areas represent non-warbler habitat (urban, agriculture, coniferous forest); white areas represent mixed-deciduous and deciduous forested habitat. Stars indicate locations of study sites. 83

Figure 2.3. Schematic of a single study site. Shaded area represents a focal warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey stations at 250m and 500m from a random center survey station. TERRITORY_SHRUB metrics were estimated from vegetation samples collected at nest locations and the center sampling point within the focal territory. PATCH_SHRUB was estimated from vegetation samples collected at all sampling points outside the focal territory. 84

Figure 2.4. Cumulative Akaike weights ($\sum w_i$) of habitat covariates for each demographic parameter. 85

Figure 2.5. Surface plot of model averaged abundance as a function of TERRITORY_SHRUB and LANDSCAPE. 86

Figure 2.6. Surface plots of model averaged probability of SY (first-year breeder) male (A) and female (B) as a function of TERRITORY_SHRUB and LANDSCAPE. .. 87

Figure 2.7. Surface plot of model averaged annual fecundity as a function of TERRITORY_SHRUB and LANDSCAPE. 88

Figure 3.1. Schematic of a single research site (n = 10 sites). Shaded area represents a randomly selected warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey points at 250m and 500m from a random center survey station, speakers represent experimental treatment points (n = 2) where playback vocalizations were broadcast.

The seven remaining sampling points were classified as controls. SHRUB metrics were estimated at each of the nine sampling points.....	126
Figure 3.2 Surface plot of model averaged probability of sampling point occupancy (ψ) as a function of LANDSCAPE and SHRUB.....	127
Figure 3.3 Surface plot of model averaged probability of sampling point extinction (ε) as a function of LANDSCAPE and SHRUB.....	128
Figure 4.1. Twenty research sites in Chittenden and Addison Counties, Vermont, USA. Location of study region in Vermont is indicated on insert map. Black areas represent water; gray areas represent non-warbler habitat (urban, agriculture, coniferous forest); white areas represent mixed-deciduous and deciduous forested habitat. Stars indicate locations of research sites.....	164
Figure 4.2. Schematic of a single research site. Shaded area represents a focal warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey stations at 250m and 500m from a random center survey station.....	165
Figure 4.3. Surface plot of model average abundance as a function of territory- and landscape-level habitat patterns.....	166
Figure 4.4. Scatter plots of model averaged abundance, model averaged daily nest survival, and model averaged annual fecundity as a function of territory- and landscape-level habitat patterns.....	167

LIST OF APPENDICES

Appendix 2.1. Coefficients (β) of abundance and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.	89
Appendix 2.2. Coefficients (β) of male age ratio and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.	90
Appendix 2.3. Coefficients (β) of female age ratio and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.	91
Appendix 2.4 Coefficients (β) of pairing success and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.	92
Appendix 2.5. Coefficients (β) of annual fecundity and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.	93
Appendix 3.1. Coefficients (β) of black-throated blue warbler detection on counts in Vermont, USA, 2002-2004, and standard errors (in parentheses).	129
Appendix 3.2. Coefficients (β) of black-throated blue warbler abundance in Vermont, USA, 2002-2004, and lower and upper 95% confidence intervals (in parentheses). Year three of this study (2005) was the reference year for all models.	131
Appendix 3.3. Coefficients (β) of black-throated blue warbler occupancy (ψ), extinction (ϵ), and colonization (γ) for the five supported models, and standard errors (in parentheses).	133
Appendix 4.1. Coefficients (β) of abundance and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.	168
Appendix 4.2. Coefficients (β) of daily nest survival and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.	170
Appendix 4.2. Coefficients (β) of annual fecundity and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.	172

CHAPTER 1. INTRODUCTION

HABITAT SELECTION IN BIRDS

Ecological significance and definitions

The study of the relationships between organisms and their environment is a fundamental topic in ecology. Birds have been a major focus of habitat selection studies, and it has long been recognized that most species of birds are associated with particular vegetation types (Cody 1985). There is a large body of literature aimed at identifying and understanding bird-habitat associations and many of these associations are now largely common knowledge to both professional researchers and amateur birdwatchers.

The process of habitat selection is influenced by abiotic conditions, resource availability, competition, and predation, the same forces that structure most ecological systems. In turn, habitat selection has profound implications for population dynamics, community structure, and ecosystem function. Thus, understanding habitat selection processes plays an important role in understanding ecological systems. Further, understanding habitat selection decisions can help conservation biologists recognize the habitat requirements that are important for predicting species presence and population viability, and thus to identify the specific habitats that should be protected or managed for species conservation.

As a result of these conservation implications, habitat selection studies have recently assumed a new urgency (Caughley 1994). Application of study findings for conservation purposes hinges on consistent use of habitat terminology (Hall et al. 1997, Jones 2001). Here, I define *habitat* as the distinctive set of physical environmental

factors that a species uses for its survival and reproduction (Block and Brennan 1993).

Habitat selection is the hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Hutto 1985, Block and Brennan 1993).

Historical overview

The body of literature on avian habitat selection provides the basis of several important cornerstones in ecological theory. The observations written by Darwin on the voyage of the Beagle (1845) are some of the earliest records of species associations with particular types of vegetation. He noted that two species of geese in the Falkland islands were segregated in different areas, one in the upland and the other on the rocky shore (Cody 1985). In the 1900s Grinnell recorded more detailed observations of the differences in chaparral and desert edge habitats occupied by California thrashers (*Toxostoma redivivum*) and introduced the concept of the ecological niche. David Lack (1933) built on niche theory with his observations of habitat affinities of a number of bird species in the pine plantations of Breckland Heath in southern England. He speculated that competition and resource partitioning might explain the observed patterns and noted that where birds were more abundant than their preferred habitat could accommodate, some species would expand into other habitats (Lack 1933). Svärdsön (1949) introduced the idea that competition from other species also played a role in habitat selection. He observed that while intraspecific competition tended to broaden habitat use, interspecific interactions tended to limit use (Svärdsön 1949). In his study of old world wood warblers (*Phylloscopus sibilatrix*), Svärdsön (1949) showed that habitat choice by younger males,

arriving later in breeding areas than older males, was innate, but was perhaps reinforced by the singing of older males in the habitat.

Niche theory

Initially, Grinnell (1917) defined the ecological niche simply as the area in which a species existed and applied the concept to California thrashers (*Toxostoma redivivium*) by describing the specific habitat in which they occurred. Hutchinson (1957) built on this idea and formally defined the niche as an “n-dimensional hypervolume” of which each dimension defined the range and limits of a particular environmental condition. He defined the fundamental niche as the range of environmental conditions in which an organism could exist and the realized niche as the actual conditions in which the species was found. The realized niche thus is a subset of the fundamental niche. The idea that organisms do not necessarily fill their fundamental niches has led to the development of additional ecological concepts such as competitive exclusion and resource partitioning, as well as the niche-gestalt (James 1971), and provides a useful framework in which to discuss habitat selection.

James (1971) introduced the niche-gestalt as the collection of visual cues which a species receives from the structure and composition of vegetation. According to James, birds have a predetermined search image for a comprehensive set of vegetation patterns which defines their ecological niche. This theory has been widely accepted over the years as evidenced by the large number of multivariate studies that have attempted to define the variables of the niche-gestalt for many species (see Cody 1985). James (1971) further noted that it is not a requirement of the niche-gestalt that the configuration of vegetation be directly meaningful to a bird. Rather, the patterns perceived by the birds

may be signals of more complex ecological processes. These signals have been referred to throughout the literature as proximate factors that provide information about underlying ultimate factors (Hildén 1965).

Ultimate and proximate factors

The underlying premise of avian habitat selection is that birds have evolved to select habitat in a way maximizes their fitness by increasing their ability to survive and reproduce. Thus, the choices they make are the product of natural selection (Hildén 1965). According to Hildén (1965) the ultimate factors that influence avian reproduction and survival include food, structural and functional requirements, and shelter from weather and predation. Food availability and shelter from predation are fairly obvious factors that can profoundly influence survival of adults and nestlings, and reproduction (Holmes et al. 1992, Zanette et al. 2000, Nagy and Holmes 2005a). Shelter from weather conditions, in terms of rain, temperature, wind, and solar radiation are important for the thermal conditions of eggs and nestlings, and of incubating adults (Walsberg 1981). Structural and functional requirements are unique to each species and are usually the result of body structure and innate activities (Hildén 1965). For example, body mass and foraging behavior may limit the size, location and type of vegetation upon which birds prefer to perch (Cody 1985). Insect-catching shrikes (*Lanius collurio*) require open watch-posts from which a bird can take flight and catch prey. This foraging behavior is not possible without suitable perch sites and habitat that lacks these is not suitable for this species (Hildén 1965).

Each of these ultimate factors is related to a series of proximate factors with which birds have been found to be associated. Hildén (1965) combined these proximate

factors into the following categories of stimuli: 1) landscape, 2) terrain, 3) nest-, song-, and feeding sites, and 4) other animals. Hildén noted that all elements need not be present to elicit a settling response, but that a combined effect of different elements must exceed some threshold to trigger settling. Additionally, one key stimulus may outweigh the others, such that in its absence birds will not settle, and in its presence birds may settle even in suboptimal environments. There are many examples in the literature of how these proximate factors are related to each of the ultimate factors. I discuss some examples in the next section.

There are numerous factors that serve as cues to the possible effects of climate. It has been found that the density and arrangement of vegetation at a nest site are related to microclimate conditions (Calder 1973, Walsberg 1985, With and Webb 1993, Martin 1992, 2002). Leaf cover over nests can provide protection from rain and solar radiation, and leaf cover around nests can protect from wind. Hummingbirds have been found to nest directly under sheltering structures (Calder 1973) and warbling vireos (*Vireo gilvus*) have been found to select nest sites beneath canopy configurations that reduced solar radiation in the warmest times of the day (Walsberg 1985).

The structure and composition of vegetation may also provide information about whether a habitat can support the physiological and morphological requirements of a species. For example, ovenbirds and waterthrushes (*Seiurus* spp.) are ground foragers and exhibit thrush-like beak morphology. These species are likely to occur only in forests with a relatively open floor where they can forage easily (Cody 1985). Similarly, black-and-white warblers (*Mniotilta varia*) forage on tree trunks and exhibit morphological characteristics of both legs and bills that allow them to walk vertically on

large trees and pick insects from the bark. Thus, they are not likely to be found in habitats that lack tall woody vegetation (Osterhaus 1962).

The availability of food resources may also be signaled by the density and arrangement of vegetation. Although some species respond directly to their food supply (i.e., bay-breasted warblers (*Dendroica castanea*) congregate at spruce budworm (*Choristoneura fumiferana*) outbreak areas in spruce forests), most birds appear to rely on the composition and structure of the vegetation as an indirect (proximate) cue of food supply (Cody 1985). Steele (1992b) found a positive relationship between understory shrub cover and caterpillar abundance, a main food source for black-throated blue warblers (*Dendroica caerulescens*) in New Hampshire.

The structure of vegetation may serve as a proximate signal of another ultimate factor, predation pressure. Specifically, the density of vegetation is a proximate cue known to be related to predation rates. Martin (1992) reported that dense vegetation around nests of many open-cup nesting birds may reduce predation risks. Dense vegetation may hide both nest sites and parental activities around the nest, particularly during the nestling stage. Further, dense vegetation may impede the movement of some mammalian predators (Bowman and Harris 1980, Holway 1991) or contain more potential nest sites for a predator to search (Martin and Roper 1988).

Similarly, vegetation structure may serve as a signal of the severity of avian brood parasitism of an area. In a study of Indigo buntings (*Passerina cyanea*), Burhans (1997) found that at the microhabitat scale, more concealed nests were less likely to be parasitized. Although brood parasitism was not mentioned by Hildén, it may also an important ultimate factor influencing reproduction and survival in some bird species in

some areas (Gates and Gysel 1978, Brittingham and Temple 1983, Robinson et al. 1995). Gates and Gysel (1978) found that open-nesting passerines nested in high abundance in field-forest edges experienced, and that in these areas, birds experienced reduced fledging success. More recently, Burhans et al. (2000) found that parasitized nests of Field sparrows (*Spizella pusilla*) and Indigo buntings exhibited reduced clutch sizes, reduced hatching success, and reduced nestling survival rates.

As shown in this review, there is a plethora of studies that have linked proximate vegetation cues with ultimate factors. There is another body of literature that focuses on the influence of competition on habitat selection. As mentioned previously, Hildén (1965) included the presence of other animals as a proximate cue that relates to the availability of a particular resource (e.g., food, territories, nest sites, mating opportunities, predation or parasitism pressures). Research in this area focuses on potential interspecific competition (McArthur 1958, Rosenzweig 1981) and intraspecific competition (Fretwell and Lucas 1970). In terms of interspecific competition, birds may perceive some habitats as suitable in terms of structure and level of productivity, but the presence of other species therewith similar ecological preferences might reduce the availability of resources, decrease habitat quality, and render habitat unacceptable to prospecting individuals (Cody 1985). McArthur's work (McArthur 1958) on resource partitioning in warblers is an example of how warbler species had their distributional limits determined by interspecific competition. More recently, in a removal experiment with orange-crowned warblers (*Vermivora celata*) and virginia's warblers (*Vermivora virginiae*) in Arizona, Martin and Martin (2001) showed interspecific competition limited access to nest sites for the subordinate virginia's warbler.

Competition between individuals of the same species may also serve as a proximate cue for ultimate factors. One large body of theory holds that, because conspecifics are competitors, individual fitness should decline monotonically as a function of conspecific density (Fretwell and Lucas 1970, Fretwell 1972, Rosenzweig 1985, 1991, Sutherland 1996). Such models suggest that the presence of previous settlers in a habitat serve as a negative proximate cue (*sensu* Hildén 1965) and should discourage newcomers from settling. This pattern was observed in great tits (*Parus major*) by Kluijver and Tinbergen (1953).

Others have suggested conspecifics may serve as positive proximate cues to habitat quality during the process of habitat selection, where settlers may benefit by choosing territories near other conspecifics (reviewed in Stamps 1988, Muller et al. 1997). Conspecifics may serve as cues to habitat quality and territory holders living in aggregations are more effective at territory defense, protection from predators, and attracting potential mates (Stamps 1988, 1994, Wagner 1993, Boulinier and Danchin 1997, Muller et al. 1997). Further, aggregation may be beneficial in territorial species if previously settled neighbors can provide valuable information about the habitat. In many species, territory quality is determined by resource abundance and distribution but assessing resource quality requires time and energy (Stamps 1987, Stamps 1988). These explanations both imply that naïve individuals should be more strongly attracted to conspecifics than would individuals already familiar with the habitat (Stamps 1988, Boulinier and Danchin 1997, Muller et al. 1997).

Despite interest in conspecific cueing by conservation biologists there are a relatively small number of empirical studies that have examined the effects of conspecific

attraction in habitat selection, particularly for territorial species (Smith and Peacock 1990, Ray et al. 1991, Reed and Dobson 1993, Lima and Zollner 1996, Muller et al. 1997). Experimental studies on the role of conspecific attraction are even rarer. To my knowledge, only two studies have experimentally examined the role of conspecific cueing for territorial migratory bird species. Ward and Schlossberg (2004) used song playbacks to experimentally establish new breeding populations of endangered Black-capped vireos (*Vireo atricapilla*) in previously unoccupied sites. Noccera et al. (2006) experimentally compared use of inadvertent social information between two habitats that varied in quality during pre- and post-breeding periods, for the Bobolink (*Dolichonyx oryzivorus*) and Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*). They found that sparrows did not respond to playback treatments, but bobolinks responded strongly to post-breeding location cues, irrespective of habitat quality.

There is strong evidence suggesting that birds use patterns of vegetation for habitat selection. Further, these proximate vegetation cues appear to relate to the ultimate factors that determine fitness. There is also some evidence that conspecific attraction may also play a role in the selection process, but this concept continues to be debated. The idea that habitat selection is driven largely by patterns of vegetation may be limited by the relatively small spatial scales at which bird-habitat relationships have traditionally been studied (e.g. McArthur and McArthur 1961, Walsberg 1985, Cody 1985, Holway 1991, Steele 1992b, Martin 1992). In more recent decades, development of the field of landscape ecology and the simultaneous application of hierarchy theory to the ecological systems, have had profound influences on the way ecologists perceive the operation of

ecological processes. These approaches have led to important insights into the processes associated with habitat selection.

THE LANDSCAPE ECOLOGY PARADIGM AND HIERARCHY THEORY

The landscape paradigm

Traditionally, ecologists assumed that the most important ecological processes affecting populations and communities operated at local spatial scales. More recently, scientists have begun to realize that ecological processes operate over a wide range of both spatial and temporal scales (O'Neill et al. 1986, Wiens et al. 1986, Wiens 1989). Further, it has become clear that habitat variation exists at a variety of spatial scales and ecologists have become increasingly aware of the importance of studying ecological process at spatial and temporal scales relevant to both the organisms and the processes under study (Wiens 1989, Allen and Hoekstra 1992, Forman 1995, Saab 1999). Recently, Turner (2005) called for investigations that evaluated the interactions among spatial scales to advance our understanding ecological systems. The field of landscape ecology developed as a means of considering the effects of spatial and temporal scales in ecological systems.

A landscape has been defined as a spatial extent (King et al. 1997), a spatially heterogeneous area (Turner 1989), and a heterogeneous mosaic of habitat patches in which individuals live and disperse (Dunning et al. 1992). The types and amounts of different habitats present in the landscape are referred to as landscape composition, while the spatial positions of the different habitats in relation to each other define the landscape configuration. Landscape ecology is the study of how the composition and configuration

of habitats affects ecological patterns and processes (Forman and Godron 1986, Urban et al. 1987, Turner 1989).

Birds and landscapes

Landscape ecology provides an essential framework for understanding habitat selection in birds. Knowledge of the structural features of local habitat may not be sufficient to understand bird distribution, abundance, and population dynamics. Because birds are highly mobile, they have the ability to assess habitat patterns at multiple spatial scales before choosing where to forage, breed, or winter (Hildén 1965). Birds may be able to recognize patterns of vegetation at spatial scales on the order of square kilometers and at small spatial scales, birds may recognize leaf and branch structures (Hildén 1965). Thus, birds have been found to be associated with the structure of vegetation at relatively small scales (e.g. McArthur and McArthur 1961, James 1971, Wiens and Rotenberry 1981) as well as landscape patterns (Freemark et al. 1995). Avian community structure (Ambuel and Temple 1983, Lichstein et al. 2002, Betts et al. *in press*), population dynamics (Pearson 1993), and habitat associations of individual species (Coker and Capen 1995, Driscoll et al. 2005) have all been found to be related to landscape patterns. Like the features of vegetation at smaller spatial scales, landscape patterns may also serve as proximate cues to which birds respond when selecting habitats. Thus, the proximate cues of landscape pattern should represent ultimate factors such as predation risks, brood parasitism risks, food availability, shelter from adverse conditions, and avoidance of competition.

The total amount or area of habitat (coverage) is viewed among ecologists as potentially the most important determinant of demographic parameters for populations

inhabiting patchy landscapes (Donovan et al. 1995a, Robinson et al. 1995, Tewksbury et al. 1998, Flather and Bevers 2002). In general, the diversity and density of birds declines as the total amount of habitat in a landscape declines (Freemark and Merriam 1986, Andren 1994, McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999, Fahrig 2001). For example, Lichstein et al. (2002) found that relative abundance of several late-successional forest songbird species, including the black-throated blue warbler, were positively correlated with the amount of older forest in the landscape. Reproductive success may also decline with the amount of habitat in the landscape. Robinson et al. (1995) found that forest cover within a 10-km radius of sites was negatively related to nest success rates for nine songbird species in the mid-western United States. Nest predation and brood parasitism by the brown-headed cowbird (*Molothrus ater*), the two most important factors causing reduced reproductive success in heterogeneous landscapes, have been found to be higher in small forest patches than in large forest patches (Brittingham and Temple 1983, Wilcove 1985, Paton 1994, Donovan et al. 1995b, Robinson et al. 1995, Hartley and Hunter 1998, Cavitt and Martin 2002, Mattsson and Niemi 2006). Birds may use the amount of a particular type of habitat in the landscape as a cue for the amount of a resource such as nest and perch sites, food, or as cues to predation and parasitism risks. Further, patch size may also be related to the overall amount of heterogeneity within a patch, where larger patches tend to have more heterogeneity.

The arrangement [configuration] of habitat patches in a landscape (i.e. isolation and edge density) may also be important proximate cue for habitat selection. The degree of isolation of habitat patches has been found to be an important predictor of species

occurrence and population abundance (Belisle et al. 2001, Harris and Reed 2001).

Further, isolation may result in lower pairing success if individuals are unable to disperse (Cooper and Walters 2002). Thus, birds may use patch isolation as a proximate cue of mate availability.

In addition to isolation effects, the quality of forest habitat is often degraded in forest fragments compared to intact habitats of the same size, primarily due to edge effects. Forest habitats near ecotonal edges experience different microclimatic conditions, changes in resource availability, and alteration of interspecific interactions such as competition, predation, and parasitism. The magnitude of these edge effects may vary as a function of distance to an ecotonal edge, as well as among species, habitats, and regions (Paton 1994, Andren 1994, Faaborg et al. 1995, Donovan et al. 1997, Dijak and Thompson 2000, Sisk and Battin 2002, Peak et al. 2004). Many studies show increased nest predation and nest parasitism rates with increasing proximity to edges, particularly in open-cup nesting birds (Gates and Gysel 1978, Andren and Angelstam 1988, Yahner 1988, Chalfoun et al. 2002; but see Paton 1994). These increased rates are accompanied by changes in predator species assemblages and the overall density of predators (Bayne and Hobson 1997). There is also evidence that food availability declines in edge habitats (Zanette et al. 2000; but see Hughes 2003). Thus, for many bird species, it is likely that forest edge may serve as a proximate cue for the ultimate factors of shelter from weather and predation and parasitism risk, food availability, and potential nest sites.

Many landscape patterns are correlated. An important area of current research is focused on disentangling the effects of landscape composition and landscape configuration on population abundance and persistence in patchy environments (Fahrig

1997, McGargal and Cushman 2002, Flather and Bevers 2002, Turner 2005). There is mounting evidence that the effects of habitat amount and arrangement are confounded in many studies, making conclusions tenuous. For example, Donovan et al. (1997) found that edge effects depended on the composition of the surrounding landscape, where edge effects had a greater effect on nest predation patterns in fragmented landscapes than in contiguously forested landscapes. Further, there is some evidence to support that there may be a primary effect of composition and a secondary effect of configuration (Trzcinski et al. 1999, McGargal and Cushman 2002, Flather and Bevers 2002). Fahrig (1997, 1998) found that the effects of habitat amount far outweigh effects associated with habitat arrangement, and that habitat placement can rarely mitigate extinction risks induced by habitat loss. In a modeling study, Flather and Bevers (2002) demonstrated that, over a broad range of habitat amounts and arrangements, population size was largely determined by the abundance of habitat. However, habitat configuration became important in landscapes with low habitat abundance, when species persistence became uncertain due to dispersal mortality. Such findings have important implications for conservation because they suggest that species abundance and persistence will depend not only on the amount of habitat loss, but that habitat configuration may act synergistically to exacerbate declines when habitat loss exceeds a critical amount.

It is clear that both small scale and large scale habitat patterns are important components of the habitat selection process for most bird species. As landscape ecology develops as a discipline, it has become increasingly apparent that ecological systems are driven by features at multiple spatial scales. It is in this sense that hierarchy theory has

offered an important framework for simplifying, organizing, and understanding the process of habitat selection.

Hierarchy theory

Hierarchy theory provides a useful theoretical framework for understanding complex ecological systems that operate across multiple scales (e.g., landscapes; Allen and Starr 1982, O'Neill et al. 1986). It considers issues of scale, levels of organization, levels of observation, and levels of interpretation (O'Neill 1989). A hierarchical system is a system of systems of systems.

According to hierarchy theory, system components are organized into levels of functional scale, where each level can itself be a system of systems (O'Neill 1989). Hierarchies are typically discussed according to a triadic structure of these functional levels (Bissonette 1997, King 1997). First, a focal level of observation interest is chosen (L). The next higher level in a hierarchy (L+1) is thought to contain and control, or constrain, components or processes of the focal level. Lower level components (L-1) are thought to be the mechanistic explanations of the focal level. The levels in this triad are typically organized according to temporal scale; that is each component has a natural rate, or frequency, of occurrence. Higher level components operate at slower rates over longer time periods. Low level components can operate at high frequencies, and often interactions occur between low level components. In addition to temporal scales, a hierarchy can be organized according to spatial scales where high levels literally occur over a larger area than smaller levels. In essence, hierarchy theory is useful for simplifying complex system interactions to help researchers understand the processes that affect a focal level of interest. One of the inherent requirements of using such a triadic

approach is that the exploration of processes at larger spatial scales must take place. Thus, the application of hierarchy theory in ecology was bolstered by the parallel progression of the field of landscape ecology. Both landscape ecology and hierarchy theory direct us to study complex systems at multiple scales simultaneously.

Habitat selection as a complex hierarchical process

Birds may select territories at multiple spatial scales in a hierarchical fashion, first by selecting patterns at large spatial scales and then continuing to make decisions at progressively smaller spatial scales until a territory and eventually a nest site is selected (Johnson 1980). The concept of hierarchical habitat selection implies that constraints are established by the decisions made at larger spatial scales (Figure 1.1; Hutto 1985). For example, if a bird chooses a riparian area in which to nest, it is then unable to select a rocky outcropping on a ridge-top. This theory of hierarchical decision making incorporates James's theory of the niche-gestalt where there may be a series of patterns perceived by a bird that results in a niche-gestalt at each spatial scale or birds make one or more decisions at a particular scale, accepting alternative patterns depending on the combination of factors present (Johnson 1980). Both of these imply that all the proximate cues combine in some additive or interactive way to produce one search image.

INFORMATION GAPS

This hierarchical decision process has been suggested in the literature for quite some time (Svärsden 1949, Hildén 1965, Johnson 1980, Hutto 1985) and has led to a number of bird studies that have addressed distribution and abundance patterns at multiple spatial scales simultaneously (e.g. Saab 1999, Sodhi et al. 1999, Lichstein et al.

2002). The majority of these studies have shown that habitat associations do exist at multiple spatial scales. Although interest in multi-scale habitat selection studies continues to grow, there remains a dearth of information on the relative importance of proximate mechanisms at each spatial scale, the interactions among habitat scales, and the roles they play in 1) restricting selection decisions at smaller spatial scales and 2) contributing to demographic consequences that affect the dynamics of populations.

This scarcity of information is likely the result of several factors, including 1) the inability of traditional frequentist statistical approaches to simultaneously evaluate the relative importance of potential proximate factors and interactions among them (Burnham and Anderson 2002), 2) logistical difficulties in obtaining adequate demographic data from marked individuals over time and at regional scales, especially for vertebrates with high dispersal capabilities, like birds, and 3) difficulties in conducting population-level experiments to evaluate the relative effects of proximate mechanisms identified in descriptive studies.

STUDY APPROACHES

Model selection and inference

A model selection and multi-model inference-based analysis approach allows for examination of proximate mechanisms of habitat selection across multiple scales and is useful for identifying interactions among scales and variation in multiple demographic parameters over time. This approach requires careful *a priori* thought leading to alternative hypotheses concerning a process or system of interest (Burnham and Anderson 2002). These hypotheses are then represented by statistical models, one for each hypothesis, that form the ‘model set’. To determine which hypothesis is best

supported by the empirical data, Kullback-Leiber information (the information lost when a model is used to approximate reality) is estimated. One quantity commonly used to estimate the K-L information is Akaike's Information Criterion, AIC (Akaike 1973). This quantity represents a relationship between K-L information and maximum likelihood:

$$\text{AIC} = -2\log_e(L\theta | \text{data}) + 2K$$

where $\log_e(L\theta | \text{data})$ is the value of the maximized log-likelihood over the unknown parameters (θ), given the data and the model and K is the number of estimable parameters in the approximating model. When K is large relative to sample size n , there is a small-sample (second-order) version called AIC_c ,

$$\text{AIC}_c = -2\log_e(L\theta | \text{data}) + 2K + ((2K(K + 1))/(n - K - 1)).$$

AIC is computed for each of the approximating models in the set. The model for which AIC is minimal is selected as best for the empirical data at hand. For ease of interpretation, the AIC values are rescaled as simple differences:

$$\Delta_i = \text{AIC}_i - \min\text{AIC}.$$

Thus, the model with the minimum information criterion has a Δ_i value of zero. These Δ_i values allow an easy ranking of the hypotheses (models). In general, models having a $\Delta_i < 2$ have substantial support, models having Δ_i within 3-7 units of the best model have less support, and models having $\Delta_i > 10$ have little support. To evaluate the strength of evidence for alternative models, it is first necessary to obtain the likelihood of each model, given the data, using the simple transformation, $\exp(-\Delta_i/2)$. These quantities are then normalized such that they sum to one, as

$$w_i = (\exp(-\Delta_i/2))/(\sum \exp(-\Delta_i/2)).$$

The w_i , called Akaike weights, are useful as the ‘weight of evidence’ in favor of model i as being the actual K-L best model in the set. They are interpreted as probabilities.

These methods are simple to understand and practical to employ across a wide range of empirical situations (Burnham and Anderson 2002). Further, they are quite effective at making strong inferences from the analysis of empirical data.

Mark-recapture analysis

The call for long-term demographic data from marked individuals has evolved in parallel to the acceptance of model selection analysis approaches. As human populations expand and habitat destruction and alteration continues to impact wildlife populations, there is increased emphasis towards monitoring wildlife populations. Mark-recapture studies play an important role in this process and are used to assess population status and trends, particularly for species that cannot be surveyed through direct counts (i.e., species that are not often seen but can be caught and released). Because birds are mobile, it is difficult to directly census the population by counting individuals. Thus, population size is typically estimated through mark-recapture sampling techniques where individual birds are captured and marked with color-coded leg bands. Marked animals are then released and move freely about the population. Follow-up recapture sessions involve capturing a random sample of individuals from the population where some individuals will be marked and some will not. This approach is based on the assumption that the proportion of marked individuals in the second sample should approximate the proportion of marked individuals in the entire population. Thus, with information on the number of marked (R) and unmarked individuals captured in the second sampling session (C = total captured in second sampling session) and the number of individuals marked in the first sampling

session (M), it is possible to estimate the original population size (N) using mathematical models (i.e. the Lincoln-Peterson model):

$$N/M \approx C/R$$

Changes in population size over time can be directly linked to the population's birth, death, immigration, and emigration rates. Changes in a combination of any, or all of these factors can cause population increases or decreases. Thus, population viability analyses require estimates of these vital population rates, which can be derived from the study of uniquely marked animals. For example, survival is a key parameter in the demographic equation for all organisms. Survival probabilities can be estimated by tracking the fates of marked individuals over time using mathematical operations in life table analyses and survivorship curves where survival and reproductive events for individuals in the population are separated by age, size, or developmental stage.

Because the analyses described above can be cumbersome for data collected on many individuals over long time periods, there has been a considerable amount of recent work on computer software development to perform such population analyses, particularly in terms of estimation of abundance, and both survival and recruitment rates. For example, White and Burnham (1999) developed Program MARK as a means for estimating survival and population size from marked animals using both live and dead re-encounters. This program can be used for estimating key demographic parameters including apparent survival, recruitment, population size, and territory occupancy from marked animals when they are re-encountered at a later time. More than one attribute group of animals can be modeled (e.g., treatment and control animals), and covariates specific to the group or individual can be considered.

The basic input for this program is the encounter history for each animal.

Encounter histories are comprised of 0's and 1's where a 1 represents an encounter with a marked individual, and a 0 indicates that a particular marked individual was not seen on a particular occasion. A zero could indicate either that an individual had died, or that it was in fact alive, but simply not encountered. For example, in a 3 occasion study, a 101 encounter history would be interpreted as the individual was captured and marked on the first occasion, alive and not encountered on the second occasion, and alive and encountered on the third occasion. Each encounter history could occur due to a specific sequence of events, each of which has a corresponding probability. Using the 101 encounter history described above, a probability expression is formalized. Let ϕ_i be the probability of surviving from time (i) to time ($i + 1$) (the time between encounters), and let p_i be the probability of encounter at time (i). Thus, $(1 - p_i)$ is the probability of not encountering the individual at time (i). The probability expression then for the 101 encounter history is

$$\phi_1(1 - p_2) \phi_1 p_i.$$

Program MARK (White and Burnham 1999) computes the estimates the various probabilities (parameters) in each expression using maximum likelihood estimation. For example, it derives estimates of ϕ_i and p_i which maximize the likelihood of observing the frequency of individuals with each encounter history. Outputs for the various models that the user has built (fit) are presented in a model selection analysis format and include the AIC value, delta AIC, AIC weight, model likelihood, the number of estimated parameters, and the model deviance. Additional outputs include parameter estimates,

standard errors, deviance residuals from the model, likelihood ratios, and goodness-of-fit tests.

The model selection analysis approach and new analysis tools for mark-recapture studies, combined with field experiments that help to tease apart the importance of proximate mechanisms of habitat selection, will help advance our understanding of this key ecological process and will help provide important information for wildlife managers and conservation planners. I employed all three of these approaches in a study of habitat selection in a paruline warbler.

STUDY SPECIES: A PARULINE WARBLER

Distribution and appearance

The Black-throated blue warbler (*Dendrioca caerulescens*) is a Nearctic-Neotropical migratory songbird. In summer months, these wood warblers are one of the most common breeding songbirds in the extensive hardwood and mixed-coniferous forests of southeastern Canada and the northeastern United States (Figure 1.2; Gough et al. 1998). This species breeds as far south as Georgia along the Appalachian Mountain range. They leave their northern breeding grounds in late summer, migrating mainly along the eastern seaboard and through the Appalachian Mountains, and arrive on their winter quarters in the Caribbean by mid-October. Most individuals over-winter in the Greater Antilles: Cuba, Jamaica, Hispaniola, and Puerto Rico. In April, warblers leave wintering grounds and migrate north again to breed, arriving back on their breeding grounds by mid-May.

Black-throated blue warblers are small with adults weighing about 9-10 grams. This species is highly sexually dichromatic. Males have a dark blue back, black face and throat, whitish underparts, and a large white wing patch. Females are grayish-green in color with a small white wing patch and a distinct white stripe over the eye. They differ so much that the two sexes were considered separate species by ornithologists in the early 1800's (Holmes et al. 2005). Their plumage varies with age and these characteristics can be used to distinguish between first year and older birds (Pyle et al. 1987, Graves 1997). Males in their first year tend to have greenish tinge on their dorsal tract feathers, and their alula covert is edged with light green. In young females, the white wing patch is small, or lacking, while that of older females is larger. Age ratios vary among habitats (Holmes et al. 1996b), perhaps reflecting differences in habitat quality.

Population status

This species prefers interior forest habitats in breeding regions. Because of this, it has probably suffered a population decline over the last 300 years as the result of extensive deforestation during settlement of North America by Europeans (Holmes et al. 2005). In more recent decades, as fields have returned to forests, populations have appeared to increase. Although many populations of migratory songbird species are currently experiencing declines, most black-throated blue warbler populations seem to be relatively stable (Sauer et al. 2003, Homes et al. 2005, Sillett and Holmes 2005), although it is identified as a species of conservation priority by both Partners in Flight and the by the state of Vermont.

The long-term stability of black-throated blue warbler populations makes this an ideal species for studying the processes that determine its distribution and abundance.

Because of this, it is one of the most intensively studied passerine species in North America and one of few species for which population demographics have been studied in both breeding and wintering areas (Holmes et al. 1992, 1996b, Holmes and Sherry 1992, Nagy and Holmes 2004, 2005a, 2005b, Rodenhouse and Holmes 1992, Rodenhouse et al. 2003, Sillett et al. 2000, 2004, Sillett and Holmes 2002, 2005, Wunderle 1992, 1995). The vast majority of studies on breeding season demography have occurred in large contiguous tracts of forest land, the most prominent being the long-term research conducted by Richard T. Holmes and colleagues at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. From these studies, we have detailed information about warbler resource requirements and population demographics in intact forests.

Habitat preferences for nesting and foraging

This species typically occurs in large continuous tracts of relatively undisturbed deciduous or mixed deciduous-coniferous forests in mountainous regions. It is most abundant at elevations of 400-700 m in New Hampshire and above 300 m in New York (Holmes et al. 2005). New England forests typically occupied are usually dominated by maples (*Acer* spp.), birches (*Betula* spp.), and beech (*Fagus grandifolia*) with eastern hemlock (*Tsuga canadensis*), spruce (*Picea* spp.) and fir (*Abies* spp.). Suitable breeding forests usually contain a dense understory layer of deciduous or broad-leaved evergreen shrubs (Holmes et al. 2005). The plant species comprising this layer vary geographically; in New Hampshire and Vermont, they are mostly hobblebush (*Viburnum alnifolium*), sugar maple (*Acer saccharum*), American Beech, striped maple (*Acer pensylvanicum*), red spruce (*Picea rubeus*), and balsam fir (*Aibes balsamea*; Steele 1992, 1993, Holmes et

al. 2005). Selection of habitats with a dense shrub layer seems most closely related to nesting requirements (Holway 1991, Steele 1992). Breeding density varies directly and positively with the thickness of the shrub layer (Steele 1992).

Black-throated blue warblers are insectivorous; during the breeding season they feed mainly on Lepidoptera larvae and adults, crane flies (Tipulidae: Diptera) and other arthropods (Robinson and Holmes 1982, Rodenhouse and Holmes 1992). They forage mainly in the lower to mid-strata of the forest (Holmes 1986), primarily by obtaining arthropod prey from the underside of leaves (Holmes and Shultz 1988). Thus, black-throated blue warblers may use understory foliage density as a proximate indicator of prey availability.

Breeding behaviors and demography

Males defend and advertise territories on the breeding grounds, responding strongly to the presence of conspecifics, and playbacks of conspecific song. Territories range in size from about 1 to 4 ha, depending on habitat; territories are smallest where shrub layer is most dense (Steele 1992). This territorial behavior makes it fairly easy to capture adult males; males are lured into mist-nets by broadcasting playbacks of conspecific song.

Most breeding males are monogamous with typically one female nesting in each territory. Polygyny does occur, but at a low frequency. Most pairs remain together during the length of the breeding season which can include multiple re-nesting attempts and multiple brooding (Holmes et al. 1992).

Females apparently choose nest site locations (Holmes et al. 2005). Males sometimes accompany female while she is searching and sometimes appears to 'show'

females potential nest sites by perching and settling in potential locations. Nest sites are typically located in the dense understory shrub layer, in conifer saplings, deciduous shrubs, ferns, raspberry thickets (Bent 1953), blue cohosh (*Caulophyllum thalictroides*; Bent 1953), and in clusters of dead leaves.

Clutch size varies from 2 to 5 eggs, but is typically 4 (Holmes et al. 1992).

Females have attempted up to 5 clutches in a season, with a median of two (Holmes et al. 1992). In New Hampshire, females laid an average of 6.6 eggs per season and fledged an average of 4.3 young per female per season (Holmes et al. 1992). At this same site, from 1996-2001, 53% of females that successfully fledged their first nests attempted second broods (Nagy and Holmes 2005b).

Predation is the leading cause of nest failure for black-throated blue warblers, but rates vary among years, sites, and habitats (Holmes et al. 1992). A suite of avian and mammalian predators that prey on adults, eggs and nestlings have been identified. Raptors typically prey on adults; blue-jays (*Cyanocitta cristata*), red squirrels (*Tamiasciurus hudsonicus*), eastern chipmunks (*Tamias striatus*), and martens (*Martes americana*) have been observed taking eggs and nestlings in New Hampshire (Rodenhouse 1986, Reitsma et al. 1990). At Hubbard Brook, the mean proportion of nests lost to predation between 1986 and 1999 ranged annually from 0.08 – 0.42, averaging about 25% (Sillett and Holmes 2005). Nest predation did not vary with conspecific density (Sillett et al. 2004), but was higher in areas of low shrub density compared to high shrub density (Holmes et al. 1996). Thus in New Hampshire, territories with high shrubs are likely to produce more offspring than territories with low shrubs.

The only known brood parasite of black-throated blue warblers is the brown-headed cowbird (*Molothrus ater*). The frequency of parasitism in this species is relatively unknown, but this species may be less subject to cowbird parasitism compared with some other Neotropical migrants because of its preference for nesting in large tracts of undisturbed forest. This dissertation is among the first studies to document the influence of Brown-headed cowbird parasitism on nesting black-throated blue warblers. Cowbirds typically lay their eggs in warbler nests during the normal laying period of its host, beginning after the first host egg appears in the nest (K. Cornell, this study). Cowbirds can lay up to four eggs in a warbler nest, although usually only 1 or 2 eggs are laid. Black-throated blue warbler females have been observed incubating cowbird eggs and feeding cowbird nestlings and fledglings (K. Cornell, this study).

Adults typically return to the same general area year after year (Holmes et al. 1992). In New Hampshire, the median distance between territory centers for individually marked males that returned to the study plot was 94 m (Holmes and Sherry 1992). In a study on marked individuals in New Hampshire from 1986-2000 (n = 336 individuals), annual survival measured on returns to the breeding grounds each spring was 51% for males and 40% for females (Silllett and Holmes 2002).

Population limitation and regulation

The long-term demographic data from Hubbard Brook indicate ways in which black-throated blue warbler populations are limited and regulated. Food, predation, and local population density appear to be the major factors affecting reproductive success (reviewed in Holmes et al. 2005). Specifically, density-independent nest predation and density-dependent fecundity, as well as climatically affected food abundance appear to be

the most critical factors driving annual fecundity for this species. The density-dependent factors appear to operate via a crowding mechanism where territories are more packed and intraspecific competition is intense (Sillett et al. 2004) and a site-dependence mechanism (Rodenhouse et al. 1997, 2003b, McPeck et al. 2001) where despotic individuals force subordinate individuals into low quality habitats (Fretwell and Lucas 1970). These two mechanisms appear to operate simultaneously, but at different spatial scales (Rodenhouse et al. 2003). In a modeling study, Sillett and Holmes (2005) showed that negative feedback on fecundity is sufficient to regulate populations. Further, annual fecundity appears to be positively related to the number of yearlings recruited into the population in subsequent years (Holmes and Sherry 1992, Sillett et al. 2000). Thus, factors affecting breeding success (e.g., habitat fragmentation) may have significant influences on population abundances.

Response to forest management and fragmentation

Black-throated blue warblers are area-sensitive, occurring mainly in forest patches >100 ha (Robbins et al. 1989). This species typically does not occur in young clear-cuts or second growth until the forest canopy develops and canopy gaps allow the shrub layer to develop (Holmes 1990). Buford and Capen (Buford and Capen 1999) found this species to be equally common in both managed and unmanaged northern hardwood forests. Age ratios can vary among habitats (Holmes et al. 1996b), perhaps reflecting differences in habitat quality. A study conducted in managed forests in Maine found that older birds occurred in forest interiors and had higher productivity than individuals breeding near edges, but pairing success and food density was highest along edges, and that males occupying territories in interiors and along edges had similar probabilities of

producing fledglings (Harris and Reed 2002). From these studies, it appears that distributions may be limited by habitat characteristics. However, most demographic studies of this species have been conducted in large tracts of relatively undisturbed forests. The potential effects of habitat change, especially human-induced fragmentation and degradation, on abundance, spatial distribution, and population dynamics remains unclear (Holmes et al. 2005).

DISSERTATION OBJECTIVES

The three studies that follow (Chapters 2, 3, and 4) emerge from a main research objective which was to understand how the degree of landscape fragmentation affects the temporal and spatial pattern of demographic traits of migratory bird populations. I chose to concentrate on demographics of black-throated blue warbler populations as a representative species, in west-central Vermont. Each chapter of this dissertation is intended to stand alone, yet each is based on the related topics and approaches outlined above.

The focus of chapter two was to investigate the relative importance of habitat features at territory-, patch-, and landscape-level spatial extents in affecting habitat selection decisions and the reproductive consequences of those decisions. I quantified four different demographic parameters during 2002-2004 and applied a model selection analysis approach to determine which levels of habitat affected abundance, age ratios, pairing success, and annual fecundity. This study represents one of the most comprehensive studies to date in the fields of avian ecology and landscape ecology. I

considered habitat factors at multiple spatial extents, simultaneously, including interactions between levels, and it considered multiple demographic parameters.

The goal of chapter three was to use an experimental approach to investigate the role of habitat features and the role of behavioral cues in the habitat selection process. Specifically, I manipulated conspecific density on sites that varied in territory-level shrub density and landscape-level patterns to determine which cues were most important for shaping settlement patterns and whether habitat cues interacted with social cues to increase occupancy and abundance. I applied model selection analysis techniques to examine territory occupancy rates, colonization rates, and extinction rates and warbler abundance. There are few studies that have used experimental approaches at the landscape scale to address the role of conspecific attraction in habitat selection. This study will contribute to the science of migrant bird ecology and the management and conservation of territorial migrant songbirds. Further, it will contribute towards understanding the importance of proximate habitat cues at different spatial extents and the role of conspecifics in territory selection.

While chapters two and three were mainly aimed at advancing theoretical knowledge of the habitat selection process, the results of chapter four directly apply to conservation. The objective of this chapter was to investigate relationships among demographic parameters to determine whether measures of abundance can be used as an indicator of habitat quality. Results of this chapter may be useful for conservation planners and managers interested in managing habitats for species conservation.

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FIGURES

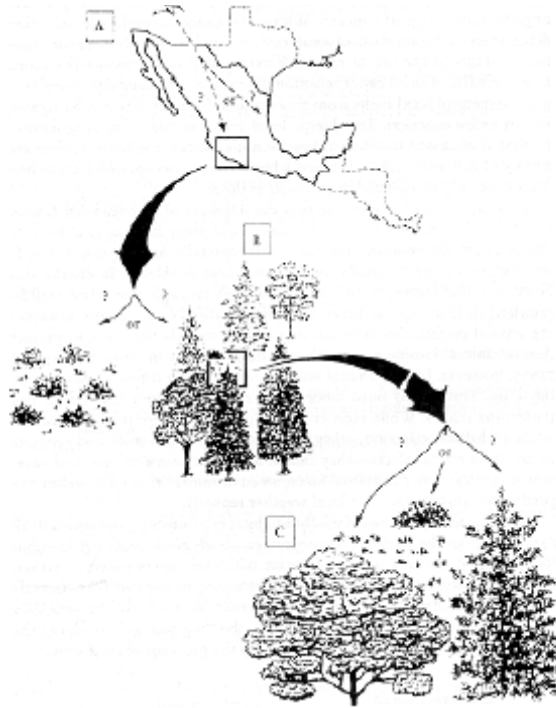


Figure 1.1. A schematic of the hierarchical decision-making process involved in selection of non-breeding habitats by a migratory bird (Hutto 1985).

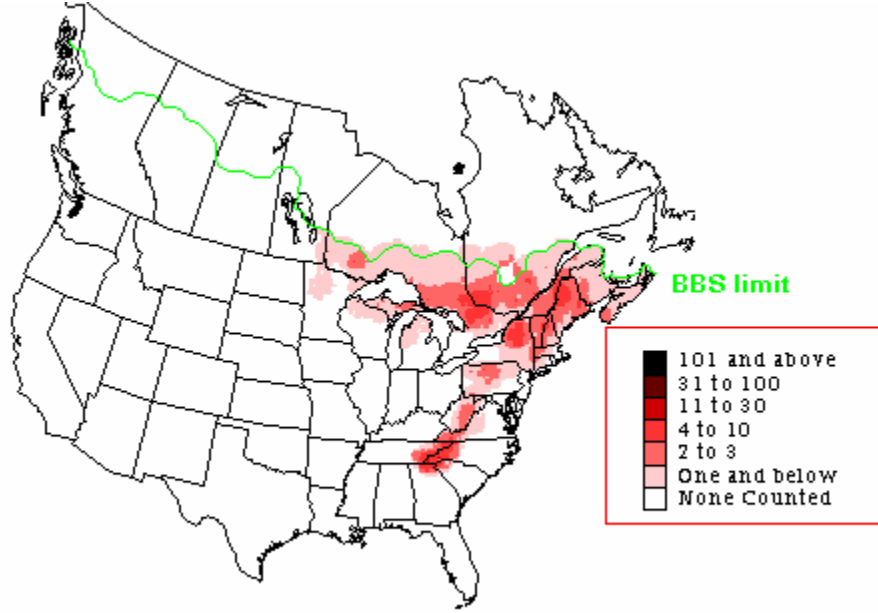


Figure 1.2. Breeding range of the black-throated blue warbler (Gough et al. 1998).

CHAPTER 2. EFFECTS OF SPATIAL HABITAT HETEROGENEITY ON HABITAT SELECTION AND DEMOGRAPHY FOR A FOREST SONGBIRD

Abstract. We used an information-theoretic approach to investigate how habitat patterns across three spatial extents influenced habitat selection decisions and demographic patterns for black-throated blue warblers (*Dendroica caerulescens*) at 20 study sites in west-central Vermont, USA from 2002-2005. These sites represented gradients of habitat patterns at different spatial extents, including: 1) territory-level understory shrub density, 2) patch-level understory shrub density occurring within 25 ha of territories, and 3) landscape-level habitat patterns occurring within 5 km radius extents of territories. We considered multiple vital population parameters including abundance, age ratios, pairing success, and annual fecundity. We found that territory-level shrub cover was most important for determining which individuals occupied which habitats but that landscape-level habitat structure strongly influenced reproductive output. Consistent with long-term studies of this species in New Hampshire, sites with higher territory-level shrub density had higher abundance, were more likely to be occupied by older, more experienced individuals, and males that were paired compared to sites with lower shrub density. However, annual fecundity was higher on sites located in contiguously forested landscape where shrub cover was low. In addition, we found evidence that the effect of habitat pattern at one spatial level depended on habitat conditions at different levels. The interaction between territory-level and landscape-level habitat structure influenced both abundance and annual fecundity. Abundance was highest at sites located in more fragmented landscapes with the highest shrub densities, but females occupying these

same sites fledged fewer offspring per year. Our results suggest that the proximate cue of territory-level shrub density used for breeding territory selection by this species may be decoupled from realized fitness, where individuals are unable to recognize and occupy habitats best suited for reproduction. We considered ecological factors associated with this disconnect including predation, parasitism, and food limitation, and suggest that cowbird parasitism is a leading factor contributing to disconnect between selection cues and fitness in this system.

INTRODUCTION

A central goal in ecology has been to understand how the spatial patterns of habitats influence the abundance and dynamics of wildlife populations (Turner 1989). This topic is even more pressing given that land use change is a current and primary driving force in the loss of biological diversity worldwide (Vitousek et al. 1997). Songbirds have long served as model organisms in studies investigating habitat associations and the consequences of changing environments (Darwin 1897, Grinnell 1917, Lack 1933, Svärnsden 1949, Hildén 1965, Ambuel and Temple 1983, Cody 1985, Villard et al. 1995). As the result of these studies, we now know that birds, in general, respond to habitat patterns at multiple spatial scales (Hildén 1965, Orians and Wittenberger 1991). These spatial extents include 1) territory-level habitat patterns measured within a 5 ha area, 2) patch-level habitat patterns measured within 25 ha area surrounding a breeding territory, and 3) landscape-level habitat patterns measured within a 5 km radius extent surrounding a breeding territory.

Numerous studies have examined how habitat factors at these scales independently affect the distribution of birds (i.e., pattern; Thompson et al. 2002). At the territory-level, the density and arrangement of vegetation within a home range may influence the availability and selection of nest sites (Calder 1973, Walsberg 1981, Rodriques 1994). At the patch-level, vegetation composition and structure (e.g., the abundance of shrubs or trees) have been shown to influence territory occupancy and density (Cody 1968, James 1971, Wiens and Rotenberry 1981, Cody 1985). At the landscape-level, the amount and arrangements of habitats in a landscape are correlated with the distribution of many bird species (e.g., Dunning et al. 1992, Hansen and Urban 1992, Faaborg et al. 1995, Freemark et al. 1995). In general, population density declines as the total amount of habitat cover in a landscape declines. Additionally, pairing success tends to be lower on small isolated patches (Villard et al. 1993, Bayne and Hobson 2001), and first-year breeders tend to dominate such populations (Richards 1999, Bayne and Hobson 2001). In some cases, the arrangement of habitats within a landscape is an important predictor of occurrence, particularly when the amount of habitat cover is low (Andren 1994, McGarigal and McComb 1995, Hinsley et al. 1996, Fahrig 1998, Trzcinski et al. 1999b, Villard et al. 1999).

Although the effects of habitat structure on distribution patterns of songbirds are well established, far fewer studies have examined how habitat factors at different spatial extents influence vital demographic parameters, such as annual fecundity, and the mechanisms shaping them. Many studies to date typically investigate these parameters in isolation. Shrub cover within a territory may also be positively correlated with food abundance, thus influencing annual fecundity (Rodenhouse et al. 2003a). Moreover, nest

concealment can influence the likelihood of parasitism and depredation (e.g., Flaspohler et al. 2000, Budnik 2002), two mechanisms which directly affect annual fecundity. Patch-level studies also show that nest predation and parasitism levels are influenced by the vegetation structure of a localized area (reviewed in Thompson et al. 2002). For instance, shrub density influences how nest predators move through a localized environment, potentially affecting predation rates within a habitat patch (Bowman and Harris 1980). Finally, landscape-level investigations in eastern North America have shown that nest survival decreases and brood parasitism levels by the brown-headed cowbird (*Molothrus ater*) increase as landscapes become more fragmented (e.g. Donovan et al. 1995, Robinson et al. 1995b, Hochachka 1999). Additionally, food resources for nesting songbirds can be lower in fragmented habitats (Burke and Nol 1998, Zarette et al. 2000).

From the studies mentioned above, it is likely that territory-, patch-, and landscape-level habitat structure are all important factors that shape demographic rates. Yet, a firm understanding of the processes responsible for fluctuating occurrence and abundance of forest bird populations across a heterogeneous landscape cannot be synthesized from these piecemeal studies. This inability is likely the result of several factors. First, comparing pattern and process across studies is difficult; different studies use different methodological approaches and evaluate different spatial extents. Second, local songbird populations are influenced by factors occurring at extents much larger than the patch-level, where populations are structured as sources and sinks (Pulliam 1988, Brawn and Robinson 1996) or metapopulations (Hanski and Simberloff 1997). Studies conducted within single habitat patches do not allow for evaluation of the effects of

ecological processes occurring at larger extents. Third, interactions among habitat features at different spatial extents may be associated with measures of population dynamics, where the effects of habitat features at one spatial extent depend on habitat conditions at other extents. Studies that examine these interactions are lacking (Turner 2005), mainly due to logistical difficulties in acquiring demographic data across multiple extents simultaneously.

To address these shortcomings, we conducted a field study to evaluate how habitat patterns at territory, patch, and landscape levels affects populations of migratory forest songbirds (Figure 2.1). We evaluated four vital population parameters (abundance, age ratios, pairing success, annual fecundity) for a forest-nesting songbird, the black-throated blue warbler (*Dendroica caerulescens*), at twenty study sites in west-central Vermont, USA. By considering territory, patch, and landscape extents simultaneously, we were able to evaluate which habitat scale most strongly influenced each demographic parameter, and to determine if habitat patterns at one level are dependent on habitat conditions at other levels.

Our objectives in this study were to: 1) Use an information-theoretic analysis approach to evaluate and compare twelve models representing univariate, additive, and interactive combinations of territory-, patch-, and landscape-level habitat patterns for four population parameters, including (1) abundance, (2) age ratios, (3) pairing success, (4) annual fecundity, and 2) Identify the most important spatial extent(s) affecting each demographic parameter, and determine how habitat conditions at one level may affect demography differently depending on habitat conditions at another level (Figure 2.1).

METHODS

Study species

The black-throated blue warbler is an insectivorous Nearctic-Neotropical migratory songbird. Males and females arrive in North America in early May to establish breeding territories, and the breeding season lasts 3-4 months (Holmes et al. 2005). Black-throated blue warblers are common to forest patches across many different landscape types throughout Vermont, but appear to be patchily distributed (K. Cornell, unpublished data). This species is typically socially monogamous during the breeding season. Black-throated blue warblers are sexually dichromatic and highly territorial; males sing to defend exclusive territories typically ranging in size from 1-4 ha during the breeding season (Holmes et al. 2005). Thus, males are easily counted in a variety of field conditions based on vocalizations, can be captured in mist-nets, and banded for individual identification. Females build nests in understory shrubs, and can therefore be flushed from nests after 6 days of incubation, captured, and banded. Mean and modal clutch size is 4 (Holmes et al. 2005), and pairs can successfully raise two broods of young in a single breeding season. Both parents feed nestlings and fledglings. Easy access to nests also allows for accurate assessment of annual fecundity, defined as the total number of offspring fledged per adult female per year.

Perhaps more is known about black-throated blue warbler demography than any other North American migratory passerine; it has been studied continuously since 1969 at the Hubbard Brook Experimental Forest (Holmes 1994, Holmes et al. 1996, Sillett and Holmes 2002, Holmes et al. 2005), a large unfragmented forested habitat in the White Mountains of New Hampshire, USA. From this long-term research program, a great deal

about how territory-level habitat elements affect demographic parameters is known. The most suitable and thus most productive territories have a high shrub density, low nest predation rates, and high food abundance (Steele 1992, Rodenhouse et al. 2003). Furthermore, annual fecundity is negatively correlated with population density (Sillett and Holmes 2005), such that average annual fecundity in New Hampshire declines as population size increases due to despotic interactions which force some birds into suboptimal habitats (Rodenhouse et al. 1997). Recruitment of first-year breeders into the population each spring is positively correlated with fecundity in the previous year (Sillett and Holmes 2002). However, little is known about how landscape-level habitat patterns affect demographic parameters, and how landscape-level habitat patterns interact with territory- and patch-level habitat patterns in heterogeneous landscapes to affect demographic rates in this species.

Study Sites

We conducted field research from May to August 2002-2005 at 20 forested sites in Chittenden and Addison counties, Vermont, USA (Figure 2.2). Suitable habitat was abundant throughout the region due to an ice storm that opened gaps in the forest canopy allowed understory growth. We selected study sites by examining digital orthophoto quadrangles to locate accessible forest patches and by conducting site visits to determine potentially suitable breeding habitat. Study sites were then chosen based on the presence of at least one black-throated blue warbler territory (i.e., one singing male) as of 1 June 2002 to ensure that the site was suitable for warbler use. At each study site, we randomly selected a single breeding pair that actively defended a territory and mapped territory boundaries based on male singing perches using a Global Positioning System (GPS). We

referred to each of these as a “focal territory” of intense study. Study sites were at least 1 km apart in order to increase statistical independence between focal territories, predator communities, and landscape extents.

Study sites were selected to span a wide gradient of forest fragmentation level (i.e., highly heterogeneous landscape composition versus homogeneously forested areas). Sites within contiguously forested landscapes were located in the northern half of Green Mountain National Forest, a relatively homogenous forest with a canopy dominated by northern hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), and an understory dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and beech saplings. Study sites in more fragmented landscapes were located in the Champlain Valley, a heterogeneous area characterized by small forest patches situated in a matrix dominated by agriculture. These lower elevation forests differed from contiguous forests in the region in that they exhibited a higher diversity of canopy tree species than the contiguous forests, and the understory was dominated by witch hazel (*Hammamelis virginiana*), *Rubus* spp., blue cohosh (*Caulophyllum thalictroides*), and elm (*Ulmus* spp.), rather than hobblebush.

Field Methods

Warbler abundance surveys.—Two 10-minute, single-observer point counts were conducted in succession at a randomly selected survey point located near the center of each mapped focal territory in all 20 study sites from 25 May to 15 July in 2002-2005. Surveys were conducted on mornings with low wind and no rain, between 0600h and 1100h. All surveys were conducted by experienced observers who recorded the number

of all black-throated blue warblers heard or seen (unlimited distance), the time at which each warbler was first detected, the distance category of detected individuals ($1 \leq 25\text{m}$, $2 \leq 50\text{m}$, $3 \leq 75\text{ m}$, $4 \leq 100\text{m}$, $5 \leq 137\text{ m}$, $6 \geq 137\text{ m}$), the sex, and when possible, the age of adults (Graves 1997).

Demographic characteristics. — On each focal territory in 2002, we first determined whether each male was paired. We used mist nets to capture adults; males were lured to nets with conspecific playback and females were flushed from nests after day 6 of incubation. We marked each adult with a unique combination of a single numbered aluminum leg band and three colored plastic bands, and determined age according to plumage characteristics as either SY (second-year; first-year breeder) or ASY (after-second-year; Pyle et al. 1987). We used a Global Positioning System (GPS) to map territory space boundaries and used these mapped locations to ensure we monitored the same focal territory space at each site across years. Overall, the band-resight data enabled us to evaluate age ratios for each sex, pairing status, and annual fecundity.

Within each year from 2002-2004, we located and documented fates of all nest attempts for each focal female across the entire breeding season (May-August). Most nests were found during the building or incubation stage and checked every two to four days until fledging or failure. At each visit, we recorded date, time of visit, nesting stage (building, laying, incubation, nestling), description of contents, parental activity, and incidence of parasitism and/or predation.

Quantifying habitat structure at three spatial scales.— For each of the 20 focal territories, we measured habitat characteristics within the territory itself, within a habitat

patch surrounding each territory, and within a 5-km radius landscape surrounding each territory. These habitat characteristics were used as explanatory variables this study: 1) TERRITORY_SHRUB, 2) PATCH_SHRUB, and 3) LANDSCAPE. We describe how each of these metrics was estimated below.

TERRITORY_SHRUB was a territory-level metric that describes the general understory shrub cover within a focal territory. We measured understory leaf density at all nests attempted by the focal pair, and in which eggs were laid, after fledging or failure, following procedures described by Sillett et al. (2004). Four, 11.2-m transects were delineated in the understory in cardinal directions within plots centered on each nest site. At the distal end of each transect, a vertical 9-m² plane was erected using two 3-m vertical poles set 3-m apart. We counted all leaves of all understory species that intersected this plane. To avoid bias resulting from measuring only locations near nest sites, we also measured understory leaf density at a single random sampling point within each mapped focal territory using the same methods. TERRITORY_SHRUB was computed for each of the 20 focal territories as the average of leaf counts across all four planes for each nest site and random sampling point (Figure 2.3).

PATCH_SHRUB was a patch-level metric that described understory shrub cover within a 25 ha area surrounding each focal territory. Eight sampling points were established at 250 m and 500 m in cardinal directions and centered at a sampling point within the focal territory (Figure 2.3). At each study site in 2002, understory leaf density was measured at each of the 8 sampling stations. Leaf counts were conducted using the same methods as described for TERRITORY_SHRUB. PATCH_SHRUB was computed

as the average total leaf counts across all four planes for each of the eight sampling points.

LANDSCAPE was a landscape-level metric that described the composition and configuration of forested areas within 5 km of each focal territory. We characterized landscape pattern surrounding each study site using USGS/EPA MRLC land cover maps derived from a version of the 1992 National Land Cover Dataset (30 m pixel size; Vogelmann et al. 2001) and updated to include extent of developed land in Vermont as of 2002 (Spatial Analysis Lab, University of Vermont). Black-throated blue warblers breed mainly in deciduous or mixed/coniferous forests (Holmes et al. 2005). Thus, we used ArcGIS 9.1 (Esri, Inc) to reduce the original 18 land-use classes to eight classes based on perceived biological relevance and ease of interpretation. The classes included (1) water, (2) barren, (3) developed land, (4), wetland, (5) deciduous and mixed-coniferous forest, (6) coniferous forest, (7) agriculture (row crop, hayfield, pasture), and (8) orchard and other agriculture.

We used the quantitative spatial analysis program FRAGSTATS (McGarigal and Marks 1995) to obtain specific measures of landscape composition and configuration within a 5 km radius area surrounding the center of each study site (Donovan et al. 2000). This scale was selected because it reflects the home range size of brown-headed cowbirds (Thompson 1994), a potentially important determinant of reproductive success in our system. In FRAGSTATS, we applied an 8-neighbor rule for delineating patches. We used the percent of landscape in the deciduous/mixed coniferous forest landuse category as a single landscape composition metric. Landscape configuration metrics included percent core deciduous/mixed coniferous forest area (defined as >120 m from edge),

mean forest patch area, mean shape index, and edge density. Landscape composition and configuration metrics were consistently collinear (Pearson's correlations, $p < 0.05$; SAS 8.2, SAS 1999). To manage this problem, we used a correlation-based Principle Components Analysis (PROC PRINCOMP; SAS 8.2, SAS 1999) to condense the five landscape composition and configuration metrics into a single measure that explained 91.0% of the total variation among research sites (Table 2.1). We termed this component LANDSCAPE. Sites with high LANDSCAPE PCA scores had high percent forest cover, high core forest area, large mean patch area, and a higher mean shape index, while sites with low PCA score were more heterogeneous with more isolated forest patches and more edge.

Statistical Analysis: An information-theoretic approach

Model set. – We used an information theoretic approach (Burnham and Anderson 2002) to determine which habitat level(s) most strongly influence the following demographic parameters: 1) abundance, 2) age, 3) pairing success, 4) annual fecundity. For each of these four dependent variables, we evaluated support for the same 12 alternative *a priori* models that reflected our habitat hypotheses (Table 2.2). For clarity, we next describe the model set, and then describe the analytical method used to assess the model set for each of the four dependent variables separately.

The model set included a territory-level model containing TERRITORY_SHRUB as the explanatory variable, patch-level model with PATCH_SHRUB as the explanatory variable, and a landscape-level model with LANDSCAPE as the explanatory variable (models 1-3, Table 2.2). The model set also considered two-way additive, three-way additive, and two-way interactive combinations of these variables (models 4-10, Table

2.2). To keep the number of candidate models manageable, we did not consider models that included more than 2-way interactions. Finally, a global model with all effects and a null model that did not include habitat variables were evaluated (models 11 and 12, Table 2.2).

This model set allowed us to determine how each of the four demographic variables (abundance, age ratios, pairing success, and annual fecundity) were explained by habitat factors at three spatial extents, and allowed us to directly assess whether the effect of habitat at one spatial extent depended on habitat features at other spatial extents (Turner 2005). In addition, evaluating the same model set across different demographic parameters allowed us to compare model rankings and weights and to identify which habitat features were consistently related to black-throated blue warbler demographics. We conducted four separate evaluations of the model set for each of the four dependent variables in either SAS (SAS 8.2, SAS 1999) or in Program MARK (White and Burnham 1999). For all evaluations, we used Akaike's Information Criteria with a small sample size correction (AIC_c) to rank candidate models from best to least supported and calculated the weighted evidence for each model (ω_i ; Burnham and Anderson 2002). We report parameter estimates and standard errors for all models.

Relative importance of habitat variables. – Because each of the three explanatory habitat variables occurred in the same number of models, we were able to assess the relative importance of each variable by summing the Akaike weights (ω_i) across all models in which the variable appeared (Burnham and Anderson 2002). The sum of the Akaike weights can be thought of as a *relative importance value* for a particular explanatory variable. One possible caveat of interpreting the true importance of an

explanatory variable in an observational study like ours is that variable importance may not be apparent unless the variable is observed at both low and high values. Therefore, in addition to relative importance values, we also report descriptive statistics for each habitat variable.

Statistical Analysis: Individual Demographic Variables

Abundance.—To assess how habitat features at different spatial extents influenced abundance, we first corrected the raw (unadjusted) point count data by detection probability (Thompson 2002). To estimate detection probability (p , the probability that a blue warbler would be detected in a 10-minute point count, given it is present), we used the Huggins closed-capture removal models (Huggins 1989, 1991) within Program MARK (White and Burnham 1999) to analyze point count data. We divided each 10 minute count into five, 2-minute intervals, and created capture histories for each bird on each survey. We assessed whether year, date, and time of survey, wind conditions, average daily temperature, understory shrub cover measured at the level of a study site, and two landscape-level metrics at the 5 km radius scale (percent deciduous/mixed-coniferous forest cover and total edge) affected p . We used an information theoretic model selection approach (Burnham and Anderson 2002) to evaluate support for 13 alternative *a priori* models (Table 2.3). We then used the Akaike weights and beta estimates associated with each model to obtain a model-averaged p for each survey conducted in the study (Burnham and Anderson 2002). The raw count data for each survey were then divided by the model-averaged p to obtain a corrected abundance estimate for each survey conducted in the study. We modeled corrected warbler abundance as a linear function of habitat variables (Table 2.2) using PROC GENMOD

(SAS 8.2, SAS 1999). For each of the 12 models, we specified the Poisson distribution and designated study site as a repeated factor. We assessed fit of the Poisson distribution by evaluating the ratio of deviance divided by degrees of freedom for the most saturated model (model 11). We corrected for underdispersion using the DSCALE option in the model statement.

Age. – All focal territory holders were classified as second-year (SY) and after-second-year (ASY) at the time of banding, where SY birds were first-time breeders and ASY birds were experienced breeders. To determine which habitat variables were most important for determining age ratios, we modeled warbler age as a linear function of habitat variables (Table 2.2) with PROC GENMOD (SAS 8.2, SAS 1999) for males and females separately. For each of the 12 models, we specified the binomial distribution and designated the variable study site as a repeated factor. We assessed goodness-of-fit and examined model residuals and influential data points for the most saturated model (Model 11, Table 2.2).

Pairing success.—In black-throated blue warblers, sex ratios at the level of the territory can either be 1:1, indicating the territorial male was paired with one or more females in a given year, or 1:0, indicating the territory was occupied by an unmated male. For this species, polygyny occurs with low frequency (0% to 15%; Holmes et al. 2005) and was not documented in this study. We modeled pairing success categories as a linear function of habitat variables (Table 2.2) with PROC GENMOD (SAS 8.2, SAS 1999) following the same specifications described for age ratios. We assessed goodness-of-fit and examined model residuals and influential data points for the most saturated model (Model 11, Table 2.2).

Annual fecundity.—Annual fecundity was calculated as the total number of warbler young fledged over all nest attempts in a given year per adult female. All nestlings present in the nest on day 6 of the nestling stage were assumed to have fledged. We modeled annual fecundity as a linear function of habitat variables (Table 2.2) using PROC GENMOD (SAS 8.2, SAS 1999). For each of the 12 models, we specified the Poisson distribution and designated study site as a repeated factor. We tested for overdispersion of the data using the DSCALE option in PROC GENMOD (SAS 8.2, SAS 1999) for our most parameterized model.

RESULTS

Habitat structure at three spatial extents.

Vegetation structure was variable among study sites (Table 2.4). At a landscape-extent, sites ranged from 13 – 81% deciduous/mixed deciduous forest cover within 5 km of the focal territory. Both PATCH_SHRUB and TERRITORY_SHRUB were correlated with LANDSCAPE (Pearson correlation coefficient $r = -0.32$ and -0.57 respectively; $p < 0.01$ for both). In general, study sites located in more fragmented landscapes had higher understory shrub cover at both the territory and patch levels, due in part to the aforementioned ice storm.

Demographic results

Abundance.—We conducted a total of 160 point count surveys. Our ability to detect warblers on point counts, given presence, was high, ranging from 93% to 100%. Average warbler abundance ranged from 0 to 3.03 singing males per site per year, where 0's indicate territory vacancy.

Multiple models were supported in the data (having $\Delta\text{AICc} < 2$; Table 2.5), but overall territory- and landscape-level habitat variables were most important for affecting abundance patterns (Figure 2.4). A model containing a two-way interaction between these two extents carried the most weight (0.20; Table 2.5). Model-averaged results show that sites with high territory-level shrub density and sites located within intact landscapes had high abundance (Figure 2.5). However, the highest abundances occurred in fragmented sites with high territory-level understory shrub density (Figure 2.5).

Age. — To determine whether age structure was related to habitat features (Table 2.2), we analyzed the probability that an individual (male or female) on a focal territory was second-year (SY) or after-second-year (ASY). We analyzed age ratios for a total of 61 males and 59 females. The global model (model 11) fit the observed values for males ($\chi^2 = 12.69$, $df = 7$, $P > 0.08$) and for females ($\chi^2 = 3.31$, $df = 7$, $P > 0.86$).

For males, territory- and landscape-level habitat patterns were most important for determining age ratios (Table 2.5, models 5 and 7, Figure 2.4). Patch-level understory shrub cover was relatively less important (Table 2.4, Appendix 2.2). In general, territories with low shrub cover were more likely to support SY males, especially in fragmented landscapes. Territories exhibiting average to high shrub cover for the sample always supported ASY males, regardless of landscape pattern (Figure 2.6).

Territory-level understory shrub cover affected female age ratios more than either patch- or landscape-level variables (Table 2.5; Figure 2.4). Overall, SY females occupied territories with lower than average shrub cover (Figure 2.6), regardless of the landscape.

Pairing success.— Over the duration of this study, only three research sites (focal territories) (1 in 2003 and 2 in 2004) were not occupied by either a male or female

warbler. These were not included in the analysis. We analyzed 61 males for pair status. Of those, 59 males exhibited a 1:1 pairing status and only 2 males at 2 different sites in 2003 exhibited a 1:0 pairing status. The global model fit (model 11) fit the observed values ($\chi^2 = 1.35$, $df = 7$, $P > 0.99$).

The probability that a male was paired with a female was most affected by territory-level understory shrub cover (Table 2.5, model 1; Figure 2.4), although there is some uncertainty in the model set. In general, males occupying territories with high density of understory shrubs were more likely to be paired with a female (Appendix 2.4).

Annual fecundity.— We monitored 65 uniquely banded female warblers for fecundity analyses across the 20 study sites from 2002-2004. Annual fecundity ranged from zero to eight warbler young fledged across all sites and all years. Over all study sites, annual fecundity averaged 2.5 warblers in 2002, 2.6 warblers in 2003, and 4.2 warblers in 2004. On average, over all years and study sites, 51% of monitored nests were successful, 32% failed due to predation, and 16% failed due to brood parasitism.

The landscape-level habitat pattern was most important for affecting annual fecundity (Figure 2.4) and the model containing a two-way interaction between territory and landscape extents carried the most weight (0.20; Table 2.5). In general, individuals that occupied sites located in landscapes that were above average for intactness in the sample fledged more offspring per year. Annual fecundity was lowest in the most fragmented sites but where territory-level shrub cover was above average (Figure 2.7).

DISCUSSION

Advancement of the field of landscape ecology calls for studies that consider interactions of patterns and processes across spatial extents because they provide a more comprehensive look at ecological dynamics in heterogeneous landscapes (Turner 2005). In this study, we found evidence that 1) patterns of habitat at different spatial extents affect different aspects of a species' demography, 2) habitat patterns at one spatial extent can be influenced by habitat patterns at different extents in shaping demographic patterns, and 3) proximate cues used in territory selection may be decoupled from realized fitness.

We found that territory-level shrub density was a major influence affecting which individuals occupied which habitats and that landscape-level habitat patterns were a primary influence on reproductive output. Black-throated blue warbler abundance was higher at sites with higher than average shrub density. Shrubby sites were also occupied by older (≥ 2 years old), more experienced breeders, and by males that were paired with females compared with forested sites with a more open shrub layer. Although shrubs strongly influenced distribution, landscape pattern most strongly influenced annual fecundity. Females occupying more intact forested sites fledged more young per season than those occupying fragments.

We also found evidence that the way in which habitat patterns at one spatial extent affect demography depend on habitat patterns at different extents (Turner 2005). Interactions among territory-level and landscape-level habitat structure influence both black-throated blue warbler abundance and annual fecundity, but in contrasting ways. Both abundance and fecundity increased as territory-level shrub density and landscape-level forest intactness increased. Although abundance was highest on highly fragmented

sites with the densest shrub layer, females occupying these sites fledged the fewest offspring.

Territory-level shrub cover as a proximate cue of habitat selection

Our results suggest that individuals use territory-level shrub density as a proximate cue for territory selection, but the realized fitness levels appear to be decoupled from the information associated with the selection cues (Schlaepfer et al. 2002). Individuals select territories with the highest shrub density, but the interaction of the landscape-level habitat structure appears to have a negative effect on reproductive success on those territories. In this discussion, we consider the factors that could account for the decoupling of selection cues from observed fitness.

Our findings on the importance of territory-level shrub cover for territory selection are consistent with the habitat-specific distribution patterns reported for black-throated blue warblers by (Holmes et al. 1996) in a large (>10,000 ha), contiguous tract of forest in New Hampshire. In a comparison between high shrub density and low shrub density study plots, they reported that warbler density was higher and there were proportionately more older (≥ 2 years old) breeders in the high shrub density plot compared to the low shrub density plot. Of the small number of males that remained unmated, significantly more of them occurred on the low shrub density plot. In the same study system, Steele (1992) found that warbler density was positively correlated with shrub density at the scale of a study plot (14 ha), but that shrub density within warbler territories was not higher than shrub density outside of territories. Based on these findings, Steele (1992) argued that territories located on plots where average shrub density is above a threshold level will contain enough small patches of shrubs for use,

especially if selection is driven by nesting requirements rather than foraging requirements. Neither of these studies considered habitat patterns at more extensive landscape scales.

Research conducted on other species or in other areas has found consistent results. Several studies conducted in heterogeneous forests found that landscape-scale habitat patterns are important predictors of forest bird occurrence (Trzcinski et al. 1999a), but tended to be less important than fine-scale variables (Villard et al. 1999, Norton et al. 2000, Lichstein et al 2002). For example, Lichstein et al. (2002) reported a positive relationship of black-throated blue warbler abundance with the amount of older forest in a managed landscape in the southeastern Appalachians, USA, but found that landscape variables explained only a small amount of variation in the counts after controlling for local habitat effects, including elevation.

Ecological determinants of reproductive output

We found evidence that when the main cue of territory-selection (territory-level shrub density) interacts with habitat heterogeneity at landscape-level, black-throated blue warblers may be unable to recognize and occupy the places best suited for their reproduction (the contiguously forested landscapes). Bock and Jones (2004) found similar patterns among species occupying human dominated landscapes and suggest that birds may fail to recognize suitable breeding habitats in landscapes that differ from those in which they evolved. Here, we consider the factors that could account for the observed decoupling of selection cue and reproductive success for black-throated blue warblers and potentially other forest passerines in this system. The most likely factors include predation, parasitism, and food limitation (Martin 1992).

Predation pressures may play an important role in determining reproductive success in our system; our research sites in fragmented areas support a more diverse predator community than sites in more intact landscapes. However, nest failure due to predation was only significantly related to landscape pattern in one year (2004) and in that year, it was *lower* in more fragmented sites (K. Cornell, unpublished data). Thus, differences in nest predation do not seem to be a major contributor explaining lower fecundity in fragmented landscapes. Holmes et al. (1996) was also unable to attribute differences in demographic patterns between low and high quality habitats to predation.

Brood parasitism by brown-headed cowbirds can negatively influence reproductive success for forest-nesting passerines (Robinson et al. 1995a). This is the first study to document the costs of parasitism incurred by black-throated blue warblers. Parasitism was significantly greater on fragmented sites in all years of this study (K. Cornell, unpublished data). In this study region in Vermont, a single brown-headed cowbird nestling in a black-throated blue warbler nest can cause complete reproductive failure. In some cases, host fledglings are successful, but their condition at fledging is unknown and may be compromised, thereby affecting longer term survival. Thus, it appears that increased reproductive failure in fragmented landscapes is strongly influenced by brood parasitism.

The negative influence of cowbird parasitism in this system may interact with the frequency of double-brooding to further effect reproductive output. This could occur in two ways: 1) a female produces a single brood, fledges a cowbird, and does not offset the loss of the first brood by attempting a second because she is expending all of her energy attending a large fledgling cowbird, or 2) a female produces a first brood, fledges a

cowbird, attempts a second brood, and fledges another cowbird. We found that younger, less experienced females are more likely to be found in fragmented sites, and previous studies have shown that younger females are less likely to produce two broods per season than are older birds, even in high shrub density habitats (Holmes et al. 1992). Thus, the first scenario is a more likely pattern for black-throated blue warblers in Vermont.

Food limitation is another possibility explaining reduced reproduction on fragmented sites with high shrub cover. Holmes et al. (1996) found that the factor that accounted for the greatest difference in reproductive output between high and low quality habitats was the frequency of double-brooding which was accomplished most often by older females on high shrub density plots. Nagy and Holmes (2005) conducted controlled food supplementation experiments and demonstrated that the observed frequency of double-brooding is positively related to food resources on a territory. If these patterns apply to our system, we would expect that food resources may drive the patterns of reproductive success in our system as well. Several studies demonstrate that food resources decrease with increasing fragmentation (Burke and Nol 2000, Zanette et al. 2000), suggesting that poor reproduction in fragmented sites could be the result of reduced local food resources on those sites. This remains uncertain in our system. Hughes (2003) found increased diversity and abundance of insect populations in edge habitats versus core habitat in sites located within fragmented sites in west-central Vermont. However, the distribution of insects across the gradient of fragmentation of sites used in this study has not been investigated.

Conclusions

The results of our study support the idea that patterns of habitat at different spatial extents affect different aspects of demography and that habitat patterns among spatial extents can interact and affect the habitat selection process and the consequences of selection decisions for some species. For black-throated blue warblers, these interactions appear to prevent individuals from recognizing and occupying habitats best suited for their reproduction in heterogeneous landscapes. Further, cowbird parasitism appears to be a major factor contributing to disconnect between selection cues and fitness in this system. How widespread and important this decoupling is throughout the range of habitats occupied by black-throated blue warblers and for other forest-breeding passerines is unknown. Our findings lend credence to the complexity of the habitat selection process and call for experimental field studies conducted at multiple spatial extents aimed at teasing apart the mechanisms driving selection decisions for territorial species.

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TABLES

Table 2.1. Principle component loadings for the four forest arrangement metrics. PC1 explained 91% of the total variation and PC 2 explained 96% of the total residual variation. Sites with high LANDSCAPE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e., they were more contiguous).

Landscape metrics	LANDSCAPE	
	PC1	PC2
Percent forest cover	0.41	0.38
Percent core forest cover	0.41	0.26
Patch density	-0.42	0.33
Edge density	-0.42	0.35
Mean patch area	0.41	-0.48
Mean patch shape index	0.38	0.57

Table 2.2. *A priori* model set. Univariate, additive, and interactive combinations of three habitat variables: TERRITORY_SHRUB, PATCH_SHRUB, and LANDSCAPE with number of estimable parameters (K).

Model No.	Model	K
1	TERRITORY_SHRUB	2
2	PATCH_SHRUB	2
3	LANDSCAPE	2
4	TERRITORY_SHRUB + PATCH_SHRUB	3
5	TERRITORY_SHRUB + LANDSCAPE	3
6	PATCH_SHRUB + LANDSCAPE	3
7	TERRITORY_SHRUB + PATCH_SHRUB + LANDSCAPE	4
8	TERRITORY_SHRUB * PATCH_SHRUB	4
9	TERRITORY_SHRUB * LANDSCAPE	4
10	PATCH_SHRUB * LANDSCAPE	4
11	Global	7
12	Null	1

Table 2.3. Models of black-throated blue warbler detection on counts in Vermont, USA, number of parameters (K), scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).

Model name	K	-2(L)	ΔAIC_c	w_i
PATCH_SHRUB	2	836.02	0.00	0.58
LAND_AMOUNT + Total edge + PATCH_SHRUB	4	833.51	1.53	0.27
Intercept	1	844.02	5.98	0.03
Wind	2	842.98	6.96	0.02
Mean daily temperature	2	843.03	7.01	0.02
Total edge	2	843.25	7.23	0.02
Time of day	2	843.48	7.46	0.01
Year	2	843.61	7.59	0.01
Date	2	843.76	7.74	0.01
LAND_AMOUNT	2	844.01	7.99	0.01
Wind + Mean daily temperature	3	842.41	8.41	0.01
Global	9	830.65	8.91	0.01
Date + Time of day + Year	4	843.3	11.33	0.00

Table 2.4. Mean and standard deviation of territory- and patch-level habitat metrics and principle component scores for the landscape-level habitat metric.

Study site	TERRITORY_SHRUB			PATCH_ SHRUB	LANDSCAPE
	2002	2003	2004		
1	271.70 (76.6)	189 (84.9)	188.5 (85.6)	1520 (35, 537)	-3.77
2	131 (94.8)	211 (148)	299.8 (207)	836 (129, 387)	-2.29
3	234 (42.8)	207 (31.1)	185 (0)	698 (0, 275)	-2.76
4	219 (46.2)	228.7 (38.7)	188.5 (88.4)	1389 (0, 324)	-1.20
5	177.7 (99.3)	137 (76.5)	161.7 (70.1)	788 (0, 199)	1.05
6	127.5 (38.9)	182 (143.3)	116.7 (23.1)	437 (0, 156)	0.27
7	253.3 (42)	252.5 (47.4)	252.5 (47.4)	1175 (0, 249)	-4.23
8	190.7 (64.6)	137 (1.4)	136.3 (15.5)	746 (66, 216)	-0.84
9	285 (19.8)	241.3 (45.5)	271 (0)	1028 (1, 299)	-1.36
10	240.5 (58.7)	241.5 (86)	285.3 (84)	1971 (123, 776)	-2.86
11	180 (132.6)	166 (61.5)	117 (64.7)	434 (0, 237)	2.49
12	212.6 (83.6)	257 (208.3)	203 (95.9)	670 (58, 249)	2.57
13	100.3 (53.4)	151 (77.1)	98 (68.4)	672 (74, 162)	3.40
14	172.3 (137.7)	131.7 (44.5)	80 (35.2)	758 (40, 273)	2.51
15	500.3 (314.7)	245.9 (200.7)	242.2 (251.2)	290 (0, 88)	1.30

Table 2.4. Continued.

Study site	TERRITORY_SHRUB			PATCH_ SHRUB	LANDSCAPE
	2002	2003	2004		
16	121.5 (12)	130 (0)	247 (165.5)	768 (16, 260)	-0.01
17	58.3 (21.2)	78 (52.3)	127.8 (90.7)	448 (22, 160)	2.99
18	205.5 (139.3)	117.7 (10.5)	127.5 (29)	305 (7, 345)	1.55
19	77.3 (16.2)	70.7 (4.6)	82.7 (15)	849 (24, 478)	1.17
20	111.5 (0.7)	112 (0)	119.3 (25.8)	352 (15, 137)	0.01

Table 2.5. Models of mean annual abundance, male and female age ratios, pairing success, and annual fecundity of black-throated blue warblers in Vermont, USA, scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Statistics for best fit models are in bold.

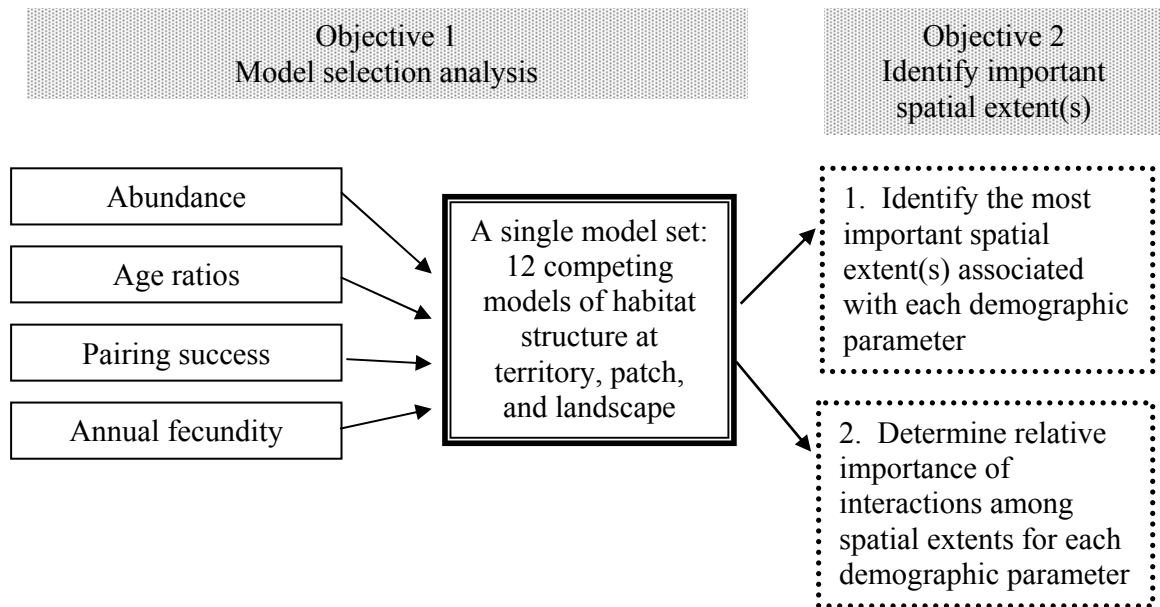
Model No.	Abundance			Male Age Ratio			Female Age Ratio		
	-2(L)	ΔAIC_c	w_i	-2(L)	ΔAIC_c	w_i	-2(L)	ΔAIC_c	w_i
1	46.14	1.60	0.09	65.96	4.90	0.05	77.74	0.00	0.20
2	47.11	2.56	0.06	70.93	9.87	0.00	80.21	2.46	0.06
3	45.43	0.89	0.13	73.98	12.92	0.00	81.36	3.62	0.03
4	46.10	3.77	0.03	64.22	5.39	0.04	75.55	0.02	0.20
5	43.52	1.20	0.11	60.81	1.98	0.21	77.43	1.91	0.08
6	45.01	2.68	0.05	69.02	10.18	0.00	79.48	3.96	0.03
7	42.83	2.80	0.05	56.54	0.00	0.55	75.52	2.30	0.06
8	45.61	5.58	0.01	63.73	7.19	0.02	75.49	2.28	0.06
9	40.03	0.00	0.20	60.25	3.71	0.09	73.55	0.34	0.17
10	41.62	1.59	0.09	66.17	9.63	0.00	79.26	6.04	0.01
11	37.65	5.05	0.02	54.49	5.38	0.04	71.95	6.19	0.01
12	47.13	0.44	0.16	74.01	10.81	0.00	81.37	1.48	0.10

Table 2.5. Continued.

Model	Pairing success			Annual fecundity		
No.	$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i
1	15.00	0.00	0.25	46.14	1.60	0.09
2	17.58	2.57	0.07	47.11	2.56	0.06
3	17.52	2.52	0.07	45.43	0.89	0.13
4	14.71	1.92	0.09	46.10	3.77	0.03
5	14.05	1.26	0.13	43.52	1.20	0.11
6	17.52	4.73	0.02	45.01	2.68	0.05
7	14.01	3.51	0.04	42.83	2.80	0.05
8	13.70	3.21	0.05	45.61	5.58	0.01
9	13.51	3.01	0.05	40.03	0.00	0.20
10	15.51	5.02	0.02	41.62	1.59	0.09
11	12.04	8.95	0.00	37.65	5.05	0.02
12	17.60	0.46	0.20	47.13	0.44	0.16

FIGURES

Figure 2.1. Overview of study design. Objective 1: use an information-theoretic analysis approach to evaluate and compare twelve models representing univariate, additive, and two-way interactive combinations of territory-, patch-, and landscape-level habitat patterns for four demographic parameters, including 1) abundance, 2) age ratios, 3) pairing success, and 4) annual fecundity. Objective 2: identify the most important spatial extent(s) affecting each parameter.



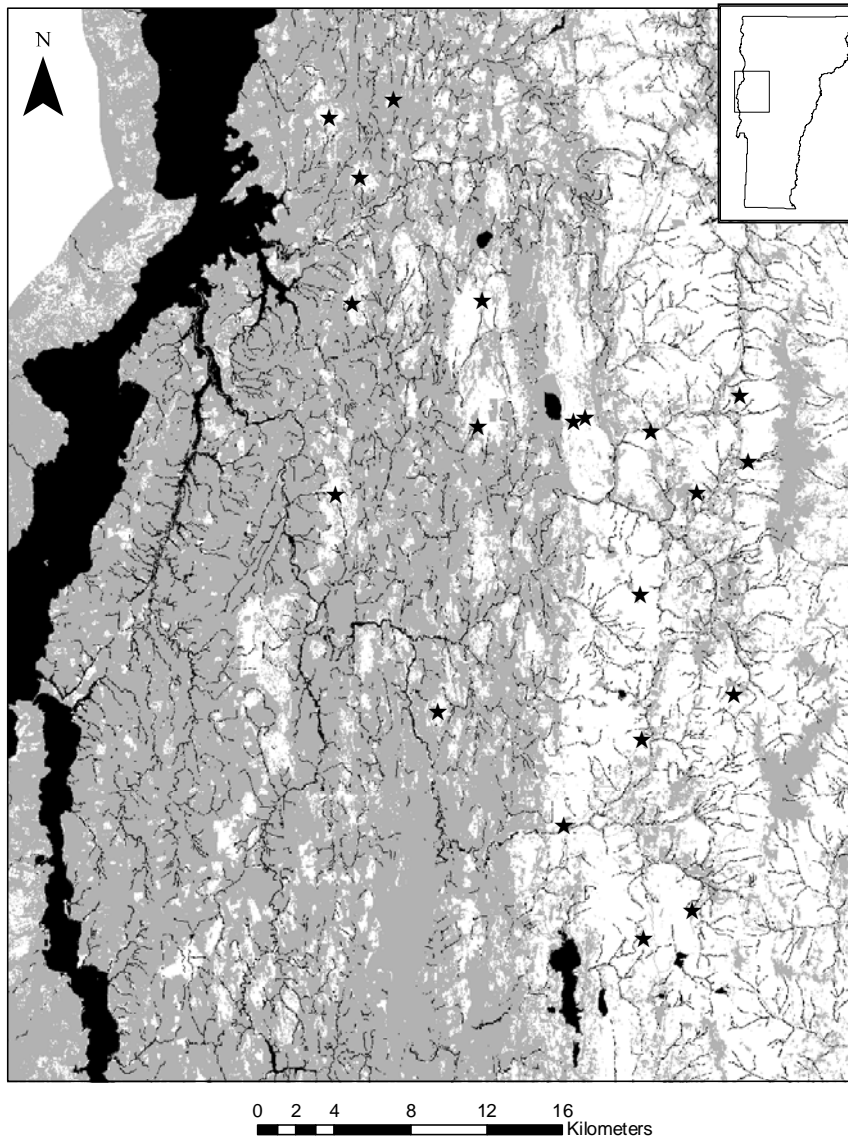


Figure 2.2. Twenty study sites in Chittenden and Addison Counties, Vermont, USA. Location of study region in Vermont is indicated on insert map. Black areas represent water; gray areas represent non-warbler habitat (urban, agriculture, coniferous forest); white areas represent mixed-deciduous and deciduous forested habitat. Stars indicate locations of study sites.

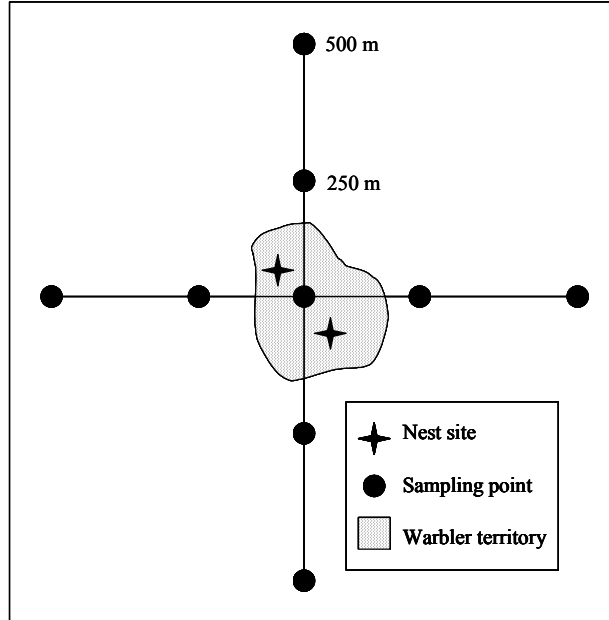


Figure 2.3. Schematic of a single study site. Shaded area represents a focal warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey stations at 250m and 500m from a random center survey station. TERRITORY_SHRUB metrics were estimated from vegetation samples collected at nest locations and the center sampling point within the focal territory. PATCH_SHRUB was estimated from vegetation samples collected at all sampling points outside the focal territory.

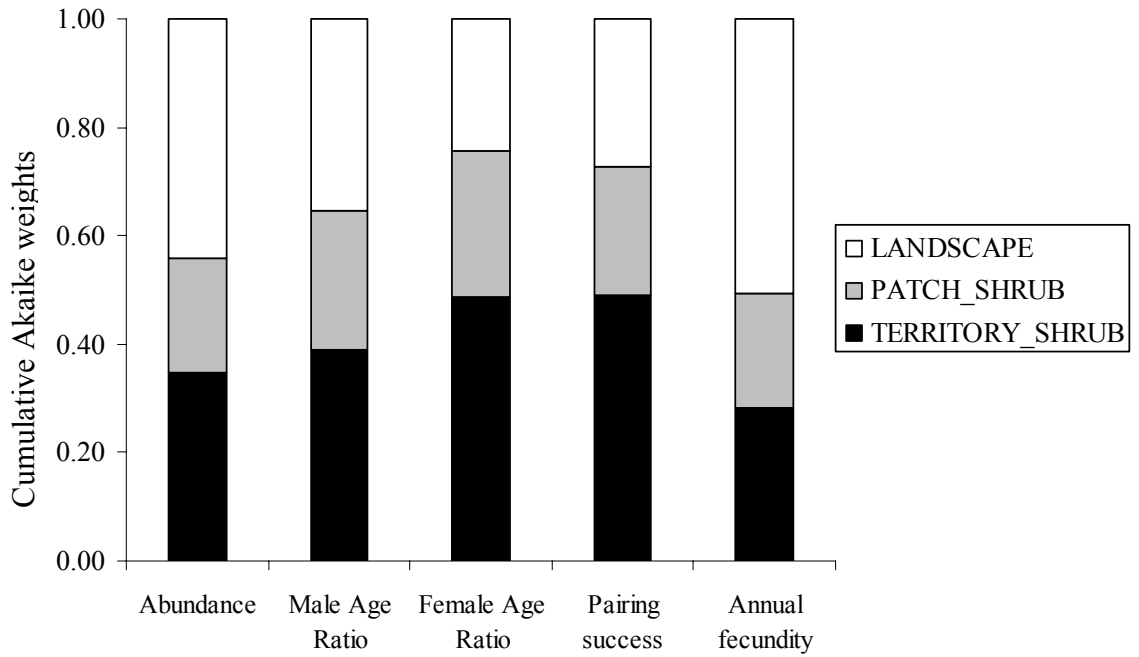


Figure 2.4. Cumulative Akaike weights ($\sum w_i$) of habitat covariates for each demographic parameter.

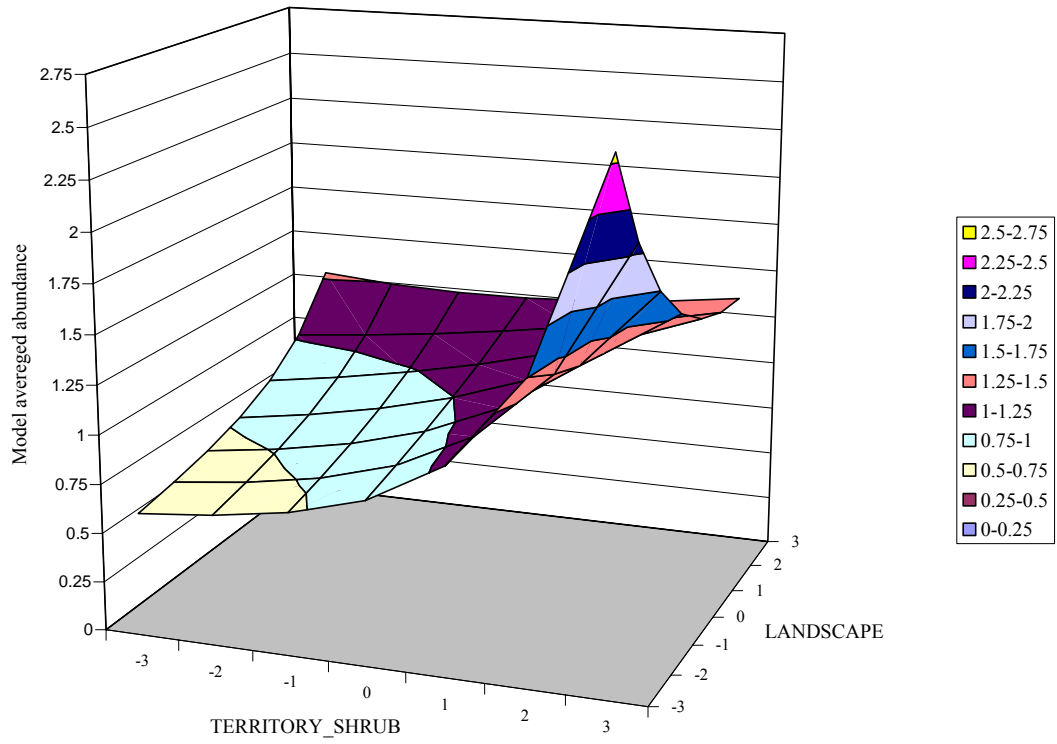
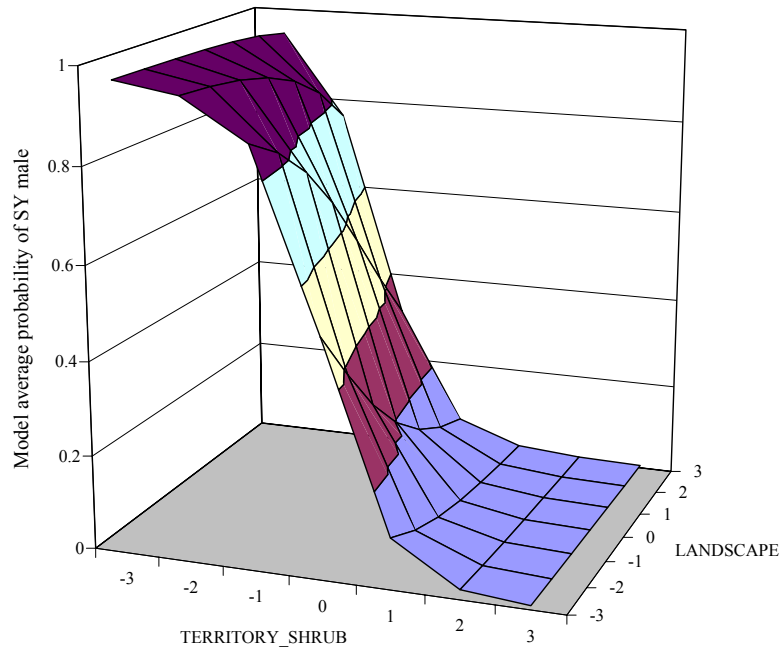
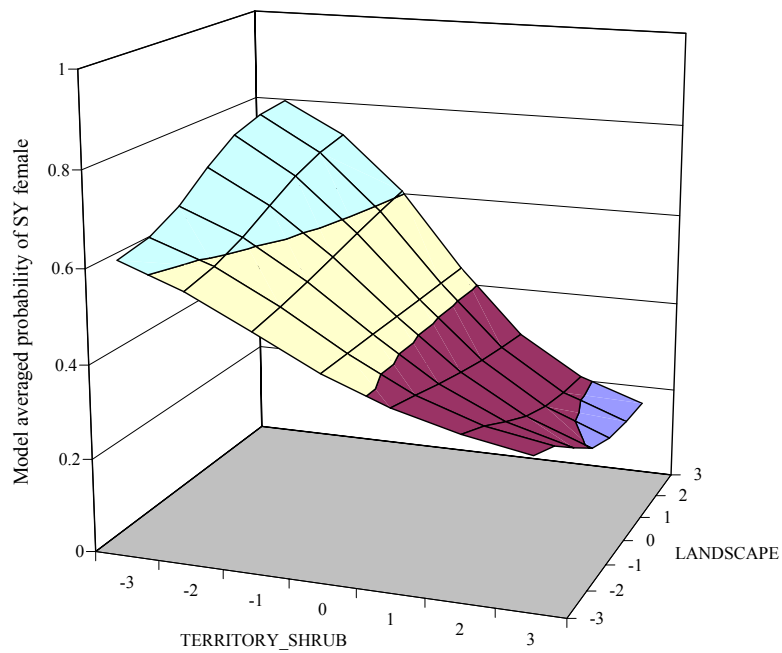
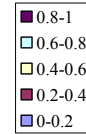


Figure 2.5. Surface plot of model averaged abundance as a function of TERRITORY_SHRUB and LANDSCAPE.



A



B

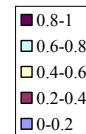


Figure 2.6. Surface plots of model averaged probability of SY (first-year breeder) male (A) and female (B) as a function of TERRITORY_SHRUB and LANDSCAPE.

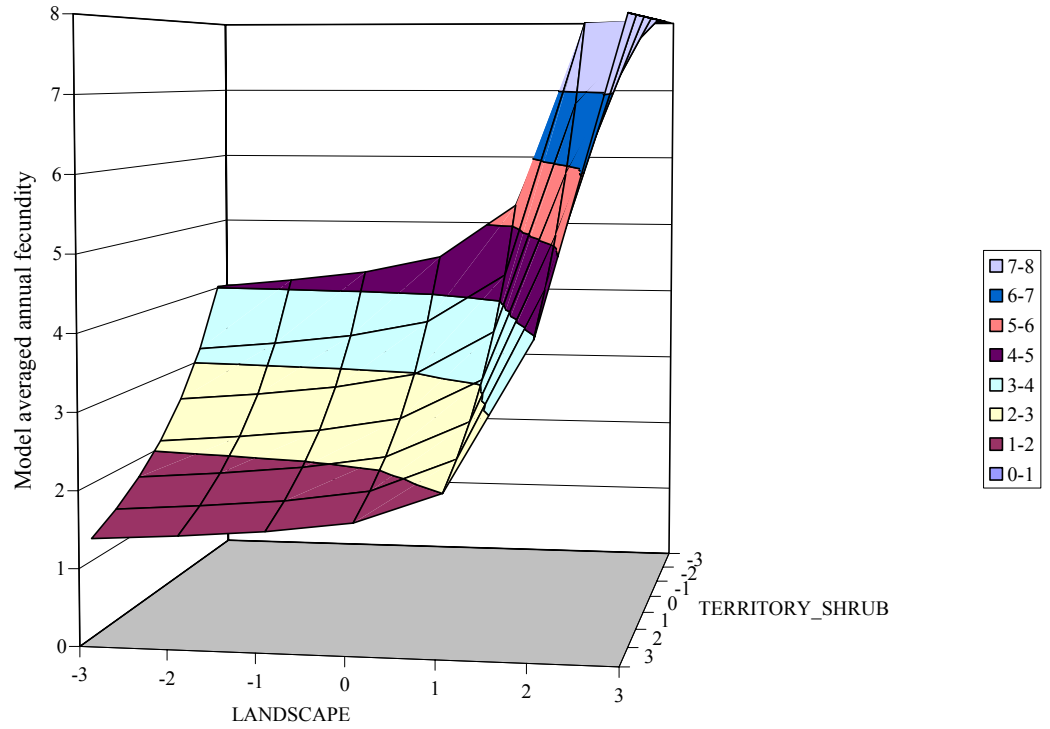


Figure 2.7. Surface plot of model averaged annual fecundity as a function of TERRITORY_SHRUB and LANDSCAPE.

APPENDICES

Appendix 2.1. Coefficients (β) of abundance and standard errors (in parentheses) for black-throated blue warblers in Vermont,

USA, 2002-2004.

Model No.	Intercept	TERRITORY_		PATCH_		LANDSCAPE		TERRITORY*		PATCH*		LANDSCAPE*	
		SHRUB	SHRUB	SHRUB	SHRUB	LANDSCAPE	LANDSCAPE	PATCH	PATCH	LANDSCAPE	LANDSCAPE	PATCH	PATCH
1	0.05 (0.11)		0.12 (0.1)										
2	0.06 (0.11)				-0.02 (0.12)								
3	0.05 (0.11)						0.07 (0.05)						
4	0.05 (0.11)		0.12 (0.1)		-0.03 (0.11)								
5	0.04 (0.11)		0.16 (0.1)				0.09 (0.05)						
6	0.04 (0.11)				0.10 (0.14)		0.10 (0.06)						
7	0.03 (0.11)		0.18 (0.10)		0.12 (0.13)		0.13 (0.06)						
8	0.06 (0.11)		0.02 (0.16)		0.06 (0.16)					-0.11 (0.14)			
9	-0.12 (0.14)		0.38 (0.14)				0.14 (0.05)					-0.17 (0.08)	
10	-0.15 (0.15)				-0.11 (0.16)		0.09 (0.06)						-0.14 (0.07)
11	-0.20 (0.19)		0.14 (0.22)		0.11 (0.23)		0.12 (0.08)			-0.23 (0.19)			-0.18 (0.11)
12	0.06 (0.11)												-0.08 (0.09)

Appendix 2.2. Coefficients (β) of male age ratio and standard errors (in parentheses) for black-throated blue warblers in

Vermont, USA, 2002-2004.

Model No.	Intercept	TERRITORY_		PATCH_		LANDSCAPE		TERRITORY*		PATCH*		LANDSCAPE*	
		SHRUB	SHRUB	SHRUB	SHRUB	LANDSCAPE	LANDSCAPE	PATCH	PATCH	LANDSCAPE	LANDSCAPE	LANDSCAPE	LANDSCAPE
1	-1.13 (0.36)		-1.21 (0.53)										
2	-0.93 (0.30)			-0.57 (0.36)									
3	-0.87 (0.28)				-0.02 (0.12)								
4	-1.11 (0.35)		-0.91 (0.47)	-0.60 (0.47)									
5	-1.55 (0.47)		-2.63 (0.97)		-0.47 (0.23)								
6	-0.93 (0.30)			-0.86 (0.42)									
7	-1.49 (0.51)		-2.14 (1.02)	-1.18 (0.62)									
8	-1.14 (0.37)		-0.72 (0.61)	-0.70 (0.50)				0.40 (0.60)					
9	-1.32 (0.54)		-2.51 (0.95)		-0.41 (0.23)				0.21 (0.29)				
10	-0.55 (0.37)			-0.65 (0.49)									0.41 (0.26)
11	-1.34 (0.59)		-2.28 (1.06)	-0.32 (0.80)				1.88 (1.34)				0.11 (0.33)	0.52 (0.47)
12	-0.87 (0.28)												

Appendix 2.3. Coefficients (β) of female age ratio and standard errors (in parentheses) for black-throated blue warblers in

Vermont, USA, 2002-2004.

Model No.	Intercept		TERRITORY_		PATCH_		LANDSCAPE		TERRITORY*		PATCH*		LANDSCAPE	
	SHRUB	SHRUB	SHRUB	SHRUB	SHRUB	SHRUB	LANDSCAPE	LANDSCAPE	PATCH	LANDSCAPE	PATCH	LANDSCAPE	PATCH	LANDSCAPE
1	-0.18 (0.27)	-0.56 (0.33)												
2	-0.18 (0.26)		0.28 (0.26)											
3	-0.17 (0.26)			0.01 (0.11)										
4	-0.26 (0.29)	-0.80 (0.48)	0.46 (0.33)											
5	-0.19 (0.27)	-0.64 (0.38)		-0.07 (0.13)										
6	-0.20 (0.27)		0.44 (0.33)	0.12 (0.14)										
7	-0.26 (0.29)	-0.77 (0.50)	0.48 (0.36)	0.03 (0.15)										
8	-0.24 (0.30)	-0.86 (0.54)	0.52 (0.44)						-0.11 (0.48)					
9	-0.49 (0.33)	-0.28 (0.50)		0.00 (0.14)						-0.42 (0.22)				
10	-0.09 (0.35)		0.56 (0.42)	0.12 (0.14)									0.08 (0.17)	
11	-0.35 (0.39)	-0.46 (0.67)	0.67 (0.56)	0.06 (0.16)							-0.34 (0.58)		-0.50 (0.27)	0.15 (0.25)
12	-0.17 (0.26)													

Appendix 2.4 Coefficients (β) of pairing success and standard errors (in parentheses) for black-throated blue warblers in

Vermont, USA, 2002-2004.

Model No.	Intercept		TERRITORY_		PATCH_		LANDSCAPE		TERRITORY*		PATCH*		LANDSCAPE*	
	SHRUB	SHRUB	SHRUB	SHRUB	SHRUB	SHRUB	LANDSCAPE	LANDSCAPE	PATCH	PATCH	LANDSCAPE	LANDSCAPE	PATCH	PATCH
1	4.59 (1.60)	2.39 (1.86)												
2	3.39 (0.72)		0.13 (0.77)											
3	3.42 (0.74)						-0.09 (0.33)							
4	4.66 (1.50)	2.67 (1.79)	-0.68 (1.21)											
5	5.24 (1.93)	3.99 (2.70)					0.59 (0.67)							
6	3.42 (0.74)		0.01 (0.93)				-0.09 (0.39)							
7	5.18 (1.88)	3.94 (2.63)	-0.25 (1.25)				0.55 (0.70)							
8	4.78 (1.92)	2.91 (2.06)	0.37 (1.99)						1.89 (1.62)					
9	5.11 (1.97)	4.5 (2.91)					0.05 (1.09)			-1.02 (1.69)				
10	3.00 (0.79)		-0.58 (1.51)				-0.08 (0.38)							-0.95 (0.81)
11	4.82 (2.14)	4.73 (3.72)	0.24 (2.15)				-0.11 (0.86)			1.88 (1.90)				-0.89 (1.46)
12	3.38 (0.72)													

Appendix 2.5. Coefficients (β) of annual fecundity and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004.

Model No.	Intercept	TERRITORY_		PATCH_		LANDSCAPE		TERRITORY*		PATCH*	
		SHRUB	SHRUB	SHRUB	SHRUB	LANDSCAPE	LANDSCAPE	PATCH	LANDSCAPE	LANDSCAPE	LANDSCAPE
1	0.99 (0.12)	-0.24 (0.14)									
2	0.99 (0.12)		-0.23 (0.14)								
3	0.92 (0.13)			0.19 (0.06)							
4	0.97 (0.13)	-0.24 (0.13)	-0.27 (0.15)								
5	0.92 (0.13)	-0.12 (0.12)		0.17 (0.06)							
6	0.92 (0.13)		-0.02 (0.16)	0.19 (0.07)							
7	0.91 (0.13)	-0.13 (0.13)	-0.07 (0.17)	0.16 (0.07)							
8	0.91 (0.13)	-0.50 (0.19)	-0.14 (0.17)					-0.34 (0.18)			
9	0.92 (0.13)	-0.15 (0.18)		0.17 (0.06)					0.02 (0.1)		
10	1.02 (0.15)		0.04 (0.17)	0.18 (0.07)							0.09 (0.08)
11	0.94 (0.16)	-0.2 (0.25)	0.04 (0.2)	0.13 (0.08)				-0.26 (0.20)		-0.08 (0.12)	0.09 (0.10)
12	1.02 (0.12)										

CHAPTER 3. SCALE-DEPENDENT MECHANISMS OF HABITAT SLECTION FOR A MIGRATORY PASSERINE: AN EXPERIMENTAL APPROACH

Abstract. A fundamental tenet of habitat selection theory is that individuals choose habitats based on indirect cues in their environment such as physical features representing habitat quality and the presence of other conspecifics. Although avian habitat selection theory has been well developed, surprisingly few experimental studies have evaluated the role that habitat and conspecifics play in shaping distribution and abundance patterns. We performed a field experiment to examine the roles that conspecific attraction and territory- and landscape-level habitat pattern play in determining territory occupancy patterns and abundance in a forest-nesting passerine, the black-throated blue warbler (*Dendroica caerulescens*). In 2004 and 2005, we broadcast warbler vocalizations in areas of previously low abundance at 10 forested sites across a gradient of landscape pattern and understory shrub density. We used multi-season occupancy models to examine the effects of the experimental treatment and two habitat features on site colonization and extinction rates. We found that 1) habitat features describing territory- and landscape-level patterns were relatively more important than conspecific cueing for determining warbler occupancy and abundance patterns, 2) abundance patterns, occupancy rates, and extinction rates were affected by an interaction between habitat features at different spatial extents, but not by interactions between habitat cues and social cues, and 3) conspecific vocal cues do not appear to either attract or deter settlement for black-throated blue warblers.

INTRODUCTION

A fundamental tenet of habitat selection theory is that individuals choose habitats based on indirect cues in their environment. These cues include the physical features representing habitat quality at multiple spatial extents and the presence of other conspecifics (Hildén 1965, Stamps 1988, Muller et al. 1997). The underlying premise is that habitat selection decisions or preferences are adaptive because individuals rely on cues that, over evolutionary time, reliably correlate with ultimate factors that relate to survival and reproductive success, such as food availability, structural and functional requirements, and shelter from weather, predation, and parasitism (Hildén 1965).

Studies of avian habitat selection have played a major role in the development of the theory. In a classic paper on avian habitat selection, Hildén (1965) discussed these indirect proximate cues that signal ultimate factors according to the following categories: 1) landscape, 2) terrain, 3) nest-, song-, and feeding sites, and 4) other animals. Hildén noted that all elements need not be present to elicit a settling response, but that a combined effect of different elements must exceed some threshold to trigger settling. Additionally, one key stimulus may outweigh the others, such that in its absence birds will not settle, and in its presence birds may settle even in very suboptimal environments.

There are many examples in the literature of how the structural features of habitat at different spatial extents may signal ultimate factors, and thus determine avian distribution and abundance patterns. For example, density and arrangement of vegetation at a nest site are related to microclimate conditions, where leaf cover over nests can provide protection from rain, solar radiation, and wind (Calder 1973, Walsberg 1985,

With and Webb 1993, Martin 2002). Vegetation structure and composition may also provide information about whether a habitat can support the physiological and morphological requirements of a species (Cody 1985), the availability of food resources (Steele 1992, Rodenhouse and Holmes 1992, Zanette et al. 2000), predation pressure (Martin 1992, Bowman and Harris 1980, Martin and Roper 1988, Holway 1991), and the severity of avian brood parasitism of an area (Burhans 1997). From these studies it has become clear that habitat patterns at multiple spatial extents influence distribution patterns for birds.

In addition to habitat cues, there is growing evidence that social cues may also influence habitat selection for territorial songbirds (Alatalo et al. 1992, Stamps 1988). Hildén (1965) included the presence of other animals as a proximate cue that relates to the availability of a particular resource (e.g. food, territories, nest sites, mating opportunities, and predation or parasitism pressures). These cues can either entice or deter settlement.

In terms of deterrents, research has focused on the effects of competition by other species (e.g. McArthur 1958, Rosenzweig 1981) and by the same species (e.g., Fretwell and Lucas 1970). In the case of interspecific competition, birds may perceive some habitats as suitable in terms of structure and level of productivity, but the presence of other species with similar ecological preferences might reduce the availability of resources and render the habitat less acceptable (Cody 1985). Competition between individuals of the same species may also serve as a proximate cue for ultimate factors. One large body of theory holds that, because conspecifics are competitors, individual fitness should decline monotonically as a function of conspecific density (Fretwell and

Lucas 1970, Fretwell 1972, Rosenzweig 1985, 1991, Sutherland 1996). Such models suggest that the presence of previous settlers in a habitat serve as a negative proximate cue (*sensu* Hildén 1965) and should discourage newcomers from settling (Kluijver and Tinbergen 1953).

Others have suggested conspecifics may serve as positive proximate cues to habitat quality during the process of habitat selection, where settlers may benefit by choosing territories near other conspecifics (reviewed in Stamps 1988, Muller et al. 1997). In this light, conspecifics may serve as cues to habitat quality because territory holders living in aggregations are more effective at territory defense, protection from predators, and attracting potential mates (Stamps 1998, 1994, Wagner 1993, Boulinier and Danchin 1997, Muller et al. 1997). Further, aggregation may be beneficial in territorial species if previously settled neighbors can provide valuable information about the habitat. In many species, territory quality is determined by resource distributions but assessing resource quality requires time and energy (Stamps 1987, 1988). These explanations both imply that naïve individuals (young, first time breeders or older dispersers) should be more strongly attracted to conspecifics than would individuals already familiar with the habitat (Stamps 1988, Boulinier and Danchin 1997, Muller et al. 1997).

Despite recent heightened interest in conspecific cueing (Reed and Dobson 1993, Ward and Schlossberg 2004, Nocera et al. 2006, Ahlering and Faaborg 2006), particularly by conservation biologists, there are a relatively small number of empirical studies that have examined the effects of conspecific attraction in habitat selection for territorial species (Smith and Peacock 1990, Ray et al. 1991, Reed and Dobson 1993,

Lima and Zollner 1996, Muller et al. 1997). Experimental studies on the role of conspecific attraction are even rarer. To our knowledge, only two studies have experimentally examined the role of conspecific cueing for territorial migratory passerines. Ward and Schlossberg (2004) used song playbacks to experimentally establish new breeding populations of endangered Black-capped vireos (*Vireo atricapilla*) in previously unoccupied sites. Noccera et al. (2006) experimentally compared use of inadvertent social information between two habitats that varied in quality during pre- and post-breeding periods for the Bobolink (*Dolichonyx oryzivorus*) and Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*). They found that first-time breeders use information about the location of adults at the end of the breeding season to make settlement decisions during their first breeding season in the following year.

These experimental studies have shown that social conspecific attraction may play an important role in determining habitat selection decisions, yet it is unknown how widespread this behavior is among territorial bird species. The strength of behavioral cues in relation to other innate cues of habitat structure is also poorly understood (Ahlering and Faaborg 2006). Further, it is unclear as to how behavioral cues interact with habitat cues at multiple extents to affect site occupancy rates and abundance patterns.

In this study, we simultaneously examined the roles of conspecific attraction and habitat structure at two spatial extents as mechanisms affecting territory occupancy rates and abundance patterns in a forest-nesting passerine, the black-throated blue warbler (*Dendroica caerulescens*). We report on the results of an experimental field study designed to tease apart the effects of territory-level shrub density measure within

breeding territories, landscape-level habitat patterns at a 5km radius extent, and conspecific cueing in a heterogeneous landscape in west-central Vermont, USA. We applied a model selection approach that enabled us to determine the effects of individual habitat and behavioral cues on selection decisions, and the effects of interactions between cues.

Our objectives were to: (1) determine the relative importance of conspecific attraction and habitat features at territory and landscape extents in determining a) black-throated blue warbler abundance patterns, and b) site occupancy rates, site extinction rates, and site colonization rates, (2) determine if behavioral cues and habitat cues interact to determine abundance and occupancy patterns, and (3) determine whether the effect of the conspecific attraction is positive or negative for this species.

METHODS

Study species

The black-throated blue warbler is a territorial migratory songbird that breeds in parts of the eastern United States and southern Canada, and winters in the Greater Antilles. During the breeding season, black-throated blue warblers are common to forest patches across many different landscape types throughout Vermont, but appear to be patchily distributed (K. Cornell, unpublished data). Males arrive on the breeding grounds in early May, before females, and select and defend breeding territories; males advertise their presence through song and by responding aggressively to the presence of male conspecifics. Territories range in size from about 1 to 4 ha, depending on habitat; territories are smallest where shrub layer is dense (Steel 1992). Males are easily counted

in a variety of field conditions based on vocalizations, and territories can be mapped by tracking males over space and time and using GPS to record perching and singing locations, and locations of aggressive interactions with neighbors.

Perhaps more is known about black-throated blue warbler habitat preferences and demography than any other North American migratory passerine; it has been studied continuously since 1969 at the Hubbard Brook Experimental Forest (Holmes 1994, Holmes et al. 1996a, Sillett and Holmes 2002a, Holmes et al. 2005), a large unfragmented forest in the White Mountains of New Hampshire, USA. From this long-term research program, we know that the most productive territories have high shrub density, low nest predation, and high food abundance (Steele 1992a, Steele 1992b, Rodenhouse et al. 2003a). However, little is known about how landscape-level habitat patterns affect territory selection and population abundance, and how territory- and landscape-level habitat patterns interact in fragmented landscapes to affect distribution for this species. Further, little is known about what role conspecific attraction plays in determining site occupancy and abundance.

Study sites

We conducted a field experiment from April to July 2003-2005 at 10 forested sites that were part of a larger study of habitat selection and demography for this species in Chittenden and Addison counties, Vermont, USA (Cornell, Chapter 2). Study sites were selected to span a wide gradient of forest fragmentation level (i.e., highly heterogeneous landscape composition versus homogeneously forested areas). Sites within contiguously forested landscapes were located in the northern half of Green Mountain National Forest, a relatively homogenous forest with a canopy dominated by

northern hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), and an understory dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and beech saplings. Study sites in more fragmented landscapes were located in the Champlain Valley, a heterogeneous area characterized by small forest patches situated in a matrix dominated by agriculture. These lower elevation forests differed from contiguous forests in the region in that they exhibited a higher diversity of canopy tree species than the contiguous forests, variable vertical structure, and the understory was dominated by witch hazel (*Hammamelis virginiana*), *Rubus* spp., blue cohosh (*Caulophyllum thalictroides*), and elm (*Ulmus* spp.), rather than hobblebush (*Viburnum alnifolium*).

Experimental design

At each of the 10 study sites, we established eight sampling points at 250 m and 500 m in cardinal directions and centered at a sampling point within a randomly chosen black-throated blue warbler territory (n = 9 sampling points total per study site; Figure 3.1). Statistical analysis for this study (see below) was conducted at the level of the sampling point, where each of the 9 sampling points per study site were assigned to experimental categories: treatment (n = 2 sampling points) and control (n = 7 sampling points).

In 2004 and 2005, we played recordings of warbler vocalizations at 2 sampling points within each of the 10 study sites (hereafter, we refer to these as ‘treatment points’; Figure 3.1). Both treatment points were chosen based on low abundance counts at those points in 2003 and because they were located in forested habitat. We classified low abundance as ≤ 1 male black-throated blue warbler detected within 100 m of the sampling

point. The other 7 sampling points at each site were controls in which no recordings were broadcast (hereafter, we refer to these as ‘control points’). Because understory shrub density may be an important proximate cue in the territory selection process (Hildén 1965, Cornell, Chapter 2), we broadcast warbler vocalizations (treatment points) in both low shrub density areas and high shrub density areas within each study site.

The conspecific cue: song playbacks

At each treatment point, we played pre-recorded vocalizations of black-throated blue warblers on portable compact disc players and stereo speakers housed in weatherproof boxes (playback boxes) and powered by 12 volt deep-cycle batteries. Because prospecting males may assess sites at dawn during the dawn chorus (Amrhein et al. 2004), vocalizations were played from 0400 to 1200 daily throughout the settlement period and early breeding season from late-April to early-July in 2004 and 2005. The experimental playbacks were not conducted in 2003 to establish baseline occupancy patterns. The compact disc players repeated all tracts on a 74 minute compact disk and included 55 minutes of black-throated blue warbler song and calls recorded in New York and New Hampshire. To prevent individuals from habituating to the playbacks, the tracts also included 10 minutes of silence, and 9 minutes of songs other species that generally occur in the same bird community with warblers, including black-throated green warblers (*Dendroica virens*), ovenbirds (*Seiurus aurocapillus*), red-eyed vireos (*Vireo olivaceus*), and wood thrush (*Hylocichla mustelina*). Vocalizations were not played at control points.

Field Methods: abundance and occupancy surveys

To evaluate abundance and site occupancy rates, we conducted two 10-minute, single-observer point counts in succession at each of the nine sampling points in each

study site from 25 May to 15 July in 2003-2005 (Figure 3.1). Surveys were conducted on mornings with low wind and no rain, between 0600h and 1100h. All surveys were conducted by experienced observers who recorded the number of all black-throated blue warblers heard or seen within 100 meters of the sampling point, the time at which each warbler was first detected, the distance category of detected individuals, and the sex of adults. The raw data were then processed for statistical analysis (see below).

Field methods: Quantifying habitat at each sampling point

Understory shrub cover. – We quantified the understory shrub cover at each of nine sampling points at each study site using two different field methods. First, we measured understory leaf density at each point following procedures described by Sillett et al. (2004). Four 11.2-m transects were delineated in the understory in cardinal directions within plots centered on each sampling point. At the distal end of each transect, a ground-level, 9-m² plane was erected using two 3-m vertical poles set 3-m apart. We counted all leaves of all understory species that intersected this plane and summed them across all four transects for each sampling point. Second, we established three, 50 meter long transects, spaced 50 meters apart, and running in the north-south cardinal directions with the center transect bisecting the sampling point. At three survey stations spaced evenly along each transect, we estimated the percentage of the ground covered by individual shrub species that black-throated blue warblers may potentially use for nesting, foraging, or perching within a 10 meter radius circle surrounding each survey station. The cover estimates were first summed across species for each survey station and then averaged across survey stations to estimate understory shrub cover for each sampling point.

We used a correlation-based Principle Components Analysis (PROC PRINCOMP; SAS 1999) to condense the two shrub measures into a single metric for each of the nine sampling points at each of the 10 study sites for our model selection analyses. This analysis incorporated information from each of the two shrub variables into a single component that explained 56.9 % of the total variation among sampling points (Table 3.1). We termed this component SHRUB. Points with high SHRUB PCA score had high leaf density and overall high cover of shrubs used by black-throated blue warblers, while sites with low SHRUB PCA score were less shrubby.

Landscape pattern. – We characterized landscape pattern surrounding each research site using USGS/EPA MRLC land cover maps derived from a version of the 1992 National Land Cover Dataset (30 m pixel size; Vogelmann et al. 2001) and updated to include extent of developed land in Vermont as of 2002 (Spatial Analysis Lab, University of Vermont). Black-throated blue warblers breed mainly in deciduous or mixed/coniferous forests (Holmes et al. 2005). Thus, we used ArcGIS 9.1 (Esri, Inc) to reduce the original 18 land-use classes to eight classes based on perceived biological relevance and ease of interpretation. The classes included (1) water, (2) barren, (3) developed land, (4), wetland, (5) deciduous and mixed-coniferous forest, (6) coniferous forest, (7) agriculture (row crop, hayfield, pasture), and (8) orchard and other agriculture.

We used the quantitative spatial analysis program FRAGSTATS (McGarigal and Marks 1995) to obtain specific measures of landscape composition and configuration within a 5 km radius area surrounding the center of each study site (Donovan et al. 2000). This scale was selected because it reflects the home range size of Brown-headed Cowbirds (Thompson 1994), a potentially important determinant of reproductive success

in our system (Cornell, Chapter 2). In FRAGSTATS, we applied an 8-neighbor rule for delineating patches. We used the percent of landscape in the deciduous/mixed coniferous forest landuse category as a single landscape composition metric. Study sites ranged in forest cover from 13%-85%. Landscape configuration metrics included percent core deciduous/mixed coniferous forest area (defined as >120 m from edge), mean forest patch area, mean shape index, forest patch density, and edge density. Landscape composition and configuration metrics were consistently collinear (Pearson's correlations, $p < 0.05$; SAS 8.2, SAS Institute 1999). To manage this problem, we used a correlation-based Principle Components Analysis (PROC PRINCOMP; SAS 8.2, SAS Institute 1999) to condense the six landscape metrics into a single landscape measure for each study site (each of the nine sampling points at each site had the same landscape score). This analysis incorporated information from each variable into a single component that explained 91.0% of the total variation among study sites (Table 3.1). We termed this component LANDSCAPE. Sites with high LANDSCAPE PCA scores had high percent forest cover in the landscape, high core forest area, large mean patch area, and a higher mean shape index, while sites with low LANDSCAPE PCA scores were more heterogeneous with a higher density of more isolated forest patches and more edge.

Statistical Analyses

We used an information theoretic approach (Burnham and Anderson 2002) to determine how social and habitat cues interact to determine site occupancy and abundance patterns separately. Recall that each analysis was conducted at the level of the sampling point where each point was assigned to a treatment category: the 2 points where playbacks were broadcast at each site were categorized as 'treatment' points and the

seven remaining points were categorized as ‘control’ points. The model sets used for each analysis thus consisted of a number of plausible candidate models reflecting univariate, additive, and two-way interactive combinations of three main effects including 1) experimental treatment, 2) SHRUB, and 3) LANDSCAPE (Tables 3.2 and 3.3). For the abundance analysis, we also considered year as an explanatory variable because we were interested in assessing changes in abundance over time.

Abundance. –The abundance analysis consisted of two steps: 1) a preliminary analysis to determine whether raw point count data required adjustment to account for detection probability (Thompson 2002), and 2) a model selection analysis to evaluate how conspecific attraction and habitat features influenced abundance. For the preliminary analysis to estimate detection probability (p , the probability that a blue warbler would be detected in a 10-minute point count, given it is present), we used the Huggins closed-capture removal models (Huggins 1989, 1991) within the Program MARK (White and Burnham 1999). We divided each 10-minute count into five, 2-minute intervals, and created capture histories for each bird on each survey. We assessed whether year, date, and time of survey, wind conditions, average daily temperature, understory shrub cover measured at the level of a study site, and two landscape-level metrics at the 5 km radius scale (percent deciduous/mixed-coniferous forest cover and total edge) affected p . We used an information theoretic model selection approach (Burnham and Anderson 2002) to evaluate support for 13 alternative *a priori* models (Table 3.4) containing various combinations of the eight covariates to determine which factor(s) affected detection of warblers in point count surveys. We used Akaike’s Information Criteria (AIC_c) to rank candidate models from best to least supported and

calculated Akaike weights for each model (ω_i ; Table 3.4, Burnham and Anderson 2002). We then calculated a model-averaged p for each 10-minute point count survey conducted in the study (Burnham and Anderson 2002). Our ability to detect warblers, given presence was high, ranging from 0.90 to 0.99. Because the corrected abundances were not truthfully Poisson distributed, and because our probability of detecting warblers, given presence, was high (> 90%), we used the raw count data for the second step of the abundance analysis. Raw counts were summed per survey at each sampling point in each year, and the maximum number of warblers counted across the two surveys at a given point was modeled in step 2.

In step 2, we modeled raw abundance as a linear function of 17 plausible ecological models containing univariate, additive, and two-way interactive combinations of treatment category, SHRUB and LANDSCAPE habitat metrics, and year (Table 3.2) using PROC GENMOD (SAS 8.2, SAS Institute 1999). For each of the 17 models, we specified the Poisson distribution and designated the sampling point as a repeated factor. We tested for overdispersion of the data using the DSCALE option for our most parameterized model; there was no evidence of overdispersion in the data.

Occupancy, extinction, and colonization.— To assess how conspecific attraction and habitat features influenced occupancy (ψ), extinction (ϵ), and colonization (γ) of warblers at a given point (MacKenzie et al. 2004), we created primary and secondary encounter histories from the raw abundance data, representing two surveys in each of the three years of the study (2003-2005) at each of the nine sampling points for all 10 study sites ($n = 90$ histories). Each history consisted of 0's and 1's, which described whether a black-throated blue warbler was detected on a survey over time. For example, an

encounter history of 11 10 00 at a sampling point indicated that at least one warbler was present within 100m of the point (occupied a territory) in the first year of the study and was detected on both surveys; in year two, at least one warbler was present and detected on the first survey, but was not detected in the second; and in year three, no warblers were detected, either because the point went locally extinct or because observers failed to detect present warblers on either survey. The collection of capture histories allowed us to estimate site occupancy (ψ), capture probability (p , the probability that an individual that is present at the site and was detected for each sampling point; Pollock et al. 1990, Lebreton et al. 1992), extinction rate (ϵ , the probability that a previously occupied site goes extinct between primary sampling occasions), and colonization rate (γ , the probability that a previously unoccupied site is colonized).

We modeled site occupancy, extinction, and colonization rates for black-throated blue warblers with the multi-season occupancy model (MacKenzie et al. 2002) option in Program MARK (White and Burnham 1999). We considered 49 plausible, linear models in total, representing univariate, additive, and interactive combinations of treatment, SHRUB, and LANDSCAPE to the set of observed capture histories (Table 3.3). In all models, ψ was modeled as a function of the interaction between SHRUB and LANDSCAPE because previous research showed that the interaction between these two habitat levels played an important role in determining black-throated blue warbler abundance in this system (K. Cornell, Chapter 2). We modeled capture probability, p , as a function of four variables known to effect detection of warblers on point counts, including wind intensity, average daily temperature, date of survey, and time of day (K. Cornell, Chapter 2; this study, Table 3.4). Capture probability was held constant across

surveys within a year (secondary sampling occasions), but was allowed to vary between years (primary sampling occasions). Thus, with ψ and p accounted for, we modeled extinction rate (ϵ) and colonization rate (γ) as functions of all combinations of the treatment and habitat variables simultaneously. In all models, the logit link option was used to allow linear modeling. We then used information theoretic approaches to rank and weight each model in the model set.

RESULTS

Abundance

We conducted a total of 540, 10-minute counts from 2003-2005. We counted 231 male black-throated blue warblers on these counts. Raw counts ranged from 0 to 4 males per 10-minute survey.

The top model explaining black-throated blue warbler abundance contained the interaction between SHRUB and LANDSCAPE (model 9) and had 89% of the total weight ($w_i = 0.89$). Only one other model in the set had any weight (model 12, $w_i = 0.11$) and this model also contained the interaction between SHRUB*LANDSCAPE as well as the additive effect of treatment, but the effect of treatment was not significant (Appendix 3.2). If conspecifics played a role in shaping abundance we would have expected that models containing the year*Treatment interaction to carry more weight in the model set, but there was little support in the data for these models (Table 3.2).

The beta coefficients for the SHRUB by LANDSCAPE interaction model show that the effects of both SHRUB and LANDSCAPE were positive and significant with a significant negative estimate for the interaction (Appendix 3.2). Thus, research points

with either 1) higher than average shrub cover in more fragmented landscapes or 2) lower than average shrub cover in more intact landscapes had higher abundances than other possible combinations. Points located in highly fragmented landscapes with low shrub cover had the lowest abundances.

Occupancy, extinction, and colonization

We estimated site occupancy, probability of extinction, and probability of site colonization at each of the 90 sampling points used in this study; 20 points were experimental points and 70 points were control points. From 2003 to 2004, 10 sites went extinct, and 18 were colonized (Table 3.5). One of the sites that went extinct one was a treatment point, while 2 sites that were colonized were also treatment points. From 2004 to 2005, 15 sites went extinct and 11 were colonized (Table 3.5). Of those that went extinct 22% (4 out of 18) were treatment points and of those that were colonized 27% (3 of 11) were treatment points.

In all of the models in the set for the occupancy analysis (Table 3.3), we modeled ψ as a function of the interaction between SHRUB and LANDSCAPE and p as a function of wind, temperature, date, and time. Recall that ψ establishes the baseline occupancy pattern in the first year of surveys, and thereafter changes in occupancy status are determined by ϵ and γ . Baseline occupancy results were consistent with the abundance results. Points with high shrub cover had highest occupancy rates, regardless of landscape level patterns. Points with lower than average shrub cover were occupied in contiguous landscapes, but were less likely to be occupied in fragmented landscapes (Figure 3.2).

When extinction and colonization were modeled with covariates, there was evidence that habitat variables affected extinction rates, but little evidence that habitat

variables or treatment affected colonization rates. Colonization rates were 0.33 for all sites regardless of the treatment or habitat conditions. Model averaged extinction probabilities (the probability a previously occupied site goes extinct) ranged between 0.08 and 0.16 (Figure 3.3). The top models in the model set indicate that extinction was function of the interaction between SHRUB and LANDSCAPE, where the interaction term was positive, but relatively weak (Appendix 3.3). The beta estimates from the top models overall suggest that as shrub cover and forest cover increase, extinction probability decreases with the landscape effect being a much stronger effect (Appendix 3.3). Points with lowest shrub density in fragmented landscapes were more likely to go locally extinct than other points (Table 3.3, Figure 3.3).

DISCUSSION

We used an experimental approach to test Hildén's hypothesis about avian habitat selection, where structural features of habitat at multiple spatial extents and the presence of other conspecifics may both be important proximate cues of habitat quality (Hildén 1965). Hildén noted that all elements need not be present to elicit a settling response, but that a combined effect of different elements must exceed some threshold to trigger settling. Additionally, one key stimulus may outweigh the others, such that in its absence birds will not settle, and in its presence birds may settle even in very suboptimal environments. We found that 1) habitat features describing territory- and landscape-level patterns were relatively more important than conspecific cueing for determining warbler occupancy and abundance patterns, 2) abundance patterns, occupancy rates, and

extinction rates were affected by an interaction between habitat features at different spatial extents, but not by interactions between habitat cues and social cues, and 3) conspecific vocal cues do not appear to either attract or deter settlement for black-throated blue warblers.

Our results for abundance and occupancy showed an effect of the interaction between territory- and landscape-level habitat patterns for both abundance and site occupancy. This interaction suggests cues at both extents are used by birds, where abundance and occurrence increase as shrub cover and forest intactness increase. In fragmented landscapes abundance is highest at points with high shrub cover and in contiguously forested landscapes abundance is higher at points with lower shrub cover. This interaction result is likely due to the overall distribution of shrubs in our study system where forest fragments have higher shrub density overall due to the effects of an ice storm that affected the region in 1998. Therefore, intact forested points had consistently adequate shrub cover, but it was lower overall than fragmented points.

Our experimental approach allowed us to examine changes in site occupancy patterns as they related to habitat and playback treatment. We found that extinction rates were also influenced by the interaction of understory shrub cover and landscape pattern, where points with low shrub cover in fragmented landscapes had higher extinction rates compared with points with low shrub cover in intact forests. Interpreting the mechanisms affecting such distribution patterns can often be difficult, especially in the absence of demographic data that can reveal population responses to habitat selection decisions. As the result of a previous study that examined the influence of habitat features at multiple spatial extents on demographic measures (Cornell, Chapter 2), we know quite a bit about

habitat patterns at different spatial extents interact to shape the abundance and occupancy patterns that were detected in this study. It appears that warblers use a combination of fine-scale understory shrub cover and landscape pattern as primary cues of territory selection decisions. However, choosing high shrub areas in fragmented landscapes may result in reduced fitness. We found that warblers breeding in such habitats were typically first-time breeders, had lower pairing success, and had reduced annual fecundity. Reduced reproductive success is likely as the result of increased brood parasitism rates in these areas, the influence of a more diverse predator community, and potentially by lower food availability. Thus, birds selecting territories in fragmented landscapes were more likely to fail in their reproductive efforts, potentially triggering them to vacate territories and move to new territories in subsequent years (Greenwood and Harvey 1982). In contrast, birds in contiguous landscape had higher annual productivity regardless of territorial shrub cover, and extinction rates of territories were lower due to either returning adults or colonization of new recruits

There are several plausible explanations for our failure to detect a strong effect of conspecific cueing on colonization. First, song may simply be the wrong cue that this species uses in social interactions. The songs we used were recorded from birds in New York and New Hampshire, but it's possible that dialects differ in Vermont. Additionally, birds may respond to the physical presence of other birds more strongly than to song. Where the boxes appeared to have triggered settling, we noticed that there typically two or more birds present such that each bird provided visual and physical stimuli in addition to increased vocal stimuli at the playback box locations. In many cases, we observed birds prospecting playback box locations but leaving if another bird was not also present.

Second, is possible that conspecific cueing plays a role in territory selection for this species at a different time during the annual cycle than when our study was conducted. Nocerra et al. (2006) found that in Bobolinks, first-time breeders use information about the location of adults at the end of the breeding season to make settlement decisions during their first breeding season in the following year. Such a seasonal influence on the importance of conspecifics may also be occurring in our system, but remains untested. We have observed that adults breeding on fragments tend to leave earlier in the season than adults breeding in contiguously forested landscapes (K. Cornell, unpublished data). If prospecting happens in the fall based on adult locations, it would suggest that site colonization would be higher in these more forested areas.

We did not find conclusive evidence that conspecific vocalizations either attracted or deterred settlement. In the occupancy analysis, models that included treatment effects on colonization were not highly supported by the data ($w_i < 0.05$). These models suggest that, if anything, the boxes were a deterrent rather than an attractant, but the precisions on these estimates were very low. If treatment did affect settlement, the signal needed to be great in order for our study design to detect it. It is possible that competition between individuals of the same species may inhibit settling, even if the features of habitat are sufficient for breeding (Hildén 1965). There is strong evidence in black-throated blue warblers that despotic interactions force birds from packing tightly in high quality areas (Rodenhouse et al. 2003b). To further elucidate the mechanisms driving settlement patterns it may be beneficial to radio-tag birds and measure interactions among individuals directly and how conspecifics affect fitness of neighbors (Silllett et al. 2004).

In summary, we found little evidence that vocal conspecific cueing influenced abundance and site occupancy patterns. The results of our field experiment showed strong evidence that habitat conditions at both the territory and landscape levels were the most important cues affecting habitat selection decisions.

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TABLES

Table 3.1 Principle component loadings for the two shrub metrics and six landscape metrics. For shrubs, PC1 explained 56.8% and PC2 explained 100%. Sites with SHRUB PC1 score had high leaf densities in the understory and an overall high amount of shrub cover of species used by warblers. For landscape, PC1 explained 91% of the total variation and PC 2 explained 96% of the total variation. Sites with high LANDSCPAE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e. they were more contiguous).

Shrub metrics	SHRUB		Landscape metrics	LANDSCPAE	
	PC1	PC2		PC1	PC2
Leaf density	0.71	0.71	Percent forest cover	0.41	0.38
Shrub cover	0.71	-0.71	Percent core forest cover	0.41	0.26
			Patch density	-0.42	0.33
			Edge density	-0.42	0.35
			Mean patch area	0.41	-0.48
			Mean patch shape index	0.38	0.57

Table 3.2. Models of abundance of black-throated blue warblers in Vermont, USA, scaled deviance ($-2 \log$ likelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).

Model No.	Model	K	$-2(L)$	ΔAIC_c	w_i
9	SHRUB * LANDSCAPE	4	502.69	0.00	0.89
12	SHRUB * LANDSCAPE + treatment	6	502.69	4.17	0.11
2	LANDSCAPE	2	519.08	12.29	0.00
5	SHRUB + LANDSCAPE	3	518.67	13.92	0.00
7	LANDSCAPE + treatment	4	519.08	16.39	0.00
8	SHRUB + LANDSCAPE + treatment	5	518.67	18.06	0.00
11	LANDSCAPE * treatment	6	519.01	20.50	0.00
13	SHRUB * treatment + LANDSCAPE	7	518.49	22.08	0.00
14	LANDSCAPE * treatment + SHRUB	7	518.60	22.19	0.00
1	SHRUB	2	533.08	26.29	0.00
17	Year*treatment + landscape	12	518.72	33.10	0.00
3	treatment	3	534.05	29.30	0.00
6	SHRUB + treatment	4	533.06	30.37	0.00
4	Year	4	533.97	31.28	0.00
10	SHRUB * treatment	6	532.87	34.36	0.00
15	Year*treatment	11	533.66	45.84	0.00
16	Year*treatment + shrub	12	532.67	47.05	0.00

Table 3.3. A 95% confidence set of models of site occupancy for black-throated blue warblers in Vermont, USA, number of model parameters (K), deviance, scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c). In all models, ψ was modeled as a function of SHRUB* LANDSCAPE and capture probability, p , was modeled as a function of the additive effects of wind intensity, average daily temperature, date of survey, and time of day.

Model	K	Deviance	ΔAIC_c	w_i
$\epsilon(\cdot), \gamma(\cdot)$	13	606.89	0.00	0.14
$\epsilon(\text{SHRUB*LANDSCAPE}), \gamma(\cdot)$	16	598.30	0.08	0.14
$\epsilon(\text{LANDSCAPE}), \gamma(\cdot)$	14	604.59	0.51	0.11
$\epsilon(\text{Treatment}), \gamma(\cdot)$	14	605.11	1.03	0.08
$\epsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{LANDSCAPE})$	17	597.08	1.90	0.05
$\epsilon(\text{LANDSCAPE}), \gamma(\text{LANDSCAPE})$	15	603.21	2.02	0.05
$\epsilon(\text{SHRUB}), \gamma(\cdot)$	14	606.58	2.51	0.04
$\epsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{Treatment})$	17	597.73	2.55	0.04
$\epsilon(\text{Treatment}), \gamma(\text{LANDSCAPE})$	15	603.79	2.60	0.04
$\epsilon(\text{LANDSCAPE}), \gamma(\text{Treatment})$	15	604.01	2.82	0.03
$\epsilon(\text{Treatment}), \gamma(\text{Treatment})$	15	604.15	2.96	0.03
$\epsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{SHRUB})$	17	598.30	3.13	0.03
$\epsilon(\text{LANDSCAPE}), \gamma(\text{SHRUB})$	15	604.58	3.39	0.03

Table 3.3. Continued.

Model	K	Deviance	ΔAIC_c	w_i
$\varepsilon(\text{SHRUB}), \gamma(\text{LANDSCAPE})$	15	604.85	3.66	0.02
$\varepsilon(\text{Treatment}), \gamma(\text{SHRUB})$	15	605.11	3.92	0.02
$\varepsilon(\text{LANDSCAPE} * \text{Treatment}), \gamma(.)$	16	603.02	4.79	0.01
$\varepsilon(\text{SHRUB} + \text{LANDSCAPE} + \text{Treatment}), \gamma(.)$	16	603.06	4.83	0.01
$\varepsilon(\text{SHRUB}), \gamma(\text{Treatment})$	15	606.13	4.94	0.01
$\varepsilon(\text{SHRUB}), \gamma(\text{SHRUB})$	15	606.56	5.37	0.01
$\varepsilon(\text{Treatment}), \gamma(\text{SHRUB} * \text{LANDSCAPE})$	17	600.60	5.42	0.01
$\varepsilon(\text{SHRUB} * \text{LANDSCAPE}), \gamma(\text{SHRUB} * \text{LANDSCAPE})$	19	594.34	5.52	0.01
$\varepsilon(\text{LANDSCAPE}), \gamma(\text{SHRUB} * \text{LANDSCAPE})$	17	601.15	5.97	0.01
$\varepsilon(\text{LANDSCAPE} * \text{Treatment}), \gamma(\text{LANDSCAPE})$	17	601.89	6.71	0.00
$\varepsilon(\text{SHRUB} + \text{LANDSCAPE} + \text{Treatment}),$ $\gamma(\text{LANDSCAPE})$	17	601.99	6.81	0.00

Table 3.4. Models of black-throated blue warbler detection on counts in Vermont, USA, number of parameters (K), scaled deviance (-2 loglikelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c).

Model No.	Model	K	-2(L)	ΔAIC_c	w_i
12	Wind + Mean daily temperature	3	1400.75	0.00	0.63
10	Wind	2	1405.90	3.14	0.13
8	Year	2	1407.59	4.83	0.06
13	Global	9	1393.55	4.86	0.06
11	Mean daily temperature	2	1408.74	5.98	0.03
6	Date	2	1408.97	6.21	0.03
1	Intercept	1	1411.89	7.13	0.02
7	Time of day	2	1410.22	7.46	0.02
9	Time of day + Date + Year	4	1407.23	8.48	0.01
4	Understory shrub	2	1411.38	8.62	0.01
2	Forest amount	2	1411.69	8.94	0.01
3	Total edge	2	1411.72	8.96	0.01
5	Understory shrub + Forest amount + Total edge	4	1411.29	12.55	0.00

Table 3.5. Summary of sampling points that went extinct or were colonized in each of the two experiment categories for each of the two time periods of the study.

Year	Experiment category	Extinct	Colonized
2003-2004	Treatment	1	2
	Control	9	16
	Total	10	18
2004-2005	Treatment	4	3
	Control	11	8
	Total	15	11

FIGURES

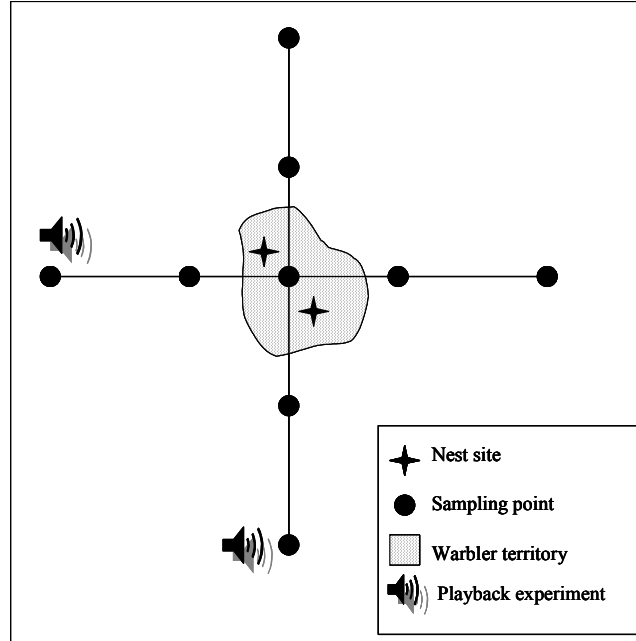


Figure 3.1. Schematic of a single research site ($n = 10$ sites). Shaded area represents a randomly selected warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey points at 250m and 500m from a random center survey station, speakers represent experimental treatment points ($n = 2$) where playback vocalizations were broadcast. The seven remaining sampling points were classified as controls. SHRUB metrics were estimated at each of the nine sampling points.

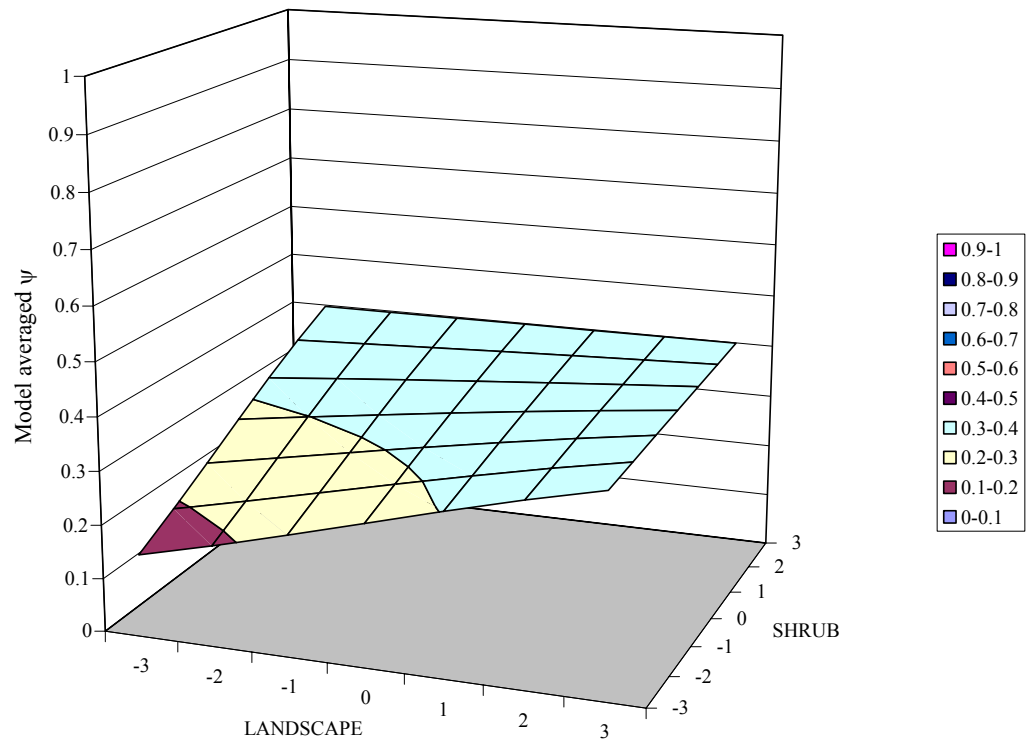


Figure 3.2 Surface plot of model averaged probability of sampling point occupancy (ψ) as a function of LANDSCAPE and SHRUB.

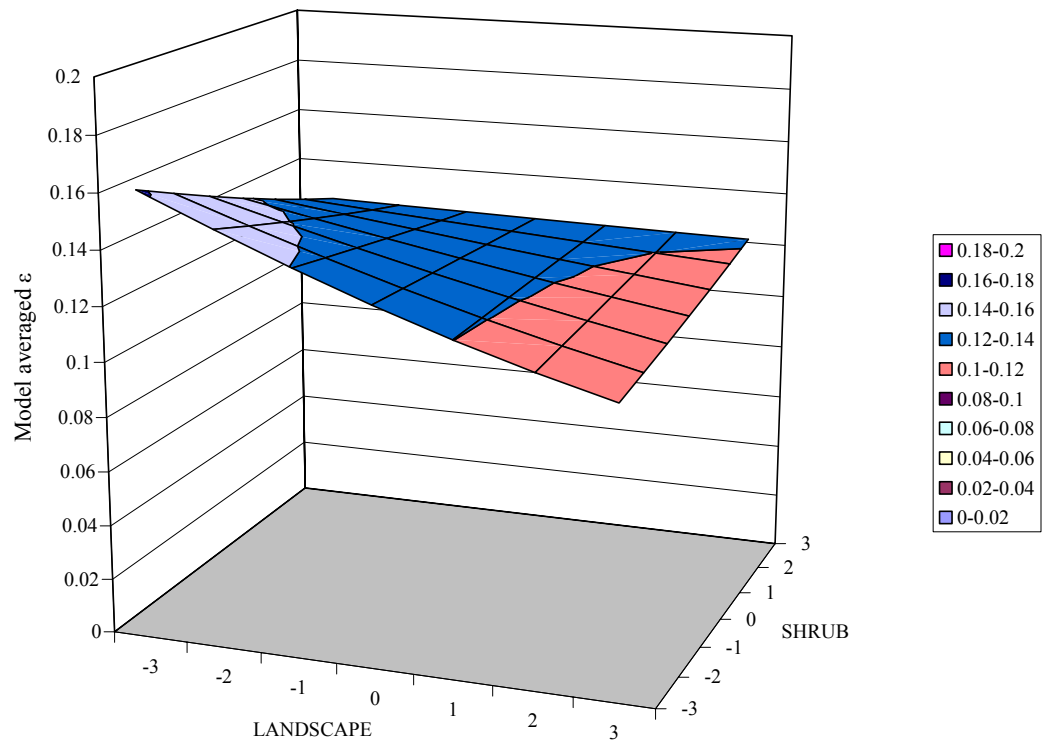


Figure 3.3 Surface plot of model averaged probability of sampling point extinction (ϵ) as a function of LANDSCAPE and SHRUB.

APPENDICES

Appendix 3.1. Coefficients (β) of black-throated blue warbler detection on counts in Vermont, USA, 2002-2004, and standard errors (in parentheses).

Model No.	Intercept	Forest amount	Total edge	Understory shrub	Date	Time of day	Year	Wind	Mean daily Temperature
1	-0.11 (0.08)								
2	-0.02 (0.21)	-0.16 (0.36)							
3	-0.11 (0.08)		-0.03 (0.08)						
4	-0.11 (0.08)			0.06 (0.09)					
5	-0.18 (0.36)	0.12 (0.64)	-0.03 (0.12)	0.07 (0.11)					
6	-0.11 (0.08)				-0.14 (0.08)				
7	-0.11 (0.08)					-0.11 (0.09)			
8	0.01 (0.10)						-0.36 (0.18)		
9	-0.03 (0.12)				-0.05 (0.11)	-0.05 (0.10)	-0.24 (0.27)		
10	-0.11 (0.08)							-0.20 (0.08)	

Appendix 3.1 Continued.

Model No.	Intercept	Forest amount	Total edge	Understory shrub	Date	Time of day	Year	Wind	Mean daily Temperature
11	-0.11 (0.08)								-0.14 (0.08)
12	-0.11 (0.08)							-0.23 (0.09)	-0.19 (0.08)
13	0.06 (0.38)	-0.09 (0.68)	-0.02 (0.14)	0.12 (0.12)	-0.04 (0.14)	0.02 (0.11)	-0.34 (-0.34)	-0.28 (0.09)	-0.2 (0.09)

Appendix 3.2. Coefficients (β) of black-throated blue warbler abundance in Vermont, USA, 2002-2004, and lower and upper 95% confidence intervals (in parentheses). Year three of this study (2005) was the reference year for all models.

Model No.	Intercept	SHRUB	LANDSCAPE	Treatment-0	Year-1
1	-0.16(0.07)	0.06(0.06)			
2	-0.24(0.07)		0.11(0.03)		
3	-0.15(0.07)			-0.03(0.18)	
4	-0.13(0.11)				-0.05(0.16)
5	-0.24(0.07)	0.04(0.06)	0.11(0.03)		
6	-0.15(0.07)	0.06(0.06)		-0.03(0.18)	
7	-0.24(0.08)		0.11(0.03)	-0.01(0.18)	
8	-0.24(0.08)	0.04(0.06)	0.11(0.03)	-0.01(0.18)	
9	-0.27(0.08)	0.12(0.07)	0.13(0.03)		
10	-0.15(0.07)	-0.07(0.17)		-0.03(0.18)	
11	-0.23(0.08)		0.11(0.03)	-0.03(0.20)	
12	-0.27(0.08)	0.12(0.07)	0.13(0.03)	0.00(0.18)	
13	-0.24(0.08)	0.05(0.07)	0.11(0.03)	0.00(0.18)	
14	-0.23(0.08)	0.04(0.06)	0.11(0.03)	-0.02(0.20)	
15	-0.14(0.13)			0.04(0.26)	-0.04(0.17)
16	-0.14(0.13)	0.04(0.26)		0.04(0.26)	-0.04(0.17)
17	-0.23(0.13)		0.11(0.03)	0.07(0.26)	0.02(0.18)

Appendix 3.2. Continued.

Model		SHRUB*	SHRUB*	LANDSCAPE*	YEAR *
No.	Year - 2	LANDSCAPE	Treatment	Treatment	Treatment
1					
2					
3					
4	-0.03(0.16)				
5					
6					
7					
8					
9		-0.12(0.03)	-0.07(0.17)		
10					
11				0.02(0.08)	
12		-0.12(0.03)			
13			-0.07(0.17)		
14				0.02(0.08)	
15	0.02(0.18)				-0.19(0.38)
16	0.02(0.18)				-0.19(0.38)
17	0.02(0.18)				-0.19(0.38)

Appendix 3.3. Coefficients (β) of black-throated blue warbler occupancy (ψ), extinction (ε), and colonization (γ) for the five supported models, and standard errors (in parentheses).

Model	Parameter	Intercept	SHRUB	LANDSCAPE	Treatment	SHRUB* LANDSCAPE
$\varepsilon(\cdot), \gamma(\cdot)$	ψ	0.62 (0.41)	0.19 (0.1)	0.15 (0.06)		-0.05 (0.02)
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\cdot)$	ψ	0.61 (0.38)	0.2 (0.11)	0.15 (0.06)		-0.05 (0.02)
$\varepsilon(\text{LANDSCAPE}), \gamma(\cdot)$	ψ	0.63 (0.39)	0.19 (0.10)	0.16 (0.06)		-0.05 (0.02)
$\varepsilon(\text{Treatment}), \gamma(\cdot)$	ψ	0.63 (0.39)	0.19 (0.10)	0.16 (0.06)		-0.05 (0.02)
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{LANDSCAPE})$	ψ	0.47 (0.34)	0.19 (0.10)	0.13 (0.05)		-0.04 (0.02)
$\varepsilon(\cdot), \gamma(\cdot)$	ε	-1.29 (0.26)				
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\cdot)$	ε	-1.02 (0.30)	-0.03 (0.10)	-0.11 (0.05)		0.04 (0.02)
$\varepsilon(\text{LANDSCAPE}), \gamma(\cdot)$	ε	-1.15 (0.27)		-0.05 (0.04)		
$\varepsilon(\text{Treatment}), \gamma(\cdot)$	ε	-1.18 (0.27)			-1.41 (1.61)	

Appendix 3.3. Continued.

Model	Parameter	Intercept	SHRUB	LANDSCAPE	Treatment	SHRUB* LANDSCAPE
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{LANDSCAPE})$	ε	-1 (0.29)	-0.03 (0.10)	-0.10 (0.05)		0.04 (0.02)
$\varepsilon(\cdot), \gamma(\cdot)$	γ	-0.71 (0.34)				
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\cdot)$	γ	-0.66 (0.33)				
$\varepsilon(\text{LANDSCAPE}), \gamma(\cdot)$	γ	-0.71 (0.34)				
$\varepsilon(\text{Treatment}), \gamma(\cdot)$	γ	-0.74 (0.34)				
$\varepsilon(\text{SHRUB*LANDSCAPE}), \gamma(\text{LANDSCAPE})$	γ	-0.47 (0.32)		0.05 (0.05)		

CHAPTER 4. LANDSCAPE FRAGMENTATION DECOUPLES ABUNDANCE AND BREEDING PERFORMANCE IN A MIGRATORY SONGBIRD

Abstract. – Habitat quality is the suite of resources and environmental conditions that determine the presence, survival, and reproduction of an individual or population. Habitat selection theory assumes that high-quality habitats will be occupied at higher abundances than low-quality habitats. The distribution of individuals in relation to habitat quality is significant for determining population persistence. As habitats become modified due to anthropogenic causes, the environmental cues that birds use to select habitats may no longer be associated with adaptive fitness outcomes and thus individuals may make poor habitat choices. In such cases the value of population counts as indicators of habitat quality may be limited. We quantified relationships between abundance, daily nest survival, and annual fecundity for a migratory songbird, the black-throated blue warbler (*Dendroica caerulescens*) at 20 research sites in a heterogeneous landscape in Vermont, USA from 2002-2005. We found that the habitats preferred by warblers do not confer the highest fitness levels in terms of daily nest survival or annual fecundity, and overall the relationships between abundance, daily nest survival, and annual fecundity were weak. These findings imply that habitat selection decisions may be decoupled from realized fitness in this system. Further, we found that the primary ecological mechanisms driving disconnect between abundance and annual fecundity for black-throated blue warblers were predation, cowbird parasitism, and the frequency of double brooding. Thus, habitat use patterns reflected in abundance estimates may provide misleading information on the suitability of habitats in terms of fitness.

INTRODUCTION

A critical facet of modern land use planning is the inclusion of measures of landscape quality, including the capacity of habitats to support viable populations of wildlife species. By definition, habitat quality is the suite of resources and environmental conditions that determine the presence, survival, and reproduction of an individual or population (Hall et al. 1997). Most species occupy both high- and low-quality habitats throughout their range. The distribution of individuals in relation to habitat quality is significant for determining population persistence. As habitats worldwide become modified due to anthropogenic causes, low-quality habitats may become a more dominant component of the landscape for some species (Vitousek et al. 1997). These changes in the landscape quality may particularly affect migratory birds because they depend on a diverse assortment of habitats in wintering and breeding grounds, and on migration routes.

Management and conservation of species typically entails habitat management that presupposes some understanding of a species' needs. For example, the U.S. Endangered Species Act requires that critical habitats for endangered species be identified wherever they occur. Additionally, Partners-in-Flight, an international consortium of agencies, researchers, and land managers whose primary mission is to conserve birds throughout North America, develops conservation plans for each physiographic region in North America and sets management objectives for high-priority species. A primary need for virtually all high-priority species identified by PIF is the identification of high-quality breeding habitat (Sherry and Holmes 1999, Donovan et al. 2002).

For birds, and many other animal taxa, count data collected during standardized surveys form a primary source of information on a species' needs, including habitat use. Based on the results of these surveys, researchers infer habitat selection and preference according to the theory that individuals should reproduce and survive better in habitats they prefer (Hildén 1965). Thus, avian conservation strategies and management plans are often guided by the assumption that estimates of population size (abundance) are positively correlated with habitat quality (Vickery 1992). In some situations, density may be correlated with habitat quality, but not always. In 1983, Van Horne reported that density could be a misleading indicator of habitat quality if it were negatively correlated with critical population parameters that determine population change and suggested that demographic information on survival and annual fecundity would aid greatly in establishing the quality of a particular habitat. Martin (1992) built on Van Horne's suggestion by noting that correlations between abundance and habitat features are often used to identify critical habitat features for management purposes, but such correlations may spur management of habitat features that do not influence populations most directly.

In some avian systems, evidence suggests that population abundance may become decoupled from reproductive output. Purcell and Verner (1998) reported reduced nest success for California Towhees (*Pipilo crissalis*) in apparent sink habitats where densities were greater than in nearby source habitats. In a review of North American and European avian habitat studies, Bock and Jones (2004) found that density was negatively related to reproductive success more often in areas of human disturbance compared with natural areas. However, how widespread and under which environmental circumstances (i.e., spatial extent) this disconnect occurs, remains unknown.

Previous research conducted on the black-throated blue warbler (*Dendroica caerulescens*) in a heterogeneous landscape in Vermont demonstrates disconnect between abundance and reproduction (Cornell Chapter 2). In this species, abundance was most affected by territory-level shrub cover, where abundance was highest in study sites with highest shrub cover. However, annual fecundity was strongly associated with landscape pattern, where fecundity was highest in study sites located in contiguously forested landscapes compared with fragmented landscapes. In this system, fragmented study sites had overall higher shrub density, suggesting the relationship between abundance and annual fecundity may be decoupled.

In this study, we quantified the relationship between abundance and two measures of breeding performance, daily nest survival and annual fecundity, for a forest-nesting migratory songbird, the black-throated blue warbler in west-central Vermont, USA, and document mechanisms that lead to decoupling of demographic parameters. Our research objectives were to 1) assess patterns of warbler abundance, daily nest survival, and annual fecundity across 20 sites in central Vermont, U.S.A., from 2002-2004 as a function of vegetation pattern at three spatial extents, 2) evaluate strength and directions of relationships among abundance, daily nest survival, and annual fecundity, and 3) identify ecological mechanisms shaping reproductive success.

METHODS

Study species

The black-throated blue warbler is an insectivorous Nearctic-Neotropical migratory songbird. Males and females arrive in North America in early May to establish

breeding territories, and the breeding season lasts 3-4 months (Holmes et al. 2005). Black-throated blue warblers are common to forest patches across many different landscape types throughout Vermont, but appear to be patchily distributed (K. Cornell, unpublished data). Black-throated blue warblers are sexually dichromatic and highly territorial; males sing to defend exclusive territories during the breeding season (Holmes et al. 2005). Thus, males are easily counted in a variety of field conditions based on vocalizations, can be captured in mist-nets using the lure of conspecific playback, and banded for individual identification. Females build nests in understory shrubs, allowing for accurate assessment of both nesting success (the probability that a given nest will successfully fledge at least one offspring) and annual fecundity (the total number of fledglings produced per adult female across the entire breeding season). The most suitable and thus most productive territories have a high shrub density, low nest predation rates, and high food abundance (Steele 1992, Rodenhouse et al. 2003). Mean and modal clutch size is 4 (Holmes et al. 2005), and pairs can successfully raise two broods of young in a single breeding season.

Study Sites

We conducted field research from May to August 2002-2004 at 20 forested sites in Chittenden and Addison counties, Vermont, USA (Figure 4.1). Study sites were selected to span a wide gradient of forest fragmentation level (i.e., highly heterogeneous landscape composition versus homogeneously forested areas). The details associated with the composition and structure of forest habitat at these sites are described in Cornell, Chapter 2. We selected study sites by examining digital orthophoto quadrangles to locate accessible forest patches and by conducting site visits to determine potentially

suitable breeding habitat. Study sites were then chosen based on the presence of at least one black-throated blue warbler territory (i.e., one singing male) as of 1 June 2002 to ensure that the site was suitable for warbler use. At each study site, we randomly selected a single breeding pair that actively defended a territory and mapped territory boundaries based on male singing perches using a Global Positioning System (GPS). We referred to each of these as a “focal territory” of intense study. Study sites were at least 1 km apart in order to increase statistical independence between focal territories and predator communities.

Field Methods

At each of the 20 study sites, we randomly selected a sampling point within the focal territory and established 4 sampling points at 250 m in cardinal directions (Figure 4.2). The area encompassed by the sampling points was thus 323m². Within this area, we intensively studied black-throated blue warblers to assess abundance, daily nest survival, and annual fecundity.

Warbler abundance surveys.—At each of the five sampling points in each study site, two 10-minute, single-observer point counts were conducted in succession from 25 May to 15 July in 2002-2004. Surveys were conducted on mornings with low wind and no rain, between 0600h and 1100h. All surveys were conducted by experienced observers who recorded all black-throated blue warblers heard or seen (unlimited distance), the time at which each warbler was first detected, the distance category of detected individuals, the sex, and when possible, the age of adults (Graves 1997).

Daily nest survival and annual fecundity.— We captured and color-banded most adults (>98%) on focal territories in each year using mist nests and conspecific playback,

and thus, individuals were identifiable. We determined age of adults at time of banding based on plumage (Graves 1997). We located nests by intensive searching within the focal territory and at other points within each study area. Our nest sample included both re-nests after nest failure and second nests attempted after successfully fledging the first. Most nests were found during the building or incubation stage and checked every two to four days until fledging or failure. At each visit, we recorded date, time of visit, nesting stage (building, laying, incubation, nestling), description of contents, parental activity, and incidence of parasitism and/or predation. Nests were considered successful if at least one black-throated blue warbler fledged. All nestlings were weighed on day 6, and were assumed to have fledged. Annual fecundity was calculated as the total number of young fledged per female annually. Cause of failure (predation, parasitism by cowbirds (*Molothrus ater*), abandonment by female, and weather) was determined by condition of the failed nest. From these data, we also assessed how life history characteristics (adult female age, number of nest attempts, clutch size, and brood size) and ecological characteristics (predation rate, parasitism rate, growth rates of nestlings) affected annual fecundity.

Quantifying habitat.— We quantified habitat structure for each of the 20 study sites at three spatial extents, including: 1) territory-level understory shrub density occurring within each breeding territory, 2) patch-level understory shrub density occurring within 323m² of territories, and 3) landscape-level habitat patterns occurring within 5 km radius extents of territories. These habitat characteristics were used as explanatory variables for objective 1 of this study. We describe how each of these metrics was estimated below.

TERRITORY_SHRUB was a fine-scale habitat metric that described the general understory shrub cover associated with breeding attempts. This metric reflects habitat used by warblers for breeding. Four 11.2-m transects were delineated in the understory in cardinal directions within plots centered on each nest site. At the distal end of each transect, a ground-level, 9-m² plane was erected using two 3-m vertical poles set 3-m apart. We counted all leaves of all understory species that intersected this plane, and then standardized counts as *Z* scores. TERRITORY_SHRUB was computed for each of the 20 focal territories as the average of leaf counts across all four planes and nests within a territory for annual fecundity, but was used as a covariate for individual nest attempts for daily nest survival analyses.

PATCH_SHRUB described shrub cover within each 323m² study area. This metric reflected the quantity of available habitat for warbler use within the study area. We measured understory leaf density at each of the five sampling points (Figure 4.2) using the same methods as described for TERRITORY_SHRUB. PATCH_SHRUB was averaged across all five sampling points per study site and standardized as *Z* scores.

LANDSCAPE was a landscape-level habitat metric that described the composition and configuration of forested areas within 5 km of a focal territory. We characterized landscape pattern surrounding each study site using USGS/EPA MRLC land cover maps derived from a version of the 1992 National Land Cover Dataset (30 m pixel size; Vogelmann et al. 2001) and updated to include extent of developed land in Vermont as of 2002 (Spatial Analysis Lab, University of Vermont). Black-throated blue warblers breed mainly in deciduous or mixed/coniferous forests (Holmes et al. 2005). Thus, we used ArcGIS 9.1 (Esri, Inc) to reduce the original 18 land-use classes to eight

classes based on perceived biological relevance and ease of interpretation. The classes included (1) water, (2) barren, (3) developed land, (4), wetland, (5) deciduous and mixed-coniferous forest, (6) coniferous forest, (7) agriculture (row crop, hayfield, pasture), and (8) orchard and other agriculture.

We used the quantitative spatial analysis program FRAGSTATS (McGarigal and Marks 1995) to obtain specific measures of landscape composition and configuration within a 5 km radius area surrounding the center of each study site (Donovan et al. 2000). This scale was selected because it reflects the home range size of brown-headed cowbirds (Thompson 1994), a potentially important determinant of reproductive success in our system. In FRAGSTATS, we applied an 8-neighbor rule for delineating patches. We used the percent of landscape in the deciduous/mixed coniferous forest landuse category as a single landscape composition metric. Landscape configuration metrics included percent core deciduous/mixed coniferous forest area (defined as >120 m from edge), mean forest patch area, mean shape index, and edge density. We used a Principle Components Analysis to condense the five landscape measures into a single metric that explained 91.0% of the total variation among research sites (Table 4.1). We termed this component LANDSCAPE. Sites with high LANDSCAPE PC1 scores had high core forest area, large mean patch area, and a higher mean shape index, while sites with low LANDSCAPE PC1 scores were more heterogeneous with more isolated forest patches and more edge.

Statistical analyses

Our general approach was to use model selection and model averaging analytic methods (Burnham and Anderson 2002) to obtain precise and unbiased estimates for

abundance, daily nest survival, and annual fecundity at 20 study sites as a function of territory-, patch-, and landscape-level habitat variables.

The model set included a territory-level model containing TERRITORY_SHRUB as the explanatory variable, patch-level model with PATCH_SHRUB as the explanatory variable, and a landscape-level model with LANDSCAPE as the explanatory variable (models 1-3, Table 4.2). The model set also considered two-way additive, three-way additive, and two-way interactive combinations of these variables (models 4-10, Table 4.2). Finally, a global model with all effects and a null model that did not include habitat variables were evaluated (models 11 and 12, Table 4.2).

Abundance— The analysis of abundance for each site in each year consisted of two steps. First, we first corrected the raw (unadjusted) point count data by detection probability (Thompson 2002). To estimate detection probability (p , the probability that a black-throated blue warbler would be detected in a 10 minute point count, given it is present), we analyzed data using the Huggins (1989, 1991) closed-capture removal models within the Program MARK (White and Burnham 1999). The Huggins model allows analysis of covariates that may influence p . These analyses are described in detail in Chapter 2. Given the beta estimates from different models and weights, we model averaged to obtain an estimate of p for each survey conducted in this study (Burnham and Anderson 2002). The raw count data for each survey was then divided by the survey-specific model-averaged p to obtain a corrected abundance estimate.

Second, we analyzed the corrected abundance as a function of habitat features at territory, patch, and landscape extents. For each of the 12 models in the model set, we specified the Poisson distribution and designated study site as a repeated factor. We

assessed fit of the Poisson distribution by evaluating the ratio of deviance divided by degrees of freedom for the most saturated model (model 11, Table 4.2). We used parameter estimates and weights associated with each model to derive a model-averaged estimate of abundance per site per year.

Daily nest survival.—For daily nest survival, we evaluated the model set containing the 12 models representing habitat features at territory, patch, and landscape extents (Table 4.2) in SAS (SAS 8.2, 1999). To estimate daily nest survival, we employed the Logistic-Exposure model (Shaffer 2004). This method utilizes a generalized-linear-model approach based on a binomial distribution and a logit link function (PROC GENMOD; SAS 8.2, 1999). We used Hosmer and Lemeshow method (1989) to evaluate goodness-of-fit of the most parameterized model to the observed data. We computed the Akaike weights from the ΔAIC_c scores, and then model averaged to derive measures of daily nest survival for each research site in each year of the study. Daily nest survival was the probability that a give nest survives a day; daily nest survival raised to the number of days in the nesting cycle (21 days) yields nest success.

Annual fecundity.—We modeled annual fecundity as a linear function of habitat features at territory, patch, and landscape extents (Table 4.2) using PROC GENMOD (SAS 8.2, SAS 1999). For each of the 12 models, we specified the Poisson distribution and designated study site and female as a repeated factor. We tested for overdispersion of the data using the DSCALE option for our most parameterized model.

Objective 2: Relationships among abundance, daily nest survival, and annual fecundity—To quantify the statistical relationship between model-averaged abundance,

daily nest survival, and annual fecundity, we examined univariate and polynomial regression and logistic models (PROC REG, PROC LOGISTIC, SAS 8.2, 1999).

Objective 3: Mechanisms shaping annual fecundity.—For each breeding female, we used generalized linear regression models to evaluate variation in annual fecundity as a function of clutch initiation dates, number of attempts per season, clutch size, brood size, female age, number of cowbird eggs and fledglings, number of broods, failure due to predation, failure due to parasitism . We also examined relationships between these same life history or ecological factors and territory-, patch-, and landscape-level habitat patterns (PROC REG, PROC LOGISTIC, SAS 8.2, 1999).

RESULTS

Objective 1: abundance, daily nest survival, and annual fecundity

Abundance.—We conducted a total of 600, 10-minute counts from 2002-2004 and counted a total of 665 male black-throated blue warblers. Our ability to detect warblers on point counts, given presence, was high, ranging from 93% to 100%.

Multiple models were supported in the data (having $\Delta\text{AICc} < 2$; Table 4.2), but overall territory- and landscape-level habitat variables were most important for affecting abundance patterns. A model containing a two-way interaction between these two extents carried the most weight (0.20; Table 4.2). Model-averaged results show that sites with high territory-level shrub density and sites located within intact landscapes had high abundance (Figure 4.3, Appendix 4.1). However, the highest abundances occurred in fragmented sites with high territory-level understory shrub density (Figure 4.3)

suggesting that habitat pattern at nest sites is an important cue used by individuals for territory selection. This pattern held across all years of the study.

Daily nest survival.--We monitored 133 black-throated blue warbler nests for daily nest survival from 2002-2004 for a total of 832 intervals. Additive effects of habitat patterns at territory, patch, and landscape levels affected daily nest survival (Table 4.2). Nest survival was lowest at sites where territory- and patch-level shrub covers were highest (Figure 4.4, Appendix 4.2). There was little effect of landscape on whether or not nests were successful (Figure 4.4, Appendix 4.2). These patterns were consistent across years, but overall, daily nest survival was lower in 2002 than in either 2003 or 2004.

Annual fecundity.--We monitored 63 females for annual fecundity analyses across the 20 study sites from 2002-2004. Annual fecundity ranged from zero to eight warbler young fledged across all sites and all years. Models with territory-level shrub cover, and the interaction between territory- and landscape-levels were most supported in the data (Table 4.2). In each year, annual fecundity increased as forested landscapes became more contiguous, but declined as TERRITORY_SHRUB increased across all sites (Figure 4.4, Appendix 4.3). The same pattern held at the patch-level, although the effect patch-level shrub cover was weaker (Appendix 4.3).

Objective 2: relationships among abundance, daily nest survival, and annual fecundity

Model averaged abundance was correlated with model averaged daily nest survival in 2004 and totaled over all years of the study (Table 4.3). There was a positive correlation between abundance and annual fecundity in 2003 and when data were pooled over all years (Table 4.3). We also examined whether annual fecundity at each site

reflected daily nest survival rates. We found that nest success and annual fecundity were correlated in 2003 and over all years of the study (Table 4.3).

Objective 3: mechanisms shaping reproductive success

We evaluated multiple life history characteristics and ecological factors to determine the mechanisms shaping reproductive success for black-throated blue warblers and to identify the factors influencing the observed disconnect between abundance and reproduction across our study area. We evaluated whether annual fecundity varied as a function of female age, clutch size, timing of breeding (clutch initiation), number of nesting attempts per female, cause of failure including predation and parasitism, number of broods, and number of cowbird eggs and fledglings. We also tested for relationships between the proportion of nests that failed due to predation or parasitism with landscape pattern and the proportion of females that double-brooded as a function of landscape pattern. For these analyses, we pooled data across all years.

Clutch size, clutch initiation, and age.— Clutches of black-throated blue warblers ranged in size from one to five eggs with a median of four. Clutch initiation dates ranged from 17 May to 10 July. Annual fecundity was not affected by clutch initiation date but increased with clutch size (Table 4.4). There was no effect of female age on annual fecundity (Table 4.4).

Nesting attempts and double brooding. – The number of attempts per female per season ranged from one to four with a median of 1.5. During the three years of this study, 13 of 70 individually marked females (18.5%) fledged a second brood after successfully fledging a first brood. Annual fecundity was not related to the number of

attempts a female made during a given season, but was influenced by whether or not a female produced two successful broods in a season (Table 4.4).

Cause of failure. – Predation and parasitism were the two major causes of nest failure in our system (K. Cornell, unpublished data). In our sample of nests for individually banded females, 40 nests of 70 (57.0%) were successful, 16 failed due to predation (22.9%) and 14 (20%) failed due to parasitism. The number of cowbird eggs observed in black-throated blue warbler nests ranged from zero to four with a median of zero, and the number of cowbird fledglings per female per year ranged from 0 to 2. Annual fecundity declined as both a function of predation and parasitism, however, the effect of parasitism was a significant factor affecting reproduction in this system (Table 4.4). Both the number of cowbird eggs and the number of cowbird fledglings had a significant negative effect on the number of black-throated blue warblers fledged per female.

Relationships of demographic mechanisms with habitat patterns. –To further address the causes of decoupling between abundance and annual fecundity, we evaluated whether predation, parasitism, and double-brooding varied as a function of landscape pattern or territory-level shrub density. Both predation and parasitism varied with landscape pattern, but the effects were in opposite directions: nests at sites in more intact landscapes failed as result of predation more frequently than nests in fragmented sites, but nests in fragmented landscape failed more frequently due to parasitism than nests in sites in contiguous forest (Table 4.5). The frequency of double brooding increased in contiguous forest sites, but the effect of landscape pattern was not significant (Table 4.5).

There was no effect of territory-level shrub cover on failure due to predation or parasitism, or on the frequency of double brooding (Table 4.5).

DISCUSSION

A potential flaw in the evaluation of habitat quality is the assumed relationship between habitat selection and fitness. Under certain circumstances, the link between population abundance and fitness may become disconnected, leading to the management of habitats which may not be the most suitable in terms of individual fitness. Thus, the best measures of habitat quality test the effects of habitat on demographic parameters related to population growth and decline, and directly quantify the relationships between population abundance and reproductive performance. In this study, we found that the habitats preferred by black-throated blue warblers do not confer the highest fitness levels in terms of reproductive output, and overall the relationships between abundance, daily nest survival, and annual fecundity were weak. These findings imply that habitat selection decisions may be decoupled from realized fitness in this system. Further, we found that the primary ecological mechanisms driving disconnect between abundance and annual fecundity for black-throated blue warblers were cowbird parasitism and the frequency of double brooding. We discuss these, and other possible mechanisms of decoupling as they relate to our system.

We observed that although black-throated blue warblers preferred high shrub density areas, as reflected in higher abundance in high shrub sites, nest success at these same sites was lowest. Thus, even nest success did not reflect habitat quality in our system. Nest success is an attractive metric for researchers because it can be measured

without color-banding individuals, which is time and labor intensive. Indeed, a recent review found that 54% of 356 articles reporting productivity estimators used variations of nest success, while only 10% reported annual fecundity (Thompson et al. 2001).

However, our results suggest the degree to which nest success accurately reflects habitat quality is questionable. The annual fecundity of a female bird is a function of the number of successful and unsuccessful nest attempts she makes, the probability that a nest will fledge young for any given attempt, and the number of young that are fledged from a successful attempt (Grzybowski and Pease 2005). All else being equal, a bird that attempts five nests that fail then fledges young on the 6th attempt may produce the same number of offspring per year as a bird that attempts a single nest that is successful.

Correlations between abundance and nest success and abundance and annual fecundity were weak overall, indicating that the applicability of abundance as a suitable measure of habitat quality is unfounded.

These patterns may become clearer when considered over longer time scales, with time lags, or by analyzing patterns at different spatial scales. First, in terms of time, we found that the relationships between abundance, nest success, and annual fecundity, were strongest when they were analyzed across all years of the study. These results emphasize the need for long-term demographic data from marked individuals (Sherry and Holmes 1999) because patterns detected from single-year studies may misrepresent longer-term patterns. Second, time lags between reproductive events and subsequent changes in population size may also be a factor influencing the lack of strong relationships within a given year (Kanick and Rotenberry 2000). Third, the spatial extent in which the analysis is conducted may influence whether abundance represents habitat quality. For example,

many forest songbird species have lower densities on small fragmented patches compared to larger patches (Faaborg et al. 1995). The strength of the relationships we observed may have been different if the spatial level of analysis was larger than the 323m² study site analyzed in this study (Brown et al. 1995).

Our observations of disconnect between abundance and nest success, and annual fecundity, are not unusual. There are plenty of studies in the literature where density or abundance has failed to predict habitat quality (e.g. Van Horne 1983, Purcell and Verner 1998, Rodenhouse et al. 2003, Bock and Jones 2004, Robertson and Hutto 2006). For example, grassland birds in the Champlain Valley of Vermont have high abundance on fields that are hayed repeatedly throughout the breeding season resulting in zero reproductive success for individuals breeding there (Perlut et al. 2006). There are also studies that show that abundance is a good predictor of quality (Brown et al. 1995). The questions that remain then are what mechanisms affect the linkage between these measures?

Our investigation of multiple life history characters and ecological factors revealed that cowbird parasitism and the frequency of double brooding were primary mechanisms working to disconnect the correlation between abundance and annual fecundity. In a previous study conducted near our study area, Coker and Capen (1995) documented that cowbird distribution was best explained by examining the area of the forest patch, the distance to the closest opening (potential feeding area), and the number of livestock areas (known feeding areas) within 7 km of a patch. Cowbirds play a dual role in reducing black-throated blue warbler annual fecundity in fragmented landscapes. First, cowbirds may have been the primary mechanism by which clutch size was reduced

in fragmented systems because cowbirds remove host eggs before parasitizing a nest (Lowther 1993). Second, they were a major cause of nest failure and abandonment in our system.

Although cowbirds play a strong role in reducing annual fecundity, the abundance on fragmented sites was higher than contiguous sites, presumably due to the higher shrub cover on these sites. High understory shrub cover in fragments was the partial result of an ice storm that affected our region and opened light gaps in the canopy layer of the forest. Thus, these sites likely appear very attractive to prospecting black-throated blue warblers resulting in relatively high abundances. Birds may not always be able to correctly perceive risks, especially in habitats affected by anthropogenic changes. Thus, their choice of habitats may not be the best in terms of their fitness (Schlaepfer et al. 2002). In human altered landscapes, the relationship between abundance and quality appears to decouple rapidly because environmental cues that birds use to select new habitats may no longer be associated with adaptive outcomes (Schlaepfer et al. 2002). Thus, individuals may make poor habitat choices because they need time to adjust to changing landscapes, either through adaptation or learning (Purcell and Verner 1998, Boal and Mannan 1999, Misenhelter and Rotenberry 2000, Battin 2004).

A second potential mechanism of decoupling was the frequency of double brooding, which could be related to a variety of ecological factors. In contiguously forested landscapes, the number of broods a pair can raise in a season is related to the availability of food resources (Nagy and Holmes 2005a, Nagy and Holmes 2005b). However, in addition to the influence of parasitism on fragments, food abundance may be lower on these sites (Burke and Nol 1998, Zanette et al. 2000) thereby limiting the

frequency of double brooding. We don't believe that double brooding is the primary mechanism causing the disconnect between abundance and annual fecundity for two reasons. First, we did not find direct evidence that landscape pattern affected whether or not females fledged second broods. Second, in a previous study conducted on forest fragments near our study areas, Hughes (2003) found that fragmented sites supported higher prey abundances than contiguous sites.

To summarize, we found no evidence of relationships between abundance, daily nest survival, and annual fecundity in our study. The disconnect between abundance and annual fecundity appears to be most affected by the influence of cowbird parasitism and the frequency of double brooding. These results emphasize the complexity of ecological systems, especially in changing landscapes, where multiple mechanisms may weaken the linkage between population abundance and habitat quality.

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TABLES

Table 4.1. Principle component loadings for five landscape metrics describing forest composition and configuration. PC1 explained 91% of the total variation and PC 2 explained 4% of the total residual variation. PC1 was used as an explanatory variable in 1 abundance, daily nest survival, and annual fecundity analyses. Sites with high LANDSCAPE PC1 score had high amount of deciduous / mixed-deciduous forest in the landscape, high amounts of core forest area, large patch sizes, and low patch density and edge density (i.e., they were more contiguous).

Landscape metrics	LANDSCAPE	
	PC1	PC2
Percent forest cover	0.41	0.38
Percent core forest cover	0.41	0.26
Patch density	-0.42	0.33
Edge density	-0.42	0.35
Mean patch area	0.41	-0.48
Mean patch shape index	0.38	0.57

Table 4.2. Models of mean annual abundance, daily nest survival, and annual fecundity of black-throated blue warblers in Vermont, USA, number of estimable parameters (K), scaled deviance ($-2 \log$ likelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Statistics for best fit models are in bold. A year effect was included in all models.

Model No.	Model name	K	Abundance		Daily nest survival		Annual fecundity				
			$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i
1	TERRITORY	4	46.14	1.60	0.09	65.96	4.90	0.05	77.74	0.00	0.20
2	PATCH	4	47.11	2.56	0.06	70.93	9.87	0.00	80.21	2.46	0.06
3	LANDSCAPE	4	45.43	0.89	0.13	73.98	12.92	0.00	81.36	3.62	0.03
4	TERRITORY + PATCH	5	46.10	3.77	0.03	64.22	5.39	0.04	75.55	0.02	0.20
5	TERRITORY + LANDSCAPE	5	43.52	1.20	0.11	60.81	1.98	0.21	77.43	1.91	0.08
6	PATCH + LANDSCAPE	5	45.01	2.68	0.05	69.02	10.18	0.00	79.48	3.96	0.03
7	TERRITORY + PATCH + LANDSCAPE	6	42.83	2.80	0.05	56.54	0.00	0.55	75.52	2.30	0.06
8	TERRITORY * PATCH	6	45.61	5.58	0.01	63.73	7.19	0.02	75.49	2.28	0.06
9	TERRITORY * LANDSCAPE	6	40.03	0.00	0.20	60.25	3.71	0.09	73.55	0.34	0.17
10	PATCH * LANDSCAPE	6	41.62	1.59	0.09	66.17	9.63	0.00	79.26	6.04	0.01
11	Global	9	37.65	5.05	0.02	54.49	5.38	0.04	71.95	6.19	0.01
12	Null	3	47.13	0.44	0.16	74.01	10.81	0.00	81.37	1.48	0.10

Table 4.3. Spearman correlation coefficients of relationships between model averaged abundance, model averaged daily nest success, and model averaged annual fecundity.

	Abundance				Daily nest survival				Annual fecundity			
	2002	2003	2004	Total	2002	2003	2004	Total	2002	2003	2004	Total
Abundance	1	1	1	1	0.426 (0.061)	0.346 (0.160)	-0.565 (0.015)	0.322 (0.016)	0.212 (0.370)	0.65 (0.002)	0.272 (0.246)	0.546 (<0.0001)
Daily nest survival					1	1	1	1	0.030 (0.900)	0.476 (0.046)	-0.327 (0.185)	0.444 (0.001)
Annual fecundity									1	1	1	1

Table 4.4. Models of annual fecundity, intercept with standard error, beta coefficient with standard error, and ANOVA summary statistics.

Response variable	Predictor variable	Intercept	Beta coefficient	F	df	P
Annual fecundity	Clutch size	-0.266 (1.262)	1.003 (0.356)	7.94	37	0.008
Annual fecundity	Clutch initiation date	2.448 (0.647)	0.005 (0.005)	1.15	56	0.288
Annual fecundity	Female age	3.047 (0.536)	0.337 (0.72)	0.22	45	0.642
Annual fecundity	Nesting Attempts	2.053 (0.849)	0.597 (0.47)	1.61	56	0.209
Annual fecundity	Number of broods	2.018 (0.273)	3.899 (0.576)	45.80	56	0.000
Annual fecundity	Predation	3.528 (0.4)	-1.255 (0.827)	2.30	45	0.136
Annual fecundity	Parasitism	3.837 (0.354)	-2.838 (0.768)	13.76	56	0.001
Annual fecundity	Cowbird eggs	3.583 (0.361)	-1.172 (0.451)	6.74	45	0.013
Annual fecundity	Cowbird fledglings	3.546 (0.365)	-1.837 (0.791)	5.40	45	0.025

Table 4.5. Logistic models of three mechanisms affecting annual fecundity (predation, parasitism, and double-brooding) as a function of landscape- and territory- level habitat features, model intercept with standard error, beta coefficient with standard error, Wald chi-square estimates, and significance value.

Response variable	Predictor variable	Intercept	Beta coefficient	Wald χ^2	df	P
Predation	LANDSCAPE	-1.445 (0.423)	0.339 (0.199)	2.91	1	0.088
Predation	TERRITORY_SHRUB	1.211 (0.353)	0.111 (0.262)	0.18	1	0.671
Parasitism	LANDSCAPE	-1.409 (0.411)	-0.461 (0.184)	6.31	1	0.012
Parasitism	TERRITORY_SHRUB	-1.387 (0.375)	0.267 (0.261)	1.05	1	0.305
Double brood	LANDSCAPE	-1.396 (0.38)	0.216 (0.175)	1.52	1	0.217
Double brood	TERRITORY_SHRUB	-1.2 (0.351)	0.066 (0.267)	0.06	1	0.805

FIGURES

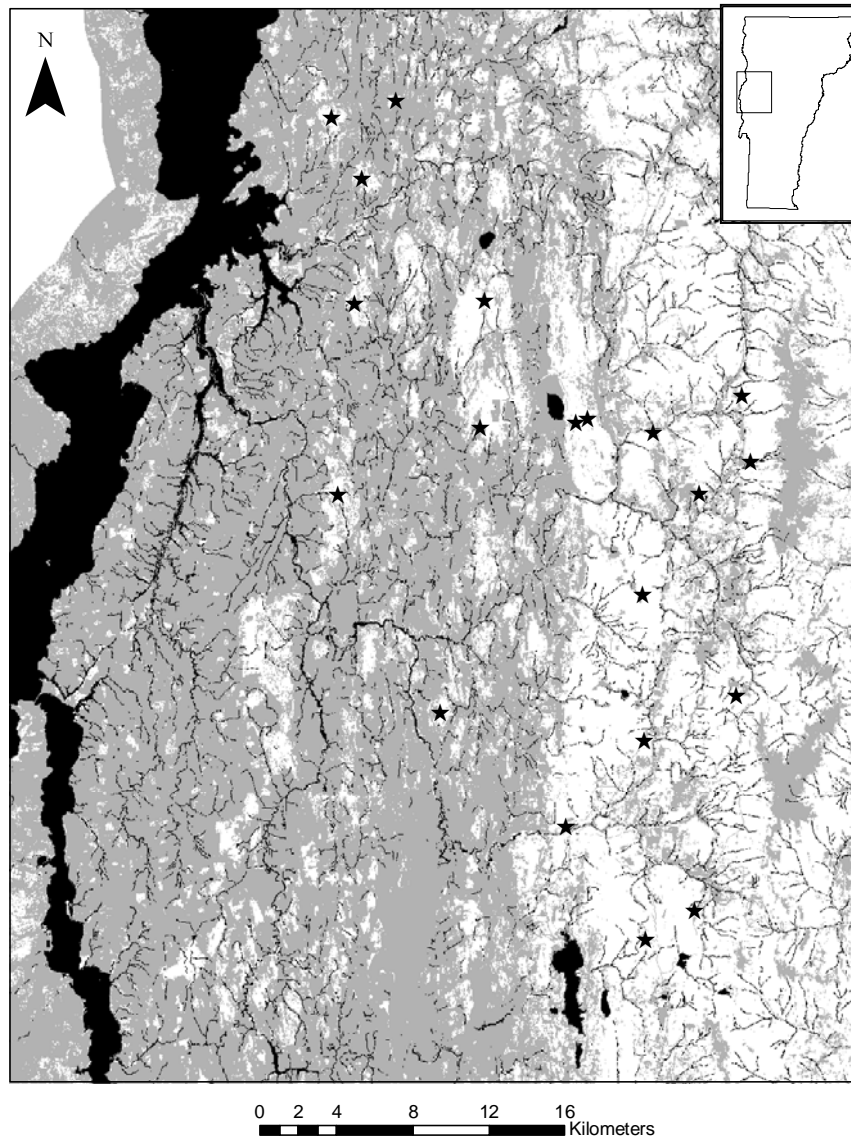


Figure 4.1. Twenty research sites in Chittenden and Addison Counties, Vermont, USA. Location of study region in Vermont is indicated on insert map. Black areas represent water; gray areas represent non-warbler habitat (urban, agriculture, coniferous forest); white areas represent mixed-deciduous and deciduous forested habitat. Stars indicate locations of research sites.

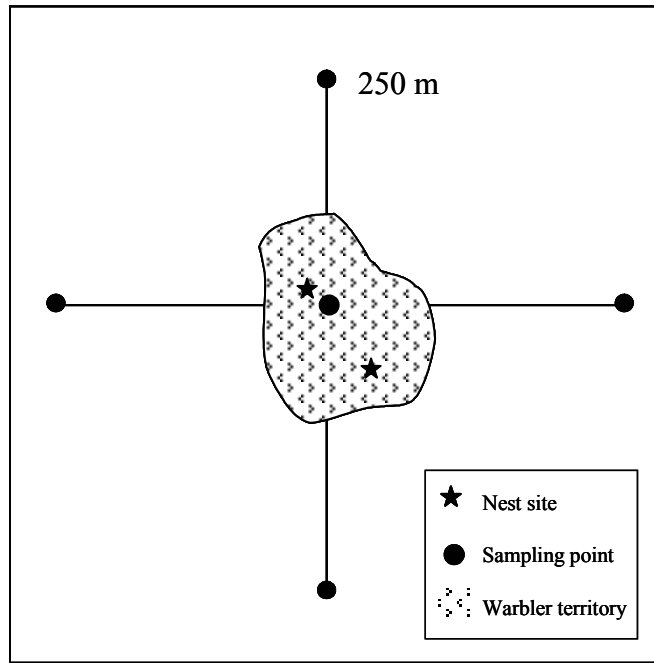


Figure 4.2. Schematic of a single research site. Shaded area represents a focal warbler territory; stars represent hypothetical nest locations; black lines indicate digital transects in cardinal directions; black circles represent survey stations at 250m and 500m from a random center survey station.

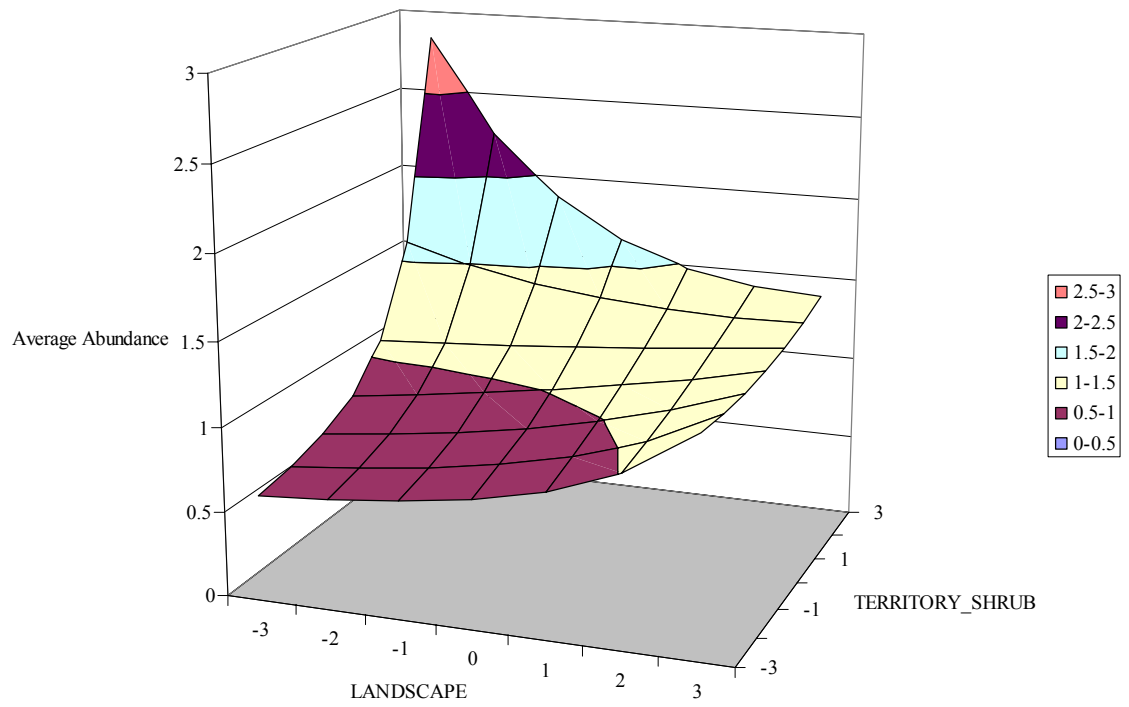


Figure 4.3. Surface plot of model average abundance as a function of territory- and landscape-level habitat patterns.

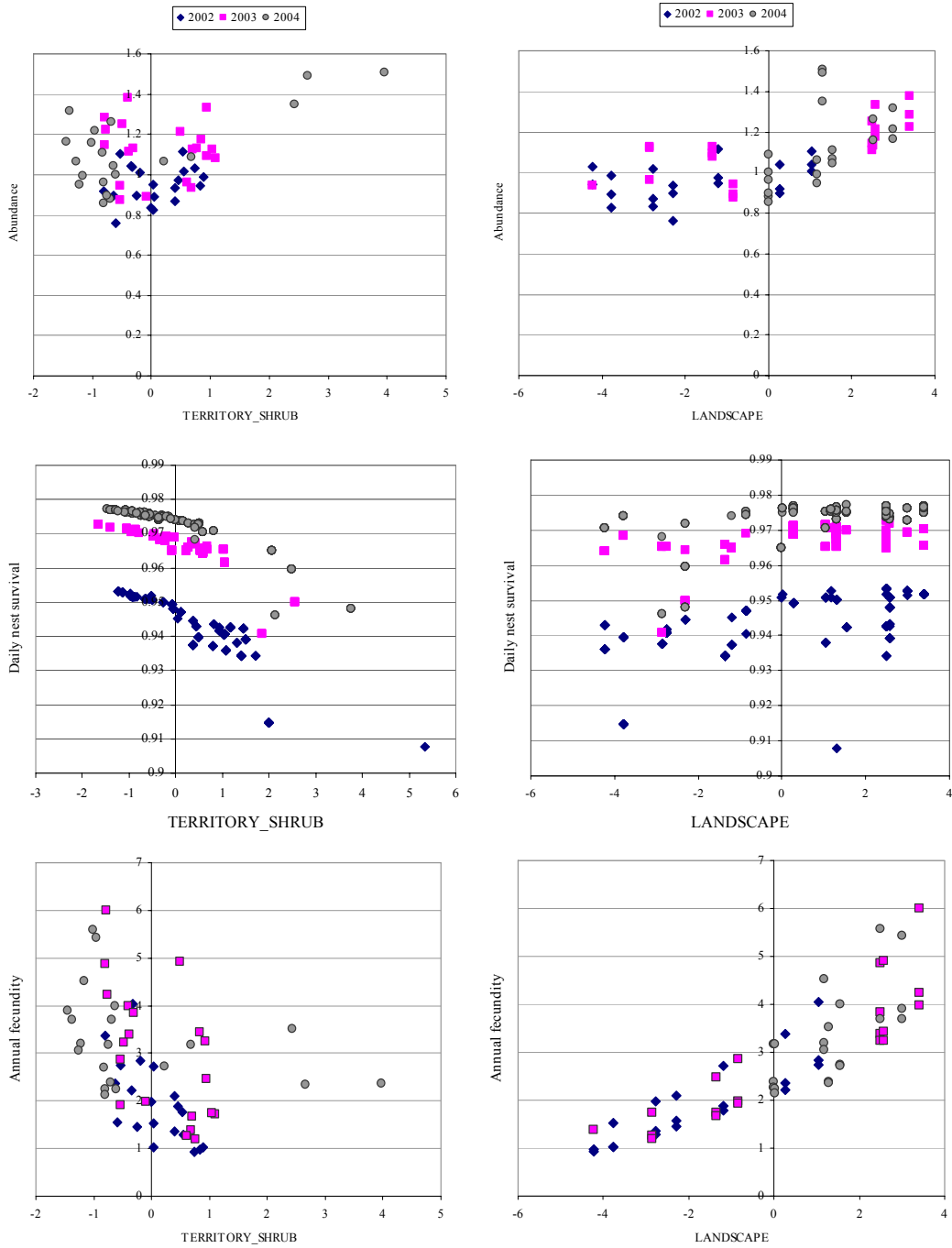


Figure 4.4. Scatter plots of model averaged abundance, model averaged daily nest survival, and model averaged annual fecundity as a function of territory- and landscape-level habitat patterns.

APPENDICES

Appendix 4.1. Coefficients (β) of abundance and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.

Model No.	Intercept	2002	2003	TERRITORY_ SHRUB	PATCH_ SHRUB
1	0.04 (0.2)	-0.05 (0.28)	0.07 (0.28)	0.12 (0.11)	
2	0.04 (0.2)	-0.02 (0.28)	0.07 (0.28)		-0.02 (0.12)
3	0.03 (0.2)	-0.02 (0.28)	0.07 (0.27)		
4	0.04 (0.2)	-0.05 (0.29)	0.07 (0.28)	0.12 (0.11)	-0.04 (0.12)
5	0.03 (0.2)	-0.06 (0.28)	0.07 (0.27)	0.16 (0.10)	
6	0.03 (0.2)	-0.02 (0.28)	0.07 (0.27)		0.13 (0.15)
7	0.02 (0.2)	-0.06 (0.28)	0.07 (0.27)	0.18 (0.10)	0.16 (0.15)
8	0.06 (0.2)	-0.05 (0.29)	0.07 (0.28)	0.08 (0.15)	0 (0.14)
9	-0.13 (0.21)	-0.07 (0.27)	0.1 (0.26)	0.39 (0.14)	
10	-0.07 (0.23)	-0.02 (0.28)	0.07 (0.27)		0.04 (0.18)
11	-0.18 (0.27)	-0.08 (0.31)	0.09 (0.3)	0.25 (0.22)	0.06 (0.21)
12	0.04 (0.2)	-0.02 (0.28)	0.07 (0.28)		

Appendix 4.2. Continued.

Model No.	LANDSCAPE	TERRITORY* PATCH	TERRITORY* LANDSCAPE	PATCH* LANDSCAPE
1				
2				
3	0.07 (0.05)			
4				
5	0.09 (0.05)			
6	0.11 (0.07)			
7	0.14 (0.07)			
8		-0.07 (0.16)		
9	0.14 (0.05)		-0.17 (0.08)	
10	0.11 (0.07)			-0.06 (0.068)
11	0.12 (0.08)	-0.24 (0.23)	-0.21 (0.11)	-0.05 (0.095)
12				

Appendix 4.2. Coefficients (β) of daily nest survival and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.

Model No.	Intercept	2002	2003	TERRITORY_ SHRUB	PATCH_ SHRUB
1	3.58 (0.23)	-0.68 (0.33)	-0.18 (0.32)	-0.21 (0.13)	
2	3.59 (0.23)	-0.75 (0.33)	-0.2 (0.33)		-0.08 (0.12)
3	3.58 (0.24)	-0.75 (0.33)	-0.21 (0.33)		
4	3.58 (0.23)	-0.67 (0.33)	-0.16 (0.33)	-0.2 (0.13)	-0.05 (0.13)
5	3.59 (0.24)	-0.68 (0.33)	-0.19 (0.33)	-0.22 (0.14)	
6	3.59 (0.24)	-0.75 (0.33)	-0.2 (0.33)		-0.07 (0.16)
7	3.61 (0.24)	-0.68 (0.33)	-0.17 (0.33)	-0.23 (0.14)	-0.11 (0.16)
8	3.67 (0.24)	-0.71 (0.33)	-0.26 (0.33)	-0.17 (0.13)	0.05 (0.15)
9	3.74 (0.27)	-0.72 (0.33)	-0.27 (0.33)	-0.24 (0.14)	
10	3.61 (0.27)	-0.74 (0.33)	-0.2 (0.33)		-0.04 (0.2)
11	3.74 (0.3)	-0.73 (0.33)	-0.28 (0.33)	-0.22 (0.15)	-0.03 (0.21)
12	3.61 (0.23)	-0.77 (0.32)	-0.23 (0.32)		

Appendix 4.2. Continued.

Model No.	LANDSCAPE	TERRITORY* PATCH	TERRITORY* LANDSCAPE	PATCH* LANDSCAPE
1				
2				
3	0.03 (0.06)			
4				
5	-0.01 (0.06)			
6	0.01 (0.07)			
7	-0.05 (0.08)			
8		-0.22 (0.13)		
9	-0.04 (0.07)		0.09 (0.06)	
10	0.01 (0.07)			0.02 (0.077)
11	-0.06 (0.09)	-0.17 (0.18)	0.04 (0.08)	-0.01 (0.087)
12				

Appendix 4.2. Coefficients (β) of annual fecundity and standard errors (in parentheses) for black-throated blue warblers in Vermont, USA, 2002-2004. Year 2004 was the reference year in the analysis.

Model No.	Intercept	2002	2003	TERRITORY_SHRUB	PATCH_SHRUB
1	1.24 (0.19)	-0.36 (0.3)	-0.4 (0.28)	-0.23 (0.14)	
2	1.26 (0.19)	-0.38 (0.3)	-0.43 (0.28)		-0.19 (0.14)
3	1.17 (0.19)	-0.35 (0.29)	-0.41 (0.27)		
4	1.22 (0.19)	-0.36 (0.3)	-0.4 (0.28)	-0.21 (0.13)	-0.18 (0.14)
5	1.15 (0.19)	-0.34 (0.29)	-0.39 (0.27)	-0.1 (0.12)	
6	1.16 (0.19)	-0.35 (0.29)	-0.41 (0.27)		0.09 (0.16)
7	1.15 (0.19)	-0.34 (0.29)	-0.39 (0.27)	-0.09 (0.13)	0.06 (0.17)
8	1.19 (0.19)	-0.34 (0.17)	-0.43 (0.15)	-0.44 (0.17)	-0.14 (0.15)
9	1.17 (0.19)	-0.35 (0.18)	-0.4 (0.06)	-0.15 (0.18)	
10	1.27 (0.2)	-0.35 (0.17)	-0.39 (0.07)		0.16 (0.17)
11	1.18 (0.23)	-0.33 (0.28)	-0.4 (0.13)	-0.2 (0.26)	0.08 (0.21)
12	1.28 (0.19)	-0.38 (0.31)	-0.43 (0.29)		

Appendix 4.2. Continued.

Model No.	LANDSCAPE	TERRITORY* PATCH	TERRITORY* LANDSCAPE	PATCH* LANDSCAPE
1				
2				
3	0.19 (0.06)			
4				
5	0.17 (0.06)			
6	0.21 (0.07)			
7	0.19 (0.07)			
8		-0.41 (0.2)		
9	0.17 (0.06)		0.03 (0.1)	
10	0.2 (0.07)			0.1 (0.078)
11	0.15 (0.09)	-0.22 (0.28)	-0.02 (0.13)	0.04 (0.105)
12				

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