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AN ASSESSMENT OF HABITAT QUALITY OF HEAVILY-AND LESS-BROWSED MICHIGAN FORESTS FOR A SHRUB-NESTING SONGBIRD

by

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of the requirements for the degree of
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CHAPTER I

CHALLENGES TO SONGBIRD CONSERVATION POSED BY ABUNDANT WHITE-TAILED DEER IN NORTHERN FORESTS

Introduction

In recent years, the effects of high populations of ungulates such as white-tailed deer (*Odocoileus virginianus*) on forested ecosystems has become recognized as a serious conservation issue in North America (e.g., McShea et al. 1997a, Warren 1997), and many other parts of the world (e.g., Teruaki 2000, Fuller and Gill 2001). For migratory songbirds that use forested habitat, alteration of that habitat by deer joins a long list of possible threats, including habitat fragmentation and loss, exposure to pesticides and other contaminants, introductions of exotic species, and collisions with human-made structures. If, as has been hypothesized by many researchers, these threats are leading to population declines for many songbird species (e.g., Askins et al. 1990, Robinson et al. 1995), understanding how deer can impact the remaining intact forests of the northern Great Lakes states may help managers protect birds that can act as sources for declining populations in other regions.

Neotropical migrant bird species are of conservation in northern forests both because of the hypothesized population declines, and because songbirds are well suited to act as indicators of the effects of deer management on forested ecosystems. Migratory bird populations make good forest-condition indicators because they are highly sensitive to changes in their habitat, are vulnerable to many different forms of environmental perturbation, and are relatively easy to monitor (Hutto 1998). Additionally, they are of great interest to the general public. From Rachel Carson's (1962) *Silent Spring*, which warned of a future in which pesticides have silenced the songs of birds, to John · Terborgh's *Where Have all the Birds Gone* (1989), conservationists have used the hypothesized decline of birds as a vehicle for raising public awareness and concern about environmental degradation and the loss of forests (Maurer and Villard 1996). By linking the study of "popular" migratory bird species with science-based ecosystem management, we expand our opportunities to increase public support for managing northern forests in ways that promote the conservation of biodiversity and maintenance of ecosystems.

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In the U.S., deer management has become a highly controversial topic. Many deer hunters and people that rely on revenues from hunters favor high populations, while groups such as the timber and insurance industries have suffered economic harm due to destructive effects of deer on regenerating trees, and increased rates of deer-car collisions (Diefenbach et al. 1997, Conover 1997). High deer populations also are a concern from the perspective of public and livestock health, as deer are a common host of the ticks that transmit the Lyme disease spirochete (*Borrelia burgdorferi*), and can be infected with and spread bovine tuberculosis (*Myobacterium bovis*) and a form of transmissible spongiform encephalopathy (TSE), chronic wasting disease (Ostfeld 1997, Daszak et al. 2000). Finally, attempts to control deer in parks and suburban areas have led to conflicts with animal rights activists and concerned citizens that enjoy watching deer (Conover 1997, Rutberg 1997). Together, the many types of deer impacts and the diverse group of stakeholders interested in deer management make deer-related conservation efforts a complex challenge that will require coordinated efforts from both scientists and policy makers.

In many parts of eastern North America, populations of white-tailed deer are currently at levels that greatly exceed densities estimated from the early 1900's (deCalesta and Stout 1997, McCabe and McCabe 1997). However, using the turn of the 20th century as a population-size reference point is potentially deceptive, because at that time deer populations were very low in most of this region, due primarily to extreme hunting pressure (McCabe and McCabe 1984, McCabe and McCabe 1997, McShea et al. 1997b). Aided by changes in land use, such as natural-area conversion to agriculture and silviculture, recovery programs for white-tailed deer populations were extremely successful. As a result of this success, many of the management practices that promoted high densities, such as supplemental feeding, habitat modification, and hunting regulations that favors bucks over does, have become firmly entrenched in the minds of many wildlife managers and deer hunters (Waller and Alverson 1997, Diefenbach et al. 1997). It is in this context of overexploitation, followed by what many researchers deem to be overabundance of deer, that conservation biologists are working to develop forest management plans that are inclusive of non-game species, and responsive to changes in deer numbers.

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The most obvious effects of high deer densities within forests are on understory plants. Where deer concentrate, there are often significant reductions in the density, height, and species diversity of shrubs and small trees (e.g., Stoeckeler et al. 1957, Tilghman 1989, Anderson and Katz 1993). Over time, as species fail to regenerate, intense browsing can change the structure and composition of forests (Anderson and Loucks 1979, Frelich and Lorimer 1985, Tilghman 1989, Anderson and Katz 1993, Van Deelen et al. 1996, Cornett et al. 2000). Although less visible than browse effects, areas frequented by deer may also show altered patterns of nutrient cycling and energy flow (Pastor and Naiman 1992, Hobbs 1996). In particular, sites supporting high deer densities are likely to have increased levels of soil nitrogen from deer wastes, a change in nutrient availability that can have strong impacts on understory species composition (McCollin et al. 2000). Similarly, the distribution of deer also can influence plant species composition through their role as seed dispersers (Gill and Beardall 2001). As information on the effects of deer on ecosystems has accumulated, researchers have hypothesized that there is potential for sustained high deer populations to lead to alternative stable states in forest plant communities (Stromayer and Warren 1997). If true, this result of alternative stable forest conditions suggests that reversing deer impacts and restoring former successional patterns will require a more complicated management approach, rather than a (theoretically) simple approach of reducing deer densities and waiting for the former forest conditions to re-appear (Stromayer and Warren, 1997).

Although most research and conservation attention on deer impacts has focused on rare plants and timber trees, evidence is accumulating that major changes in deer density can produce effects that ripple through all forest trophic levels (Waller and Alverson, 1997, McShea 2000). One complex set of interactions in which deer populations play a key role has been described by researchers studying gypsy moths (*Lymantria dispar*), acorn production (*Quercus* spp.), white-footed mice (*Peromyscus leucopus*), and black-legged ticks (*Ixodes scapularis*), the primary vector for Lyme disease (Ostfeld et al. 1996, Jones et al. 1998, Ostfeld and Keesing 2000). This research suggests that defoliation of trees by gypsy moths and the incidence of Lyme disease can be strongly influenced by masting oaks, because both deer and mice concentrate in oak forests to feed on acorns. This attraction of mice and deer to acorns leads to increased

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Lyme disease risk because deer are a common and highly mobile tick host, and white-footed mice are a highly competent reservoir-host for the spirochete that causes the disease. Mice also feed on pupae of the gypsy moth, which can reduce the chances of an outbreak of this introduced forest defoliator by keeping low populations from increasing. Additional research by McShea (2000) suggests that deer population densities may mediate the strength of these and other ecological chain-reactions associated with masting trees. In McShea's study, white-footed mouse and eastern chipmunk (*Tamias striatus*) population densities were significantly higher in non-mast years within deer exclosures, presumably due to reduced competition for the few acorns available. Adding another set of links to the chain, McShea (2000) also found that the best predictor of annual depredation rates on artificial bird nests was acorn production in the previous fall.

The complexity of possible interactions between high deer populations and other species makes predicting impacts on species of conservation concern particularly challenging. So far, evidence suggests that impacts can vary widely both by and within taxonomic groups, and that the highest levels of biodiversity for some taxa may occur at moderate levels of browse (McShea and Rappole 2000, Fuller and Gill 2001). For example, some butterflies in the United Kingdom benefit from deer keeping open fields in an early successional condition, but woodland butterfly populations may be reduced when deer consume the understory plants that species use for egg deposition or obtaining nectar (Feber et al. 2001). A key factor for butterflies is alteration of microclimate, which is likely also the case for many other forest invertebrates (Stewart 2001). More generally, invertebrate biodiversity and abundance are likely strongly linked to complexity of forest habitat, so browse-related reductions in habitat complexity are likely to lead to declines in invertebrate biodiversity (Stewart 2001).

Forest and deer management in the Great Lakes region
In the forests of the Great Lakes states, managers and conservation biologists face the challenge of finding a balance between the management of forests for timber, game species, and other sources of economic gain for local residents, and maintenance of ecosystem processes and biodiversity. In the eastern Upper Peninsula (U.P.) of Michigan, much of the forested land has traditionally been managed by the Michigan

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Department of Natural Resources or the U. S. Forest Service with goals of maximizing harvest of both timber and white-tailed deer. Together, timber and hunting-related resources are major contributors to local economies, so any change in management is likely to have wide-ranging influence and interest from local communities. Although many current land managers are working to broaden the scope of forest management goals to include non-game wildlife, in many areas promotion of high deer populations has already led to changes in habitat conditions (The Nature Conservancy 2000). Within the U.P., there is a gradient of higher browse pressure to lower from the south to the north due to concentration of deer in southern "deer yards," conifer stands that provide thermal protection during the winter (Van Deelen 1995). High deer densities have been further encouraged near deer yards through the creation of wildlife openings, and clear-cutting of aspen forests, both of which provide forage for deer. The Nature Conservancy (2000) has ranked high deer populations and the associated ecological damage as a top threat to ecosystem and biodiversity conservation in the Great Lakes region.

Linking deer and timber management to effects on songbirds in northern forests
Although studies of the effects of different types of timber management on bird species are becoming fairly common (e.g., Probst et al. 1992, Schulte and Niemi 1998, King and DeGraaf 2000), less work has been done to identify the effects of deer populations on songbirds. The primary effect of deer on songbirds is alteration of habitat, as low vegetation layers consumed by deer are used by many bird species for foraging and nesting. In general, there tends to be a link between understory vegetation volume and bird species richness and total abundance (Mills et al. 1991, Fuller and Henderson 1992). High deer populations have been correlated with reductions in some bird species' density, especially those that nest and forage in the shrub layer of the forest (Casey and Hein 1983, DeGraaf et al. 1991, deCalesta 1994, McShea et al. 1995, McShea and Rappole 2000, Perrins and Overall 2001). Within the same forest stand, however, effects on bird species can be mixed, as some species favor the habitat conditions produced by abundant deer (Casey and Hein 1983, McShea and Rappole 2000, Fuller 2001, Perrins and Overall 2001). Similarly, guilds of birds, such as ground-nesters, may respond positively to high deer densities in some areas, and negatively in other areas, due to differences in the

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species composition of understory and groundcover vegetation promoted by deer in particular areas (deCalesta 1994, McShea and Rappole 2000).

Browsing of forest-understory vegetation by deer can potentially impact breeding birds through many different mechanisms. As described above, the most obvious effects are likely to be related to changes in the structure and/or density of understory vegetation, which may alter the availability of nest sites or foraging habitat. Other possible links between deer browse intensity and bird populations include (1) changes in plant species composition, which may also alter food supplies or the availability of preferred nest sites; (2) changes in food supplies, through effects on the abundance of invertebrate prey species that utilize and compete with deer for particular types of understory foliage (Lynch and Whigham 1984, Fuller 2001); (3) changes in nesting success through reduction in nest-site vegetative cover, indirect effects on nest predator population sizes, or direct nest depredation or trampling (Martin and Roper 1988, Reitsma et al. 1990, McShea 2000, Pietz and Granfors 2000); and (4) changes in habitat characteristics that alter the abundance of other bird species that might compete for food or nest sites, or act as brood parasites. It is likely that eventually researchers will be able to tease apart the relative importance of various mechanisms for particular species, but first much remains to be done in terms of identifying patterns of bird distribution and reproductive success in a variety of forest types that experience different levels of deer browse.

Scope of the study

The first component of this study (Chapter 2) identifies general patterns in the distribution of migratory bird species in heavily-browsed and less-browsed sites within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula (U.P.). The hardwood forests in the HNF are managed for timber production, and those near traditional deer yards are heavily-browsed. For this component, I surveyed breeding birds in many hardwood stands, and used these data to estimate the relative abundance of species in forests with different understory conditions (high vs. low shrub density, heavily- vs. less-browsed). I hypothesized that bird species that require a dense understory would be less abundant in areas with low shrub-densities and/or high

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browse pressure, and other groups such as ground- and canopy-nesters would not show a consistent pattern with shrub density or browse level. In addition, I also tested whether the abundance of a browse-resistant conifer, balsam fir (*Abies balsamea*), in high shrub-density, heavily-browsed forest stands was a useful predictor of the abundance of birds and groups of bird species. My goal for this chapter was to identify species that are likely to be impacted, both positively and negatively, by the effects of abundant deer. This information can help to focus future research on those species most at risk, and provide information that managers can use to help incorporate conservation of songbirds into forest management plans.

In the second component of my study (Chapter 3), I focused on the demography and behavior of the black-throated blue warbler (*Dendroica caerulescens*), which may be particularly sensitive to browse effects because it requires a dense understory for both nesting and foraging (Holmes 1994). Blue warblers are also considered to be of conservation concern in northern Michigan by the Nature Conservancy (2000). Since browsing by deer reduces the total foliage area available for caterpillars, the preferred prey of blue warblers, it is possible that removal or reduction of the complexity of the understory layer will reduce the habitat quality of browsed habitats for this species. To examine whether there is evidence that heavily-browsed habitats are of lower quality, I tested the hypotheses that blue warblers in heavily-browsed habitats will have lower reproductive success (fewer second broods), a higher percentage of younger (second year) birds, and lower breeding-site fidelity than sub-populations in habitats with less evidence of deer browse. Examining the demographic parameters of a bird population provides information that allows a better understanding of what ecological factors might be leading to changes in population size. If these factors can then be manipulated through variations in deer or timber management, managers will have a better chance of developing long-term management plans that favor songbird population persistence.

Managing birds in heterogeneous landscapes requires information on what types of habitats are used, and the distribution of birds within those habitats. In the third component of my study (Chapters 4 and 5), I compare the territory sizes and spatial distributions of black-throated blue warblers within heavily-browsed and less-browsed forest stands. As described above, if food or other resources are less abundant or more

patchy due to the effects of deer, differences in the size of territories defended by birds, and/or how territories are arranged in space are likely to result (Chapter 4). In Chapter 5, I use a novel spatial analysis method, geographic boundary analysis, to help describe the patterns in understory vegetation on the two habitat types, and the distribution of blue warbler territories within these heavily- and less-browsed sites. In particular, these techniques allow forests to be visualized as mosaics, and provide a tool for understanding how the juxtaposition of different understory types might attract breeding birds to a particular location.

Finally, In Chapter 6 I present a summary of results, and a brief list of suggestions on how this information on the relationship between songbird distributions and demography can be further examined and incorporated into management of northern forests. The premise of this chapter is that it is likely that within the range of density levels typically seen in the HNF, browsing by deer will reduce habitat quality for some migratory bird species, while improving quality for others with different resource needs. In some cases, it may be beneficial to maintain some areas as heavily browsed to promote species that survive and reproduce the best in these types of habitats (McShea and Rappole 2000). On the other hand, browse-sensitive species may need special protection in order to persist, and there may be opportunities for managing browse-resistant plants to provide additional habitat. As the managers at the HNF have little control over how deer are managed throughout the U.P., management suggestions focus on approaches that might be possible through landscape-scale management plans. Through careful selection of the locations of various management actions such as forest cutting or thinning, deer effects could be concentrated in areas where they will do the least damage.

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CHAPTER II

SONGBIRD DISTRIBUTION PATTERNS IN MANAGED FORESTS: DEER-BROWSE PRESSURE IN NORTHERN MICHIGAN

Introduction

Unlike the fragmented forests found in much of the Midwest (e.g., Thompson et al. 1993, Robinson et al. 1995), the northern forests of the Great Lakes States are likely to provide important "source" habitats for many species of migratory songbirds. Many of these forests are on public lands, and managers face the challenge of finding a balance between managing the forests for timber and game species, and maintenance of ecosystem processes and biodiversity. As a result, efforts to protect songbirds and other non-game species must be developed within a complex management framework, which requires that conservation plans utilize information on how various forms of timber or wildlife management influence non-target species, such as songbirds. As is true of most changes in an ecological system, a change in forest characteristics that results from management actions is likely to benefit some species by improving habitat, and reduce habitat available for other species. Through providing information on distributions of songbirds in forests with different management histories, researchers can help resource managers meet the goal of assessing costs and benefits to these species within proposed forest management plans.

In many parts of eastern North America, populations of white-tailed deer (*Odocoileus virginianus*) are currently at levels that greatly exceed densities estimated for the early 1900's (deCalesta 1997, McCabe and McCabe 1997). Many negative effects have been linked to these high deer densities, ranging from reduced rates of timber-tree regeneration (e.g., Tilghman 1989, Rooney 2001), reduction of rare plant populations and associated insects (Miller et al. 1992, Feber et al. 2001), and local increases in ticks that carry Lyme disease (*Ixodes sp.*, Wilson et al. 1990). However, using the turn of the 20th century as a population-size reference point is potentially deceptive for the Great Lakes States because deer populations were very low at that time, with many local extirpations, due primarily to extreme hunting pressure (McCabe and

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McCabe 1984, McCabe and McCabe 1997, McShea et al. 1997). Aided by changes in land use (natural area conversion to agriculture and silviculture), recovery programs for white-tailed deer populations in the Great Lakes region have been extremely successful. As a result, many of the management practices that promoted high densities, such as supplemental feeding, habitat modification, and buck-biased hunting regulations, have become firmly entrenched in the minds of many wildlife managers and deer hunters (Waller and Alverson 1997, Diefenbach et al. 1997). The continuing debate as to whether there are too many, too few, or just enough deer can be best approached when information on how deer populations impact other species is available: Effects of deer on other species such as migratory birds helps provide a context and set of consequences to go along with various options for "ideal" deer population levels.

Like many other forested habitats used by migratory songbirds in eastern North America, Great Lakes forests have a high potential to be modified by the browsing of white-tailed deer. Although identifying the forests that receive high levels of browse is fairly straightforward (e.g., an obvious "browse line" exists in the forest vegetation, low plants show evidence of multiple foraging events), understanding the impacts of deer browse on birds and other species is more difficult. White-tailed deer have been described as "keystone species" because intense browse pressure can produce changes that influence species at many different trophic levels within an ecosystem (Waller and Alverson 1997, McShea and Rappole 2000, McShea 2000). As a result, high deer densities can produce a potentially complex web of both direct and indirect effects on species of conservation concern. Assessing the potential impact of high deer-densities on other species, such as migratory birds, is challenging because effects can vary widely both by and within taxonomic groups (McShea and Rappole 2000, Fuller and Gill 2001). Similarly, the effects of reducing deer density on a particular non-managed species can vary with time, as the species responds to successional changes in the recovering plant community (McShea and Rappole 2000). Linking deer management to impacts on other wildlife species is further complicated by the fact that most northern forests are also managed for timber, and timber management activities can lead to major changes in the distribution of both deer and birds.

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Migratory bird species are ideal subjects for a study of the effects of deer and timber management because they are highly sensitive to changes in the structure of their habitat (Morse 1976, Mills et al. 1991), and are relatively easy to monitor (Hutto 1998). Factors affecting the distribution of forest-dependent migratory songbirds are also a critical conservation focus, as many of these species are believed to be declining, especially in regions where most forest habitat has been fragmented or lost (Askins et al. 1990, Robinson et al. 1995, Faaborg et al. 1995). Taking actions now to understand the effects of management within the large expanses of forest that remain in the northern Great Lakes States can be seen as both a prudent management action at the local scale, and as a method for helping to buy time through protecting healthy populations that may provide immigrants to restored habitats throughout a species' range.

Browsing of forest understory vegetation by deer can potentially impact breeding birds through many different mechanisms. The most obvious effects of high deer densities are changes in the structure and/or density of understory vegetation, which may alter the availability of nest sites or foraging habitat. Other possible links between deer browse intensity and bird populations include (1) changes in plant species composition, which may also alter food supplies or the availability of preferred nest sites; (2) changes in food supplies through effects on the abundance of invertebrates that compete with deer for particular types of understory foliage (Fuller 2001); (3) changes in nesting success through reduction in nest-site vegetative cover, indirect effects on nest predator population sizes, or direct nest depredation or trampling (Martin and Roper 1988, Reitsma et al. 1990, McShea 2000, Pietz and Granfors 2000); and (4) changes in habitat characteristics that alter the abundance of other bird species that might compete for food or nests sites, or act as brood parasites. The first step in determining which of these potential mechanisms influence bird populations is identifying how bird distributions vary among of forests exposed to different levels of deer browse-pressure

Due to the wide range of life history traits seen in forest-breeding songbirds, and the variety of mechanisms through which deer can change ecosystem characteristics, it is likely that various bird species within the same landscape will show different responses to deer browse-pressure. Similarly, the same species in different habitat conditions may show a different response to deer effects. In spite of this complexity, some basic patterns

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have emerged in recent years. As might be expected, studies have linked heavily-browsed conditions with reduced abundances of species that require a dense understory layer for nesting or foraging (e.g., American redstart, black-throated blue warbler, chestnut-sided warbler; species names are listed in Table 1), while migratory species that nest and forage in forest canopy vegetation tend to show little or no response to browse level (e.g., Casey and Hein 1983, deCalesta 1994, McShea and Rappole 2000, Perrins and Overall 2001).

In contrast to shrub- and canopy-nesting species, the responses of ground-nesters, such as ovenbirds and hermit thrushes, have varied among studies. Ovenbirds increased in density after deer were excluded from oak-hickory forests in Virginia (McShea and Rappole 2000), but showed no detectable response to browse level in oak-pine forests in Massachusetts, where hermit thrush were more common in areas with high deer densities (DeGraaf et al. 1991). Ground nesters as a group (including both ovenbirds and hermit thrushes) showed no response to browse level in cherry-maple-beech forests in Pennsylvania (deCalesta 1994). McShea and Rappole (2000) point out that the apparent conflict between their positive response of ovenbirds to deer density reduction and deCalesta's (1994) lack of an effect may be because in their Virginia study sites, groundcover tends to be dominated by grasses when deer densities are high, while in deCalesta's Pennsylvania sites, high deer densities tend to promote ferns in the groundcover. Based on the few studies currently available, it seems likely that responses of ground nesters will be most difficult to predict across studies and over time, due to the potentially complex responses and interactions between understory and groundcover vegetation.

In this work, my goal was to identify patterns in the distribution of songbirds in heavily-browsed (HB) and less-browsed (LB) hardwood forests within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula. Unlike most studies that look at deer browse effects, I compare sites that vary in terms of deer browse due to natural patterns of deer behavior, rather than from the use of deer exclosures or enclosures. As a result, I was able to survey sites across a wide range of forest conditions within both HB and LB regions. Of particular interest, some of the sites surveyed in this work had patchy distributions of a plant that is not preferred by deer in

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this region, balsam fir (*Abies balsamea*). So far, little work has been done to assess how browse resistant plants might provide refuge habitat for shrub-nesters in otherwise heavily-browsed habitats. Understanding how birds, especially ground- and shrub-nesters, may shift their distributions to include browse-resistant species in their territories could provide a direct link between conservation of forest birds and concrete, on-the-ground management activities. These Michigan sites also are unusual when compared to other sites where deer browse and bird relationships have been studied, in that much of the browse pressure is occurring in the winter, when the shortest vegetation is protected by snow. As a result of protection by snow, strong effects of deer are still visible, but instead of being removed, most browse-sensitive woody plants are kept at heights of roughly 0.5-0.75 m through repeated browsing. Ground- and shrub-nesters in northern Great Lakes forests are likely to respond differently to this uniformly-short, but often dense understory layer than they would to browsed conditions in more southern forests without snow protection.

To simplify the results and facilitate comparison with other studies, I grouped bird species by typical nesting/foraging height based on Ehrlich et al. (1988), McShea and Rappole (2000), and my personal observations on the study sites. I hypothesized that shrub-low canopy nesting species would be negatively associated with deer browse level, and positively associated with shrub density, while other groups would not show a pattern with respect to browse level or shrub density. Although results for all common bird species detected are presented and discussed, I focused on common neotropical migrant songbirds, as these are the species for which northern Great Lakes forests may provide important source habitats.

Study sites

I conducted this research in hardwood forests within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula (U.P.; Figure 2.1). Two main bands of hardwood forest cross the eastern half of the HNF; one in the southern section (high winter deer densities) along the Niagara Escarpment (lat 46°04 N, long 84°55 - 84°40W), and a second in the northern half (lower winter deer densities),

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between approximately 0 and 15 km south of Lake Superior (lat 46°27 N, long 84°37 -
85°07 W, Figure 2.1). A gradient of browse levels occurs naturally in the U.P. due to the
fall-early winter migration of deer to southern areas where there is less snow and weather
conditions are less severe (Van Deelen 1995). Within these southern U.P. forests,
wintering deer tend to concentrate in "deer yards," conifer stands dominated by northern
white-cedar (*Thuja occidentalis*) and white spruce (*Picea glauca*) that provide thermal
protection, and then move out from these areas during the day to forage (Van Deelen
1995). High concentrations of deer have been further encouraged, especially near the
deer yards, through the creation of wildlife openings, and clear-cutting of aspen forests,
which provide forage as they re-sprout.

I established point-count survey sites in forest stands dominated by sugar maple
(*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*),
with lower densities of ironwood (*Ostrya virginiana*), yellow birch (*Betula
alleghaniensis*), balsam fir (*Abies balsamea*), and occasional white spruce (*Picea alba*),
white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), black cherry (*Prunus
serotina*), and linden (*Tilia americana*). In the LB sites, understory vegetation
composition was very similar to the overstory composition, and was dominated by maple
and beech sapling and seedlings in high-shrub density areas. On high shrub-density HB
sites, sugar maple seedlings and saplings were also very common, and tended to form
fairly uniform, dense patches 0.5 - 0.75 m tall. In contrast to most LB areas, many of HB
forest stands had dense patches of understory firs, typically between 0.5 - 4 m tall. Firs
rarely showed browse damage, and some of the differences in fir distribution between the
HB and LB sites may be due to the effects of deer on populations of less browse-tolerant
understory species. Beech, ironwood, and other less-common overstory species were
also present in the HB site understory, although these two species in particular tended to
be very heavily-browsed. At both site-types, groundcover at low shrub-density areas
typically consisted of patches of leaf-litter, seedlings of overstory trees, and a sparse layer
(5-15% by area) of herbaceous vegetation, including some large ferns.

All hardwood stands that I surveyed were at least 40 ha in size, and were located
within a forest-dominated landscape divided by gravel and dirt roads, and interspersed
with small disturbed areas. Most stand boundaries were determined by a change in forest

type or management history, rather than a transition from forest to some other form of land-cover. All of the sampled stands were managed as even-aged stands through selective thinning, and I only included stands that were at least 5 years-post thinning, and on flat terrain (this eliminated stands near the shore of Lake Superior) to minimize any potential effects of management or site conditions on habitat occupancy by songbirds. To further ensure that the southern areas received strong browse pressure, most HB sites that I sampled were located within a few km of northern-white cedar/spruce stands consistently used as deer yards by wintering deer.

Field methods

To determine patterns of relative abundance for bird species, I conducted point-count surveys in 14 HB (all southern) and 11 LB (all but one northern) hardwood forest stands in the HNF. Within both the HB and LB sites, point count locations were categorized by shrub/sapling density and then grouped by density in the analyses to reduce variation in the abundance estimates. To explore the potential role of browse-resistant understory firs as refuge habitat for shrub nesters in HB sites, I also compared bird distributions in areas with high or low fir densities within high-shrub/sapling density sites. Together, results from these counts provide a large-scale perspective of how the relative abundances of forest birds varied with changes in forest understory density, species composition, and browse intensity in the HNF.

Point count samples and bird mapping
I estimated the relative abundance of birds in HNF hardwood forest stands using fixed-radius point count surveys, the method most often recommended for determining patterns of bird distribution across variable habitats (Ralph et al. 1993, 1995, Nur et al. 1999). I surveyed stands between 07:00 and 10:00 EDT in June and July of 1998-2001 on days with wind speeds less than 10-12 miles per hour, and no rain (Ralph et al.1995). Sunrise at HNF occurred between 05:45 and 06:15 EDT during the study season. At each point, I counted all birds seen or heard for 10 minutes within a 100 m radius. During the point counts, I estimated the distance and direction to each bird (Reynolds et al.1980, Scott et

al. 1981). If a bird appeared to move during the count, I recorded the new location and it was not double counted.

I began each survey at a point accessible by road, and determined transect start points by walking to a point at least 100 m from the stand edge (determined by where forest type or management condition changed), and then starting a transect at a randomly selected distance up to 50 m from this point. I conducted counts every 200 m along the transects, with the first count located at a randomly selected distance between 20 and 50 m from the start of the transect. Additional transects were parallel to the first, and were at least at least 200 m away. I determined the distances between transects and sampling points through a combination of pacing and verification with a Global Positioning System (GPS). Although it is likely that samples on the same transect are not statistically-independent estimates of bird abundance, the fact that understory conditions varied along transects, and that transect lengths could not be easily standardized due to the range of stand shapes in the HNF, made the transect an inappropriate sampling unit. I visited each point once over the course of the study, and did all counts myself to avoid observer bias.

To complement the point count data, I collected spot mapping data for common shrub- and ground-nesting species at two HB hardwood forest stands (HB-Wishbone and HB-Wilderness) and two LB stands (LB-McNearney and LB-Slash). The mapping results provide a means for visualizing relationships between the distributions of potentially browse-impacted bird species and within-stand patterns of understory vegetation characteristics. Each hardwood stand had a heterogeneous understory, with the two HB stands varying in understory plant species composition (heavily-browsed hardwoods vs. conifers), understory density, and understory height, while the LB sites were dominated by hardwoods, and varied primarily in terms of understory density and height. At each site, I mapped birds on a 25 ha (500 m by 500 m) areas, recording observations of six common ground- and shrub/low canopy-nesting species: ovenbird, hermit thrush, veery, black-throated blue warbler, American redstart, and Swainson's thrush. To map birds, assistants and I walked the eleven 500 m long north-south and east-west transect lines within each plot twice between late June-mid July of 2000 and 2001. All observed birds of the focal species were recorded on gridded maps with a 25-m grid-square resolution. If a bird moved to a different grid-square during the mapping

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process we added the new locations to the maps, because the goal of mapping was to indicate habitat use within the sites rather than bird abundance. I combined all observations for each species on yearly maps, and created presence/absence (within 25 m pixels) GIS layers for each species/year.

Vegetation data categorization and collection

As described above, I categorized point-count locations as high (HS) or low shrub/sapling density (LS), and heavy or low deer-browse pressure (HB or LB). I defined shrubs as woody plants between 0.5 - 1.5 m tall, and saplings as plants taller than 1.5 m, but less than 2.5 m in diameter (measured at 1.5 m). The browse level and shrub density of stands was often consistent within a stand due to similarity in distance from deer yards and recent management history (more recently thinned areas had higher shrub/sapling densities). To account for smaller scale variation, however, I recorded shrub density, browse pressure, and proportion of firs in the understory at each point-count location.

To classify vegetation at a point, I focused on an estimated 50-m circle around the count location, and categorized the "cover" of shrubs and saplings within this area. I categorized vegetation density based on cover, rather than by an estimate of number of stems, to allow comparisons among areas dominated by plants with different heights and growth forms (e.g., a balsam fir sapling typically fills more space than a maple sapling of similar height). If at least 30% of the ground was covered by vegetation within the shrub and sapling size classes, the area was considered high shrub-density. Within the HS-HB sites, I further classified points as having a high (> 30%) or low proportion of balsam fir in the understory vegetation. Based on data collected at a subset of point count locations, high shrub/sapling densities in hardwoods likely ranged between 130 - 370 stems/10 m^2, with high densities of firs equaling about 38 - 145 stems/10 m^2 (unpublished data).

To map understory vegetation on the 25 ha bird-mapping plots, I used a subset of data collected for a related study (Chapters 4 and 5) in which I estimated vegetation characteristics every 25 m along marked transects at the four (40 – 75 ha) sites described above. The sampling frame approximated the James and Shugart (1970) method, in that I estimated understory-vegetation characteristics within a 5-m radius circle at each

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sampling point. At these points, I estimated the most common (mode) understory seedling/sapling height, vegetation density, and the percentage of coniferous vs. hardwood vegetation. I estimated mode vegetation heights to the nearest 0.25 m from 0.5 -1 m, the nearest 0.5 from >1 m to 3 m, and nearest 1 m above heights of 3 m. As described above, I estimated density in terms of shrub/sapling cover, and values were recorded in four coverage categories which seemed to represent natural breaks in density distribution: 0-10%, 11-40%, 41-80%, and >80%. I also estimated the species composition of the understory vegetation by % coverage (nearest 5%) to account for the different growth forms of the two species groups (conifers and hardwoods). I collected all vegetation mapping data in August and September of 2000 and 2001.

Analysis methods

I examined the effects of understory characteristics on the number of birds, number of species, number of ground nesting birds, and number of shrub-nesting birds observed per point with two-way ANOVAs, with shrub density and browse level as main factors. Sample sizes differed between the various understory types due to the relative frequency of these types in the landscape. As a result, the two-way ANOVAs were unbalanced. I used the "Type III" method for partitioning the total sums of squares in the ANOVAs, as this method is recommended for unbalanced designs when there are no missing values, although it may show reduced power to detect main effects (Shaw and Mitchell-Olds 1993). These data met the assumptions of normality and homogeneity of variances as assessed by histograms of values and residuals, normal probability plots, and Levene's test. Data for the two most common species, the ovenbird and red-eyed vireo, also met the assumptions required for use of two-way ANOVAs. For these groups and species, I compared point counts in areas with low and high fir densities within HB-HS sites with Student's t-tests, following assessment of similarity of variances with F-tests.

For the less abundant bird species, as well as for grouped canopy- and cavity-nesters, the high frequency of zero values led to violation of the assumption of data normality. The high frequency of tied values (e.g., counts of 0, 1, 2, etc.) suggested that non-parametric tests based on ranks would also not be appropriate. To assess the effect

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of browse pressure and shrub density on these species and groups, I first tested for interactions between the presence/absence of various species across the browse and density levels. Testing for interactions was done using a log-linear model approach, which involved comparing the Likelihood Ratio (L.R.) Chi-Square value for a model including the browse-density interaction to one without this interaction (SPSS 2000a). The difference between the L.R. Chi-Square value for the two models can be tested for significance (a Chi-Square test with one degree of freedom), and in all cases, the comparison suggested a significant interaction between factors. Due to the significant interactions, I completed four Chi-Square Tests of Independence for each species: two tests assessed browse effects within the two density levels, and two tests assessed density effects within the two browse levels. For the pooled canopy- and cavity-nesting groups, I used three categories (0, 1, 2+) in the comparison of distributions, rather than presence/absence. For nesting groups and species with enough observations, I also compared bird distributions at points with high and low fir density within the HB-HS density sites with Chi-Square Tests of Independence. I used SYSTAT® 10 (SPSS 2000b) for all statistical tests and tests of assumptions, and set alpha at 0.05 for all tests. I present the set of four Chi-square tests for browse and density with their calculated p-values, but have highlighted only those results that were significant following a Bonferroni correction to maintain an error rate for each species or group at 0.05 (calculated as 0.05, divided by 4 tests = 0.0125).

Results

I conducted 239 point counts: 32 in LS-HB areas; 43 in LS-LB areas; 97 in HS-HB areas, and; 67 in HS-LB areas. In these counts, I detected a total of 2168 birds of 44 species. The totals by site-type were: LS-HB - 281 birds, 27 species; LS-LB - 372 birds, 30 species; HS-HB - 896 birds, 35 species, and; HS-LB - 619 birds, 30 species (Table 2.1). I found that the mean number of birds detected per point ranged from 8.7 (LS-LB) to 9.3 (HS-HB and HS-LB), and the number of species detected per point ranged from 5.9 (LS-LB) to 6.5 (HS-LB) (Table 2.1). Among the most common neotropical migrants, relative abundance varied widely between species, and ground- and shrub-nesters

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displayed the strongest responses to understory conditions (Figure 2.2, species name abbreviations are defined in Table 2.2).

Ground-nesters had significantly higher relative abundances in low shrub-density areas, and were also significantly more common in HB rather than LB sites (Table 2.3). Within the ground-nester group, ovenbirds showed the same pattern of significant results, and dominated the group numerically (Table 2.3). In contrast, shrub-nesting species as a group were significantly more abundant in the densely-vegetated sites, and significantly more abundant in LB, rather than HB, areas (Table 2.3). The higher abundance of shrub-nesters in LB sites should be interpreted with caution, however, because in high shrub-density areas much of the difference between means was due to the presence of Swainson's thrushes (Table 2.1), which may be less common in HB sites because these sites are closer to the species' southern range boundary in Michigan (distribution map in Brewer et al. 1991, page 353). Within the density comparisons for shrub-nesters, black-throated blue warblers and American redstarts were significantly more common in high density areas within less browsed sites, while veeries and black-throated blue warblers were significantly more common in high density areas in HB sites. Within high-shrub density areas, I found that rose-breasted grosbeaks and Swainson's thrushes were more common on the LB sites (but see note above about Swainson's thrushes), while veeries had a strong trend toward higher abundance in the HB sites (Table 2.4). No shrub- or low canopy-nesting species showed a detectable browse effect in low shrub-density sites (Table 2.4)

I found that canopy-nesters were more common in the low shrub-density areas within both HB and LB sites, although the distributions were not significantly different (Table 2.4). In particular, least flycatchers and cedar waxwings displayed a strong trend of being more common at low density locations within HB sites (Table 2.4). When I tested for browse effects on grouped and individual species of canopy-nesters in both high- and low-shrub density sites, I found no significant differences in distributions (Table 2.4). Cavity-nesters were significantly more common at low density locations in HB sites, but had a strong trend toward being more common at high density locations within LB areas (Table 2.4). This group also showed conflicting responses to browse: Cavity-nesters were significantly more common in low density areas that were HB,

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however, in high density areas I found a strong trend toward higher abundance at LB sites. For the cavity-nesters, I found no significant patterns with respect to browse or shrub density, although black-capped chickadees had a strong trend of being more common in HB areas with low rather than high densities, and yellow-bellied sapsuckers had a strong trend of being more common in high density areas that were less-, rather than heavily-browsed (Table 2.4).

When I divided the HS-HB points into locations with high (N=60), or low (N=37) balsam fir densities, I found no difference in the mean number of birds detected per point (9.2 ±0.27 vs. 9.2 ± 0.41, high and low fir densities, respectively; t=0.021, p = 0.98). Similarly, I found no difference in the number of species detected between high and low fir density HS-HB points (6.3 ± 0.18 vs. 6.2 ± 0.41, high and low fir densities, respectively; t=0.20, p= 0.84). I found that ground-nesters, shrub-nesters, and canopy-nesters as groups did not seem to respond to fir density, but two shrub-nesting species, the veery and black-throated blue warbler, were significantly more common in areas with many firs, and two other shrub nesters, the American robin and Eastern wood-pewee, were more significantly more common in areas with few understory firs (Figure 2.3, Table 2.4). The least flycatcher, a canopy-nester, and cavity-nesters as a group, also were more common in HS-HB sites with few firs (Figure 2.3, Table 2.4).

The bird mapping results (Figures 2.4 - 2.7) agree with and add detail to the point count results. For example, ovenbirds were more common on the HB study areas, and I found hermit thrushes in lower shrub-density areas within sites (especially noticeable on the LB sites). Similarly, the maps suggest that the distribution of veeries was closely linked to the prevalence of firs on the HB sites, and to increased shrub density on the LB-McNearney site. These maps also demonstrate that black-throated blue warblers typically occupied high shrub-density areas on both HB and LB study areas. In general on the HB sites, blue warblers were most often seen in fir-dominated areas, although, especially on the HB-Wilderness site, they were also commonly seen in areas with few firs and dense, short, hardwood shrubs. The addition of the shrub height variable was particularly useful for describing the distribution American redstarts, which I usually found in areas with taller vegetation, especially on HB sites. Similarly, the height variable helped explain the difference in frequency of Swainson's thrushes between the

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two LB sites; these thrushes were more common on the McNearney site, which had taller understory vegetation.

Discussion

In the northern forests that I studied, balsam fir appear to supply refuge habitat for two shrub-nesting species that prefer forests with high understory vegetation densities, the black-throated blue warbler, and veery. The abundance of these two species appears to be well predicted by the proportion of understory firs in relatively-recently thinned forests (i.e., high shrub-densities). As a result of this refuge effect, the response of shrub-nesters to browse impacts was mixed. I found that species that utilized firs (e.g., veery, black-throated blue warbler, magnolia warbler) were more common in HS-HB areas, and species less likely to use firs (e.g., American redstart, rose-breasted grosbeak) showed a browse-related decrease in abundance. When data for these species were pooled into the shrub-nesting group, I found the expected relationship of significantly higher relative abundances of shrub-nesters in LB sites. This result, however, should be interpreted with caution, as for at least the high shrub-density counts, differences in abundance between HB and LB sites can be explained by variations in Swainson's thrush abundance. Swainson's thrush prefer coniferous understory (Noon 1981), and thus would be expected to be among the species that were more common in the HB sites. Instead, this thrush was most common on high-shrub density LB sites, which were 30 - 40 km north of the HB sites. As northern Michigan is part of the southern range boundary for this species (Brewer et al. 1991), the lower abundance of Swainson's thrush on HB sites seems more likely to be related to larger scale factor such as climate, rather than understory conditions. Ground-nesting species, dominated numerically by the ovenbird, were most common where deer browse-pressure was high, regardless of whether forests had firs in the understory were more-recently thinned, or had a closed canopy (low shrub density). Interestingly, some species, such as the least flycatcher and eastern wood-pewee, were significantly less common in stands with understory dominated by the refuge habitat (firs). Together these results suggest that, as found by McShea and Rappole (2000), any

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change in management to favor one of these neotropical migrant species is likely to reduce habitat available for another species in this potentially at-risk group.

When all individual birds and species were pooled, there was no evidence of an impact of browse-pressure or shrub density on bird abundance or species richness. In contrast, when species were grouped by nest height, distribution patterns emerged that should help link proposed changes in deer or timber management to predictable effects on local bird populations. Both of these general observations agree with previous work on the impacts of abundant deer (Casey and Hein 1983, DeGraaf et al. 1991, deCalesta 1994). In a long term-study exclosure study of the effects of deer browse on forest birds, McShea and Rappole (2000) found a similar lack of a pattern in species richness with time since exclosure, but demonstrated that total bird abundance values can be dynamic as vegetation changes following reductions in deer density. In addition, my result of many species and groups showing an interaction between browse and shrub density-effects highlights the importance of considering time since thinning (the main factor influencing understory density) in assessment of browse impacts, especially in forests where some short understory vegetation is protected from deer by snow cover.

In agreement with the studies cited above, the nesting group with the strongest response to understory conditions in this study was the shrub-nesters. Processes such as thinning can produce noticeable patterns in the shrub-nesting species present, leading to increases in both species diversity and abundance as understory plants respond to increases in light availability (King and DeGraaf 2000). As suggested by the often strong responses of various nesting groups to the shrub-density variable, in these northern Michigan forests, time since thinning, rather than deer-browse pressure, is likely to be the main factor determining species distributions, a pattern also found by DeGraaf et al. (1991). Under current conditions, thinning is the main mechanism producing high understory-densities in northern Michigan hardwood forests, because canopy gaps that would allow light to reach the forest floor rarely develop when trees are cut before they grow old. Even if forests were not managed as even-aged stands, canopy gaps and other features typical of old growth conditions would still be rare in northern Michigan because most of the area was logged in the early 1900s (McCann 1991). The fact that there are few shade tolerant shrubs in Great Lakes forests further increases the importance of

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thinning as a mechanism for creating understory habitat. For example, species like *Rhododendron* and mountain laurel (*Kalmia latifolia*) in the Appalachians, and hobblebush (*Viburnum alnifolium*) in New England, provide important understory habitat for shrub-nesting black-throated blue warblers (Holmes 1994, Guzy 1995, Holmes et al. 1996). One native, shade-tolerant shrub, Canada yew (*Taxus canadensis*), is similar in structure to a patch of small firs, and may have formerly provided important habitat for shrub nesting songbirds in Great Lakes forests. Deer readily browse Canada yew, and it has been locally extirpated in this and many northern forests (Beals et al. 1960, Alverson et al. 1988, Van Deelen et al. 1996).

The positive relationship between ground-nester relative abundance and browse intensity was driven by the ovenbird, a very common species in these northern forests. As described in the introduction, previous studies of browse impacts have had mixed results for the ovenbird, which seem to be linked to the type of groundcover that persists under browse pressure (McShea and Rappole 2000). Ovenbirds may be more common in the HB forests because, although both firs and short hardwoods occur in dense patches, there were often large expanses of open leaf-litter beneath closed-canopy areas that these ground-foragers and nesters may have preferred. The hermit thrush was most common in low shrub-density, HB sites, a pattern also found by DeGraaf et al. (1991) in oak woodlands in Massachusetts. The interaction between browse and density was particularly notable for the hermit thrush, which only had a significant response to density in HB sites, and showed a strong trend toward preferring browsed sites in low, but not high, shrub-density areas. As suggested for the ovenbird, hermit thrush may prefer the higher frequencies of open expanses of leaf litter at HB sites.

The fact that there were only two common ground nesters in these Michigan forests, both of which were also ground foragers, has led to a fairly unambiguous set of results for this group. The lack of ground-nester species diversity may relate to again to timber management. When compared to more natural conditions, even-aged forests tend to not have some of the complexity in groundcover conditions (e.g., fallen logs, dense tangles of vegetation) that might attract higher population of other ground-nesters detected at low levels in this study, such as Nashville warblers, black-and-white warblers, and the low-cavity nester, the winter wren.

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As expected, most shrub-nesting species were more common in high shrub-density areas, while the pattern with respect to browse level was more mixed. Some species, such as the magnolia warbler, were likely more common in HB sites because they prefer a coniferous understory (Brewer et al. 1991). The veery may also prefer a dense coniferous understory, as suggested by the strong trend toward higher abundance in HB rather than LB, high shrub-density sites. For the black-throated blue warbler, however, which did not seem to have a strong preference for firs, these browse-resistant shrubs and saplings appear to be providing an important habitat resource that mediates the impacts of abundant deer. It remains to be seen whether fir-dominated understory habitats are similar in quality (as measured by adult survival and reproductive success) to high density, less-browsed habitats for blue warblers and veeries. For example, blue warbler, foraging habitat is likely to be reduced in areas where firs are patchy and hardwood saplings are all very short (Steele 1993, Whelan 2001).

Species that did show a browse effect (or a trend suggesting an effect) such as the rose-breasted grosbeak and American redstart, may not be as flexible in terms of nest sites or other habitat requirements, or may be prevented from using these resources by interspecific competitors. On the LB sites, grosbeaks and especially redstarts were frequently found nesting in hardwood saplings between 2-5 m in height, but were not found nesting in firs of similar height on the HB sites (unpublished data). Redstarts showed a strong positive response to deer exclusion in Virginia forests (McShea and Rappole 2000), and preferred early successional northern hardwood forests with few conifers in New Hampshire (Sherry and Holmes 1985, Hunt 1996 & 1998). The fact that there were many disturbed areas within the HB part of the Hiawatha National Forest may provide a short-term benefit to redstarts, grosbeaks, and similar species that prefer taller saplings and small trees. On HB sites, I typically found these species along the edges of forest openings, or in small areas with dense, tall (>5 m) saplings and little overstory, such as re-generating wildlife cuts. Whether a small area like this (e.g., 2-4 ha) cut today would regenerate to this sapling stage is hard to predict, as heavy deer browsing would certainly slow, if not prevent, shrubs from growing above the protective snow cover.

For many of the shrub-nesters, even age-age management, which produces a pulse of dense understory habitat beneath a relatively intact canopy, is likely to lead to strong

variations in relative abundance over time. However, when these habitats are browsed, the dense but short shrub-layer may persist, leading to reduced hardwood regeneration and reduced habitat for species that prefer hardwood saplings and small trees such as rose breasted grosbeaks (Brewer et al. 1991) and American redstarts (Hunt 1996). In regions such as the Great Lakes with persistent snow cover, shrub- nesters that use lower nest sites may be less impacted, and a decade or two following thinning may be more common in browsed areas due to deer maintaining short clumps of understory. When coupled with browse-resistant species like firs that provide some structural diversity, deer browse may be severe in terms of reductions in hardwood forest regeneration, but may not have strong negative impacts on all shrub-nesting species.

As with the ground-nesting group, there were some shrub-nesting species typical of hardwood forests in the northern Great Lakes states that had low abundances in the even-aged stands studied here. Although close to their northern range limit in the UP, wood thrush, a species of particular conservation concern in Eastern and Midwestern forests (Thompson et al 1993, Robinson et al. 1995) are more common in Michigan forests with dense, multi-layered understory vegetation and a closed canopy (Brewer et al. 1991). Dense understory and closed canopy conditions are not typically found together in even-aged stands, as forests typically must be fairly recently thinned for dense understory to be present. Wood thrush had a significant positive response to removal of deer from Virginia oak-hickory forests (McShea and Rappole 2000), but a mixed, non-significant pattern in Massachusetts oak-pine forests (DeGraaf et al. 1991). Only a few wood thrush were observed during in this study, but this species might be more common under different management conditions, especially if climate warming favors a northward shift in wood thrush distribution. Indeed, there is evidence that the wood thrush range has been expanding into northern Canada (Robbins et al. 1986), and the relatively intact forest of the northern Great Lakes region are likely to have lower rates of nest predation and parasitism than the heavily fragmented forest in the center of this species current range (Robinson et al. 1995). If "hotspots" for breeding wood thrush were found in northern forests, particular care should be taken to evaluate how both local and regional-scale management (e.g., activities that attract deer, such as clearcutting aspen) could alter important habitats.

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Most canopy-nesters, which tended to be more common at sites with low shrub-densities, were probably responding to the higher canopy-foliage density in areas that have been thinned less recently (few understory shrubs). The least flycatcher was significantly less abundant in areas with high fir densities, a pattern also described by Sherry and Holmes (1985). Possibly, the least flycatcher, along with the eastern wood-pewee, prefer more open habitat with hardwoods rather than firs below the canopy, as it may provide a more suitable structure for "hawking" prey from the undersides of leaves (Robinson and Holmes 1982, Sherry and Holmes 1985).

Cavity-nesters were not very common at any site type, and showed strong interactions between browse and shrub density. This group was significantly more common in low shrub-density areas within HB sites, but had a strong trend in the opposite direction in LB sites. Similarly, while cavity nesters were significantly more common in low shrub-density sites that were HB, they had a strong trend toward higher abundance in LB areas within the high shrub-density sites. In the fir comparisons, while overall mean abundance was very similar between sites with high and low proportions of fir in the understory, birds were more clumped in the high fir locations. These complex patterns are probably related to differences in overstory tree species composition, as well as variations in the frequency of standing-dead trees, that are not well reflected by tests of understory conditions.

Songbird conservation and management implications

From these results, I suggest that a landscape-scale approach will be key to managing deer populations and timber in ways that protect migratory songbird populations in Great Lakes forests. Due to the opposite distribution patterns shown by various neotropical migrants with respect to variation in shrub density and browse intensity, following any local-scale management action, there will be species that benefit and species for which available habitat is reduced. Although further study is needed to determine if the patterns of abundance here can be used to infer habitat quality (reproductive success and survival would have to be equal across various site-types, Van Horne 1983), as suggested by McShea and Rappole (2000), in some cases, it may be beneficial to maintain areas as heavily-browsed to promote species that survive and reproduce most successfully in these

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types of habitats. In northern forests, landscape-scale management plans could be developed with the goal of concentrating deer in particular areas through careful selection of the location of management actions such as forest clearcutting or thinning. Similarly, particular care could be taken within HB habitats to make sure that if hardwoods are to be thinned, at least some areas with high fir densities are left undisturbed so that species that utilize firs do not lose large expanses of these important habitats.

The apparent habitat value of understory firs in these hardwood forests poses an interesting management problem. In the short term, firs appear to be providing a very important resource for species in HB sites, especially veeries, black-throated blue, and magnolia warblers. However, if these high densities of firs persist and begin to recruit into the overstory, these forests will eventually shift away from a northern hardwoods forest type. In addition, the growth form of mature firs tends to prevent a dense understory layer from developing. Long before they reach canopy level, the current clumps of firs will become less valuable as habitat to the veery and black-throated blue warbler, which tend to nest in 2 - 5 m and 0.5-1.5 m tall saplings, respectively (unpublished data). Potentially, large firs could be removed from the forest understory, and small ones could be planted in HB areas, although both of these options would be quite costly if applied at a large scale. How firs are managed is likely to be a key factor determining future songbird species distributions in the HNF, and options should be tested now to determine what might be feasible in terms of long-term approaches.

To better understand the effects of deer in northern Great Lakes forests, future studies should include a set of forest conditions that better represent the possible range of understory conditions within these landscapes. This range should include forest stands with old-growth characteristics, or at least stands managed with this goal. Over time, these stands may support higher abundances of species of conservation concern that were rare or absent in these stands, such as wood thrush, black-billed cuckoos, and Nashville warblers, which may be sensitive to browse, and may require different approaches to deer management. Similarly, deer browse may be particularly important in forests with early successional conditions, which are typically rare in managed hardwood forests due to fire suppression. This study compared current conditions, and as a result provides an incomplete picture of how conditions might change if the deer herd was reduced, or even

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just concentrated in particular areas. In McShea and Rappole's (2000) nine year study in Virginia, excluding deer from heavily browsed sites led to a rapid change in understory conditions, starting from grasses and leading to woody vegetation. Their observed rapid vegetation change led to dynamic changes in bird distributions that varied both with time and with site conditions. In contrast, I suspect that changes in the species composition of understory and groundcover vegetation in these northern forests would not be as dramatic, as snow cover tends to protect at least most of the typical species from being completely removed. The speed of recovery from browse, and whether understory species like Canada yew can be successfully reintroduced, however, are important information gaps. These information gaps suggest that monitoring of the effects of management, and adapting management approaches in response to new information will be important planning tools if these large expanses of forest are to be effectively managed for songbird conservation.

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Table 2.1. Mean detections ± SE per point, and percent of points where species were detected for birds in the four understory types. Based on 10-minute, 100-m radius point counts in northern Michigan hardwood forests, 1998-2001. Only species with a mean of 0.05 or higher in at least one understory type were included in the table.[1] Within the shrub- to low canopy-nester group, species are arranged by typical nests heights observed on the sites (low to high).

	Low shrub density		High shrub density		High shrub density, and heavily-browsed	
	heavily-browsed N = 32	less-browsed N = 43	heavily-browsed N = 97	less-browsed N = 67	few firs N = 37	many firs N = 60
All birds	**8.78 ± 0.35**	**8.65 ± 0.48**	**9.23 ± 0.23**	**9.24 ± 0.34**	**9.23 ± 0.41**	**9.24 ± 0.27**
All species	**6.19 ± 0.28**	**5.90 ± 0.33**	**6.23 ± 0.15**	**6.48 ± 0.22**	**6.17 ± 0.41**	**6.31 ± 0.18**
Ground-nesters	**2.59 ± 0.18**	**1.65 ± 0.18**	**2.09 ± 0.09**	**1.18 ± 0.13**	**2.11 ± 0.19**	**2.06 ± 0.11**
Ovenbird	2.03 ± 0.15	1.33 ± 0.15	1.88 ± 0.08	0.94 ± 0.10	1.93 ± 0.14	1.81 ± 0.10
Seiurus aurocapillus	97%	84%	96%	69%	95%	96%
Hermit Thrush	0.47 ± 0.10	0.28 ± 0.08	0.20 ± 0.05	0.22 ± 0.06	0.11 ± 0.07	0.25 ± 0.07
Catharus guttatus	44%	23%	17%	19%	8.1%	22%
Nashville Warbler	0.09 ± 0.05	0.02 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.03 ± 0.03	0
Vermivora ruficapilla	9.4%	2.3%	1.0%	1.5%	2.7%	0%
Shrub- to low canopy-nesters	**3.21 ± 0.23**	**4.16 ± 0.25**	**5.23 ± 0.21**	**5.79 ± 0.32**	**4.93 ± 0.40**	**5.44 ± 0.23**
Mourning Warbler	0.03 ± 0.03	0.05 ± 0.03	0.05 ± 0.02	0	0.08 ± 0.05	0.03 ± 0.02
Oporonis philadelphia	3.1%	4.7%	5.2%	0%	8.1%	3.3%
Veery	0.25 ± 0.09	0.21 ± 0.07	0.70 ± 0.08	0.42 ± 0.08	0.41 ± 0.10	0.86 ± 0.11
Catharus fuscescens	22%	19%	52%	33%	35%	60%
Black-thr. Blue Warbler	0.25 ± 0.08	0.28 ± 0.07	1.00 ± 0.09	1.03 ± 0.09	0.73 ± 0.12	1.17 ± 0.11
Dendroica caerulescens	25%	28%	70%	70%	57%	77%
Chestnut-sided Warbler	0	0.07 ± 0.04	0.21 ± 0.05	0.13 ± 0.05	0.19 ± 0.07	0.22 ± 0.06
Dendroica pensylvanica	0%	7.0%	19%	12%	19%	18%
Magnolia Warbler	0.03 ± 0.03	0	0.06 ± 0.03	0	0	0.10 ± 0.04
Dendroica magnolia	3.1%	0%	5.2%	0%	0%	8.3%
Swainson's Thrush	0.09 ± 0.07	0.19 ± 0.06	0.01 ± 0.01	0.45 ± 0.09	0	0.02 ± 0.02
Catharus ustulatus	6.3%	19%	1.0%	33%	0%	1.7%
American Redstart	0.50 ± 0.01	0.65 ± 0.14	0.85 ± 0.10	1.31 ± 0.15	0.84 ± 0.16	0.86 ± 0.11
Setophaga ruticilla	44%	42%	54%	67%	51%	55%
Rose-breasted Grosbeak	0.19 ± 0.07	0.12 ± 0.05	0.09 ± 0.03	0.25 ± 0.06	0.06 ± 0.11	0.12 ± 0.04
Pheucticus ludovicianus	19%	12%	9.3%	24%	5.4%	12%
Red-eyed Vireo	1.53 ± 0.16	1.88 ± 0.14	1.72 ± 0.08	1.65 ± 0.09	1.84 ± 0.14	1.67 ± 0.10
Vireo olivaceus	91%	93%	94%	94%	95%	92%
American Robin	0	0.21 ± 0.07	0.08 ± 0.03	0.08 ± 0.03	0.19 ± 0.07	0.02 ± 0.02
Turdus migratorius	0%	19%	8.2%	7.5%	19%	1.7%
Eastern Wood-Pewee	0.34 ± 0.10	0.44 ± 0.12	0.38 ± 0.06	0.42 ± 0.07	0.57 ± 0.11	0.27 ± 0.06
Contopus virens	31%	33%	33%	37%	46%	25%
Canopy-nesters	**1.94 ± 0.26**	**2.11 ± 0.22**	**1.32 ± 0.11**	**1.47 ± 0.15**	**1.45 ± 0.23**	**1.19 ± 0.18**
Least Flycatcher	0.53 ± 0.16	0.79 ± 0.18	0.30 ± 0.08	0.49 ± 0.12	0.68 ± 0.17	0.07 ± 0.04
Empidonax minimus	34%	37%	18%	27%	38%	5.0%
Blackburnian Warbler	0.13 ± 0.06	0.09 ± 0.05	0.05 ± 0.02	0.09 ± 0.04	0	0.09 ± 0.04
Dendroica fusca	13%	9.3%	5.2%	9.0%	0%	8.3%
Black-thr. Green Warbler	0.72 ± 0.15	0.72 ± 0.11	0.61 ± 0.07	0.64 ± 0.09	0.62 ± 0.11	0.59 ± 0.09
Dendroica virens	50%	58%	49%	49%	51%	47%

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Table 2.1 continued.

	Low shrub density		High shrub density		High shrub density, and heavily-browsed	
	heavily-browsed N = 32	less-browsed N = 43	heavily-browsed N = 97	less-browsed N = 67	few firs N = 37	many firs N = 60
Cedar Waxwing	0.44 ± 0.13	0.26 ± 0.11	0.18 ± 0.06	0.12 ± 0.05	0.05 ± 0.04	0.25 ± 0.09
Bombycilla cedrorum	28%	12%	10%	7.5%	5.4%	13%
Scarlet Tanager	0.06 ± 0.04	0.19 ± 0.06	0.14 ± 0.04	0.09 ± 0.04	0.08 ± 0.05	0.19 ± 0.06
Piranga olivacea	6.3%	19%	13%	9.0%	8.1%	17%
Cavity-nesters	**1.00 ± 0.22**	**0.70 ± 0.14**	**0.54 ± 0.09**	**0.78 ± 0.11**	**0.53 ± 0.17**	**0.55 ± 0.11**
Yellow-bellied Sapsucker	0.25 ± 0.09	0.21 ± 0.07	0.09 ± 0.03	0.24 ± 0.06	0.11 ± 0.05	0.09 ± 0.04
Sphyrapicus varius	22%	19%	9.3%	22%	11%	8.3%
Hairy Woodpecker	0.09 ± 0.05	0.16 ± 0.07	0.08 ± 0.03	0.15 ± 0.05	0.11 ± 0.05	0.07 ± 0.03
Picoides villosus	9.4%	12%	8.2%	12%	11%	6.7%
Northern Flicker	0	0.05 ± 0.03	0.02 ± 0.02	0.08 ± 0.03	0	0.05 ± 0.04
Colaptes auratus	0%	4.7%	2.0%	7.5%	0%	5.4%
Black-capped Chickadee	0.28 ± 0.10	0.19 ± 0.08	0.10 ± 0.04	0.19 ± 0.07	0.15 ± 0.06	0.03 ± 0.03
Parus atricapillus	22%	14%	7.2%	15%	10%	2.7%
White-breasted Nuthatch	0.06 ± 0.04	0.02 ± 0.02	0.08 ± 0.03	0.02 ± 0.02	0.03 ± 0.02	0.16 ± 0.07
Sitta carolinensis	6.3%	2.3%	7.2%	1.5%	3.3%	14%
Brown Creeper	0.25 ± 0.09	0.07 ± 0.05	0.11 ± 0.03	0.10 ± 0.04	0.12 ± 0.04	0.11 ± 0.05
Certhia americana	22%	4.7%	11%	10%	12%	11%

1. Species detected at mean rates less than 0.05 (all understory types) included: Ground nesters: Ruffed Grouse (*Bonasa umbellus*), Black-and-white Warbler (*Mniotilta varia*), Shrub-low canopy nesters: Black-billed Cuckoo (*Coccyzus erythropthalmus*), Blue Jay (*Cyanocitta cristata*), Wood Thrush (*Hylocichla mustelina*), Indigo Bunting (*Passerina cyanea*), Chipping Sparrow (*Spizella passerina*), White-throated Sparrow (*Zonotrichia albicollis*); Canopy nesters: Broad-winged Hawk (*Buteo platypterus*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*Regulus calendula*), Northern Parula (*Parula americana*), Yellow-rumped Warbler (*Dendroica coronata*), American Goldfinch (*Carduelis tristis*); Cavity nesters: Downy Woodpecker (*Picoides pubescens*), Pileated Woodpecker (*Dryocopus pileatus*), Great Crested Flycatcher (*Myiarchus crinitus*), Red-breasted Nuthatch (*Sitta canadensis*), Winter Wren (*Troglodytes troglodytes*).

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Table 2.2. Key for bird name abbreviations (AOU Code) used in Figures 2.2 and 2.3.

AOU Code	Common name
AMRE	American Redstart
BTBW	Black-throated Blue Warbler
BTNW	Black-throated Green Warbler
CSWA	Chestnut-sided Warbler
EWPE	Eastern Wood-Pewee
HETH	Hermit Thrush
LEFL	Least Flycatcher
OVEN	Ovenbird
RBGR	Rose-breasted Grosbeak
REVI	Red-eyed Vireo
VEER	Veery

Table 2.3. Two-way ANOVA results for 100 m radius, 10-minute point counts conducted in sites with low or high shrub densities and heavily- or less-browsed vegetation in northern Michigan, 1999-2001.

	d.f.	MS	F	P
All birds				
shrub density	1	13.65	2.08	0.15
browse level	1	0.21	0.031	0.86
density*browse	1	0.22	0.033	0.86
error	235	6.54		
All species				
shrub density	1	5.15	1.71	0.19
browse level	1	0.046	0.015	0.90
density*browse	1	3.14	1.04	0.31
error	235	3.02		
Ground-nesting birds				
shrub density	**1**	**11.87**	**11.36**	**0.00087**
browse level	**1**	**40.10**	**41.36**	**<0.00001**
density*browse	1	0.01	0.01	0.92
error	235	1.04		
Ovenbird				
shrub density	**1**	**3.67**	**5.16**	**0.024**
browse level	**1**	**33.80**	**47.64**	**< 0.00001**
density*browse	1	0.67	0.94	0.33
error	235	0.71		
Shrub to low canopy nesting birds				
shrub density	**1**	**169.60**	**38.86**	**<0.00001**
browse level	**1**	**26.99**	**6.18**	**0.014**
density*browse	1	2.22	6.51	0.48
error	235	4.36		
Red-eyed Vireo				
shrub density	1	0.017	0.025	0.87
browse level	1	1.04	1.53	0.22
density*browse	1	2.18	3.23	0.074
error	235	0.68		

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Table 2.4. Chi-Square tests comparing bird distributions between different understory types for individual species and species grouped by nest-site in northern Michigan hardwood forests, 1998-2001. For all species, values tested were "presence/absence", while for the grouped canopy- and cavity-nesters, tests compared 0, 1, or 2+ birds per count. A dash in the X^2 column indicates sample sizes were too small to conduct the test. To account for multiple tests related to browse and density, a Bonferroni correction was applied, and only those with p-values less than 0.0125 are shown in bold, indicating statistical significance at the grouped-test 0.05 alpha level. The low/high or LB/HB columns indicate the understory type where a species or group was more common for each comparison.

	Test of density in LB		Test of density in HB		Test of browse level in low density		Test of browse level in high density		Test of fir abundance in HB, high density	
	X^2 (p-value)	low/high	X^2 (p-value)	low/high	X^2 (p-value)	LB/HB	X^2 (p-value)	LB/HB	t or X^2 (p-value)	low/high
Ground-nesters[1]		low		low		HB		HB	t = 0.13 (0.90)	high
Ovenbird[1]		low		low		HB		HB	t = 0.95 (0.34)	low
Hermit Thrush	0.235 (0.62)	low	**12.2 (< 0.001)**	low	4.61 (0.032)	HB	0.23 (0.63)	LB	3.1 (0.081)	high
Shrub- to low-canopy nesters[1]		high		high		LB		LB	t = 0.91 (0.36)	high
Veery	2.67 (0.10)	high	**8.59 (0.0034)**	high	0.12 (0.73)	HB	5.63 (0.017)	HB	**6.5 (0.011)**	**high**
Black-throated Blue Warbler	**18.8 (< 0.001)**	high	**20.2 (< 0.001)**	high	0.079 (0.78)	LB	< 0.01 (0.99)	LB	**5.1 (0.024)**	**high**
Chestnut-sided Warbler	-	high	-	high	-	LB	1.30 (0.25)	HB	0.005 (0.94)	high
Swainson's Thrush[2]	2.67 (0.10)	high	-	low	-	LB	**33.2 (< 0.001)**	LB	-	high
American Redstart	**6.85 (0.0089)**	high	0.93 (0.33)	high	0.027 (0.87)	HB	3.01 (0.083)	LB	0.12 (0.73)	high
Rose-breasted Grosbeak	2.10 (0.15)	low	2.55 (0.11)	high	0.74 (0.39)	HB	**6.53 (0.011)**	LB	1.06 (0.30)	high
Red-eyed Vireo[1]		low		high		LB		HB	t= 1.1, (0.26)	low
American Robin	3.12 (0.077)	low	-	high	-	LB	0.033 (0.85)	HB	**9.0 (0.0027)**	low
Eastern Wood-Pewee	0.26 (0.61)	high	0.0056 (0.94)	high	0.014 (0.90)	LB	0.51 (0.47)	LB	**4.5 (0.033)**	low
Canopy-nesters	3.80 (0.15)	low	4.25 (0.12)	low	0.093 (0.95)	LB	0.97 (0.61)	LB	4.6 (0.10)	low
Least Flycatcher	1.31 (0.25)	low	4.02 (0.045)	low	0.064 (0.80)	LB	2.06 (0.15)	LB	**17.1 (< 0.001)**	low
Black-throated Green Warbler	0.45 (0.50)	low	0.13 (0.72)	low	0.053 (0.81)	LB	< 0.01 (0.98)	LB	0.08 (0.77)	low
Cedar Waxwing	-	low	6.08 (0.014)	low	3.29 (0.069)	HB	0.39 (0.53)	HB	1.55 (0.21)	high
Scarlet Tanager	2.19 (0.14)	low	-	high	-	LB	0.77 (0.38)	HB	1.44 (0.23)	high
Cavity-nesters	7.38 (0.025)	high	**10.23 (0.0060)**	low	**11.5 (0.0032)**	HB	5.98 (0.050)	LB	**7.0 (0.030)**	[3]
Yellow-bellied Sapsucker	0.23 (0.63)	high	-	low	0.12 (0.72)	HB	5.45 (0.020)	LB	0.17 (0.68)	low
Hairy Woodpecker	-	low	-	low	-	LB	0.61 (0.43)	LB	-	low
Black-capped Chickadee	0.020 (0.89)	high	5.34 (0.021)	low	0.80 (0.37)	HB	2.53 (0.11)	LB	1.8 (0.18)	high
Brown Creeper	-	high	2.22 (0.14)	low	-	HB	0.032 (0.86)	HB	0.017 (0.90)	high

Notes: (1) Tested with ANOVAs (Table 2.3), but abundance patterns are indicated here to facilitate comparison with other species; t-test rather than Chi-Square test were used for fir abundance comparisons. (2) Swainson's Thrush tests for browse effects should be interpreted with caution, see text. (3) Two or more cavity nesters per point were more common on high fir sites, but cavity nester presence (1 or 2+) was more common on low fir sites.
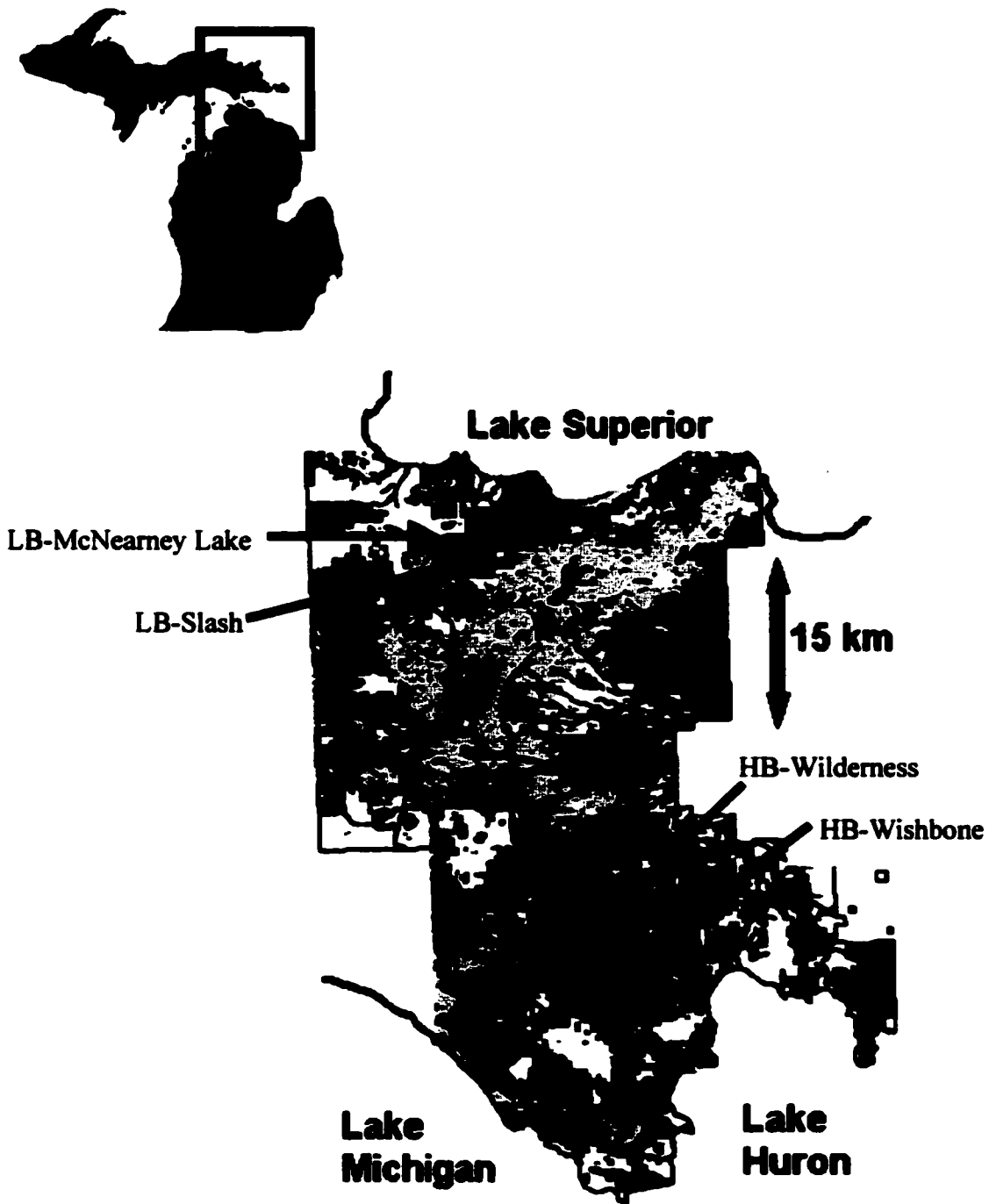
Figure 2.1. Forest types and locations of the four study areas in the eastern half of the Hiawatha National Forest. Point counts were conducted in many locations in hardwood forests (shown in green), including the four study sites. Other forest types include northern-white cedar and spruce (pink), aspen stands (orange), and red and jack pine stands (yellow), with blue representing bodies of water, and private land shown in white.

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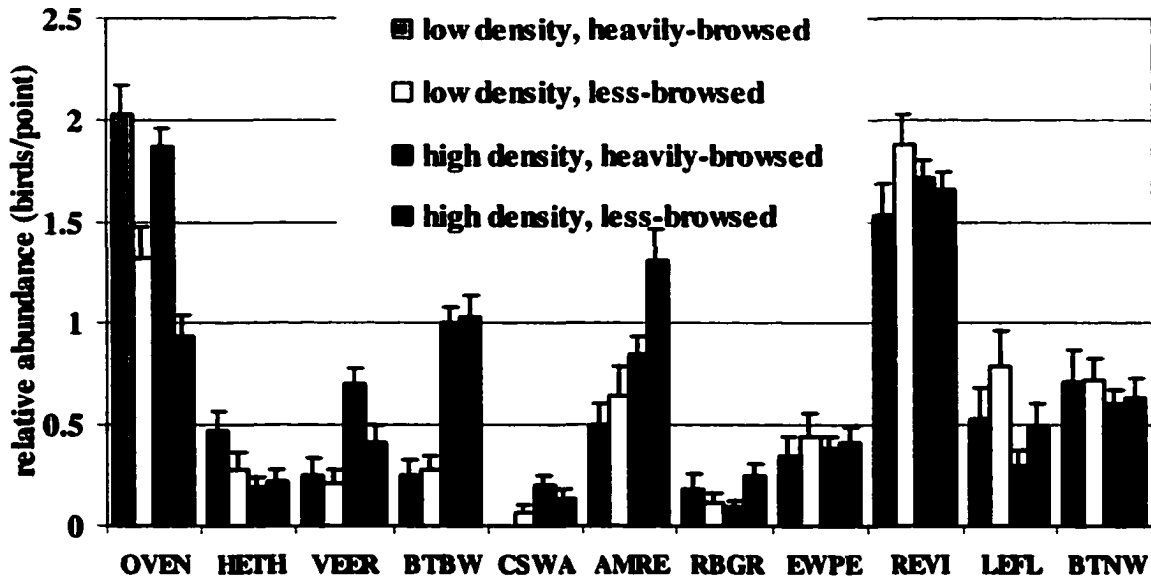
Figure 2.2. Relative abundance (mean +SE) of common migratory species in four understory types based on 100-m radius, 10-minute point counts. Understory vegetation categories are arranged from lowest to highest total volume, and bird species are arranged by typical nesting height (from OVEN & HETH on ground, through middle species at increasing shrub and low canopy heights, to LEFL and BTNW at canopy level).
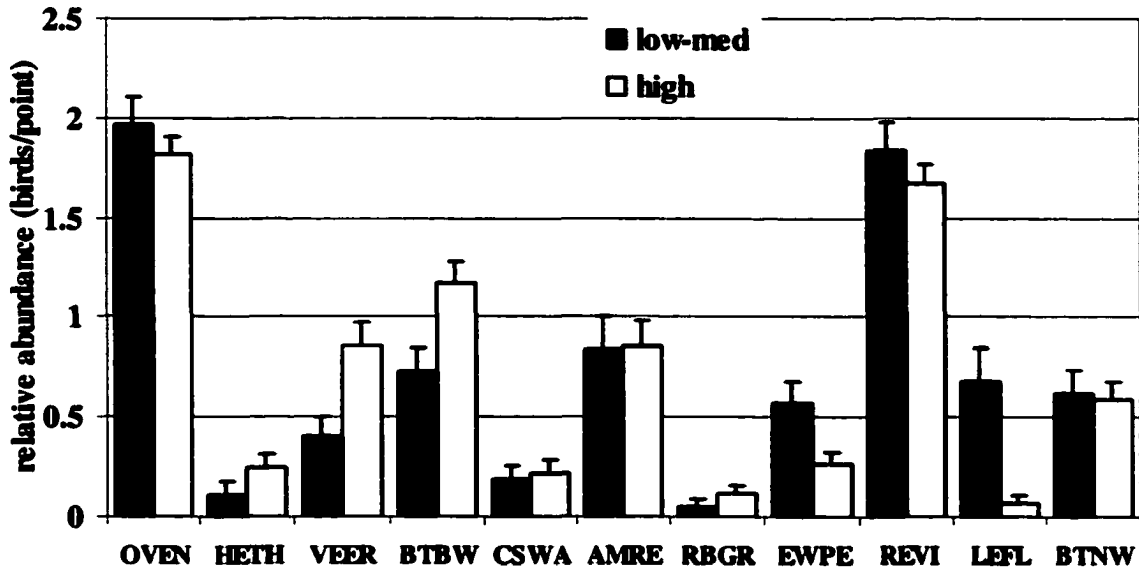
Figure 2.3. Relative abundance (mean +SE) of common migratory species in high density, heavily-browsed sites that varied in terms of balsam fir density, based on 100-m radius, 10-minute point counts. Bird species are arranged by typical nesting height (from OVEN & HETH on ground through middle species at increasing shrub and low canopy heights, to LEFL and BTNW at canopy level).
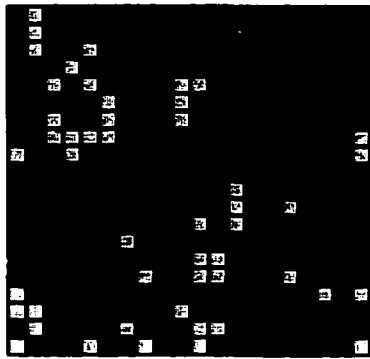
understory density   understory height   percent deciduous
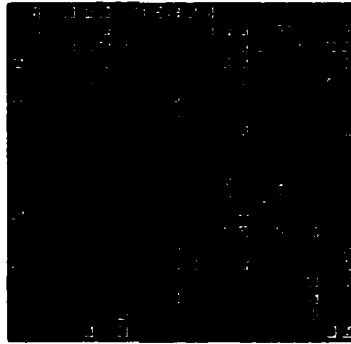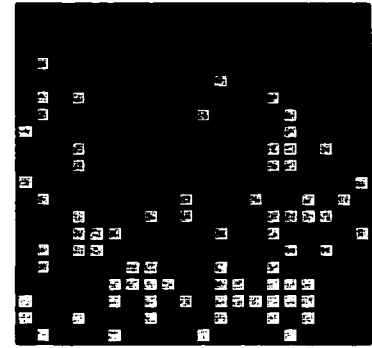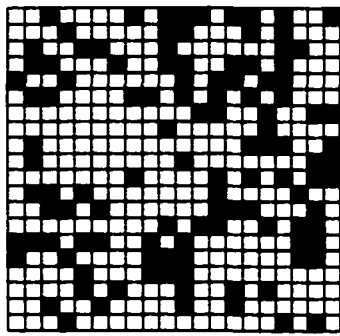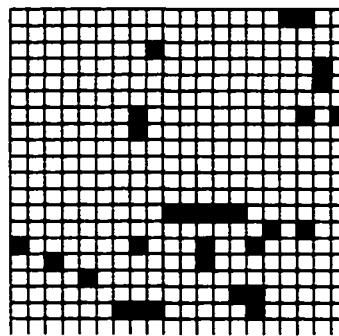
ovenbird   hermit thrush   black-thr. blue warbler
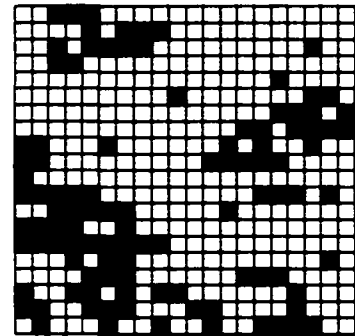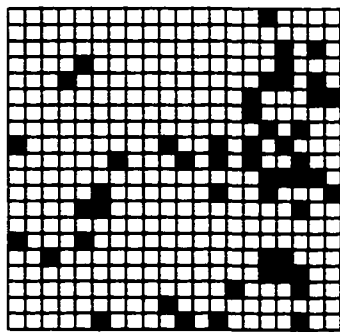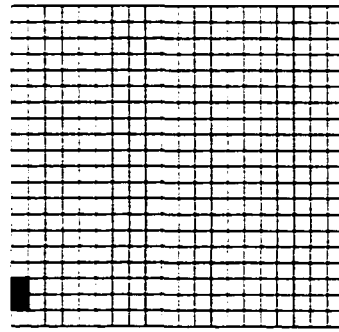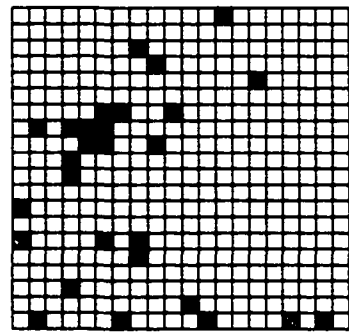
veery   Swainson's thrush   American redstart

Figure 2.4. Understory vegetation and bird distributions on the heavily-browsed Wishbone site. In the vegetation maps, five categories of mode vegetation height are shown: from light to dark, they are (in m) 0.5-1, 0.75-1.5, 2-3, 4-5, and 6-9. Similarly, density values range from light (low density) through dark shades. Finally, five categories of % deciduous are shown: 0-15 (lightest), 20-35, 40-60, 65-85, and 90-100 (darkest). For bird species, grid squares are shaded lightly if a bird was observed in one of the two years, and darkly if a bird was observed there both years (2000-2001).

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understory density   understory height   percent deciduous
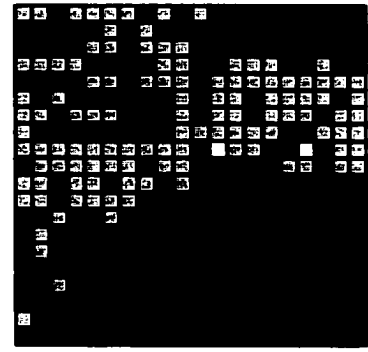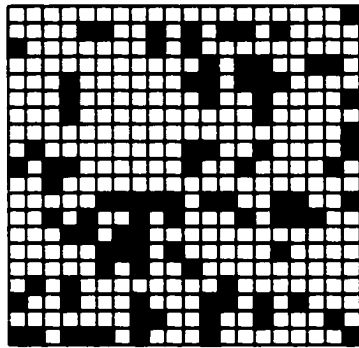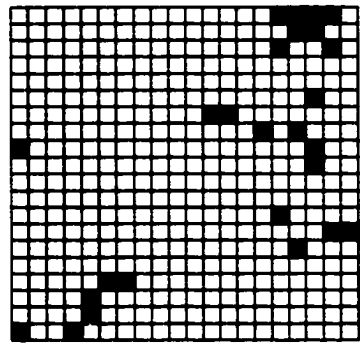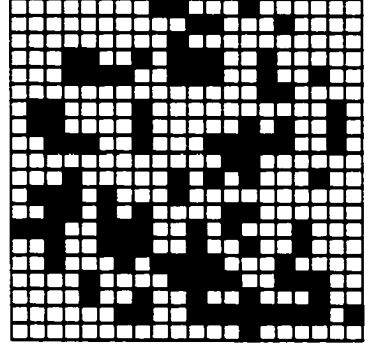
ovenbird   hermit thrush   black-thr. blue warbler
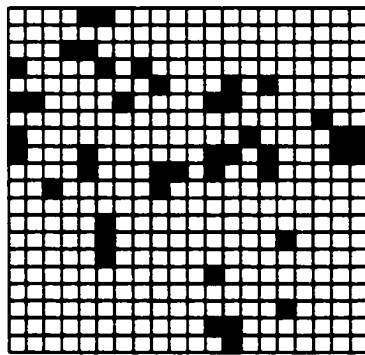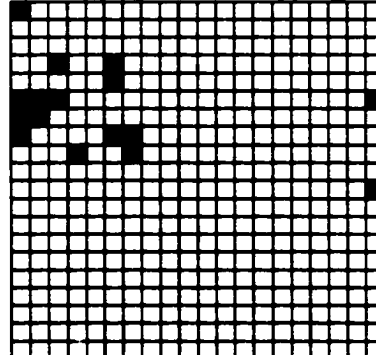
veery   American redstart

Figure 2.5. Understory vegetation and bird distributions on the heavily-browsed Wilderness site. In the vegetation maps, five categories of mode vegetation height are shown: from light to dark, they are (in m) 0.5-1, 0.75-1.5, 2-3, 4-5, and 6-9. Similarly, density values range from light (low density) through dark shades. Finally, five categories of % deciduous are shown: 0-15 (lightest), 20-35, 40-60, 65-85, and 90-100 (darkest). For bird species, grid squares are shaded lightly if a bird was observed in one of the two years, and darkly if a bird was observed there both years (2000-2001).

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understory density   understory height   percent deciduous
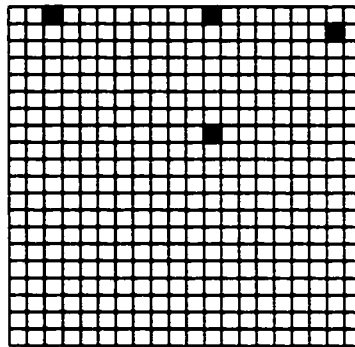
ovenbird   hermit thrush   black-thr. blue warbler
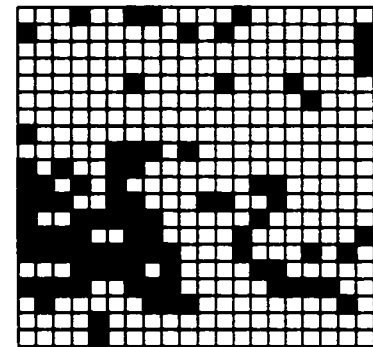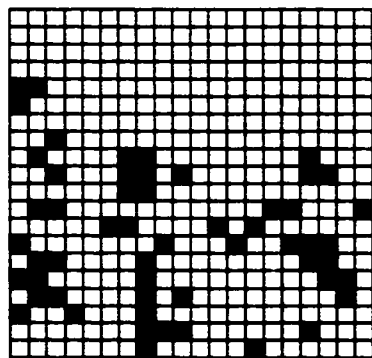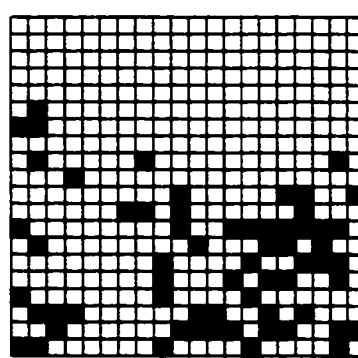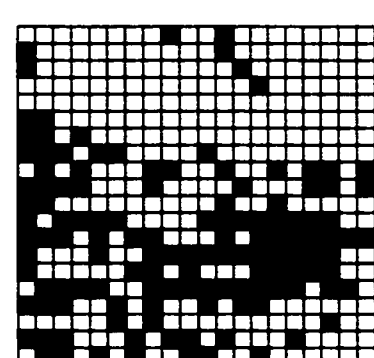
veery   Swainson's thrush   American redstart

Figure 2.6. Understory vegetation and bird distributions on the less-browsed McNearney site. In the vegetation maps, five categories of mode vegetation height are shown: from light to dark, they are (in m) 0.5-1, 0.75-1.5, 2-3, 4-5, and 6-9. Similarly, density values range from light (low density) through dark shades. Finally, five categories of % deciduous are shown: 0-15 (lightest), 20-35, 40-60, 65-85, and 90-100 (darkest). For bird species, grid squares are shaded lightly if a bird was observed in one of the two years, and darkly if a bird was observed there both years (2000-2001).

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understory density   understory height   percent deciduous
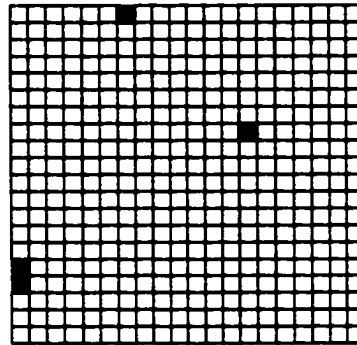
ovenbird   hermit thrush   black-thr. blue warbler
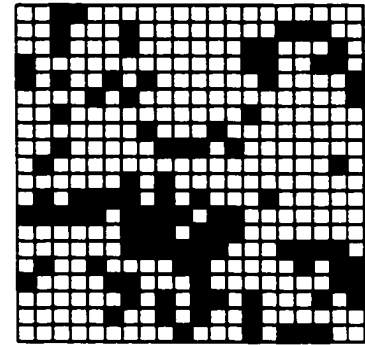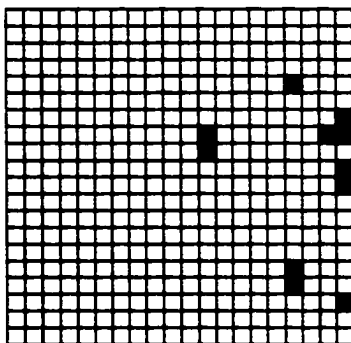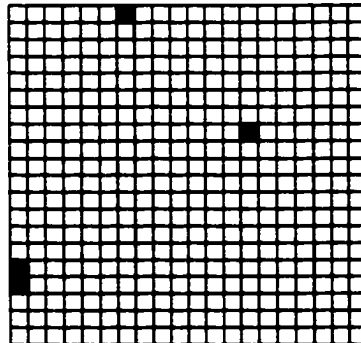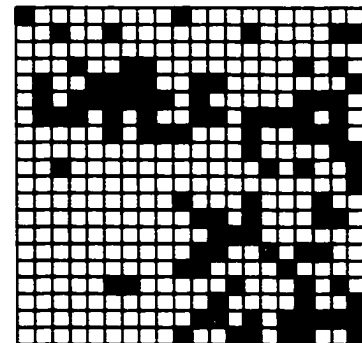
veery   Swainson's thrush   American redstart

Figure 2.7. Understory vegetation and bird distributions on the less-browsed Slash site. In the vegetation maps, five categories of mode vegetation height are shown: from light to dark, they are (in m) 0.5-1, 0.75-1.5, 2-3, 4-5, and 6-9. Similarly, density values range from light (low density) through dark shades. Finally, five categories of % deciduous are shown: 0-15 (lightest), 20-35, 40-60, 65-85, and 90-100 (darkest). For bird species, grid squares are shaded lightly if a bird was observed in one of the two years, and darkly if a bird was observed there both years (2000-2001).

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CHAPTER III

AGE RATIOS, RETURN RATES, AND REPRODUCTIVE SUCCESS OF BLACK-THROATED BLUE WARBLERS IN HEAVILY-BROWSED AND LESS-BROWSED HABITATS

Introduction

To effectively protect migratory bird species in managed northern forests, conservation planners need to understand how variations in habitat characteristics due to timber and wildlife management affect habitat quality. Although many monitoring plans rely on survey data to identify forest types and management techniques that support various songbird species, surveys typically only provide information on how bird density varies between forested areas. Although understanding how density varies with changing forest conditions is necessary, it is not sufficient information for planning, because density may not reliably indicate how well individuals survive and reproduce in a particular area (Van Horne 1983, Vickery 1992). Differences in reproduction and survival may eventually lead to local-scale density decreases that can be detected through monitoring, but in "sink" habitats, bird dispersal may mask these patterns (Brawn and Robinson 1996). Even if population changes can be detected with monitoring data, there may be a time lag between the point at which degradation of habitat has begun to cause a population decline, and the detection of this decline (Doak 1995, Hall 1996, Nur et al. 1999). As a result, managers might find that after investing years of population monitoring, statistical detection of the decline came after the "window of opportunity" to protect critical habitat had closed (Doak 1995).

To create large-scale forest management plans that incorporate effects of habitat change on bird population dynamics, it is helpful to understand the links between various habitat characteristics and the demographics of bird populations using that habitat (Van Horne 1983, Bernstein et al. 1991, Holmes et al. 1996). Besides influencing how many individuals settle in a habitat, management-related changes within habitats can lead to changes in the potential fitness of birds through effects on the abundance of resources, such as food or nest sites (Martin 1993). Similarly, changes in forest characteristics may influence the abundance of nest predators and nest parasites; for example, both of these

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groups tend to increase near "edges" in heavily fragmented landscapes (e.g., Wilcove and Robinson 1990, Andrén 1992, Robinson et al. 1993). Negative effects in terms of local rates of survival and reproduction may be compounded if, following a particular management action, only individuals that are unable to successfully compete for territories in "better" habitats settle in an area. For example, younger birds often have lower pairing and/or reproductive success, so habitats with more young birds may have lower reproductive output that is at least in part unrelated to the actual quality of the habitat (Sæther 1990, K. Martin 1995). By assessing male pairing-success, reproductive success of pairs, ages of birds, and breeding site-fidelity, as well as the density of breeders in habitats with different characteristics, researchers can have greater confidence that areas that are conserved or created through management efforts will actually contribute to the protection of populations.

In the forests of the Great Lakes states, managers and conservation biologists face the challenge of finding a balance between the management of forests for timber, game species, and other sources of economic gain for local residents, and maintenance of ecosystem processes and biodiversity (The Nature Conservancy 2000). In the eastern Upper Peninsula (U.P.) of Michigan, much of the forested land has traditionally been managed with a focus on maximizing harvest of both timber and white-tailed deer (*Odocoileus virginianus*). Although the effects of timber management on bird distributions have been studied for many years in a wide variety of forests (e.g., reviews by Thompson et al. 1995, Hejl et al. 1995, Dickson et al. 1995), the effects of abundant deer on birds are less-well known. To effectively include birds in large-scale forest management plans, managers should have access to information that allows them to predict how birds will respond to timber management, and understand how the effects of deer may further change the quality of forested habitats.

The most obvious effects of high deer-densities within forests are on understory plants. In areas where deer concentrate, there are often significant reductions in the density, height, and species diversity of shrubs and small trees (e.g., Stoeckeler et al. 1957, Tilghman 1989, Anderson and Katz 1993). Over time, as species fail to regenerate, intense browsing can change the structure and composition of forests (Anderson and Loucks 1979, Frelich and Lorimer 1985, Tilghman 1989, Anderson and Katz 1993, Van

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Deelen et al. 1996, Cornett et al. 2000). The primary effect of deer on songbirds is likely to be alteration of habitat, as the low vegetation layers consumed by deer are used by many bird species for foraging and nesting. High deer populations have been correlated with reductions in some bird species' densities, especially shrub-nesting species (Casey and Hein 1983, DeGraaf et al. 1991, deCalesta 1994, McShea et al. 1995, McShea and Rappole 2000, Perrins and Overall 2001). However, within the same forest stand, effects on bird species can be mixed, as some species or groups of species favor the habitat conditions produced by abundant deer (Casey and Hein 1983, McShea and Rappole 2000, Fuller 2001, Perrins and Overall 2001). Variation in response to deer browse may also be found between sites within the same group of birds. For example, ground-nesters have displayed positive responses to high deer densities where more open understory characteristics have been created, and negative impacts where browse led to replacement of shrubs by grasses and forbs (deCalesta 1994, McShea and Rappole 2000).

My purpose in undertaking this study was to assess the influence of deer browsing the forest understory on habitat quality for one of northern Michigan's neotropical migrant songbirds, the Black-throated Blue Warbler (*Dendroica caerulescens*). Heavily-browsed (HB) hardwood forests in northern Michigan typically have hardwood understory vegetation that is kept at a fairly uniform maximum height range (0.5 - 0.75 m tall) by browsing deer. These plants are usually not completely browsed, as browse effects in forested areas are most intense in the winter, when short vegetation is protected by snow. Both HB and less-browsed (LB) northern forests may also have dense clumps of understory balsam fir that foraging deer tend to avoid. Browse effects and variations in understory species composition are likely to be important to black-throated blue warblers because these birds typically nest in low shrubs, and forage primarily by gleaning caterpillars from shrub layer - mid canopy foliage (Holmes 1994, Whelan 2001). Blue warbler densities have been found to be positively associated with shrub-density (Holmes et al. 1996), and decreased blue warbler densities have been found where deer abundances were high in deer exclosure/enclosure studies (DeGraaf et al. 1991, deCalesta 1994).

In this work, I focused on high-shrub density forest stands to see if habitat quality in HB areas, where the total volume of hardwood understory was typically reduced, was

lower than habitat quality in LB forests. In particular, I examined whether there was evidence that the reduced understory-vegetation volume typical of HB forests seemed to reduce habitat quality by limiting blue warbler reproduction. Although browsing by deer was not examined, Holmes et al. (1996) found that high shrub-density areas contained more older birds that had higher reproductive success than birds with territories in low shrub-density areas. Blue warblers commonly produce up to two broods per breeding season (Holmes 1994), and Holmes et al. (1996) found that variation in the frequency of double brooding explained the observed higher reproductive success in high-shrub density areas. Although I focused on comparing the number of broods produced in HB and LB forests, I also examined five other demographic parameters that could indicate habitat quality-related preferences of blue warblers, and that may help explain mechanisms behind any variations in quality. These factors were: rates of nest survival/success; overall age distribution of adults; age distribution of "new" birds (those breeding for the first time on the sites); pairing success of males, and; return rates of breeding adults.

I predicted that birds on LB sites, which potentially supply more resources (e.g., insects associated with understory vegetation) to breeding pairs than HB sites, would have higher reproductive success, especially in terms of frequencies of second broods. I estimated nest success, as well as number of broods, because any differences in numbers of broods per pair could result from variations in rates of nest depredation, as well as from variations in resource availability. For the next factor, age distribution, if LB habitats were of higher quality for this shrub-nesting and foraging species, I would expect a higher percentage of older birds (rather than yearlings) in LB sites when compared to HB sites. I based this prediction on studies that suggest older male songbirds often arrive at breeding grounds earlier and have first choice of territories, and that older males sometimes actively exclude younger males from settling in preferred areas (Ficken and Ficken 1967, Sherry and Holmes 1989, Møller 1991, Petit and Petit 1996). Similarly, because at least some adult songbirds disperse between breeding seasons (Lemon et al. 1996, Holmes et al. 1996), I predicted that a higher percentage of the "new" birds on LB-sites would be older males when compared to HB sites. I assessed female site-preference through a test of the hypothesis that pairing rates on LB sites would be higher than on HB

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sites, because it is common for some male songbirds to remain unpaired, especially in less-preferred habitats (Probst and Hayes 1987, Gibbs and Faaborg 1990, Vickery et al. 1992, Hunt 1996). Finally, breeding-site fidelity in birds has been shown to increase directly with reproductive success, especially for females (Greenwood and Harvey 1982, Payne and Payne 1993). I predicted that both male and female return rates would be higher at LB, rather than HB, sites.

I conducted this assessment of blue warbler demographic parameters concurrently with a comparison of blue warbler relative abundances, territory sizes, patterns of habitat occupancy, and density in HB and LB forests (Chapters 2, 4, 5). Together, these studies provide an unusually comprehensive assessment of habitat quality for a songbird breeding in a set of hardwood forest stands that vary in terms of understory characteristics. In addition, this study is a valuable contribution to the body of work addressing the impacts of abundant deer because it takes place on large study areas within a naturally-occurring gradient of deer-browse intensity, rather than utilizing deer relatively small exclosures or enclosures to modify density levels.

Study sites

I conducted this research in hardwood forests within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula (U.P.; Figure 2.1). Within the eastern HNF, there are two bands of hardwood forest, one in the southern section (high winter deer-densities) along the Niagara Escarpment (lat 46°04 N, long 84°55 - 84°40W), and a second in the northern half (lower winter deer-densities), between approximately 0 and 15 km south of Lake Superior (lat 46°27 N, long 84°37 - 85°07 W). In most of the U.P., there is a gradient from higher deer-browse pressure to lower from the south to the north due to the concentration of deer in southern areas (near Lake Michigan) during the winter (Van Deelen 1995). Within these bands of hardwood forest, I selected two HB and two LB sites where black-throated blue warblers were locally abundant. HB sites were within a few kilometers of coniferous forest stands that consistently functioned as "deer yards," places where wintering deer concentrate at night to take advantage of thermal protection provided by coniferous vegetation. All four sites

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were within actively managed sections of hardwood forest that have re-grown following extensive logging in the U.P in the early 1900's (McCann 1991).

Canopy trees on the four sites were dominated by sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*), with lower densities of ironwood (*Ostrya virginiana*), yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), and occasional white spruce (*Picea alba*), white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), and linden (*Tilia americana*). Vegetation data for all sites are presented in Appendix A. Tree species varied somewhat between HB and LB sites, for example red maples were more common on LB sites, and small ironwood trees (10-15 cm diameter) were more common on HB sites. Understory at HB sites was a mosaic of patches of browsed hardwoods (mostly sugar maples), and dense patches of balsam fir. On HB sites, hardwood stems taller than approximately 0.75 m were rare, primarily due to the effects of wintering deer foraging on vegetation available above snow cover. Most hardwood stems showed evidence of repeated browsing and re-sprouting, and many saplings, especially beeches and ironwoods, had been stripped of all but a few small branches. Understory vegetation on LB sites consisted primarily of seedlings and saplings of the common overstory trees, especially beech, red maple, and sugar maple, with lower densities of yellow birch and balsam fir. On LB sites, the understory layer was typically multi-layered, with many areas of dense hardwoods between 0.5 and 3 - 5 m tall. The height and density of shrubs at LB sites showed variation across space, and was strongly linked to time since thinning or other disturbance.

To determine the extent of each site, I walked parallel transects until I found 10-12 singing male warblers. My goal was to establish rectangular sites dominated by hardwood forest, but some site boundaries were irregularly-shaped because they followed roads, or because the site was truncated due to a change in forest type. The sizes of each site were: HB-Wishbone at 78 ha; HB-Wilderness at 62 ha; LB-McNearney at 62 ha, and; LB-Slash at 40 ha. To facilitate bird mapping and vegetation sampling, I established sets of parallel transects on each site to create a 50-m interval grid of marked trees.

Vegetation sampling

I collected vegetation data at LB and HB sites to facilitate comparisons with other studies. I used a modification of the James and Shugart (1970) method, and sampled between 48-71 (number of samples varied with plot size and vegetation variability) randomly located points on each plot (Appendix A). To characterize trees, I recorded all trees present in 11.3 m radius (0.04 ha) circles centered on the random points, and grouped them by diameter classes (measured at 1.5 m height). To estimate shrub density, I counted all woody stems within a 5 m radius of the center of the sampling circle and assigned each stem to one of the following classes: (1) shrubs - 0.5 to 1.5 m tall; (2) saplings – over 1.5 m tall, but less than 2.5 cm in diameter (at 1.5 m in height); and (3) small trees – between 2.5 and 7.5 cm in diameter. I also assigned each shrub and sapling to a browse category based on the following criteria: no browse (no evidence of browse); low browse (some branches/stem appeared browsed, but fewer than 50%), and; high browse (more than 50% of branches/stem appeared browsed). I collected approximately one third of the vegetation samples each year from 1998-2000.

Methods

Individual identification, age determination, site fidelity, and territory mapping
I began field work in spring of 1997 with a pilot study at the HB-Wishbone site, and continued work at all four sites from May - August, 1998-2001. To identify individual black-throated blue warblers, I caught and banded birds with unique combinations of a numbered U.S. Fish and Wildlife Service aluminum leg band, and two colored plastic leg bands. I caught males by playing tape-recorded songs near a mist net, or when this method failed, caught them in a net placed near a nest when the birds were feeding nestlings. Females were caught in nets placed near active nests. When birds were in-hand for banding, I determined their relative age as either yearling (second-year, SY) or older (after second-year, ASY) based on plumage characteristics (Pyle 1997: 467-469, Graves 1997a). After two years of practicing age determination of free-living birds (1998-1999), in 2000 and 2001 I determined the ages of a few unbanded males through field observations (Graves 1997a). The age-ratio (older:yearling) data includes

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information for all birds with all or part of their territory on a research site. When banded birds returned to areas off the research sites in years following banding, I did not include them in the age-ratio results for those later years.

I estimated return rates (breeding site-fidelity) by searching for banded birds on the four sites, and in an area approximately 200 m wide around the perimeter of each site. In the 200 m zone around the sites, I used song playback to ensure that males were detected. I am confident that males that returned to or near the study sites were identified, because males sang frequently and typically responded strongly to recorded blue warbler songs, and thus were relatively easy to detect. However, I may have missed some females that returned to the area near, but not on, the research sites. I did not include birds that were presumed to have died during the breeding season when estimating return rates for the next year. I first banded birds in 1997 at the HB-Wishbone site, and in 1998 on the other three sites, although many birds were not caught on the LB-Slash site in 1998. As a result, I had four years (1998-2001) of return data for the HB-Wishbone site, and three years on the remaining sites (1999-2001). To determine territory boundaries, I mapped bird locations at each site throughout the breeding season (mid May through the first week of August). My assistants and I visited each site every 2-4 days, and we attempted to observe and evaluate reproductive status for each male at least once a week, with more frequent visits paid to birds or pairs with unknown status.

Pairing success and breeding productivity

I classified male black-throated blue warblers as paired if a female was consistently observed in their territory. In a few cases, we rarely or never observed a female, but I classified the male as paired because he was observed feeding fledglings. I classified males as polygynous if they were observed feeding nestlings at two or more nests with different females, at least one of which had to have been banded. It is possible that I missed some cases of polygyny, especially in the early years of the study.

To estimate each pairs' reproductive success, my assistants and I searched for nests, followed the fate of nests, and recorded observations of adults caring for fledglings. When nests were found, we checked them every 3-4 days until they were depredated, abandoned, or fledged young. I classified a nest as successful if it fledged at least one

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young, which required that we had observed a fledgling with a known parent bird after the nest was found empty. I considered a nest to be abandoned if it had been active when found (e.g., female seen building nest, or incubating eggs) and the nest appeared complete (e.g., fully lined), but later became inactive (no eggs laid, existing eggs not incubated) without evidence of predation. When we observed a known bird feeding fledglings in a territory where we had not found a nest, I classified the pair as having fledged a brood. I did not include these inferred successful nests in estimates of nest success or daily nest survival. To assess whether focusing on number of broods might mask important variation in reproductive success due to variations in the clutch size or number of fledglings produced per nest, I compared clutch and brood sizes for the different site-types as well. In addition, because work by Holmes et al. (1996) suggested that blue warblers of different ages may vary in terms of reproductive success, I compared the frequency of double brooding, clutch sizes, and number fledged per nest within each habitat type by age of both male and female.

Statistical analyses

I pooled data from the two sites of each type (HB and LB) for statistical analyses. For all categorical data types (e.g., age ratios, return rates, male breeding status, number of broods, simple nest success), I compared the distribution of values for the two site-types with Chi-Squared Tests of Independence. To avoid violation of the sample size assumptions of the Chi-Squared Test, for the comparison on number of broods per year, I pooled data for the two and three brood categories because only a few (polygynous) territories produced three broods. Similarly, when I analyzed the number of broods produced within each site-type by age of parent, I pooled data for the 0 and 1 brood groups for most tests (all but the test for males on LB sites) because of the small number of pairs producing 0 broods.

I have presented nest success data in two ways: simple success (% of active nests that fledged at least one offspring) and a maximum likelihood estimate of daily nest survival rates based on the Mayfield method (Mayfield 1961 & 1975, Bart and Robson 1982). I included nest success estimates based on the modified Mayfield method as an addition to simple success because many nests were found after egg laying had begun,

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which can lead to serious positive biases in estimates of nest success (Mayfield 1961 & 1975, Hensler and Nichols 1981, Bart and Robson 1982). The calculation method I used for estimating modified Mayfied daily survival was presented by Bart and Robson 1982, and I used software created by Hines (1996) to perform the calculations. The modified Mayfield method required that I include only nests active for at least 2 visits. Due to this rule, some of the successful nests that I included in the estimates of simple nest success were not reflected in the modified Mayfield estimates, because these nests were found a few days prior to fledging, and nestlings had fledged by the second visit. To convert the Mayfield daily survival estimates to probabilities of fledging success for the entire laying-to-fledging period, I raised the estimated daily rate to the power of 25, the typical number of days between laying of the first egg and the fledging of young (Holmes 1994, Hall personal observation). I used a two-sided Z-test to compare the two estimates of daily survival (Bart and Robson 1982). I set alpha at 0.05 for all statistical tests.

Results

In total, I observed 65 individual banded male black-throated blue warblers between 1997-2001 on HB sites, and 67 banded males between 1998-2001 on LB sites. I also collected data on a few (3-6) unbanded males at each site-type. I caught fewer females each year, with 46 banded on HB sites, and 40 banded on LB sites. Many females were unbanded, especially in the early years of the study, and many banded individuals of both sexes were observed for multiple years on the same site.

Age ratios and return rates

I found that age ratios for male black-throated blue warblers on both site-types were biased toward older birds (Table 3.1), with 78% and 63% of males on HB and LB sites, respectively, in the older age class. Although both site-types had more older males, this bias in age distribution was significantly stronger on the HB plots ($X^2 = 5.06$, df = 1, p = 0.025). Female age-ratios were highly variable between plots and years, but on average just over half of the banded females on a plot were older (54% and 58% on HB and LB

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sites, respectively, Table 3.1), and I detected no difference in age distribution between the habitat types ($X^2 = 0.188$, df $= 1$, p $= 0.66$).

Just under half of the banded male blue warblers present in a given year returned to breed at the same site in the following year (Table 3.2). I found no difference between male return rates on HB and LB sites (46% and 44%, respectively, $X^2 = 0.077$, df $= 1$, p $= 0.78$). Return rates were highly variable between sites and years, with some individuals returning multiple times, including one male banded on the HB-Wishbone plot that was present all five years of the study (Figure 3.1). I found that the HB-Wilderness plot had consistently high male return rates (Figure 3.1). When I separated male return rates by age class of birds, the older males tended to return at higher rates on both site-types, although this trend was not significant (HB sites: $X^2 = 3.01$, df $= 1$, p $= 0.083$; LB sites: $X^2 = 0.77$, df $= 1$, p $= 0.38$). The rates at which each age class returned to the two site-types also were not significantly different (older: $X^2 = 0.096$, df $= 1$, p $= 0.76$; yearling: $X^2 = 0.42$, df $= 1$, p $= 0.51$).

The proportion of new males (birds arriving at a site in a year after most males had been banded) that were older tended to be higher on HB rather than LB sites (58% vs. 40%), but I did not find a significant difference between the sites ($X^2 = 2.77$, df $= 1$, p $= 0.096$). Just over half of all new females banded at all sites were older (54% and 58% at HB and LB sites, respectively), and I found no difference in the age ratios of new females between the two site-types ($X^2 = 0.12$, df $= 1$, p $= 0.73$).

Male pairing success, measures of reproductive success

I found that the majority of male blue warblers on all sites appeared monogamous (95% on HB sites, 92% on LB sites), and that mating status was very similar between the two site-types (Table 3.4). In the five years of the study, I classified only four males (one on an HB site, three on LB sites) as unpaired, and found that six were polygynous (three for each habitat type). I could not use a X^2 test to compare these distributions due to a violation of the test's assumptions, but there appears to be no evidence for a difference in mating success between site-types.

The number of broods produced per male territory was also very similar between the two habitat types; I found 70% and 68% of pairs (or male and two females) produced

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one brood, and 27% or 23% of pairs produced two or more broods per season (HB and LB sites, respectively; Table 3.4, $X^2 = 1.26$, df = 2, p = 0.53). On the HB sites, I found no significant relationship between bird age and number of broods, although both older males and especially older females were more likely to have a second brood. Twenty-nine percent (N = 63) of older HB-site males had two broods, compared to 23% (N=18) of yearling males ($X^2 = 0.29$, df = 1, p = 0.59), while 38% (N=29) of older females and 23% (N=22) of the younger females displayed this high level of reproductive success ($X^2 = 1.34$, df = 1, p = 0.25). Many HB site females were unbanded, and 21% (N=29) of these females were known to have produced second broods. In contrast, on LB sites, I found that older males were significantly more likely to have a second brood than younger males: 36% (N=50) of older males had second broods, compared to only 10% (N=29) of younger males ($X^2 = 11.9$, df = 2, p= 0.0026). I found a similar, but not quite significant pattern for females on the LB sites, where 41% (N=31) of older females produced two broods, while only 16% (N=19) of yearling females produced two broods ($X^2 = 3.70$, df = 1, p = 0.054). As on the HB sites, many females (31) were unbanded, and therefore of unknown age; of these females, 13% produced 2 broods.

Clutch sizes were similar on the HB and LB sites. Most clutches had four eggs, although we commonly found three-egg clutches late in the season, and found one five-egg clutch (a first brood on an LB site), and one two-egg clutch (a replacement clutch on an HB site). The average clutch size for nests that were first-brood attempts (including both first attempts and replacement nests) was 3.82 (SE 0.061, N = 51) for HB sites, and 3.95 (SE 0.048, N = 42) for LB sites. Second-brood attempt clutch-sizes were significantly smaller on both site types at 3.53 eggs (SE 0.13, N = 15; t = 2.18, df = 64, p= 0.033) on HB sites, and 3.56 eggs (SE 0.13, N = 16; t = 2.85, df = 54, p = 0.010) for LB sites. I did not find a significant difference between clutch sizes for either first- or second-brood attempts when the two site-types were compared (first attempts: t = 1.67, df = 89, p = 0.099, second attempts: t = 0.157, df = 29, p = 0.87).

The numbers of fledglings produced per successful nests were also similar on the two site-types. I found that HB-site first-brood nests produced 3.60 (SE 0.11, N = 40) fledglings, and LB site first-broods produced 3.77 (0.097 SE, N = 27) young per nest (t = 1.12, df = 65, p = 0.24). Second-brood sizes were the same for both site-types at 3.43

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(0.14 SE, N=14) fledglings produced per nest (t = 0, df = 26, p = 1). I found a lower number of fledglings than suggested by the clutch size because some nests had eggs that did not hatch, and a few nests lost one or more fledglings or eggs during the nesting cycle. For all nests where I knew the clutch size and number hatching, 19% (N = 58) and 9% (N = 56) on HB and LB sites, respectively, had one or more eggs that did not hatch (not a significant difference X^2 = 2.38, df = 1, p = 0.12). Of nests that successfully fledged young, one nest on each site lost a hatchling before the nest fledged, and one lost an egg (N = 48 on HB, N = 46 on LB). Of the lost nestlings, one was from the five-egg clutch, and this hatchling was much smaller than the others by nestling day 4, and may have starved. The other nestling and the egg may have been removed by a predator, or the egg may have broken and been removed by a parent bird. In addition, one other nest that did not end up fledging young lost nestlings that had been of similar size to remaining nestlings before the entire nest was lost, and two nests found to be depredated had partially-chewed dead nestlings in them at their last nest check. These observations suggest that in some cases predators did not remove all nestlings (or eggs) at once.

Rates of nest depredation

Overall, I found that simple estimates of depredation rates for blue warbler nests were fairly low, but tended to be higher on the LB sites (HB 17%, N = 71 vs. LB 30%, N = 69, Table 3.5). This trend was not statistically significant (depredated compared to successful, X^2 = 3.09, d.f .= 1, p= 0.078). Only one blue warbler nest was parasitized by a brown-headed cowbird (*Molothrus ater*); this nest was on the LB-McNearney site within 100 m of a dirt road, and was depredated before hatching. A total of 55 HB-site nests and 54 LB-site nests met the criteria for being included in the modified Mayfield estimation of daily nest survival. As I found in the simple nest depredation/success results, the estimate of daily survival probability was higher for HB-site nests, with a value of 0.986 (0.0042 SE, 95% confidence interval = 0.979 to 0.995), compared to 0.972 (0.0065 SE, 95% confidence interval = 0.960 to 0.985) for nests on LB plots. Again, the trend toward higher depredation rates on LB sites was strongly suggested, but not statistically significant (Z = 1.84, p = 0.066). When converted to daily survival

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probabilities, the Mayfield estimates suggested a nesting-period survival probability of 71.2% for nests on the HB plots and 49.4% for nests on the LB plots.

Discussion

Overall, the populations of black-throated blue warblers breeding on HB and LB study sites displayed very similar demographic patterns, and had high older:yearling ratios, high return rates, and high reproductive success. These results contradict the suggestion by Graves (1997b) that forests in the Great Lakes region are "sink" populations made up of yearling warblers produced in the Appalachian region. With nearly all males on both types of sites able to attract mates, over 90% of pairs producing at least one brood, and nearly a quarter of pairs producing two broods, these populations are more likely to act as source populations for neighboring areas. Holmes and colleagues have estimated that to maintain steady population levels (i.e., replace adults that die at an assumed rate of 40-50% per year) blue warbler pairs would need to produce 3-4 young per year (Holmes et al. 1992). Based on the average number of fledglings per first and second broods, as well as the frequency of various number of broods per female (not per male territory, as shown in the tables), females on both HB and LB sites produced an average of 4.2 fledglings per year. Even if second broods were not included, females produced an average of 3.4 fledglings at both site-types per season as a result of both relatively low nest depredation rates, and frequent renesting when nests were lost.

Age ratios

I found that male age-ratios were a reasonable predictor of within-site reproductive success, in that both site types had high percentages of older males, and also had high reproductive success. However, success was not significantly higher on HB sites, even though these sites had a higher proportion of older males. Also, when compared on an individual basis within sites, older males had significantly higher frequencies of second broods on LB, but not HB, sites. Female age-ratio data were likely slightly biased toward older females, as it was much easier to see a banded returning female and count her as an older bird than it was to catch an unbanded female that could be of either age. However,

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the similarity in patterns of female age-ratios and returns between the site-types suggests that this bias is not likely to impact a comparison between the two types. With over half of known-age females in the older age group, and high reproduction at both site-types, the relationship between female age-ratio and reproductive success was consistent with those found by Holmes et al. (1996) at the scale of sites, as was the suggestion of higher reproductive success for older females (stronger at LB rather than HB sites).

Overall, the male age-ratios that I found were very similar to Holmes et al.'s (1996) results for their high-shrub density plots (68%, N = 100, average values at these Michigan sites were 78% and 63% for HB and LB sites, respectively), while Holmes et al.'s estimates for females were somewhat higher (71%, N= 86, Michigan sites ranged from 40-62%). However, my male age-ratio values were higher than the 56% found by Graves (1997b) for 293 birds collected at 9 locations north of 40 degrees north Latitude (including one location in northern Michigan, and two in southern Ontario) and were more similar to the value of 72% that he found for southern birds (N=272, from 13 locations south of 40 degrees). Based the higher frequencies of young birds that he observed in the northern margins of the blue warblers' range, Graves (1997b) suggested that these range-margin areas function as sink habitats for birds produced by source populations in the center of the range (e.g., the southern portion of the Appalachian Mountains), a conclusion with which my results strongly disagree.

Based on the significant difference in the male age-ratios on HB and LB sites, I suggest that age ratios vary on a much smaller scale than Graves hypothesized (1997b). This idea of smaller-scale variation is also strongly supported by Holmes et al.'s (1996) study, in which high shrub density areas had more older males than nearby sites with experimentally reduced shrub-densities (65 vs. 35% older, respectively). It is possible that forests in Michigan show particularly high meso-scale variation in blue warbler age-ratios across space due to natural variation in soil and forest types, and the often strong impacts of forest management on understory characteristics. The understory layer in most hardwoods forest of northern Michigan is predominantly comprised of small seedlings and saplings of overstory tree species, rather than dense patches of shade tolerant shrubs such as the abundant *Rhododendron* species and mountain laurel (*Kalmia latifolia*) in parts of the Appalachians (Guzy 1995) or hobblebush (*Viburnum alnifolium*)

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in New Hampshire (Holmes 1994, Holmes et al. 1996). As a result, time since thinning is likely to have a particularly strong impact on shrub density, and patterns of habitat occupancy shown by shrub-nesters like blue warblers. In addition, the physiognomies of the shrubs mentioned above that are common in other regions provide many potential nesting sites for blue warblers (e.g. low branch forks), while the tree seedlings and saplings that dominate northern Michigan forest understory vegetation are often relatively straight with one or two forks (although browsing can lead to more forks). One native, shade-tolerant shrub, Canada yew (*Taxus canadensis*), may have provided important habitat for shrub nesting songbirds, but is a preferred food for deer, and has been locally extirpated in many northern forests where deer densities are, or have been, high (Beals et al. 1960, Alverson et al. 1988, Van Deelen et al. 1996). So, habitat in other regions may have higher blue warbler densities due to higher densities of potential nesting and foraging sites, but northern Michigan breeding areas are likely still important, because they can support populations with high reproductive output.

A typical northern Michigan forest condition related to this lack of shade-tolerant shrubs may have led to a sampling bias in Graves' work. Graves typically collected birds for aging and estimated densities "along trails or old logging roads" (1997b:2525), which, in northern Michigan, and perhaps Ontario, often have thin strips of dense understory along each side due to increased light penetration from the removal of canopy trees. As a result, he may have found linear strings of bird territories in areas that did not have large expanses of dense understory due to closed canopy conditions. If dominant older males avoided these narrow bands of habitat, this would lead to lower older:yearling age ratios. Although Grave's collection method was presumably consistent for all of his sample locations, it would potentially cause a stronger bias in areas like Michigan with few shade-tolerant shrub species.

I found that 46 - 44% of adult males (both age classes combined; HB and LB sites, respectively) returned, and these values are similar to those found for other forest songbird species in "good" habitat (e.g., Lemon et al. 1996, Weinberg and Roth 1998, Porneluzi and Faaborg 1999). In particular, these results are very similar to the 46% (N= 130) return rate that Holmes et al. (1996) found in "control" high shrub-density plots, while they found a non-significant trend toward lower returns on low-shrub density plots

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(33% returned, N=61). Although return rates, especially of older males, were high, dispersal of adults between breeding seasons was common at both site-types, as evidenced by many older birds appearing as new birds on the research sites. The tendency of yearling male blue warblers to have lower return rates, which was also found by Holmes et al. (1996), and by Lemon et al. (1996) for American redstarts, suggests that these younger birds are more likely than older ones to switch locations between breeding seasons. If the trend of a higher percentage of older birds among the new arrivals at HB sites (58% of 45 at HB sites, vs. 40% of 47 at LB sites) persists as larger sample sizes accrue, this could suggest variation between the HB and LB sites in one or more of at least two different population-level processes. First, more older males could be dispersing between areas in the HB sites and out-competing young males for a limited number of preferred breeding territories. This sort of pattern could result if understory firs, which provided complex understory habitat in spite of high deer densities in the HB sites studied here, act as limiting resources within HB forests. If true, I would expect to find many young males in nearby forests with few firs, and that these young males would have relatively low return rates, suggesting dispersal into areas with more firs in the second breeding season. Second, the pattern of high percentages of older birds at HB sites could indicate lower recruitment of yearling males. Testing this hypothesis would be very difficult, as birds produced on these relatively small sites are highly unlikely to be observed again (Holmes 1994, personal observation), making direct comparisons of recruitment a near impossibility.

Return rates

On both HB and LB plots, about 30% of females returned per year. Female returns, and thus inferred female survival, may be lower in part because females move further between breeding attempts (reviewed by Greenwood and Harvey 1982, Clarke et al. 1997). Based on my observations, returning females occupied different territories more often than returning males, which we almost always found on or very close to their former territory. This result should be interpreted with caution, as we did not catch 15-50% of females at a site in a given year, so if these birds returned and then were banded, they would be counted as new, rather than returning, birds.

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Reproductive success

The frequency of double-brooding that I found suggests that second broods may be slightly less common in Michigan than in New Hampshire: Holmes et al. (1992) found that 10% of females fledged 0 broods, 54% fledged 1 brood, 35% fledged two broods, and 1% fledged 3 broods (N=71). In Michigan, I found quite a bit of yearly variation in the frequency of double-brooding, with 1999 a low-frequency year on all sites (4% HB, 10% LB), and 2001 a high year when about 40% of all pairs produced two successful nests. Some of this variation may have been related to variation in food supply; for example, in 2001 much of the HNF experienced an outbreak of forest tent caterpillars (*Malacosoma disstria*), which was especially noticeable on the more southern HB sites. During the outbreak, birds did not seem to eat the forest tent caterpillars, but we often saw them eat or carry the moths, which were very common in late June and July. Although rates of double-brooding were fairly similar between the two HB sites, there was some between-site variation at LB sites, with 31% double brooding at Slash (N=35), compared to 17% at McNearney (N=29). Although I pooled data for analyses due to small sample sizes, McNearney Lake also had lower female return rates (4 of 19, vs. 8 of 19 for Slash), suggesting that something about this site makes it of lower quality than the HB-Slash site.

At Hubbard Brook, yearly blue warbler nest survival probability (Mayfield method) has ranged from 46 to 79% (N = 12 years; Holmes et al. 2001). Based on inclusion of all data from 3-5 years per site, nest survival probabilities in these Michigan forests appear similar, although LB sites were closer to the low end of this range at 49%, and HB sites were near the high end at 71%. Values for the LB sites were very similar to the 47% (N=85) value estimated by Guzy (1995) for a high-density population of blue warblers in the southern Appalachians. Birds in Guzy's (1995) study were not banded, so how this rate of nest survival contributed to overall per-pair reproductive output is unknown. In a recent review, Martin estimated that 48.5% of nests of forest shrub-nesting species were lost to predators (T. Martin 1995:10, based on success/failure data for 13 species). The black-throated blue warblers studied here and also in New Hampshire by Holmes and colleagues tended to have lower rates of depredation by this measure (17% and 30% for HB and LB sites, respectively), which may be related to the

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fact that both my and Holmes et al.'s sites support relatively low density-populations in large forest tracts within primarily forested landscapes.

The strong trend toward higher nest success at HB sites is intriguing, and I suggest that it may help explain the higher male age-ratios on these sites (e.g., areas with lower depredation rates were in high demand) and the lack of a relationship between bird age and reproductive success on HB sites (all birds tended to do well). At least two deer and timber-management factors may contribute to this pattern. First, high deer densities may alter habitats in ways that make these habitats less suitable for nest predators, leading to lower predator populations, and lower depredation rates. In these northern Michigan sites, the most obvious likely predators were chipmunks, (*Tamias striatus*), although white-footed mice (*Peromyscus leucopus*) were probably common, and I observed a garter snake (*Thamnophis sirtalis*) consuming eggs at one nest. Corvids were uncommon, but mid-sized, secretive mammals may also depredate nests. For chipmunks and other mammals, the higher vegetation complexity at LB sites may provide better habitat, or high deer populations on HB sites in winter may reduce food supplies for rodents, leading to lower populations. In addition, management may have increased chipmunk habitat on the LB-Slash site, as this site was named due to the presence of "slash", or branches from trees were removed from the site when it was last thinned in the early 1990s. Chipmunks seemed more common on the LB sites, but I did not attempt to estimate relative population sizes.

A second, and not mutually exclusive hypothesis for lower depredation rates on HB sites is the idea of density-dependent nest depredation (Martin 1988, 1993, 1996, Martin and Martin 2001). Although the density of blue warblers tended to be higher on LB sites (Chapter 4), higher densities of American redstarts on LB sites (Chapter 2) may allow nest predators to experience higher success in finding nests, leading to higher rates of depredation. Although not a focus of this study, whenever nests of other species were found, they were monitored using the same methods described here for blue warblers. In general, most nests found were either shrub or ground nests, and were located within parts of the site occupied by blue warblers. On the LB sites, we found over 60 redstart nests, most of which were between 1 and 3 meters high, while blue warbler nests on these sites were typically 0.5 - 1 m high. Especially on the LB-Slash site, where blue warbler

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densities were highest and taller saplings were rare, the height range of redstart nests overlapped with the range of heights used by blue warblers, leading to at least a doubling of the density of nests in the 0.5 - 2 m height range. Evidence supporting the idea that high densities of redstart nests may increase depredation rates for blue warblers comes from a study by Martin and Martin (2001) on two co-existing, ground-nesting wood-warblers. In Martin and Martin's study, removal of either species led to increased rates of nest success for the other, suggesting a density-dependent shift in search strategies by predators. Redstarts were present in much lower densities on the HB sites, perhaps because these sites had few hardwood saplings and small trees (Chapter 2, Appendix A). Management of LB hardwood forests as even age stands probably contributes to overlap in nest site height distributions for these two species because, at least for a decade or so after thinning, dense patches of saplings are typically available, but there are few small trees to provide higher nest sites that would likely be preferred by redstarts.

Conclusions

Browsing of forest understory vegetation by deer can potentially impact breeding birds through many different mechanisms. The most apparent effects are likely to be related to changes in the structure and/or density of understory vegetation, which may alter the availability of nest sites or foraging habitat. Other possible links between deer browse intensity and bird populations include (1) changes in plant species composition, which may also alter food supplies or the availability of preferred nest sites; (2) changes in food supplies through effects on the abundance of invertebrates that use and may compete with deer for particular types of understory foliage (Lynch and Whigham 1984, Fuller 2001); (3) changes in nesting success through reduction in nest-site vegetative cover, indirect effects on nest predator population sizes, or direct nest depredation or trampling (Martin and Roper 1988, Reitsma et al. 1990, McShea 2000, Pietz and Granfors 2000); and (4) changes in habitat characteristics that alter the abundance of other bird species that might compete for food or nest sites, or act as brood parasites.

In this study, although some of these mechanisms may be at work, at the territory scale areas used by black-throated blue warblers were of equal quality on HB and LB sites. It is likely that the very similar levels of season-long reproductive success result

from a different set of constraints at each site type; for example, second broods may be limited on HB sites by food supplies, but limited on LB sites by higher rates of nest depredation. My results emphasize the importance of in-depth studies of banded birds, as very similar, high numbers of fledglings per pair were estimated for both site types, while estimates of nest success alone would suggest that HB territories were of higher quality. On a per-territory scale, both habitat types appear to function as source habitats. However, as density tended to be lower on HB sites (Chapter 4), when examined from the scale of forest stands rather than territories, most HB sites would be slightly lower quality than LB sites in terms of offspring produced per unit area. At the forest-stand scale, at HB sites the presence of balsam fir in the understory is likely to be an important component determining habitat quality, as HB areas with high densities of hardwood shrubs, but few firs, had significantly lower densities of black-throated blue warblers (Chapter 2).

In conclusion, within these high shrub-density Michigan forest sites, blue warbler density was a reasonable indicator of total reproductive output. Although even high-density populations in Michigan would be low density when compared to most other populations, the quality of individual territories was high, as birds had high levels of reproductive success. As a result, a direct comparison of density alone between populations in different regions, especially when other regions are likely to have higher rates of nest depredation, would likely under-estimate the quality of Michigan forests for blue warbler populations.

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Table 3.1. Age ratio, presented as percentage of older birds (n), of black-throated blue warblers in heavily-browsed (HB) and less-browsed (LB) northern Michigan forests.

	1997	1998	1999	2000	2001	1997-2001
Males						
HB-Wishbone	92% (12)	80% (15)	76% (17)	72% (14)	62% (13)	76% (71)
HB-Wilderness	-	64% (11)	75% (8)	100% (8)	89% (9)	81% (36)
LB-McNearney	-	79% (14)	77% (13)	54% (13)	54% (13)	66% (53)
LB-Slash	-	33% (6)	46% (13)	67% (12)	79% (14)	60% (45)
Females						
HB-Wishbone	33% (3)	33% (9)	88% (8)	67% (9)	75% (8)	62% (37)
HB-Wilderness	-	-	17% (6)	67% (6)	38% (8)	40% (20)
LB-McNearney	-	38% (8)	66% (6)	40% (5)	80% (5)	54% (24)
LB-Slash	-	50% (2)	25% (8)	78% (9)	80% (10)	62% (29)

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Table 3.2. Return rates of black-throated blue warblers in heavily-browsed (HB) and less-browsed (LB) northern Michigan forests. Data are presented as the percentage of the banded blue warblers present in the previous year that returned in the listed year (n).

	1998	1999	2000	2001	1998-2001
Males					
Older in previous year					
HB sites	64% (11)	47% (19)	42% (19)	56% (18)	**51% (67)**
LB sites	-	62% (13)	50% (16)	33% (15)	**48% (44)**
Yearling in previous year					
HB sites	100% (1)	29% (7)	17% (6)	25% (4)	**28% (18)**
LB sites	-	43% (7)	11% (9)	55% (11)	**37% (27)**
All males combined					
HB sites	67% (12)	42% (26)	36% (25)	50% (22)	**46% (85)**
LB sites	-	55% (20)	36% (25)	42% (26)	**44% (71)**
Females					
Older in previous year[1]					
HB sites	0% (1)	66% (3)	38% (8)	22% (9)	**33% (21)**
LB sites	-	75% (4)	17% (6)	44% (9)	**42% (19)**
Yearling in previous year					
HB sites	0% (2)	50% (6)	33% (6)	0% (9)	**26% (19)**
LB sites	-	17% (6)	25% (8)	20% (5)	**20% (20)**
All females combined					
HB sites	0% (3)	56% (9)	36%(14)	14%(14)	**29% (41)**
LB sites	-	40% (10)	21% (14)	36% (14)	**32% (38)**

Notes: (1) Total number of banded birds from previous year omits a bird presumed killed during the breeding season.

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Table 3.3. Age ratio, presented as percentage of older birds (n), of new (unbanded birds present in a year following a year when most males or many females were banded) black-throated blue warblers in heavily-browsed (HB) and less-browsed (LB) northern Michigan forests.

	1998	1999	2000	2001	1997-2001
Males					
HB sites	57% (7)	57% (14)	69% (13)	45% (11)	58% (45)
LB sites	-	40% (15)	38% (16)	44% (16)	40% (47)
Females					
HB sites	-	75% (4)	50% (10)	50% (14)	54% (28)
LB sites	-	33% (3)	55% (11)	70% (10)	58% (24)

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Table 3.4. Mating status and reproductive success (number of broods) of male black-throated blue warblers in heavily-browsed (HB) and less-browsed (LB) northern Michigan forests. When polygynous males are included in a category for number of broods, the number of these males is indicated in superscript. Unmated males are not included in listing of number of broods.

Mating status, years, (N)		unmated	mated	polygynous
HB sites, 1997-2001 (83)		1%	95%	4%
LB sites, 1998-2001 (79)		4%	92%	4%

Number of broods (N)	0 broods	1 brood	2 broods	3 broods
HB sites				
1997 (5)	0%	80%	20%	0%
1998 (14)	0%	71%	29%	0%
1999 (23)	4%	91%	4%	0%
2000 (20)	10%	60%[1]	30%	0%
2001 (20)	0%	50%	45%[1]	5%[1]
HB Total (82)	**4%**	**70%**	**26%**	**1%**
LB sites				
1998 (12)	8%	67%	25%	0%
1999 (21)	10%	81%	10%	0%
2000 (21)	10%	67%[1]	24%[1]	0%
2001 (22)	5%	55%	36%	5%[1]
LB Total (76)	**8%**	**68%**	**22%**	**1%**

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Table 3.5. Fate of all active black-throated blue warbler nests found in heavily-browsed (HB) and less-browsed (LB) northern Michigan forests.

sites, year (N)	abandoned	depredated	fledged at least one young
HB sites			
1997 (6)	0%	0%	100%
1998 (12)	8%	0%	92%[1]
1999 (18)	11%	22%	67%
2000 (17)	11%	29%	59%
2001 (18)	0%	17%	83%
HB sites total (71)	7%	17%	76%
LB sites			
1998 (14)	7%	14%	79%
1999 (19)	0	42%	58%
2000 (18)	0	39%	61%
2001 (18)	6%	22%	72%
LB sites total (69)	3%	30%	67%

Notes: (1) Includes two nests that lost one or more nestlings, apparently due to predation.

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Heavily-browsed sites
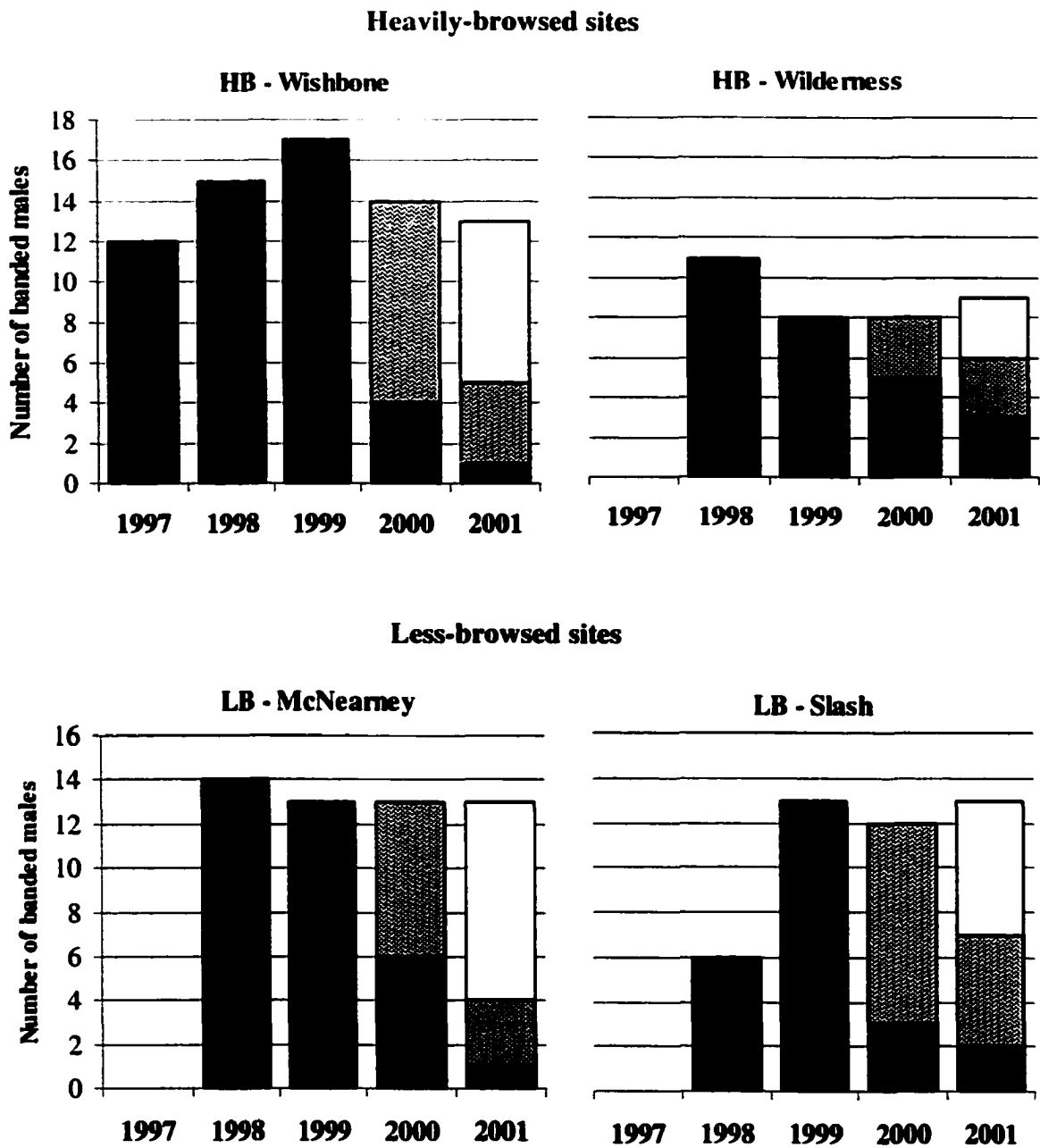
Figure 3.1. Yearly returns of banded male black-throated blue warblers in heavily-browsed (HB) and less-browsed (LB) forest sites by year of banding. Banding began in 1997 at HB-Wishbone, and in 1998 at the other sites. The banding year for each bird is indicated by the following patterns: ■ 1997 ■ 1998 ■ 1999 ▨ 2000 □ 2001 ·

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Appendix A. Vegetation characteristics of the two heavily-browsed (HB) and less-browsed (LB) northern Michigan sites. Large and medium tree values are means (± SE) from 11.3 m radius samples, while small trees, saplings, and shrubs were measured within 5 m radius circles. Percentage of the saplings and shrubs with >50% of branches browsed are shown after the values for each species.

	HB-Wishbone (N=71)	HB-Wilderness (N=50)	LB-McNearney Lake (N=61)	LB-Slash (N=47)
Large trees >23 cm				
sugar maple	3.9 ± 0.29	4.7 ± 0.36	2.2 ± 0.27	2.5 ± 0.38
American beech	0.5 ± 0.12	0.6 ± 0.17	1.2 ± 0.23	1.1 ± 0.23
red maple	0	0	2.9 ± 0.33	2.6 ± 0.36
balsam fir	0.1 ± 0.055	0.1 ± 0.0	0.18 ± 0.10	0.04 ± 0.03
other deciduous	1.2 ± 0.31	1.3 ± 0.33	0.08 ± 0.04	0.45 ± 0.14
other conifer	0.6 ± 0.44	0.36 ± 0.16	0	0.19 ± 0.11
Medium trees >7.5 - 23 cm				
sugar maple	11.5 ± 0.92	14.8 ± 1.2	13.6 ± 1.5	10.4 ± 1.3
American beech	2.4 ± 0.33	2.2 ± 0.48	2.3 ± 0.39	4.1 ± 0.76
red maple	0	0	4.5 ± 0.64	5.1 ± 1.3
balsam fir	3.0 ± 0.85	2.6 ± 0.92	0	0.96 ± 0.58
other deciduous	4.2 ± 0.72	2.7 ± 0.42	0.38 ± 0.15	1.4 ± 0.38
other conifer	0	0.06 ± 0.04	0	2.9 ± 1.7
Small trees >2.5-7.5 cm				
sugar maple	2.3 ± 0.45	1.7 ± 0.40	1.5 ± 0.39	1.0 ± 0.29
American beech	0.25 ± 0.19	0.02 ± 0.02	0.41 ± 0.11	0.33 ± 0.15
red maple	0	0	0.77 ± 0.22	0.31 ± 0.22
balsam fir	4.6 ± 1.0	6.9 ± 1.5	0.36 ± 0.08	1.1 ± 0.65
other deciduous	0.06 ± 0.03	1.6 ± 1.1	0.23 ± 0.09	0.29 ± 0.23
other conifer	0.30 ± 0.14	0.88 ± 0.80	0	0
Saplings				
sugar maple	3.3 ± 0.84 (33%)	4.2 ± 2.1 (24%)	3.3 ± 0.91 (0%)	3.6 ± 1.6 (0%)
American beech	0.68 ± 0.36 (76%)	0.06 ± 0.03 (30%)	26.7 ± 4.1 (0%)	18.2 ± 3.9 (<1%)
red maple	0	0	15.5 ± 3.7 (0%)	4.8 ± 19 (0%)
ironwood	4.0 ± 1.4 (89%)	3.8 ± 1.0 (71%)	0	0
balsam fir	11.1 ± 1.7 (0%)	10.2 ± 1.8 (0%)	0.31 ± 0.08 (0%)	1.3 ± 0.55 (0%)
other deciduous	0.03 ± 0.03 (0%)	2.7 ± 2.2 (37%)	1.6 ± 0.29 (0%)	3.6 ± 1.2 (0%)
other conifer	0.28 ± 0.11 (0%)	0.08 ± 0.04 (0%)	0	0
Shrubs				
sugar maple	70.9 ± 9.1 (52%)	62.5 ± 9.8 (35%)	13.9 ± 2.1 (0%)	30.1 ± 5.9 (0%)
American beech	2.9 ± 0.63 (84%)	2.0 ± 0.88 (65%)	42.6 ± 5.0 (<1%)	45.5 ± 6.61 (0%)
red maple	0	0	45.9 ± 5.9 (0%)	52.4 ± 9.6 (0%)
ironwood	26.4 ± 4.0 (78%)	14.9 ± 3.4 (56%)	0	0
balsam fir	23.4 ± 3.0 (3.8%)	14.5 ± 2.7 (0%)	0.61 ± 0.17 (0%)	1.1 ± 0.48
other deciduous	6.5 ± 1.7 (15%)	19.2 ± 5.7 (6.0%)	12.8 ± 3.0 (2%)	27.6 ± 9.2
other conifer	0.60 ± 0.18 (0%)	0.78 ± 0.37 (0%)	0.13 ± 0.04 (0%)	0.90 ± 0.54

CHAPTER IV

TERRITORY SIZES OF BLACK-THROATED BLUE WARBLERS IN HEAVILY- AND LESS-BROWSED HARDWOOD FORESTS

Introduction

A necessary first step toward predicting how changes in forested habitats will affect breeding migratory birds is understanding how species are distributed across heterogeneous landscapes. When available, bird-distribution data can be incorporated into landscape-scale management models, allowing the potential effects of proposed management actions on habitat availability to be assessed prior to actual changes in the landscape (Liu et al. 1995, Raphael et al. 1998). Management models can be further improved by ranking various habitats in terms of quality, which is best measured as the density of individuals multiplied by their average reproductive success (Van Home 1983, Vickery et al. 1992). At a local scale, the density component of the habitat-quality equation can be seen as a combination of two factors, territory size and territory distribution. Territory densities in a local area can vary between locations if the territory sizes defended by pairs are different due to differences in resource availability, differences in bird population density, or a combination of the two (see below). If territories do not significantly overlap and distributions are fairly uniform, typical territory size could be a useful predictor of how many pairs of birds a particular patch of "preferred" forest could support. Many songbird populations, however, exhibit low population densities and/or clumped distributions, with seemingly appropriate habitat left unoccupied (Sherry and Holmes 1985, Mikkonen 1985, Jones and Robertson 2001). As a result, when two patches of habitat are compared, they may support different densities of a species due to variation in territory sizes, variation in territory overlap, and/or differences in patterns of occupied and empty space.

The biological significance of territoriality and territory size has been a long-term focus in avian ecology. Studies of territoriality are closely linked to another long-term focus in avian ecology, habitat selection, in that preferred habitats are typically occupied by territorial individuals first, with territorial behavior potentially limiting the number of pairs breeding in that preferred area (e.g., Hinde 1956, Brown 1969, Fretwell and Lucas

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1970, Patterson 1980). For species that defend exclusive breeding territories, territory size can be described as the mechanism by which the availability of resources per unit area is translated to local breeding-population density (Newton 1992). When examined from a habitat-patch perspective, the percentage of habitat that is occupied by birds, especially over multiple years, can be used to infer the extent to which that area exceeds some minimum density of the resources required by a particular species. If spatial patterns of habitat occupancy are similar between years, comparing used areas to unused areas may be very useful in terms of developing and testing hypotheses about the basis of habitat selection at the territory scale (Petit and Petit 1996). If indeed territoriality acts to regulate population size, comparing territory sizes and distributions in different locations within a landscape could not only help better describe and predict the distribution of bird populations, but could also help identify mechanisms underlying differences among the dynamics of bird populations in habitats with different characteristics.

Most studies examining breeding-season habitat occupancy and territory size interpret these measures, typically along with others, as indicators of habitat quality. As described above, habitat quality incorporates season-long reproductive success and survival of birds in an area, as well as bird density (Van Horne 1983, Vickery et al. 1992). Since detailed reproduction and survival data are difficult to obtain, quality is often measured by proximate variables thought to be correlated with reproduction and survival, such as the density of food sources and potential nesting sites. The idea that locations within a habitat type can differ enough in quality to lead to variable occupancy rates is supported by bird removal studies, in which territories in "poor" sections remain open, while birds removed from "high quality" areas are quickly replaced by new birds, or birds that shift their territory locations (Newton 1992). Like habitat occupancy, territory size has been used to infer habitat quality from bird behavior (e.g., Hunt 1996, Jones et al. 2001), but this inference requires more assumptions in terms of how territory sizes are determined. This link between territory size and habitat quality is based on the idea that birds will attempt to secure a territory in the highest quality habitat that their individual level of fitness (e.g., age, size) allows, and then defend a territory large enough to meet their resource needs, and not larger, due to energy constraints associated with territorial defense. As with density, many field studies suggest that territory size is

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responsive to potential predictors of habitat quality, especially food availability (e.g., Cody and Cody 1972, Enoksson and Nilsson 1983, Mikkonen 1985, Smith and Shugart 1987). These observations support predictions from mechanistic behavioral models of feeding territory size, which suggest territory size will decrease as prey resources increase (Schoener 1983, Lima 1984). In recent work, evaluation of potential nest sites has also been included in measures of habitat quality and territory size, based on the idea that territories with many potential nest sites may offer a lower risk of depredation (see below, Martin 1988, 1993).

For insectivorous birds that forage and nest in the understory-vegetation layer of the forest, habitat quality may be closely linked to understory characteristics. The structure and density of understory vegetation may be a good predictor of prey density, because these characteristics determine the volume of understory substrate available for insects, especially those species that feed on plants. Understory characteristics may also predict habitat quality for shrub-nesters through effects on nesting success, as areas with few shrubs/saplings are likely to have fewer appropriate nest sites, and these sites may be at higher risk from predators that actively search appropriate microsites for nests (Martin 1988, 1993). Similarly, for predators that take eggs or nestlings by searching or incidental encounters, reduced foliage volume may increase the visibility of nests; lower nest cover was associated with higher rates of nest depredation in most studies (29 of 36) examined by Martin (1992). Finally, understory characteristics may influence habitat quality through determining the amount of cover available for young fledglings of shrub-nesting species (Holmes 1994, Moskoff 1995).

Timber management can strongly influence the characteristics of forests, including understory characteristics, leading to strong patterns of bird-species turnover as these systems are cut and later regenerate (e.g., Conner and Adkisson 1975, Probst et al. 1992, Hejl et al. 1995, Dickson et al. 1995). For some species, management history may provide a reliable indicator of aspects of habitat quality beyond measures of distribution and density. For example, Hunt (1996) found that American redstart (*Setophaga ruticilla*) territories in early and mid-successional habitats (following cutting) were about one fifth the size of territories in mature forest. Additionally, the early and mid-successional habitats also had higher densities, higher proportions of older males, and

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higher rates of paired yearling males. If the reproductive success of redstart pairs in these habitats shows the same pattern (higher in the same habitats where pairing success and density is high), knowledge of forest overstory type and management history alone could be useful predictors of habitat quality. Similar relationships may exist for other shrub- and small tree-nesting species, and potentially could be predicted from management history and stand type, as these factors typically account for most of the variation in understory plant characteristics in managed forests. However, for other species, availability of preferred microsites may not be well predicted by management history and overstory, especially when stands are exposed to different densities of browsing species such as white-tailed deer (*Odocoileus virginiana*).

In this study, I have used a Geographic Information System (GIS)-approach to explore relationships between understory-vegetation characteristics and the territories of a shrub-nesting songbird, the black-throated blue warbler (*Dendroica caerulescens*). In many northern Michigan hardwood forests occupied by blue warblers, browsing by white-tailed deer is a particular conservation concern (TNC 2000). High deer-densities can cause significant reductions in the density, height, and species diversity of shrubs and small trees (Tilghman 1989, Anderson and Katz 1993), and have been correlated with decreases in the abundance of shrub-nesting bird species in a number of deer exclosure and enclosure studies (Casey and Hein 1983, DeGraaf et al. 1991, deCalesta 1994, McShea and Rappole 2000).

Black-throated blue warblers tend to select territories with high shrub/sapling densities (Steele 1992, Holmes et al. 1996, Chapter 2), and tend to be less common in high deer-density areas (DeGraaf et al.1991, deCalesta 1994). In addition, Holmes et al. (1996) found that shrub density was a good indicator of habitat quality, as birds in areas with high shrub-densities tended to be older, and to have higher reproductive success when compared to birds breeding in low shrub-density areas. In particular, browsing of understory vegetation in northern forests reduces the availability of vegetation within the 0.5 - 1.5 m-high zone, which likely reduces the availability of blue warbler nest sites and habitat used by adults with new fledglings (Steele 1992, Holmes 1994, personal observation). The heavily- and less-browsed (HB and LB) hardwood forest stands that I studied varied in terms of understory species composition, height distributions, and

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patterns of shrub/sapling density. Of particular interest from a conservation perspective is that HB sites used by blue warblers tended to have dense patches of balsam fir (*Abies balsamea*), a species that deer rarely browse in this region, and that could be managed to provide browse-resistant understory habitat. This research is one part of a study assessing habitat quality in terms of both reproductive success and distribution patterns for blue warblers in HB and LB habitats, and is one of very few studies that examine deer-browse effects utilizing a natural gradient in deer-browse intensity. In addition, the sites that I studied differ from those used in previous work in that some low vegetation is protected, even in HB sites, by persistent snow, leading to patches of uniformly short (0.5 – 0.75 m) hardwood vegetation.

Based on the premise that browsing by deer may reduce habitat quality for black-throated blue warblers by reducing shrub/sapling height diversity and total volume, I tested the hypothesis that territories in HB habitats would be larger than those in LB habitats. To help characterize the distribution of territories between the HB and LB sites, I also present the overlap and arrangement of territories, along with maps of understory characteristics. In addition, I have summarized the territory size and overlap results to provide a description of how much area within the study sites is occupied by one or more territories. Finally, as an aid to interpreting results, I took advantage of the analytical capabilities of GIS to test the sensitivity of the territory size estimation method, minimum convex polygons (MCPs), to variations in numbers of bird observations. Although the MCP approach is frequently used by ornithologists (see methods), potential effects of differing numbers of bird-location records among territory size estimates is rarely addressed, and could be particularly problematic in analyzing data from low-density populations with potentially "loose" territory boundaries.

Study sites

I conducted this research in hardwood forests within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula (U.P.; Figure 2.1). Within the eastern HNF, there are two main bands of hardwood forest, one in the southern section (high winter deer densities) along the Niagara Escarpment (lat 46°04 N, long

84°55 - 84°40W), and a second in the northern half (lower winter deer densities), between approximately 0 and 15 km south of Lake Superior (lat 46°27 N, long 84°37 - 85°07 W). In most of the U.P., there is a gradient from higher deer-browse pressure to lower from the south to the north due to the concentration of deer in southern areas (near Lake Michigan) during the winter (Van Deelen 1995). Within these bands of hardwood forest, I selected two HB and two LB sites where black-throated blue warblers were locally abundant. The HB sites were within a few kilometers of coniferous forest stands that have consistently functioned as deer yards, places where wintering deer concentrate at night to take advantage of thermal protection from coniferous vegetation. All four sites were within actively-managed sections of hardwood forest that have re-grown following extensive logging in the U.P in the early 1900's (McCann 1991).

Canopy trees on the four sites were dominated by sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*), with lower densities of ironwood (*Ostrya virginiana*), yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), and occasional white spruce (*Picea alba*), white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), and linden (*Tilia americana*). Tree species varied slightly between HB and LB sites, for example red maples were more common on LB sites, and small ironwood trees (10-15 cm diameter) were more common on HB sites. Understory vegetation on HB sites was a mosaic of patches of heavily-browsed hardwoods (mostly sugar maples), and dense patches of balsam fir of a variety of sizes. Hardwood stems above approximately 0.75 m tall (they were not completely browsed due to protection by snow) were rare, primarily due to the effects of foraging deer. Most hardwood stems showed evidence of repeated browsing, and many saplings, especially beeches and ironwoods, had been stripped of all but a few small branches. Understory vegetation on LB sites consisted primarily of seedlings and saplings of common overstory-tree species, especially beech, red maple, and sugar maple, with lower densities of yellow birch and balsam fir. On LB sites, understory vegetation was typically multi-layered, with many areas of dense hardwoods between 0.5 and 3 m tall. Heights and densities of shrubs at LB sites showed some variation across space related to variation in time since thinning, or other types of canopy disturbance.

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To determine the rough size of each site, I walked parallel transects until I found 10-12 singing male black-throated blue warblers. The sites were all primarily hardwood forest, and some boundaries were irregular, as they followed roads, or because the site extent was limited by a change in overstory vegetation, or the presence of forest openings created for deer habitat (e.g., southwest corner of HB-Wilderness site). The final sizes of each site were: HB-Wishbone at 78 ha; HB-Wilderness at 62 ha; LB-McNearney Lake at 62 ha, and; and LB-Slash at 40 ha. To facilitate bird mapping and vegetation sampling, I established sets of parallel transects on each site to create a 50-m interval grid of trees marked with a band of labeled flagging tape.

Field Methods

Identifying and mapping blue warblers

I caught and color-banded black-throated blue warblers so they could be individually identified, and observed between 9 and 14 pairs at each site per year (1998-2001 for HB-Wishbone and LB-McNearney, 1998-2001 for the other sites). I banded birds to facilitate mapping territories, and because capturing and banding birds also allowed me to group birds by age (see below) and return status (e.g., a new bird, or one that had been on a site in a previous year), factors that might be correlated with territory size. I began banding birds in 1997 at HB-Wishbone, and in 1998 at the other sites. Therefore, birds could be identified as new or returning in 1998 at HB-Wishbone, and in 1999 at all other sites. When birds were in hand for banding, I aged them as either yearling (second year, SY) or older birds (after-second year, ASY) using plumage characteristic described by Pyle (1997) and Graves (1997a). All returning birds were by definition at least in their second breeding year or older (ASY), while new birds could be first time breeders or ASY birds that had dispersed between breeding seasons.

To test the hypothesis that blue warbler territories would be larger on HB sites, I mapped locations as birds moved throughout their territories. My assistants and I observed male warblers an average of 1-2 times per week throughout the breeding season (late May - early August) at all sites. A mapping session started after we had located a male warbler (typically singing) and recorded his location on a gridded data sheet. As the

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bird moved, we recorded new locations, continuing until we either lost the bird and could not relocate it within a 20-30 minute period of searching, or until we had observed the bird for 1-1.5 hours. My assistants and I did not record short-distance movements (e.g., 2 m or less, typically associated with foraging). Although maps focused on one bird, we recorded locations and behaviors of other birds encountered as we followed particular males. These territory size estimates can be described as "singing" territories (Hanski and Haila 1988), as I only included locations where male warblers were engaged in territorial behaviors such as singing, counter-singing, or fighting in the territory-size estimations.

During a typical early-season mapping session, male blue warblers made frequent, long flights across the territory to counter-sing with various neighbors. Once nestlings hatched, birds typically made fewer long trips around the territory, sang less, and were often observed silently bringing food to nests. Similarly, while male birds actively tended to young fledglings, they were less mobile, with an occasional song. By only including locations where birds sang or fought in the set of observations used to estimate territory size, I have prevented the many non-singing observations of birds near nests or with fledglings from biasing the estimation of territory boundaries. Bias could result because as birds feed nestlings or fledglings, they made many relatively short movements in a limited area, and were easier to follow than birds moving 50-150 m at a time. My territory-size estimation method involved removal of the most distant locations based on a harmonic mean calculation, so including many close-together observations could potentially strongly "weight" nests or fledgling habitat in ways that would influence which locations were considered "outliers"(see below). Although not directly reflected in the territory boundary estimate, all nests and the vast majority of observations of males with fledglings occurred within the singing territory boundaries identified here. It is likely that birds did move silently far away from territory centers at times (Hanski and Haila 1988), and locations used during these behaviors are potentially not reflected in the singing territory estimates.

Due to differences between birds' behaviors, and breeding success (less successful birds tended to sing more; see above) some birds were easier to locate than others, leading to differences in the number of observations available per male. In

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addition, the number of field assistants funded, their skill in following birds, and the time available for mapping vs. other duties (for a related study of reproductive success), varied between years. In particular, in the 2000 season, my assistants and I recorded more observations per bird than in other years due to an extra focus on mapping, and the above-average bird-finding skills shown by my assistants in that year.

Mapping understory vegetation

To create maps of understory vegetation for the four study sites, I estimated vegetation characteristics every 25 m along and between the marked transects at each study site. I developed this sampling method in order to sample vegetation at a fine scale over a large area in a relatively short amount of time (5-8 days of data collection per site). The sampling frame approximated the James and Shugart (1970) method, in that I estimated understory vegetation characteristics within a 5-m radius circle at each sample point. At each point, I estimated the most common (mode) understory seedling/sapling height, the height range of the middle 90% of understory stems, vegetation density, and the percentage of coniferous vs. hardwood vegetation. I defined seedlings and saplings as woody plants taller than 0.5 m, but less than 7.5 cm in diameter (all diameters measured at 1.5 m height). For both mode and 90% range of seedling/sapling heights, I estimated heights to the nearest 0.25 m from 0.5 -1 m, the nearest 0.5 from >1 m to 3 m, and nearest 1 m above heights of 3 m. I categorized vegetation density based on the percentage of the 5-m radius circle "covered" with vegetation. I used a cover approach rather than an estimate of number of stems because estimating cover allowed me to directly compare areas dominated by plants with different heights and growth forms (e.g., a balsam fir sapling typically fills more space than a maple sapling of similar height). To simplify density estimation, I recorded density in four coverage categories which seemed to represent natural breaks in density distribution: 0-10%; 11-40%; 41-80%, and; >80%. I also determined the percentage species composition of the understory vegetation by estimating coverage (to the nearest 5%), rather than number of stems. I collected all vegetation mapping data in August and September of 2000 (all sites but HB-Wilderness) or 2001 (HB-Wilderness). To avoid observer bias, I estimated all vegetation values myself.

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Analysis methods

Choice of the territory-size estimation method

In this study, as in most studies of territory sizes for most small songbirds, I mapped bird territories by plotting locations where individually identifiable (e.g., color-banded) male birds sang, counter-sang, fought or otherwise aggressively interacted with neighbors. We typically recorded many observations of the same male warblers during each mapping session. In most bird studies that estimate territory shape and size, a series of straight lines is typically drawn around some minimum number of the outer points, or some percentage of these points, forming a minimum convex polygon (MCP; Mohr 1947). Using a percentage, such as 95%, of observations allows some "unusual" observations to be left out that might strongly influence the estimated territory size. The many studies that have used this basic approach for estimating territory sizes of forest birds include work on nuthatches (*Sitta europea*; Enoksson and Nilsson 1983), two species of Hawaiian honeycreepers (Ralph and Fancy 1994), chaffinches and brambling (*Fringilla coelebs*, *F. montifringilla*; Mikkonen 1985), black-throated blue warblers (Steele 1992), American redstarts (Sherry 1979, Hunt 1998), cerulean warblers (*Dendroica cerulea*; Jones et al. 2001), and ovenbirds (*Seiurus aurocapillus*; e.g., Stenger 1958, Zach and Falls 1979, Smith and Shugart 1987).

Most of the GIS-based methods for estimating territories, or home ranges, come from the radio-tracking literature. I chose to delineate territory boundaries with MCPs, even though there are some problems with this method (see below), rather than some form of spatial density function (e.g., kernel home range) because the bird mapping methods that I used do not provide independent locations, a key assumption for many methods (White and Garrot 1990). I could have used, or collected, only one observation per visit, but this would have greatly reduced the number of observations possible with a set amount of field effort, since it often required a relatively long search-period to locate a bird for the first time. In addition, even if relatively independent, the set of observations for most birds would probably have violated the assumption of bivariate

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normality inherent in many home range estimation methods, as many bird observations occur at the edges of territories where birds interact with neighbors.

The territory mapping typically used for bird (described above) is different from methods used in radio-tracking studies, in that radio-tracking studies typically collect one sample at regular time intervals (e.g., White and Garrott 1990, Naef-Danzer 1994, De Solla et al. 1999). Although using the time-interval approach would provide a way to control for the amount of time a bird is observed, the mapping method, in which observers only record a new location when a bird has moved, is likely to produce data with less spatial autocorrelation, and should lead to a larger set of unique locations being recorded when compared to constant time-interval data sets with similar numbers of locations. The main difficulty with switching to a time-interval approach is the choice and logistics of various time interval lengths. Naef-Danzer (1994) estimated that to reproduce the route of a foraging songbird using observations at a regular time interval, data would have to be collected every 5 to 10 seconds. Recording locations this quickly with a manual mapping technique would be very difficult, especially if foraging was interrupted by a 50-100 m flight across densely-vegetated terrain.

Estimation of territory size and overlap

To estimate MCPs, I digitized all bird locations by overlaying the field data sheets on geographically referenced maps of the study sites, and compiled them into GIS coverages with ArcInfo and ArcView software (developed by Environmental Systems Research Institute, Redlands, California). I calculated MCPs using a 100-run bootstrap approach with the ArcView software extension Animal Movement (Hooge and Eichenlaub 1997). I selected the bootstrap approach because it provided a way to control the number of locations used to generate a MCP, even though the total number of locations per bird were different. In addition, by basing the territory-size estimates on an average of 100 MCP calculations, the importance of any single point in determining the MCP size was reduced, especially as the number of locations increased. These two traits were appealing, as the MCP has been criticized as being particularly sensitive to number of locations (e.g., White and Garrott 1990, Hooge and Eichenlaub 1997), and also can be strongly influenced by apparent outliers, defined here as observations that are far away

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from most locations where an individual was observed (see below). To examine the effect of sample size and outliers on territory size estimates, I plotted year 2000 data for 20 birds with high numbers of observations (five from each HB or LB site). I chose this year because it had unusually high numbers of locations for many birds. For these plots, I used the MCP sample-size bootstrap function in the Movement software (Hooge and Eichenlaub 1997) to generate a set of territory-size estimates for each bird. The first MCP was estimated from a sample of 10 locations, with additional estimates made in 20-location intervals up to the total number of locations for that bird. Each bootstrapped estimate of MCP size was determined by averaging values from 100 runs, and the locations were sampled from the total set with replacement. To examine the effect of outlier removal on the territory-size estimate, I repeated this process following the removal of the outer 5%, 10%, 15% and 20% of the sample points as identified by the harmonic mean outlier function in the Movement program. I pooled data for the 10 birds on each type of site (HB and LB), and determined means and SDs for the bootstrapped territory-size estimates for numbers of locations between 10 and the maximum value for which data were available for all 10 birds per group (Figure 4.1).

Based on the pattern of sample size and outlier effects, as well as the range of number of locations available per bird, I chose to compare territory sizes between HB and LB sites using a 65-location MCP, with 5% of the total outliers removed (birds with at least 66 locations were included, and location samples were taken with replacement). My method included a standardized way for removing outliers, because in some cases, inclusion of a few distant points would have nearly doubled the size of territory estimates, and I wanted to use the same method for all some birds. I estimated MCPs based on 65 locations because this number captured the area of most rapid increase in size with increasing locations, while also allowing me to estimate territory sizes for least 50% of birds on each site-type per year. Following the removal of the outliers, I calculated MCPs using all remaining data (referred to as "all-data" MCPs), and using the 65-location bootstrap MCP method. I assessed relationships between the number of locations and the two sets of territory-size estimates with simple linear regression in SYSTAT 10 (SPSS Inc. 2000). In both cases I found a significant positive relationship between the number of locations and the estimate of territory size (all-data MCP: F-ratio

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= 28.8, p < 0.00001; 65-location MCP: F-ratio = 15.6, p = 0.00014, Figure 4.2). The bootstrapping approach reduced the strength of the relationship between the number of locations and MCP size (all-data MCP R^2 = 0.20; 65-location MCP R^2 = 0.12), so I chose this method as the focus of analyses, but present results from both methods.

I used both the 65-location bootstrap, and all-data territory-size estimates from the three years with territory map and bird return data from all sites (1999-2001) to test whether the intensity of browse, year, or return status influenced territory size. To perform these tests, I used a mixed-model three-way ANOVA with site, year, and return status as fixed effects, and bird identity as a random effect in SAS Version 8.2 (SAS Institute 2001). I included bird identity as a random effect because territory sizes estimated for the same bird in different years were not independent, and including bird identity as a random effect allowed within-bird variability to be included in the model. I found that the variance components covariance structure provided the best mixed-model fit to these data, and used a model that included all possible interactions between the fixed effects. I did not perform a similar test with age as a fixed effect because very few birds on HB sites were yearlings. To verify that the number of samples available for estimating MCPs were similar between site and return status groups, I used a simple three-way ANOVA to test the main effects of site type, year, and return status on the number of locations available for each territory-size estimate. I used SYSTAT 10 (SPSS 2000) for this test. To meet the assumption of a normal distribution, I log-transformed the territory sizes and numbers of locations prior to analyses. Also, one extremely large territory from LB-McNearney was identified as an outlier in SYSTAT, and removed from the analysis. I set alpha at 0.05 for all comparisons, and used a Bonferroni post-hoc multiple comparison approach to test for differences in the one multi-level factor, year.

To assess the overlap of adjacent territories, I mapped the all-data MCPs in ArcView, and determined the amount of overlap between two or three adjacent territories using the "intersect" function. For all birds that met the number of locations criterion (66 locations), I totaled the amount of overlap per bird, and expressed overlap as a percentage of total territory size, based on the all-data MCP. In these comparisons, I did not attempt to control for the number of locations by using a bootstrapped assessment of overlap, as generating an MCP for each territory involved in the overlap 100 times, and then

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overlapping them 100 times, would have been exceedingly labor intensive. In most site-years, some "focal" territories overlapped with birds for which there were fewer than 66 points, and/or with birds that had most of their territory off the plot. I determined MCPs for these other birds using all available data (rather than 95%) for the purpose of overlapping them with the territories of focal birds. I decided not to remove outliers because most of these territories were not included due to low sample sizes, so removing more locations seemed unnecessary. To help interpret how variations in territory size and overlap combined to determine how much forest space was occupied by warblers, I determined the total area for each site that was included in zero, one, or more than one territory, based on all-data MCPs.

To aid in comparisons with other studies, I used the final maps of territory boundaries at each site and each year to estimate the density of warblers. Because I established the site boundaries with the goal of containing roughly 10-14 pairs of birds per site, rather than randomly, density estimates are potentially positively biased. To estimate density, I counted the number of territories completely and partially on each plot, and rounded values to the nearest half of a territory. In most cases, the number of birds in each territory was two, but in cases where unmated males or two females used the territory, I counted 1 or 3 birds, respectively, per territory. Birds observed only one or two times were not included in density estimates, but do appear on territory maps.

Results

Territory size estimates

I estimated singing territory sizes using the 65-location bootstrap and all-data MCP methods for 57 territories on both HB and LB sites (Figure 4.3 - 4.6). Territory sizes based on 65-location bootstrap MCPs typically ranged from 0.8 ha to 4 or 5 ha in a given year for all sites combined, with one unusually large territory of 8 ha recorded on the LB-McN site in 2001 (Figure 4.7). Territory sizes at HB sites showed a roughly normal distribution, but were skewed toward smaller sizes at the LB sites (especially for the Slash site, Figure 4.7). Territory sizes varied considerably within and between years, and were consistently larger when estimated using all-data MCPs (Figures 4.3 - 4.6, Table

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4.1). Although variable in size, territory locations on the sites were typically similar between years, with high shrub-density areas most frequently used (Figures 4.3 - 4.6).

Only the year factor was significant in the mixed-model three-way ANOVA for the MCP methods (Table 4.2). Territory sizes were larger in 2000, the year with the highest numbers of locations. Year was also the only significant factor in the three-way ANOVA testing for differences between the number of locations used to estimate MCPs (Table 4.3).

The mean territory sizes (1999-2001) at both site-types for returning and new males were very similar, with HB returns averaging 2.5 ± 0.20 SE (N=25), and HB new males averaging 2.5 ± 0.22 (N = 23), and LB returns and new males averaging 2.1 ± 0.20 (N=24), and 1.9 ± 0.20 (N= 25), respectively. At both sites, there was also no apparent difference in the size of territories by age group (older vs. yearling means for HB sites: 2.5 ± 0.16, N = 40, and 2.4 ± 0.41, N=8, and; LB sites: 2.0 ± 0.16, N=33, and 2.1 ± 0.29, N=15). The outlier bird, which was removed from these means and ANOVAs, was a yearling from the LB-McNearney site with a bootstrapped territory-size estimate of 7.9 ha (north-central territory on 2001 map in Figure 4.5; the other east-central very large MCP for that year was a bird with few observations that switched territory locations).

Territory overlap and density estimates

As was true for territory size, measures of territory overlap were highly variable from year to year (Table 4.1). At the LB-Slash and HB-Wishbone sites, I found that territory overlap increased with increasing territory-size estimates, while overlap was similarly low across years at HB-Wilderness, and variable with no obvious link to territory size at LB-McNearney. When territory sizes and overlap were expressed in terms of how much of each forest site was occupied by one or more warbler territories, the main difference was that, at least in 2000 and 2001, more of the habitat at LB-Slash was part of a territory (just under 70%), while use at other sites tended to be lower (30-55%, Figure 4.8). The density of blue warblers at each site was relatively steady across the study time period (Table 4.1). Similar densities were recorded for the two HB sites, while the LB-McNearney site tended to have slightly higher densities, and the LB-Slash site had densities that were roughly double those on the HB sites. While the densities of blue

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warblers were highest on the Slash site, this site did not display a major difference in shrub-density distribution when compared to the other sites (Figure 4.9).

Method evaluation

Although the 65-location bootstrap method reduced some of the dependency of MCP size on number of locations (see above), the relationship still appears strong enough to have caused the significant difference between territories mapped in different years. In this case, the most likely explanation for most of this difference had to do with sampling effort and field assistant skill level, which were both high in 2000 compared to the other years. Within a year, some of the relationship between number of samples and territory size is likely a valid relationship, in that birds that continued to sing frequently were typically those with unsuccessful nests, and may have been exploring larger areas than birds with nestlings or fledglings to care for. Similarly, as total time following a bird was not rigorously standardized, birds tended to be followed longer when they continued to move into different areas not already reflected in a daily map. Further standardization could theoretically help with this problem, but would be challenging to implement in the field. While it is not difficult to provide an upper limit to the number of observations taken per visit to each bird, it is hard to make sure that a minimum number is collected per bird at every visit. Standardization may be particularly hard when researchers are studying species such as blue warblers where territories are large and in densely-vegetated areas, and where birds may sing frequently and cover a large area on one visit, and then sing from one location, or not sing at all, during an hour of observations at another time. I conclude that when the effect of sample size is evaluated and included in analyses, MCPs represent an acceptable, if imperfect, method for comparing territory sizes.

Discussion

Singing-territory sizes of black-throated blue warbler at HB sites tended to be larger than those at LB sites, however this was not a statistically significant pattern. Rather than suggesting a strong browse-effect, most variation in territory sizes occurred within, rather

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than between, study sites. This result suggests either that resource distributions were very uneven within all forest stands, leading to high within-site variability, or that, within these relatively low-density populations, territory sizes do not provide a reliable indicator of habitat quality. Birds with territories within a cluster of other territories may have defended areas that were scaled to the distribution of resources, but I suggest that birds with territories with few near neighbors traveled out from their territories to interact with other birds, leading to very large territory-size estimates, and a wide range in territory sizes at each site.

As predicted by previous work on blue warblers (e.g., Steele 1992, Holmes et al. 1996), shrub density and height appeared to influence both territory size and location at HB and LB sites, although specific patterns differed between the two site-types. Within the LB-McNearney site, smaller territories were clumped in areas with the highest shrub densities, especially where shrubs were 3 m high or less. The LB-Slash-site, which was dominated by shrubs and saplings within the height range of nest-plants typically used by blue warblers (1 - 3 m), had the.highest bird densities, and smallest territories, of all sites. Of the four sites studied here, the rather even coverage of small to moderately-sized territories at the LB-Slash site was most similar to the regular pattern of 1-4 ha blue warbler territories typically seen at Hubbard Brook (Sherry and Holmes 1985, Steele 1992, Holmes 1994). Patterns of territory placement at the HB sites were less clear, but many high-density hardwood areas were not used, probably because the vegetation was uniformly short (0.5 - 0.75 m) due to browsing by deer. Territories seemed to be located in parts of the plot that offered moderate to high vegetation densities, and a mix of coniferous and hardwood vegetation, although very tall, dense conifers (e.g., northwest corner of the HB-Wishbone site) were avoided.

Territories estimated here tended toward the large end of those identified for forest songbirds, but were similar to those found for blue warblers in New Hampshire. Of seven common species studied in hardwood forests in New Hampshire, black-throated blue warblers, the only shrub-nesting species, had the largest estimated territory sizes (3.6 ± 0.35 ha), with the other most common species averaging between 0.18 and 2.10 ha (Sherry 1979, Holmes and Sherry unpublished data, as cited in Sherry and Holmes 1985). Three canopy-nesting and one shrub-nesting *Dendroica* warblers were studied in spruce

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forests in Maine, and mean territory sizes for all species were estimated to be between 0.25 and 1.0 ha (Morse 1976). Similarly, yearly estimates for cerulean warblers (*Dendroica cerulea*), a canopy nesting congener, ranged from 0.6 - 1.2 ha in Ontario, including two years following an ice storm that significantly reduced canopy foliage (Jones et al. 2001). Why are blue warbler territories so large when compared to congeners? I suggest that these warblers select territory sites in response to particular microsites that are often patchily distributed (such as clumps of shrubs), and then "stretch" these territories to interact with neighbors. Use of understory vegetation for foraging by blue warblers probably also contributes to large territories, because when compared to canopy-level foliage, the total leaf-surface area per unit land area in the shrub layer is likely to be much less, suggesting that shrub-nesters and foragers would need to defend larger territories than canopy-specialist congeners.

As suggested above, given the very large range of territory sizes I observed, it seems unlikely that resource availability is the main factor influencing variation in territory size in either HB or LB habitats. Maximum values within a site, year, and MCP estimation method were up to five times the minimum value (Table 4.1). The dispersion of song locations, especially within the large territories, suggests that birds may simply continue out from a central location until they meet resistance from neighbors. This pattern has also observed by other researchers; Mikkonen noted that chaffinches (*Fringilla coelebs*) in northern Finland tended to expand their territories until "checked by other males" (1985:143). Although not independent of resource availability, the main factor influencing territory size in these forests appears to be local bird density, with birds with the most neighbors having the smallest territories.

While the "clusters" of blue warblers found here can be seen as local areas of high bird densities, these densities are low-medium when compared to other studies on this species. In 30 years of data from a high shrub-density 10 ha plot at Hubbard Brook, New Hampshire, Holmes and Sherry (2001) found a mean of 10.7 (range 4-16) blue warblers, so in most years, densities were quite a bit higher than the 2-4, or 3-7 birds per 10 ha (HB and LB sites, respectively) seen in these Michigan forests. Although density was not directly estimated, Graves (1997b) found that the relative abundance of blue warblers in the southern Appalachian Mountains was up to 5 to 6 times higher than abundances near

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the Great Lakes. (It is likely that Graves' Great Lakes areas had lower densities than the ones I studied, because his maximum abundances in southern forests were only about 1.5 times higher than his estimates for New Hampshire). At higher population densities, territory sizes would probably be compressed as pairs crowd together into a patch of habitat, and relationships between territory sizes and habitat conditions, or age/experience level of the territorial male would be more likely, and easier to detect. However, in low bird density areas, any differences in the "true" territory use of birds may be masked by including observations of birds moving long distances to interact with neighbors in the territory estimation calculations.

Even though densities in the present study were low, most black-throated blue warblers shared a territory boundary with at least one other bird, and local densities experienced by some birds were fairly high, with other parts of the study sites empty of blue warblers. This uneven distribution pattern suggests either that variation in resources led to birds concentrating in certain areas, that birds were in some way attracted to one another, or both. The concept of individuals.of the same species being attracted to one another has a long history in ornithological work (Stamps 1988). Stamps suggests this phenomena, which has been observed in a wide range of taxa, could have many benefits, including a broadly interpreted set of "mating success" benefits. One possible benefit of clustering is that males defending territories near other singing males may attract females to an area more quickly, allowing earlier establishment of nests, which may increase the chances of pairs' being able to raise a second brood. Clustering may also improve mating success for some birds by allowing opportunities for extra-pair copulations. Recent work by Chuang-Dobbs, Webster, and Holmes showed that male blue warblers both pursued copulations and were successful at fertilizing eggs in nests of females in adjacent territories (Chuang-Dobbs et al. 2001). Most of these extra-pair sires came from neighboring or nearby territories (Webster et al. 2001), suggesting that positioning a territory near those defended by other males may improve the chances that a male is able to mate with females outside of his territory.

Following this line of thought, interactions with conspecifics may affect the observed size, as well as the placement, of territories. Work focusing on the relationship between food abundance and territory size has suggested that, rather than resulting from a

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direct assessment of food abundance, birds may regulate the size of the territory that they defend based on the rate of invasion by neighbors (Myers et al. 1979, Norton et al. 1982, Hixon et al. 1983, Newton 1992). Although developed in the context of feeding rather than breeding territories, response to invasion rate may also provide a very useful hypothesis to test for explaining variation in territory sizes during the breeding season. If densities of birds are fairly low, and food, or females receptive to extra-pair copulations are in nearby but not directly adjacent territories, there may be little cost to defending a large area, and much to gain. Shifts in behavioral patterns and nesting duties throughout the breeding season may lead to different birds wandering farther at different times, leading to the overlap in territories that was seen, especially at the HB-Wish and LB-Slash sites.

Territory size estimation

Although often estimated in bird habitat-selection studies, determining territory sizes is challenging, because boundaries can't be directly observed, and may shift during a breeding season as territories expand and contract, or shift in location (Sherry and Holmes 1985). For example, defended areas may be particularly large in the early spring (Newton 1992), and then decrease as more males come into an area, and then may decrease again as food becomes more abundant through changes in the abundance of new vegetation and insects (Mikkonen 1985). It is likely that territory measurements will always be highly variable, especially in low density populations. MCPs, the most common method for estimating territory size, may be particularly challenging to use in studies of low density populations, because it may take many more location observations before an asymptote is reached in the relationship between territory size number of locations (*see Method evaluation*).

To avoid what would have been an arbitrary determination of what areas were being defended and what were not, I chose to determine an MCP based on all singing locations, as well as any observations of actual interactions with neighboring birds. More reliable estimates of territory size, or at least patterns of habitat use within territories, in low density populations could result from a "time-weighted" approach, where, instead of dropping out small-scale movements of birds with fledglings and near nests, the value of

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these habitats would be emphasized. This method could be quite challenging in terms of collecting field data, however, as it would require collecting data at regular time intervals, which is often difficult in densely-vegetated habitats (see *Choice of the territory-size estimation method*). The main benefit of this approach is that it would allow study of within-territory patterns of habitat use, which could help identify the particular habitat characteristics that are highly utilized, and presumably describe habitat selection preferences of by focal bird species breeding in heterogeneous landscapes.

Conclusions

The distribution of territory sizes that I found in these northern Michigan forests suggests that the lower-limit in terms of the amount of area required to support a pair of breeding black-throated blue warblers is lower on LB, rather than HB, habitats. However, mean territory sizes did not differ significantly between the two site-types. This could be because habitat quality did not differ between the sites, or because differences were masked by birds expanding their territories until they encountered other males. Although useful as an indicator of the habitats required by blue warblers, I suggest that territory size alone is not likely to provide a reliable indication of habitat quality in forest stands such as these with low population densities of the focal species.

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Table 4.1. Number of bird locations used to estimate minimum convex polygon (MCP) territories, estimated territory sizes (in ha), percent overlap of territories, and densities (birds per ha) for black-throated blue warblers on two heavily-browsed (HB) and two less-browsed (LB) hardwood forest sites. Means are presented ± SE, and data ranges are below means for number of locations and size estimates.

	1998	1999	2000	2001	all years
Number of bird locations used for estimates, (N)					
HB-Wishbone	95 ± 5 (9)	105 ± 10 (8)	244 ± 19 (10)	86 ± 5 (10)	135 ± 12 (37)
	(66 - 114)	(70 - 142)	(142 - 323)	(71 - 120)	(66 - 323)
HB-Wilderness	-	116 ± 16 (5)	229 ± 29 (8)	107 ± 10 (7)	158 ± 18 (20)
	-	(66 - 154)	(94 - 353)	(69 - 149)	(66 - 353)
LB-McNearney	89 ± 6 (7)	105 ± 12 (6)	183 ± 11 (8)	111 ± 6 (7)	125 ± 8.5 (28)
	(66 - 110)	(73 - 162)	(141 - 226)	(83 - 133)	(66 - 226)
LB-Slash	-	92 ± 10 (5)	200 ± 27 (12)	97 ± 8 (12)	139 ± 15 (29)
	-	(71 - 126)	(93 - 408)	(70 - 168)	(70 - 408)
65-location bootstrap MCP					
HB-Wishbone	2.2 ± 0.4	2.3 ± 0.3	3.3 ± 0.4	1.9 ± 0.3	2.4 ± 0.2
	(1.0 - 5.2)	(1.2 - 3.5)	(1.3 - 4.9)	(0.86 - 3.3)	(0.86 - 4.9)
HB-Wilderness	-	2.3 ± 0.5	2.7 ± 0.3	2.6 ± 0.4	2.6 ± 0.2
	-	(0.81 - 3.6)	(1.0 - 3.7)	(1.2 - 3.9)	(0.81 - 3.9)
LB-McNearney	2.7 ± 0.3	1.5 ± 0.2	3.0 ± 0.4	1.4 ± 0.2[1]	2.2 ± 0.2[1]
	(1.5 - 3.9)	(0.95 - 2.5)	(1.0 - 4.4)	(0.69 - 2.0)[1]	(0.69 - 4.4)[1]
LB-Slash	-	1.4 ± 0.2	2.3 ± 0.3	1.9 ± 0.3	2.0 ± 0.2
	-	(0.93 - 2.2)	(0.96 - 3.9)	(1.0 - 3.7)	(0.93 - 3.9)
All data MCP					
HB-Wishbone	2.6 ± 0.4	2.7 ± 0.3	4.3 ± 0.5	2.2 ± 0.3	2.9 ± 0.2
	(1.3 - 5.7)	(1.4 - 4.0)	(1.6 - 6.8)	(0.88 - 3.7)	(0.88 - 6.8)
HB-Wilderness	-	2.7 ± 0.6	3.6 ± 0.4	3.1 ± 0.4	3.2 ± 0.3
	-	(0.95 - 4.0)	(1.6 - 4.9)	(1.4 - 4.7)	(0.95 - 4.9)
LB-McNearney	3.4 ± 0.3	1.8 ± 0.2	3.6 ± 0.5	1.7 ± 0.2[1]	2.7 ± 0.3[1]
	(1.9 - 5.0)	(1.1 - 2.8)	(1.3 - 5.7)	(0.87 - 2.3)[1]	(0.87 - 5.7)[1]
LB-Slash	-	1.7 ± 0.2	3.0 ± 0.4	2.2 ± 0.3	2.4 ± 0.2
	-	(1.1 - 2.7)	(1.4 - 5.4)	(1.1 - 4.5)	(1.1 - 5.4)
Territory overlap from all data MCPs (%)					
HB-Wishbone	33 ± 3	31 ± 10	34 ± 8	13 ± 5	27 ± 3
HB-Wilderness	-	9.3 ± 4	6.3 ± 1	9.4 ± 5	8.1 ± 2
LB-McNearney	26 ± 5	16 ± 6	8.3 ± 2	26 ± 5	18 ± 3
LB-Slash	-	17 ± 3	40 ± 5	26 ± 5	30 ± 3
Density[1]					
HB-Wishbone	3.6	3.7	3.2	3.2	3.4 ± 0.1
HB-Wilderness	-	3.1	2.7	3.1	3.0 ± 0.1
LB-McNearney	4.0	3.7	3.7	3.4	3.7 ± 0.1
LB-Slash	-	5.8	6.3	6.8	6.3 ± 0.2

Notes: (1). Value does not include a 7.9/9.6 ha (bootstrap/all-data method) territory identified as an outlier. If included, the 2001mean was 2.4 ± 1.0/2.8 ± 1.1, and the overall mean was 2.4 ± 0.3/3.0 ± 0.3. Because this outlier was dropped, sample size for 2001 was 6, and for all years at McNearney Lake was 27.

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Table 4.2. Comparison of black-throated blue warbler territory sizes, 1999-2001, estimated with a 65-location bootstrap method, or with all available data (following removal of outliers). Territory sizes were compared with a mixed-model three-way ANOVA with site, year, and return status as fixed effects, and bird identity as a random effect.

response variable	fixed effects	d.f.	F	P
territory size estimated from 65-location bootstrapped MCP	site	3	1.99	0.17
	year	2	10.99	0.0023
	return status	1	1.19	0.29
	site*year	6	1.52	0.25
	site*return	3	0.10	0.95
	year*return	2	0.36	0.70
	site*year*return	6	0.51	0.79
territory size estimate from all-data MCP	site	3	2.20	0.14
	year	2	15.45	0.0004
	return status	1	1.83	0.20
	site*year	6	1.38	0.29
	site*return	3	0.10	0.95
	year*return	2	0.51	0.61
	site*year*return	6	0.59	0.73

Table 4.3. Comparison of the number of locations available for estimating black-throated blue warbler territory sizes, 1999-2001, using a three-way ANOVA.

response variable	factors	d.f.	F	P
number of locations per territory size estimate	site	3	1.13	0.34
	year	2	47.46	<0.0001
	return status	1	1.30	0.26
	site*year	6	1.68	0.13
	site*return	3	0.69	0.56
	year*return	2	0.97	0.38
	site*year*return	6	0.55	0.77

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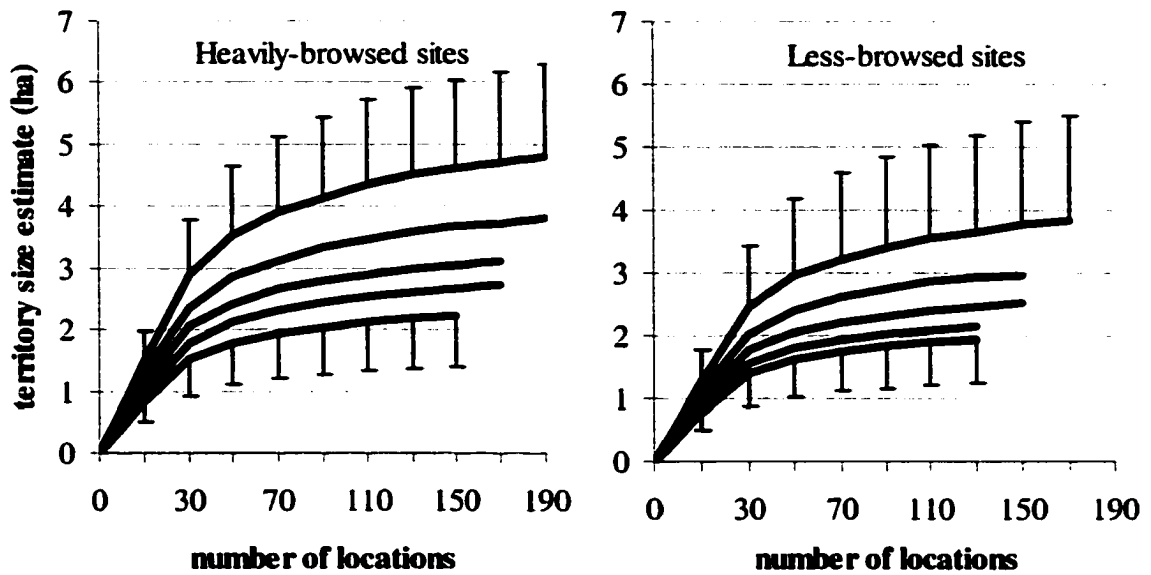
Figure 4.1. Bootstrapped estimates of average black-throated blue warbler territory size as a function of total number of locations used in the estimate and the percent of outliers removed. The highest values (top line in each figure) are for locations sampled from all data; the next lines down represent estimates after 5%, 10%, 15% or 20%, respectively, of the outlier values have been removed. Based on data for 10 birds on each type of site. Error bars indicate SD for the all data (top curve) and 20% outlier (bottom curve) data sets.
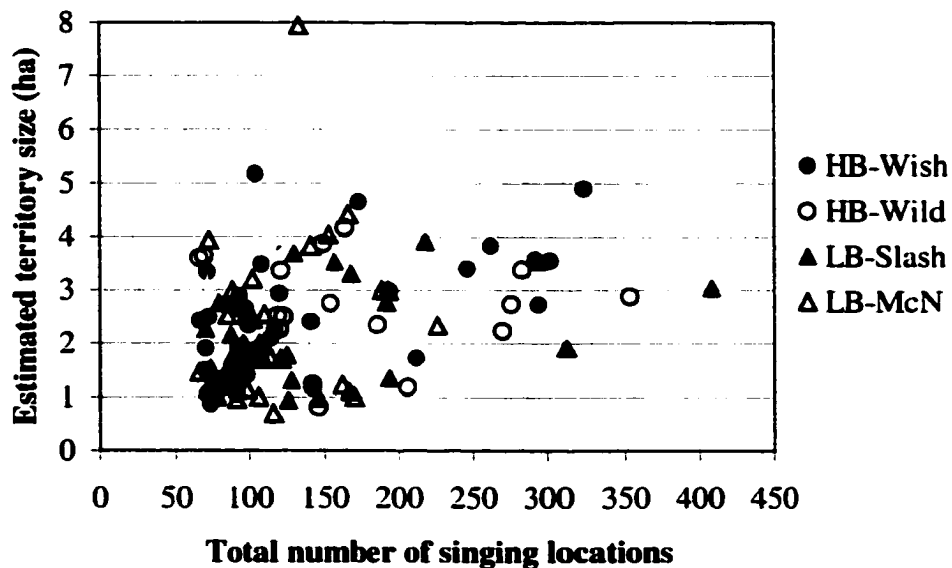
Figure 4.2. Black-throated blue warbler territory size estimates, based on a bootstrapped 65-location minimum convex polygon, as a function of total number of locations recorded.

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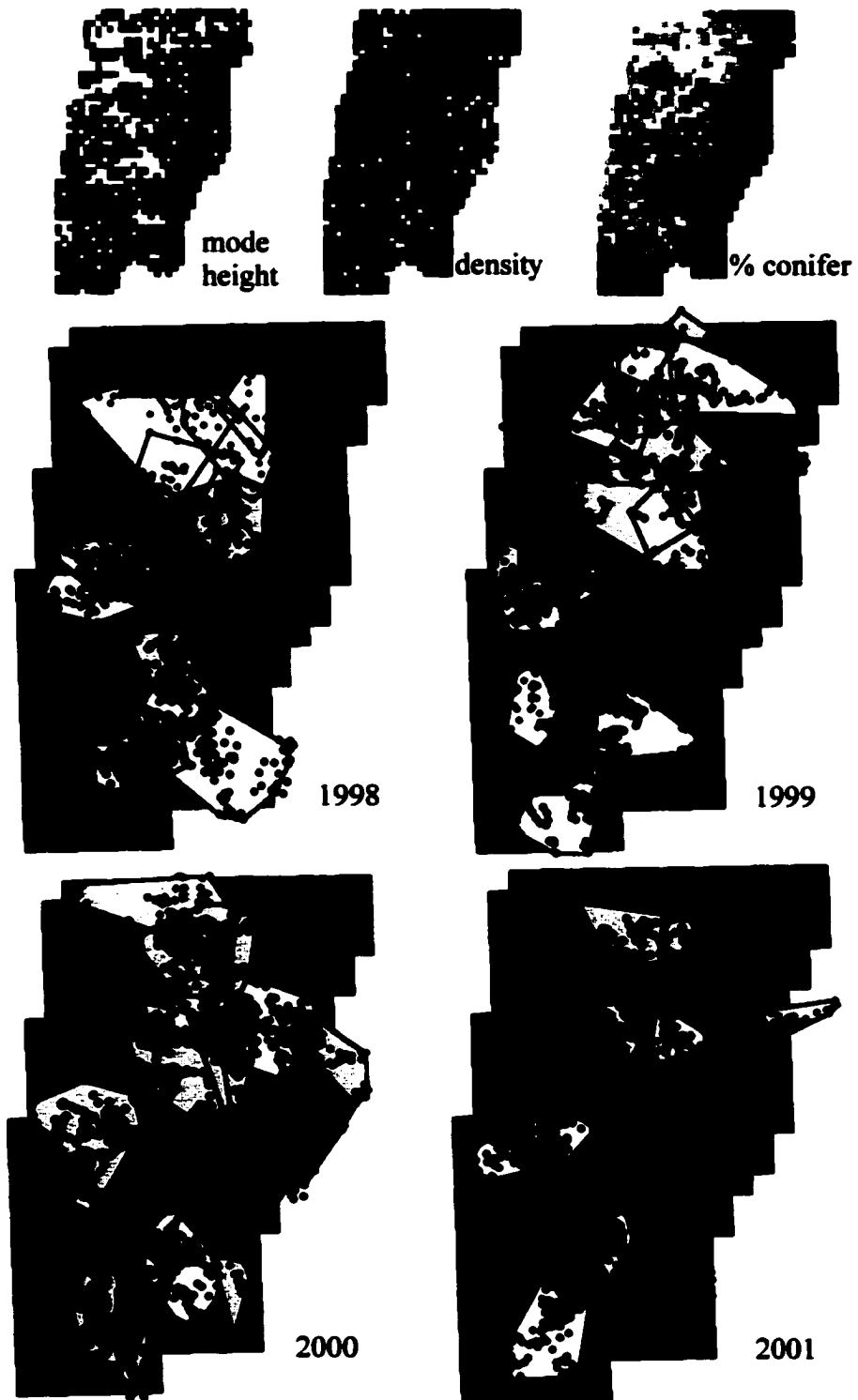
Figure 4.3. Minimum convex polygon territories for black-throated blue warblers on the HB-Wishbone site (5% outliers removed). Territories for returned ASY (white), new ASY (yellow), and SY (red) males are shown on a 50 m grid. Observations are blue if the territory met sample size requirement for size analyses and was completely on the research plot, otherwise, points are gray. Vegetation maps (top), show values ranging from low or short in black, to high or tall in white (specific categories described in the text).

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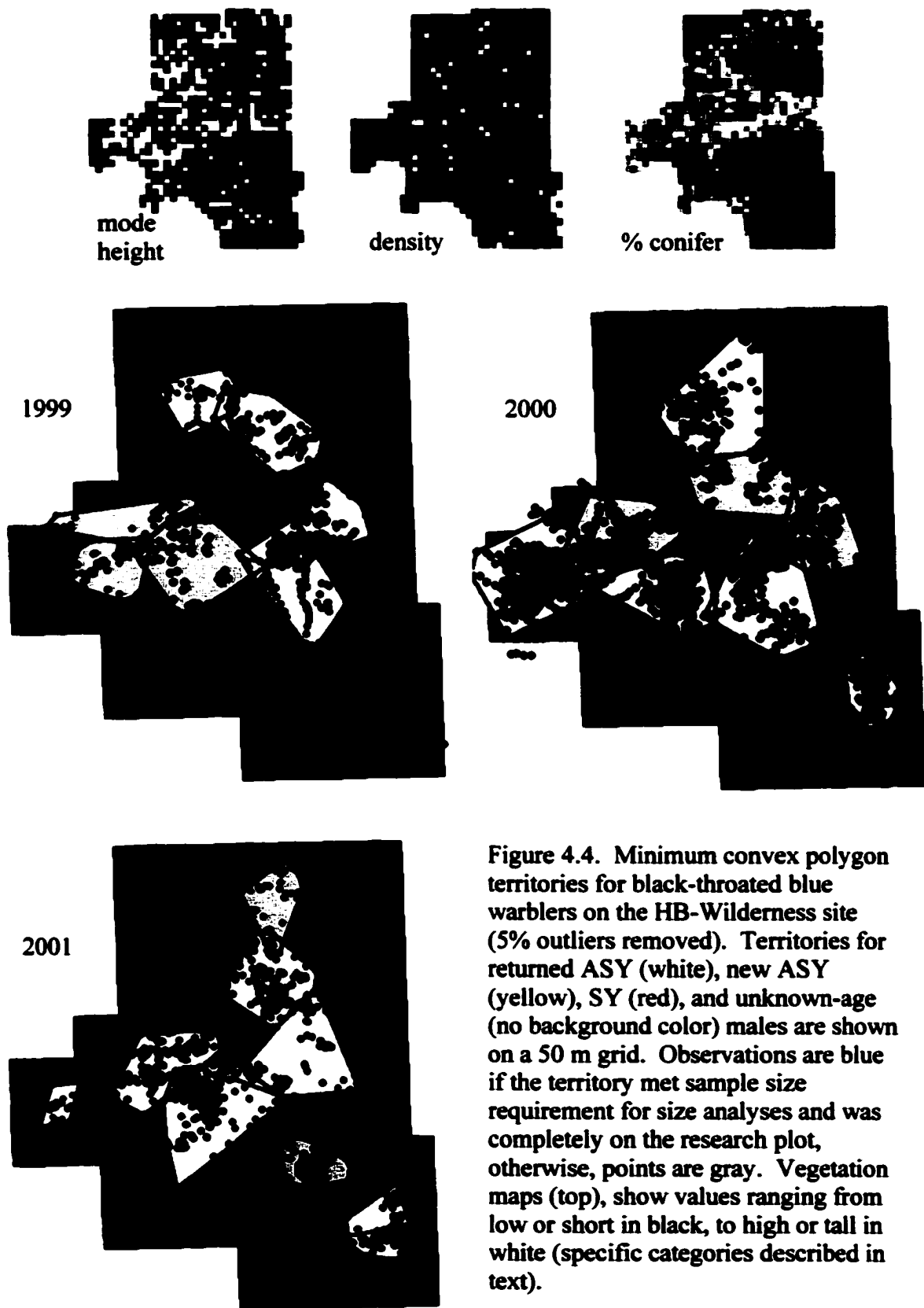
Figure 4.4. Minimum convex polygon territories for black-throated blue warblers on the HB-Wilderness site (5% outliers removed). Territories for returned ASY (white), new ASY (yellow), SY (red), and unknown-age (no background color) males are shown on a 50 m grid. Observations are blue if the territory met sample size requirement for size analyses and was completely on the research plot, otherwise, points are gray. Vegetation maps (top), show values ranging from low or short in black, to high or tall in white (specific categories described in text).

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Figure 4.5. Minimum convex polygon territories for black-throated blue warblers on the LB-McNearney Lake site (5% outliers removed). Territories for returned ASY (white), new ASY (yellow), SY (red), and unknown-age (no backgound color) males are shown on a 50 m grid. 1998 was the first year of banding, so there are no returns that year. Observations are blue if the territory met sample size requirement for size analyses and was completely on the research plot, otherwise, points are gray. Vegetation maps (right), show values ranging from low or short in black, to high or tall in white (specific categories described in text).

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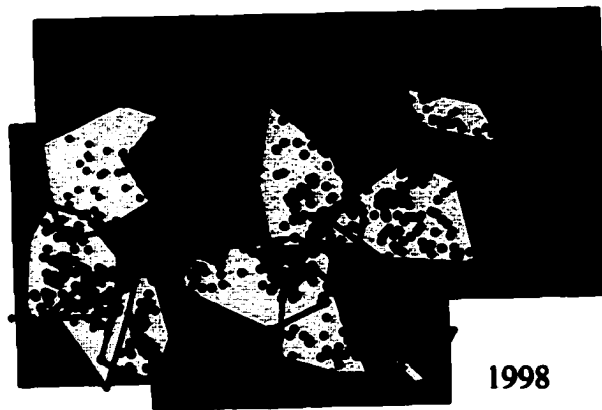
mode
height

density

% conifer

1999

2000
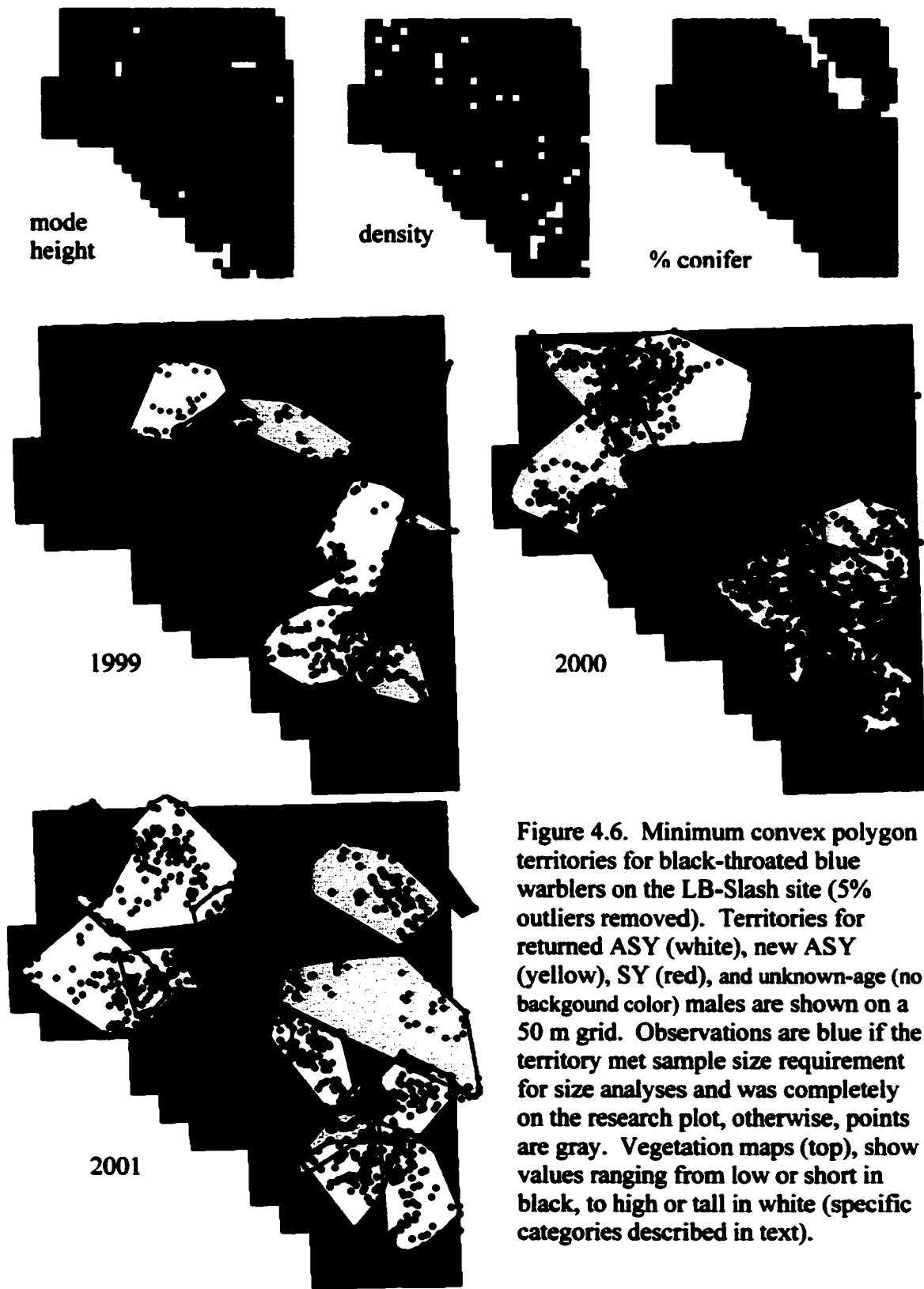
Figure 4.6. Minimum convex polygon territories for black-throated blue warblers on the LB-Slash site (5% outliers removed). Territories for returned ASY (white), new ASY (yellow), SY (red), and unknown-age (no backgound color) males are shown on a 50 m grid. Observations are blue if the territory met sample size requirement for size analyses and was completely on the research plot, otherwise, points are gray. Vegetation maps (top), show values ranging from low or short in black, to high or tall in white (specific categories described in text).

2001

Figure 4.7. Distribution of 65-sample bootstrap estimates of black-throated blue warbler territory sizes from heavily-browsed (left) and less-browsed forests (1998-2001).
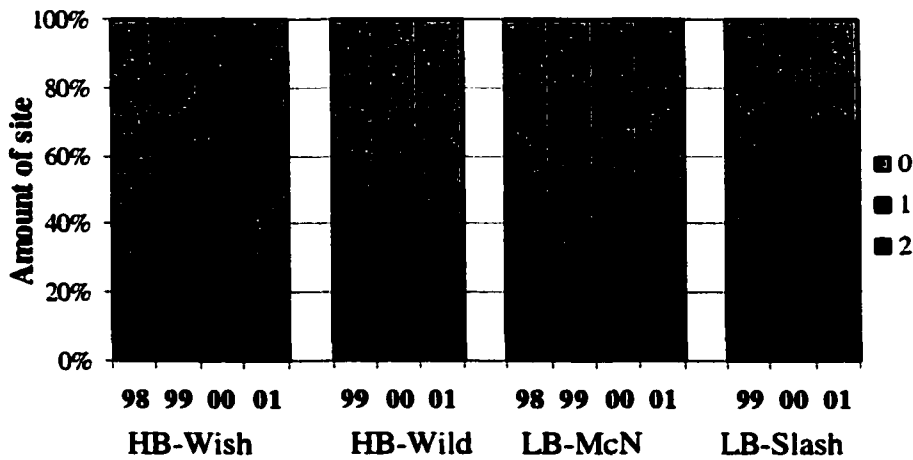
Figure 4.8. Percentage of each heavily-browsed (HB) or less-browsed site (LB) that was included in zero, one, or two or more black-throated blue warbler territories each year.
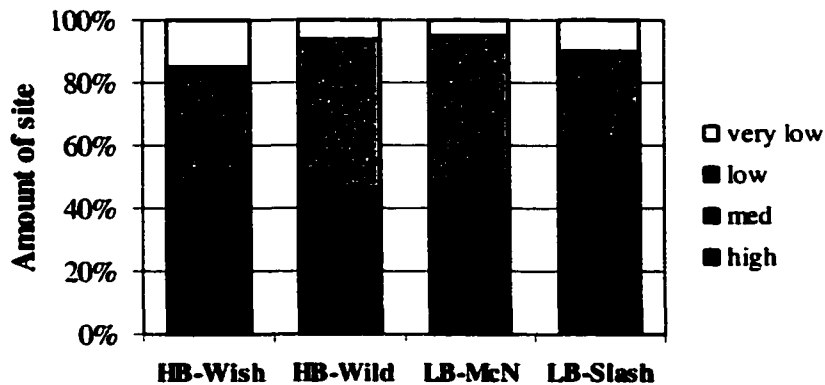
Figure 4.9. Percentage of each heavily-browsed (HB) or less-browsed (LB) study site with seedling/sapling densities in the very low, low, medium, or high category.

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CHAPTER V

GEOGRAPHIC BOUNDARY ANALYSIS OF BLACK-THROATED BLUE WARBLER TERRITORIES IN HEAVILY- AND LESS-BROWSED HARDWOOD FORESTS

Introduction

Protecting habitat for migratory songbirds is a conservation challenge because bird species typically have large ranges, and often occur at low densities in most of the range (Brown et al. 1995). Our best opportunity for conserving forest-breeding migratory songbirds and their habitats is to include birds in landscape-scale management plans for the large tracts of forest that remain in North America (Faaborg et al. 1998). Researchers can aid in the development of management plans that include migratory birds by describing how species are distributed across heterogeneous landscapes. When bird distribution data are available, spatially explicit models that break large forests down into various stand types can be used to evaluate the effects of proposed management actions on target species before final management plans are developed (e.g., Liu et al. 1995, Raphael et al. 1998). However, for species that depend on particular microsites, such as those provided by understory vegetation, heterogeneity in the distribution of those microsites can strongly influence bird distributions within a particular stand-type (Wenny et al. 1993, Faaborg et al. 1998, Martin 1998). Much of the variation in understory-plant density and species composition within a forest stand is correlated with canopy-species composition and management history, however strong differences between the understory in stands with similar vegetation types and management histories stands still may exist. As a result, relying on stand-scale measurements of overstory-tree composition as the primary definition of the management unit may lead to a weakened ability to predict habitat occupancy for understory-dependent species that respond to smaller-scale habitat features (DeGraaf et al. 1998, Haufler 1998).

In unmanaged landscapes, heterogeneity in forest understory characteristics is typically due to variations in site conditions such as soil types and position on the landscape (e.g., slope, aspect), as well as time since disturbances such as fire or outbreaks of defoliating insects (Pickett and White 1985). In managed landscapes, additional

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spatial variation can arise due to management actions, such as thinning of hardwood forests, proximity to management actions (i.e., changes in the surrounding landscape), and due to activity patterns and foraging preferences of abundant herbivores such as white-tailed deer (*Odocoileus virginianus*) (DeGraaf et al. 1991, Hagan et al. 1997, DeGraaf et al. 1998). The factors that create heterogeneity in understory-plant characteristics within managed forests influence the habitat quality of those forests for breeding migratory birds (Roth 1976, Freemark and Merriam 1986, Martin 1992). In particular, shrub-nesting birds are sensitive to changes in the structure and density of understory vegetation because these birds typically nest, forage, and care for fledged young in this low component of the forest (e.g., Holmes 1994, Moskoff 1995). Changes in understory characteristics may alter food supplies by simply reducing foraging habitat, or through more subtle effects on the abundance of invertebrate prey species that utilize and compete with deer for particular types of understory foliage (Lynch and Whigham 1984, Fuller 2001). In addition, changes in understory characteristics can decrease the availability of microsites used for nesting, and, through this decrease, increase the associated depredation risk of nest sites (Martin 1993). Similarly, reduced foliage volume may increase the visibility of nests, and lower nest cover has been associated with higher rates of nest depredation in most studies (29 of 36) examined by Martin (1992).

Although Geographic Information System (GIS)-based spatial approaches have been used to understand patterns of songbird distributions at large scales such as landscapes and regions (e.g., McGarigal and McComb 1995, Mitchell et al. 2001), they have rarely been used to understand the distribution of territories within a relatively uniform feature such as a patch of hardwood forest. This level of habitat selection has been referred to as second-order habitat selection by Johnson (1981), and local-scale selection by Villard et al. (1998). That fact that many GIS-based studies focus on larger scales is probably related to the availability of remotely-sensed vegetation data. Forest cover types can be readily identified in remotely sensed images, allowing large volumes of cover-type data to be efficiently incorporating into a GIS. Representatives of various stand types can then be surveyed for birds to give estimates of relative abundance of bird species in each type. Although these large-scale approaches provide many interesting

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and useful results, there is still typically a large amount of variation in bird distributions that is not explained by resultant habitat models (Conroy et al. 1995). The predictive abilities of management models are likely to be improved if we can include some measure of understory characteristics, and develop a better understanding of vegetation factors influencing local-order selection.

In the past, descriptions of the patterns in and boundaries between complex vegetation types have not been common in GIS-based research because these systems did not provide a means for integrating multivariate data. In part because they can use multivariate data, analytical tools for geographic boundary analysis provide new ways to explore relationships between bird distributions and vegetation characteristics by allowing users to highlight, rather than ignore, the heterogeneity that is typical of managed forests (Hall and Maruca 2001). The term "boundary" is typically used to describe ecotones, or patterns of disturbance (Johnston et al. 1992, Hansen and diCastri 1992, Fortin and Drapeau 1995, Fortin et al. 1996). However, both the term boundary and the analytical tools used to detect boundaries can also be applied within an ecosystem type to help illustrate more subtle changes, such as variations in understory characteristics in forests with similar overstory-tree composition.

Geographic boundary analysis tools provide a means for identifying "objects", such as patches of a particular vegetation type, or areas of sharp transition between vegetation types, from continuous "fields" of spatial data (Jacquez et al. 2000). There are two main types of boundary analysis tools, edge detection methods, and spatial forms of cluster analysis (Jacquez et al. 2000). Edge-detection boundary analysis methods provide a way to look for patterns of strong change in vegetation characteristics across space (i.e., spatial fields), and the boundaries identified through this process are often referred to as difference boundaries (Fortin 1994, Fortin and Drapeau 1995, Jacquez et al. 2000). Difference boundaries, or locations indicating rapid change over space, may be linked (contiguous), or scattered across the spatial field (diffuse), and may be well-defined (crisp) or imprecise (fuzzy), depending on the characteristics of the variables being analyzed (Jacquez et al. 2000). Once detected, the extent to which difference boundaries are statistically unusual in terms of their contiguity (measured as the length and branchiness of linked locations of rapid change) can be assessed by comparing

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measurements of observed boundaries to distributions of boundary measurements generated using null spatial models (Jacquez et al. 2000).

Rather than highlighting areas with the greatest change in variable values across space, spatial forms of cluster analysis delineate sets of boundaries that identify similar regions within heterogeneous areas (Jacquez et al. 2000, Hall and Maruca 2001). Like "ordinary" cluster analysis, these tools group sampled locations based on the similarity of their attributes, but then also use spatial proximity to determine the boundaries that define clusters (Legendre and Legendre 1983, Fortin and Drapeau 1995, Gordon 1999). In effect, clustering methods produce boundaries that outline different objects in space (closed boundaries), such as vegetation patches. Once boundaries have been detected with either method, the extent to which similarities between one set of boundaries (e.g., vegetation boundaries) and a second set of boundaries (e.g., from patterns in bird distributions) are statistically unusual can be assessed by comparing measures of "overlap" between the two boundaries to distributions generated from null models (Jacquez et al 2000). Overlap analysis can be thought of as a data exploration tool that is used to identify relationships between patterns in different features (such as birds and vegetation) that can form the basis of later correlation or regression models of this relationship (Jacquez et al. 2000).

In this study, I used geographic boundary analysis to explore relationships at the within-stand scale between understory-vegetation characteristics and the territory distributions of a shrub-nesting songbird, the black-throated blue warbler (*Dendroica caerulescens*). In the northern Michigan hardwood forests where I worked, browsing of understory-vegetation by white-tailed deer has been a particular conservation concern (The Nature Conservancy 2000), and two of my four study sites were heavily-browsed by deer. High deer densities can significantly reduce the density, height, and species diversity of shrubs and small trees in a forest (Tilghman 1989, Anderson and Katz 1993), and deer-related changes in vegetation have been correlated with decreases in the abundance of shrub-nesting bird species in a number of deer exclosure and enclosure studies (Casey and Hein 1983, DeGraaf et al. 1991, deCalesta 1994, McShea and Rappole 2000). I chose black-throated blue warblers as my focal species because these birds select territories that include areas with high shrub/sapling densities (Steele 1992,

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Holmes et al. 1996, Chapter 2), and have been found to be less common in heavily-browsed forests (DeGraaf et al. 1991, deCalesta 1994). In particular, browsing of understory vegetation in these northern Michigan forests has reduced the availability of vegetation within the 0.5 - 1.5 m high zone, which has probably reduced the availability of nest sites, foraging habitat, and habitat used by blue warblers caring for new fledglings (Steele 1992, Holmes 1994, Whelan 2001, personal observation).

The spatial patterns of understory species-composition, height distribution, and shrub/sapling density varied among the four northern forest stands that I examined. Of particular interest from a conservation perspective is that heavily-browsed sites used by blue warblers had dense patches of balsam fir (*Abies balsamea*) in the understory, a tree species that deer rarely browse in this region. Understory firs can be seen in spring (leaf-off) aerial photos, so understanding how bird territories are arranged in space relative to firs could provide a useful management tool that would allow managers to take advantage of the availability of remotely-sensed vegetation data. Geographic boundary analysis provides a way to integrate this set of understory-vegetation variables (species composition, height, and density), and describe how heterogeneity in understory features within forest stands relates to the distribution of black-throated blue warblers. Specifically, I used edge detection techniques to look for patterns of strong change in vegetation across space, and to test whether patterns of blue warbler habitat use mirror this variation. In addition, I used a spatial form of cluster analysis to delineate vegetation patch types within the sites, and tested whether these boundaries could be used to predict where the edges of bird territories occur. My intention in this investigation of understory vegetation and bird distributions patterns was to provide information on what vegetation features best predicted blue warbler abundance, and therefore would be appropriate features to manage within a landscape (Martin 1992). I hope to demonstrate that geographic boundary analysis tools can be used to facilitate integration of within-stand (local-scale) data with large-scale forest-cover data, with the goal of improving the predictive ability of bird-habitat models.

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Study sites

I conducted this study in northern hardwood forests within the eastern half of the Hiawatha National Forest (HNF), in Michigan's eastern Upper Peninsula (U.P., Figure 2.1). Within the eastern HNF, there are two main bands of hardwood forest, one in the southern section (high winter deer densities) along the Niagara Escarpment (lat 46°04 N, long 84°55 - 84°40W), and a second in the northern half (lower winter deer densities), between approximately 0 and 15 km south of Lake Superior (lat 46°27 N, long 84°37 - 85°07 W). In most of the U.P., there is a gradient from higher deer-browse pressure to lower from the south to the north due to the concentration of deer in southern areas (near Lake Michigan) during the winter (Van Deelen 1995). Within these bands of hardwood forests, I identified two heavily deer-browsed (HB), and two less-browsed (LB) sites where black-throated blue warblers were locally abundant. The HB sites were within a few kilometers of coniferous forest stands that consistently function as "deer yards", or places where wintering deer concentrate at night to take advantage of the thermal protection provided by coniferous vegetation. All four sites were within actively-managed sections of hardwood forest that have re-grown following extensive logging that took place in the U.P in the early 1900's (McCann 1991).

Canopy trees on the four sites were dominated by sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*), with lower densities of ironwood (*Ostrya virginiana*), yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*), and occasional white spruce (*Picea alba*), white pine (*Pinus strobus*), paper birch (*Betula papyrifera*), and linden (*Tilia americana*). Tree species varied slightly between HB and LB sites, for example red maples were more common on LB sites, and small ironwood trees (10-15 cm diameter) were more common on HB sites. These Michigan sites differed from sites where black-throated blue warblers have been studied intensively by Holmes and colleagues (e.g., Holmes et al. 1992, Holmes et al. 1996), in that they do not have high densities of any shade-tolerant shrub species, such as hobblebush (*Viburnum alnifolium*). Hobblebush can form dense patches, and is commonly used as nest sites by warblers at Holmes and colleagues' New Hampshire, sites. Instead, the Michigan forest understory was dominated by saplings and seedlings

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of overstory trees, and the density and height of the understory vegetation layer was strongly linked to time since thinning of the forest stand.

Understory vegetation heterogeneity within and between the four Michigan study sites resulted from natural variation (e.g., local-scale differences in plant-species composition, presumably related to differences in soils and seed sources), management activities (e.g., 2-5 ha "wildlife habitat" openings created for deer, in various stages of succession back toward forest), and larger-scale management effects such as time since last thinning of overstory trees. All study sites also contained old, overgrown logging roads, and were either bisected (HB-Wilderness site) or bordered on at least one side by gravel roads.

The main differences between HB and LB sites were that hardwood seedlings (stems less than 1.5 m tall) on HB sites were heavily-browsed, and HB sites also had many more balsam fir saplings and seedlings in the understory. Understory at HB sites consisted of a mosaic of dense patches of balsam fir of a variety of sizes (most were in fairy uniform clumps < 1m tall, or 1-3 m tall, although some taller saplings were present as well), and patches of browsed hardwoods (mostly maples and beeches, with other canopy species present at lower densities). Hardwood-species seedlings taller than approximately 0.75 m (they are not browsed completely due to protection by snow) were rare, primarily due to the effects of foraging deer. Most hardwood stems showed evidence of repeated browsing and re-sprouting, and many saplings, especially beeches and ironwoods, had been stripped of all but a few small branches. Understory vegetation on LB sites consisted primarily of seedlings and saplings of common overstory-tree species, especially beech, red maple, and sugar maple, with lower densities of yellow birch and balsam fir. On LB sites, understory was typically multi-layered, with many areas of dense hardwoods between 0.5 and 3 m tall. Heights and densities of vegetation at these sites showed some variation across space, with taller, higher density patches in areas with a more open canopy, or near disturbed areas such as old logging tracks. The LB-McNearney site was particularly variable, in that the south-western portion had been thinned more recently than the rest, and the site included a regenerating wildlife cut.

To determine the rough size of each site, I walked parallel transects until I encountered 10-12 pairs of birds. The sites were primarily in hardwood forest, but site

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perimeters were often irregular in shape, as vegetation used by blue warblers was often adjacent to other forest types, or to open fields created by managers to provide deer habitat. The final sizes of each site were: HB-Wishbone at 78 ha; HB-Wilderness at 62 ha; LB-McNearney at 62 ha, and; LB-Slash at 40 ha. To facilitate bird mapping and vegetation sampling, I established sets of parallel transects on each site to create a 50-m interval grid of flagged, labeled trees.

Methods

Mapping black-throated blue warbler locations

To determine the within-site distribution of black-throated blue warblers, I recorded locations of birds as they moved within the study sites. I caught and color-banded warblers so they could be individually identified, and observed between 9 and 14 pairs at each site per year. I recorded blue warbler observations throughout the breeding season (late May - early August), and mapped males an average of 1-2 times per week at just the HB-Wishbone and LB-McNearney Lake sites in 1998, and at all sites from 1999-2001. A mapping session began when I detected a target bird (typically singing), and I recorded bird locations on gridded data sheets that corresponded to the set of marked trees at each site. As birds moved, I recorded their new locations, and continued this process until I lost and could not relocate the bird in a 20-30 minute period of searching, or until I had obtained 1-1.5 hours of observations. Warbler territory sizes typically ranged from 1.5 - 4.5 ha, and birds often visited many sites along territory boundaries during observation periods (Chapter 4). Very short-distance movements (e.g., 2 m or less, typically associated with foraging) were not recorded. Females were harder to locate, but were mapped when encountered. I digitized all bird location observations by overlaying the field data sheets on geographically referenced maps of the study sites, and then compiled these observations using a Geographic Information System (GIS) with ArcInfo and ArcView software (developed by Environmental Systems Research Institute, Redlands, California). I created blue warbler presence/absence maps for each year at each site by determining which 25 m grid cells overlapped bird observations. To create composite presence/absence maps, I summed the presence/absence values from individual years.

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For the two sites with four years of data (HB-Wishbone and LB-McNearney), occupancy values ranged from 0-4 years, while for the two other sites, occupancy values ranged from 0-3 years.

Mapping understory vegetation

To create maps of understory vegetation for the four study sites, I estimated vegetation characteristics every 25 m along and between the marked transects. I developed this sampling method in order to sample vegetation at a fine scale over a large area in a relatively short amount of time (5-8 days of data collection per site). The sampling frame approximated that of the James and Shugart (1970) method, in that at each sample point, I estimated understory-vegetation characteristics within a 5 m radius circle. At these points, I estimated the most common (mode) understory seedling/sapling height, the height range of the middle 90% of understory stems, vegetation density, and the percentage of coniferous vs. hardwood vegetation. I defined seedlings and saplings as woody plants taller than 0.5 m, but less than 7.5 cm in diameter (all diameters measured at 1.5 m height). For both mode and 90% range of seedling/sapling heights, I estimated heights to the nearest 0.25 m from 0.5 -1 m, the nearest 0.5 from >1 m to 3 m, and nearest 1 m above heights of 3 m. I categorized vegetation density based on the percentage of the 5 m-radius circle "covered" with vegetation, rather than by an estimate of number of stems, to allow comparisons among areas dominated by plants with different heights and growth forms (e.g., a balsam fir sapling typically fills more space than a maple sapling of similar height). To simplify density estimation, I recorded density in four coverage categories which seemed to represent natural breaks in density distribution: 0-10%, 11-40%, 41-80%, and >80%. I also described the species composition of the understory vegetation by coverage (to the nearest 5%). I collected all vegetation mapping data in August and September of 2000 (all sites but HB-Wilderness) or 2001 (HB-Wilderness).

Detecting difference boundaries

The methods that I used for geographic boundary analysis follow those described in Hall and Maruca (2001). For the edge-detection approach, analyses involved two steps: difference boundary detection, and difference boundary evaluation (Fortin 1994, Fortin et

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al. 1996, Jacquez et al. 2000). To detect difference boundaries, I used the wombling method for grid data (Womble 1951) to identify zones of rapid change in surface gradients of the four understory-vegetation variables (multivariate wombling), and of the bird distribution data (univariate wombling). The algorithm for grid-wombling computes a rate of change for the first-order partial derivative of values measured at each of four locations that form a square, with the centroid of that square assigned as the "location" for the calculated rate of change (Fortin 1994). With multivariate data, these surface-gradient magnitudes are determined for each variable and then averaged. When values measured at the four corners of the square are very different, the surface-gradient magnitudes are high; locations with the highest magnitudes are identified as boundary elements (BEs).

The number of BEs detected in a particular spatial field is determined through the researcher's selection of a (relatively arbitrary) threshold for number of locations, typically between 5 and 15% (Barbujani et al. 1989, Fortin 1994, Hall and Maruca 2001). Because BEs are identified as some percentage of the total number of locations (those with the highest gradient magnitudes), boundaries (the collection of BEs) will always be found, regardless of how different or similar measured values are across a spatial field. To provide a comparison to related work on bird species diversity and wetland vegetation (Hall and Maruca 2001), when possible, I used a BE threshold value of 15% of locations. Attaining this threshold was not a problem with the vegetation data, but because the bird data were univariate and had a small range (0-3 or 0-4 years of occupancy), there was a relatively small number of possible surface-gradient magnitude values (9 or 13 values), leading to many ties. When a BE threshold value, such as 15%, falls within a group of tied gradient magnitude values, all locations with that value are treated as BEs, leading to a higher effective threshold than the chosen percentage. To determine appropriate threshold values, I evaluated the collection of surface-gradient magnitude values estimated at each study site with histograms. I found that a threshold of 20% represented a natural "break" in the distribution of gradient magnitudes for all bird data except for those from the LB-Slash site, for which thresholds of 17% or 25% were the next closest increments. For the Slash site, I present bird boundary results using both 17% and 25% BE threshold values.

In difference boundary delineation, after BEs have been identified, adjacent BEs are linked into subboundaries if their surface gradients describe similar directions of change across space (Oden et al. 1993, Jacquez et al. 2000). Two connection criteria are used to evaluate similarity in surface-gradient directions (Oden et al. 1993, Fortin 1994, Fortin et al. 1996). The first criterion prevents two adjacent locations with surface gradients in opposite directions from being linked, and the second criterion prevents linkages between two locations for which a link would occur parallel to the direction of change. The second rule is needed because drawing a link between two BEs implies that the direction of change in the measured variables is across (i.e., perpendicular to) the link. As with the BE threshold percentage, connection criteria for linking boundary elements are also typically arbitrary. In these analyses, to meet the first criterion, I determined that adjacent gradient vectors could differ in direction by no more than 100 degrees, and to meet the second criterion, each vector could be no closer in direction to its connecting line than 30 degrees. When there are many linkages between BEs, the set of sub-boundaries is considered to be a cohesive difference boundary, while a boundary comprised of many scattered subboundaries with infrequent linkages reflects a lack of a large-scale (relative to the sampling scale) spatial pattern.

For both the edge-detection and spatially-agglomerative clustering techniques, I used four variables to describe the forest understory: (1) mode vegetation height, (2) 90% range of vegetation heights, (3) vegetation density, and (4) percentage of vegetation that was coniferous (see "Mapping understory vegetation"). As the density data were collected within ranges, I used the midpoints of each range in the analyses. I also modified one variable, mode vegetation height, by truncating values at 3 m. I chose to use this shorter range (0.5 - 3 m, rather than 0.5 - 9 m) because it corresponded to heights of vegetation preferentially used by black-throated blue warblers for nesting and tending new fledglings. Limiting the values in this way focused the assessment of "change" between neighboring values in the vegetation-height spatial field on a more biological meaningful habitat characteristic. Without this limitation, differences among mode vegetation heights in ranges that were less likely to be utilized (e.g., a difference between 8 m and 6 m tall vegetation) would have the same effect in terms of determining the location of BEs and membership in a cluster (see below) as would differences of the

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same magnitude (2 m in this example) in the heavily-used height range. In addition, limiting mode height in this way reduced the correlation between this variable and the second vegetation variable, 90% height range, for which values tended to increase with increasing mode height. In both the edge-detection and clustering analyses, I standardized values for each of the four vegetation variables to a 0-1 range, so that differences in values between the variables would have roughly the same "weight" in the analyses. The bird data that I used in both the difference boundary and cluster analyses were univariate estimates of the frequency (number of years, ranging from 0-3 or 0-4) of use of each 25 m grid square of forest within the study sites.

Evaluating difference boundaries

To evaluate the cohesiveness of the understory vegetation and warbler boundaries found through edge-detection, I calculated subboundary statistics and then evaluated the "rarity" of the observed values using Monte Carlo procedures. The statistics, developed by Oden et al. (1993), are: number of subboundaries, number of singletons (subboundaries comprised of a single BEs), maximum and mean length of subboundaries (i.e., number of connected BEs), and maximum and mean subboundary diameter. Subboundary diameter is defined as the minimum number of connections between the most spatially separated pair of BEs within a subboundary. A cohesive boundary, e.g., one that delineates a pronounced linear feature in the landscape, is likely to be characterized by a small number of subboundaries, few singletons, and high mean and maximum lengths and diameters (Fortin and Drapeau 1995). I used a null model of complete spatial randomness to evaluate these statistics, and performed 1000 simulations to amass the null distribution. As specific tests of the hypothesis of boundary cohesiveness, all of these tests were one-sided. For these and all simulation-based evaluations, I considered the null hypothesis of complete spatial randomness to be useful more as a means of comparison between sites rather than as a true null hypothesis.

Detecting boundaries with spatially-constrained agglomerative clustering

I used a second boundary analysis tool, spatially-constrained agglomerative clustering, to group the heterogeneous understory vegetation into relatively homogeneous clusters. I

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determined the number of clusters to delineate by plotting $G(k)$, the goodness-of-fit index, for a range (10 - 30, inclusive) of cluster totals (Caliński and Harabasz 1974). I chose this range so that it would encompass approximately twice the expected final number of clusters, based on my experience that the method often identifies many one-grid-cell (singleton) clusters that I would later merge with other clusters. I used the resulting 2 - 4 cluster totals with the best fit to delineate cluster boundaries.

To determine which locations should be in the same cluster, I used the squared Euclidean distance measure of dissimilarity to compare vegetation variables measured at each pair of sample locations within the study areas. I agglomerated these locations into the pre-determined total number of clusters (referred to as a partition of the data) using flexible-link linkage with a connectedness value of 0.5 (see Legendre and Legendre 1983, Legendre 1987, and Hall and Maruca 2001 for details). Following the agglomerative step, I applied a k-means clustering algorithm to refine the partition. I visually compared the partitions of vegetation produced by each of the cluster totals with high "fit" values, and chose the one for each site that provided a good match to observed vegetation patterns and had the fewest singletons as the final set of clusters. To simplify the final cluster partitions, I merged singleton clusters with either a surrounding cluster, or with the adjacent cluster with which it shared low dissimilarity values for the four vegetation variables. For all sites, the final number of clusters prior to the merger of singletons ranged from 12 to 21. To facilitate interpretation of the maps of vegetation clusters, I treated spatially isolated clusters with similar vegetation characteristics as the same cluster type. The choice to group clusters was based primarily on cluster-cluster dissimilarity values for the four variables, but I also examined cluster means calculated from the original data (e.g., non-standardized, and mode height not limited to 3 m).

Evaluating boundary overlap

To examine the coincidence between the warbler difference boundaries and (1) vegetation difference boundaries, and (2) vegetation cluster boundaries (O_W only, see below), I used the distance-based boundary overlap statistics developed by Jacquez (1995): For this work the statistics are (all measured in m):

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- O_W: average geographic distance from a BE in a warbler boundary to the nearest BE (or cluster edge) in a vegetation boundary.

- O_V: average geographic distance from a BE in a vegetation boundary to the nearest BE in a warbler boundary.

- O_{WV}: average geographic distance from a BE in either the warbler or vegetation boundary to the nearest BE in the other boundary.

- O_E: number of BEs in vegetation and warbler boundaries that exactly overlap (are at the same location).

O_W and O_V measure directional association between boundaries, while O_{WV} reflects the overall degree of overlap between vegetation and warbler boundaries, regardless of direction. To find out if the observed values for these measures were statistically unusual, I compared them to a distribution developed under the assumption of complete spatial randomness. To do this, I chose a null model that preserved vegetation boundaries and randomized only the warbler distribution data during Monte Carlo simulations (1000 runs). The overlap statistics were evaluated as one-sided tests, testing the hypothesis that bird distributional boundaries at the four sites would show similarities (overlap with) boundaries in vegetation. All boundary detection and analysis procedures were performed using BoundarySeer software for geographic boundary analysis (TerraSeer 2002). For all simulation-based evaluations of the rarity of observed values, the 0.05 level was also used as benchmark, although these tests are best thought of as exploratory tools, rather than strict tests of hypotheses. The main point of these tests was to permit comparison between sites of the strength of various relationships between patterns in bird and vegetation distributions.

Results

Within-site distributions of warblers and understory vegetation

Based on black-throated blue warbler distribution maps for the four sites, some areas were used by birds every year, while many areas, especially on the HB sites, were typically unoccupied (Figures 5.1 - 5.4, map in lower left, or center for LB-McNearney).

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The specific pattern of habitat occupancy varied between years, leading to a "fringe" of lower occurrence values around most heavily used regions. These patterns of habitat occupancy reflect the behaviors of 12-14 pairs of blue warblers per year at HB-Wishbone, 8-9 pairs at HB-Wilderness, 10-13 pairs at LB-McNearney, and 12-14 pairs at LB-Slash. At all but the LB-Slash site, there were one or two territory-sized areas that were only used for one or two years, and some territory-sized areas that were not used at all. To help in interpreting the maps, typical territories included between 26 - 64 of the 25 m grid cells (1.5-4 ha); an isolated territory that was frequently used can be seen in the south-eastern corner of the HB-Wilderness site (Figure 5.2). Overall, a higher proportion of the total site area was used per year at the LB-Slash site than was occupied at the other sites (Figure 5.4).

All four sites had heterogeneous understory vegetation, as indicated by the distributions of the four understory-vegetation variables (tops of Figures 5.1-5.4). The most obvious difference between HB and LB sites was that HB sites had higher percentages of understory conifers. On HB sites, the mode and ranges of heights in conifer-dominated areas were highly variable, while the hardwood-dominated areas had short modes and small ranges, reflecting browsing by deer. Understory vegetation at LB-McNearney had a trend of decreasing mode height and height range from the southwest to the northeast corner of the site, with an especially tall patch of hardwood saplings near the center of the site. Understory vegetation on the LB-Slash site was the most homogeneous of the four sites, with contrast in understory conditions provided by a section of sparse, mixed hardwood and conifer understory that occurred around the edges of a patch of white spruce trees (*Picea glauca*) in the northeast corner.

Detection and evaluation of difference boundaries

The difference boundaries for both warblers and vegetation are shown overlaid upon the bird distribution data in Figures 5.1-5.4. The statistical evaluations of these boundaries, which were based on a comparison with a frequency distributions amassed through 1000 randomly arranged sets of BEs, are shown in Table 5.1. As these values have not been adjusted for multiple tests, and also because the null of complete spatial randomness is likely to provide an overly lenient source of comparative data, p values are presented, but

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the significance of various tests have been used primarily as indicators of various patterns in the results. Overall, the results were strikingly similar across all sites for both vegetation- and warbler-boundary significance values. For all sites and both variable sets, I found that the number of subboundaries and number of single BEs were lower than expected, and that the mean length and mean diameter were longer than expected, suggesting cohesive boundaries. Although the two remaining boundary statistics, maximum length and maximum diameter, were also similar for vegetation data across sites, HB-Wilderness and LB-McNearney had unusually large values, suggesting that vegetation had a stronger large-scale pattern at those sites. I found that the significance values for maximum subboundary length and diameter were more variable for the bird-boundary data, with most not statistically unusual when compared to the null distribution. Interestingly, the choice of threshold percentage for determining the number of BEs (see methods) had a strong influence on the two maximum-based statistics for the LB-Slash site. With 17% of locations selected as BEs, the two maximum measures were so small that they suggested boundary fragmentation, or a tendency for boundary elements to not be adjacent (p values of 1). However, when I added additional BEs by raising the inclusion threshold to 25%, the observed values for maximum length and diameter of subboundaries were unusually long rather than unusually short when compared to the null distribution.

Overlap between warbler- and vegetation-difference boundaries

When compared to the null model of complete spatial randomness, I found that distances between bird difference boundary elements and vegetation boundary elements suggested significant overlap at two sites, HB-Wishbone and LB-McNearney (O_W; Table 5.2). Overlap as measured from the warbler boundary elements was weaker at HB-Slash (strongest with the 25% threshold level), and I found no relationship suggested by the distances from warbler boundaries to vegetation boundaries at HB-Wilderness. In contrast, distances from vegetation boundaries to the nearest bird boundary (O_V) suggested boundary avoidance (very high p values), rather than overlap at all sites. Distances from BEs in bird boundaries to the nearest BE in vegetation boundaries (O_W) tended to be longer than the respective measure from each vegetation BE (O_V),

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suggesting clumping of vegetation boundaries, and a more even distribution of bird boundaries. As might be expected due to the mixed nature of the O_V and O_W results, both overlap and avoidance were suggested by the O_{WV} measures, with the HB-Wilderness site presenting the strongest indication of avoidance ($p = 1$), and other sites having a weak tendency toward overlap (p values between 0.07 - 0.2). The measure of exact overlap, O_E, again suggested boundary avoidance at the HB-Wilderness site, with avoidance also indicated by the 25% threshold data from LB-Slash, and less strongly at the HB-Wishbone site.

Detection of spatially constrained clustering boundaries

The clusters that I identified through spatially-constrained clustering of the understory vegetation data are shown at the bottom (LB-McNearney) or lower right of Figures 5.1-5.4. To aid in the interpretation of the vegetation clusters, I have presented the mean and SE for each of the four understory vegetation variables, along with the mean and SE for the number of years in which blue warblers were observed within the 25 m grid cells that comprised each cluster, in Table 5.3. The HB-Wishbone site was dominated by a vegetation type that is roughly two-thirds conifers, with a mode height of 1.9 m, height range of 3.4 m, and moderate density (cluster type 1). This dominant habitat type was interspersed with some irregularly shaped clusters of very tall (over 4 m), lower density hardwoods (cluster type 3), and there were also large sections of very short (0.74 m), dense hardwoods with highly irregular boundaries (cluster type 2). HB-Wilderness had a similar set of vegetation types, although the basic pattern was reversed, with a fairly short, mostly deciduous (but more diverse than HB-Wishbone cluster 2) vegetation cluster dominating the site.

For both HB-sites, when the larger cluster-types were compared, blue warbler observation frequencies were highest in areas with high percentages of firs, and mean heights of 2-3 m (cluster 1 for Wishbone, cluster 2 for Wilderness, Table 5.3). However, when I compared occupancy patterns of blue warblers and spatial locations of clusters, I found that many of the locations that were occupied in most or all study years could be characterized as places where taller fir-dominated vegetation patches were adjacent to or surrounded by shorter, hardwood-dominated clusters (Figures 5.1 and 5.2). Two

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exceptions to this pattern still support the idea that birds selected territories that encompassed areas with short and tall vegetation. The heavily-used 2-3 territory-sized zone in the west-central portion of the HB-Wishbone site was dominated by firs that were shorter than most in the fir cluster (see "height range," at top of Figure 5.1), but these territories also included some taller vegetation in cluster types 3 and 5. Similarly, the territory in the southeast corner of the HB-Wilderness site was primarily in the relatively short vegetation cluster 1, but included a dense stand of tall aspen saplings adjacent to the hardwood forest, which was primarily used by birds when they were caring for dependent fledglings.

Most of the variation within the LB-McNearney site was due to differences in mode height, height range, and density of hardwoods, because conifers were rare in the understory. This site was dominated by fairly short (1.4 m), moderate density vegetation (cluster 1), but also included an intricately-shaped patch of slightly taller (2.6 m) and denser vegetation (cluster type 3), and clusters of much taller (4.1 m) and denser vegetation (cluster type 2). At the LB-Slash site, cluster 1 was very similar in mode height, height range, and species composition to cluster type 1 at LB-McNearney, except sapling densities were higher. The fact that I found only a few clusters at LB-Slash again highlights the relative homogeneity of understory vegetation at this site, with variation primarily due to a patch of less dense, partly coniferous vegetation (cluster 2).

At the LB-McNearney site, I found the highest bird frequency values in cluster 3 (characterized by the highest average vegetation density, and an average height of 2.6 m), and cluster type 2 (taller, dense vegetation; Table 5.3). At the LB-Slash site, I found cluster type 1 (dense vegetation averaging 1.4 m tall) had the highest bird frequency values (Table 5.3). As in the HB sites, the areas most commonly occupied by warblers at the LB-McNearney site had a mixture of tall and shorter vegetation (e.g., the area where cluster 3 is surrounded by cluster 1), although sapling density alone was also good predictor of habitat use by warblers. At the LB-Slash site, blue warblers avoided the less dense, shorter (<1 m) vegetation in cluster 2, and the distribution of high occupancy areas showed a strong similarity to the distribution of high-sapling density areas within cluster 1 (Figure 5.4). Overall, the occupancy rates for all cluster types combined were highest within the LB-Slash site (Figure 5.5).

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Overlap between warbler-difference boundaries and vegetation clusters

At the LB sites, bird-difference boundaries and vegetation-cluster boundaries tended to overlap somewhat (LB-McN: $O_w = 35$ m, $p = 0.062$; LB-Slash with 17% bird BE threshold: $O_w = 35$ m, $p = 0.14$; LB-Slash with 25% bird BE threshold: $O_w = 35$ m, $p = 0.035$), while the HB-Wishbone site results suggested boundary avoidance ($O_w = 41$ m, $p = 0.96$). Although the HB-Wilderness site had the shortest distance between bird boundaries and vegetation cluster boundaries (O_w), I found no relationship between the two boundary types at this site ($O_w = 29$ m, $p = 0.58$).

Discussion

Local-scale vegetation heterogeneity appears to be a key factor influencing the location of blue warbler territories in three of the four managed-forest sites studied in Michigan. Rather than being best predicted by the distribution of one understory-vegetation type or variable, blue warbler territories at sites heavily-browsed by deer often occurred where patches of understory with different heights (e.g., 0.7 - 1.2 m, vs. 2 - 5 m) were adjacent. Typically, these heavily-used sites were found where areas dominated by taller, browse-resistant firs were near heavily-browsed hardwoods, or where areas dominated by small firs were near disturbed areas with a dense mix of taller vegetation. Heterogeneity with respect to vegetation height also seemed to influence distributions at the less-browsed McNearney site, although at that site, vegetation density alone was also a good predictor of territory distributions. Vegetation density was also a good predictor of habitat occupancy at the most uniform site, LB-Slash, which was dominated by saplings and seedlings in the "preferred" height range for black-throated blue warblers. Heterogeneity of understory habitat has long been identified as a key factor to consider when looking at patterns of bird species diversity (MacArthur and MacArthur 1961, Karr and Roth 1971, Roth 1976, Boecklen 1986, Urban and Smith 1989), yet I am aware of no other study that has attempted to describe the importance of local-scale heterogeneity in determining the distribution of an individual species.

In old growth hardwood forests, there was probably heterogeneity in the heights, species, and densities of understory plants over fairly small spatial scales as a cumulative

result of tree-fall gaps and other small-scale forms of disturbance (Pickett and White 1985). However, within forests managed as even-aged stands, similar ranges of variation in vegetation height and density are more likely to occur at the scale of management (i.e., wildlife cuts, or units selected for thinning) as the effects of management may overwhelm or eliminate other sources of small-scale variation. In areas where herbivores like white-tailed deer are very abundant, they can further homogenize the forest understory through reducing the height distribution of preferred species, but may simultaneously increase the scale of heterogeneity in vegetation heights if preferred and non-preferred plant species have patchy distributions. This study provides evidence that a shrub-nesting species, the black-throated blue warbler, may be responding to this reduced small-scale heterogeneity by selecting territory areas that include more than one distinct understory type within managed forests, potentially because more preferred understory conditions, such as those observed at the site with the highest occupancy rates (LB-Slash site), are not available. Boundary analysis techniques, especially spatially agglomerative clustering, provided useful tools for visualizing these patterns of heterogeneity in the understory vegetation, and examining similarities and differences in the bird and vegetation distributions.

Although perhaps counter-intuitive, browsing by deer does not appear to reduce the number of micro-sites available for nesting, although it may reduce their quality. On HB sites, most black-throated blue warbler nests were in vegetation less than 1 m tall, with actual nest heights typically ranging between 0.2 and 0.4 m from the ground (unpublished data). Just under half of these nests were in dense patches of heavily-browsed maples, while roughly half were in tiny firs (< 0.75 m), that while not browsed, offered little vegetative cover. Many taller firs seemed to provide suitable sites for nesting, although larger firs were often used by veeries (*Catharus fuscescens*), and may not have been available to blue warblers. Typically, once nests had fledged, birds were found in the taller parts of their territories, or in a few cases, shifted territories towards areas with taller vegetation. Steele (1992) found that foraging blue warblers were more likely to forage in taller foliage (3 - 9 m high), although they tended to forage lower when with fledglings (1 - 3 m; although low, this height range was rare in HB-site hardwood patches). Based on these observations, the habitat mosaic found within HB territories

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may reflect birds choosing locations that provided sections of low, often dense vegetation for nesting, while also providing taller areas for foraging and tending fledglings.

Difference boundary analyses

The difference boundaries within the four sites suggested that overall there were many spatially-grouped locations with high rates of change in understory characteristics, but BEs at these locations did not tend to form cohesive boundaries. At the two HB sites, although subboundaries (including both linked and single BEs) were often adjacent, their directions of change must have been different, as they were not frequently connected into larger subboundaries. This was particularly clear at the HB-Wishbone site, where many BEs formed an arc in the west-central portion of the site (Figure 5.1), but still the longest subboundary was only 7 BEs long (Table 5.1). For the two HB sites, the difference-boundary analysis typically highlighted locations where conifer-dominated areas were adjacent to hardwoods of different heights. The relatively large-scale transitions between conifer- and hardwood-dominated understory evident from the "% conifer" maps at both sites were suggested, but do not emerge as dominant features within the boundary as whole. Instead, the analysis picked up many areas where various types of disturbance have created small-scale strong contrasts in understory conditions, such as those visible in the southern part of the "arc" at HB-Wishbone (described above), that were associated with a regenerating wildlife cut. At both HB sites, with the exception of these small, disturbed areas with tall hardwoods, areas dominated by hardwood vegetation had uniformly short heights and similar densities, leading to few BEs.

Difference-boundary results at the two LB sites show how spatial patterns of heterogeneity in understory vegetation differed between the sites. At LB-McNearney, subboundaries were scattered throughout the site, with a concentration in the southern section (Figure 5.3). As at the HB sites, many of the LB-McNearney subboundaries were associated with management activities such as regenerating wildlife openings, and open areas around old roads. The south-western portion of this site was also thinned more recently than the rest, and some diversity in understory is likely due to variation in canopy-gap sizes and micro-site conditions, leading to variation in hardwood understory heights and densities across space. In contrast, I did not find similar small-scale variation

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in heights in hardwood-dominated patches of similar size at the HB sites. The majority of subboundaries at the LB-Slash site were near a patch of overstory conifers and the associated transition zone back to hardwoods (diagonal patch in northeast corner), and near a transition to a different forest type near the southern plot edge (Figure 5.4). The rest of the site was fairly uniform, reflecting similarities in recent management history, and less time since thinning to allow for variations in site conditions to produce diversity in understory heights and densities.

My use of edge-detection methods to detect boundaries in bird distributions can be seen as an effort to separate larger patterns of habitat use from autocorrelation of nearby values at a particular scale. Based on the bird distribution maps, blue warbler habitat occupancy appears to have been strongly autocorrelated in both space (nearby areas are similar) and time (there are typically frequently used areas, and areas that are rarely or never used within a site). A main contributor to this autocorrelation is the fact that bird territories were much larger than the sampling scale, so many nearby sites were part of the same territory. The tests for difference-boundary significance were designed to see if the edges of distributions (i.e., territories) were in the same location over time, and if these edges matched edges in vegetation. However, instead of sharp edges, most areas that were heavily used by birds (white in the figures) transitioned into less-used areas gradually. As a result, short subboundaries were frequent (to the point of being statistically unusual at all sites), reflecting similarity in adjacent values (autocorrelation), but long subboundaries were uncommon. These results may indicate that the actual boundaries of territories were less strongly related to habitat, and may instead have been fairly fluid, with birds responding to small-scale features in the territory, or being drawn away from territory centers to interact with neighbors.

One challenge associated with identifying links between habitat heterogeneity and bird distributions is that, for many species, when a wide range in understory conditions exists, variation within part of the range will be very important in determining habitat occupancy, while variations of similar magnitudes in other parts of this range will not. Vegetative responses to management-related disturbances tended to dominate the difference boundary analyses, and as a result may have masked some relationships between bird distributions and habitat conditions. For example, at two of the sites, HB-

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Wilderness and LB-Slash, the difference boundaries highlighted areas of vegetation change due to changes in forest type (HB-Wilderness site: subboundaries near two wildlife openings in the southwest portion, Figure 5.2; LB-Slash: subboundaries near a strip of planted spruce trees, Figure 5.4). Bird-difference boundaries seemed to respond to (overlapped with) vegetation-difference boundaries at the Wishbone and McNearney sites (O_w p- values, Table 5.2). In contrast, the high Ov values (in m) suggested that much of the change in vegetation at all four sites occurred relatively far away from the areas with high variation in bird distribution, suggesting "avoidance" of bird boundaries by vegetation boundaries. In many cases, the areas with vegetation-difference subboundaries showed very low occupation by birds on both "sides" of the detected subboundaries, suggesting that, at these locations, variations in understory conditions were outside of the range of conditions used by black-throated blue warblers.

One potential solution for situations where much of the variation in a spatial field is outside of a biologically meaningful range for a target species is to compare results using a set of different BE thresholds. Instead of using just one BE threshold (here 15% for vegetation) in the difference-boundary detection step, boundaries could be produced for 5, 10, 15, etc. percent of BEs, and compared. If boundaries with more BEs provided more information on variation within a meaningful range, BEs with the highest surface-gradient magnitudes (e.g., those associated with strong variation due to disturbance), could be masked out prior to overlap analyses. Similarly, the detection of biologically meaningful difference boundaries could probably be improved through the choice of variables. For example, I chose to limit the mode height variable to values ≤ 3 m, so that variations between neighboring locations that both had mode heights above 3 m would not influence the determination of boundaries. However, in these forests, because disturbances like old roads or wildlife cuts change many vegetation characteristics at once, vegetation near disturbed areas would likely always be detected as BEs. This effect could be minimized by not including habitat within some threshold distance from a change in forest type or management history, although for some species and individuals, these transition zones and edge habitats are important (e.g., use of regenerating aspen, in cluster 3 at HB-Wilderness, Figure 5.2).

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Cluster-based boundary analyses

For some species, spatially-agglomerative clustering may be used to identify particular habitat types within forest mosaics where birds are most abundant (e.g., Hall and Maruca 2001). In this study, however, cluster-based boundary analysis was a particularly useful spatial analysis tool because it allowed me to demonstrate that, rather than specializing on one habitat type, many blue warblers in these heavily-browsed, managed forests were found where two complementary sets of understory conditions were present. Like non-spatial forms of cluster analysis, this method allowed me to summarize vegetation characteristics by grouping vegetation samples into similar units. I could then link vegetation characteristics with bird-occupancy rates (Table 5-3), but, more importantly, I could also show these units in maps. Interpretation of patterns of habitat use by blue warblers required both of these pieces. For example, although the bird-occurrence means for cluster 1 (dominated by conifers) at HB-Wishbone was the highest of clusters at that site, examination of the map suggested that birds were using locations within cluster 1 that are adjacent to other clusters (Figure 5.1). Thus, the map allowed me to detect "hotspots" for blue warbler territories (e.g., where cluster 8 and the western portions of cluster type 3 are adjacent to cluster 1, or in north-eastern areas where cluster type 2 is adjacent to cluster 1). Although the composition of the "matrix" habitat type for the HB-Wilderness site was reversed (here the majority of the site had low, primarily deciduous vegetation, with patches of more dense, taller confers), this site had the same pattern of high frequencies of birds occurring where the different cluster-types intermingled (Figure 5.2).

The overlap analyses for both HB sites indicated avoidance of cluster boundaries by bird-difference boundaries, suggesting that variations in bird-occupancy rates occurred unusually far from cluster edges. This result agrees with the interpretation that blue warblers selected areas where two cluster-types were adjacent as a central portion of their territory, with territory edges farther away.

At the LB sites, the location of territories appears to have been most influenced by they density of vegetation with mode heights between one and three meters. This results agrees with work by Holmes et al. (1996), who found that understory-shrub density was an important habitat characteristic determining local patterns of blue warbler densities.

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Interestingly, Steele (1992) found that within New Hampshire forests with dense understory shrubs, blue warblers did not select the highest shrub-density areas for territories. A tendency for blue warblers to occupy the most dense areas may occur in Michigan due to overall lower densities of understory vegetation. In Michigan forests that are not exposed to high deer densities, time since thinning, which strongly influences the height and density of understory vegetation, is likely to be a good predictor of the density of blue warblers.

Future research in boundary analysis methods

A key consideration in any ecological analysis is the effect of sampling scale on the results obtained and conclusions drawn from the study (Wiens 1989, Levin 1992). The effects of scale can be especially apparent in spatial analyses such as this one, where much of the small-scale heterogeneity between grid cells would likely appear less important if a larger grid-cell had been used. For example, the larger-scale transition between coniferous and hardwood vegetation at the HB-sites would probably have emerged more strongly from the difference-boundary analyses if larger grid cells were used, because many of the areas where conditions were sharply different between one or two pixels would have been homogenized. A larger sampling scale would also be appropriate for reducing autocorrelation in the bird data, and a scale that more closely matched territory sizes would probably show more cohesive difference-boundaries. However, a larger scale could have masked the pattern of birds in HB sites selecting a combination of tall and short areas for use as habitat. Before boundary-detection methods are applied widely to characterize diverse understory habitats, an analysis of the effects of sampling scale, such as the one conducted by Fortin (1999) for boundaries based on forest vegetation, should be conducted to determine the scale at which vegetation boundaries best predict bird distributions.

Additional future applications of edge-detection methods include quantifying the effects of different types of forest fragmentation on breeding birds and other wildlife species. The type of edge (gradual or distinct, straight or sinuous) is likely an important factor determining the effects of fragmentation on both birds and the "usual suspects" in terms of edge-effect mechanisms, nest predators and nest parasites (Faaborg et al. 1995,

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Hawrot and Niemi 1996). Future work could use boundary-analysis techniques derived from fuzzy set theory to quantify the nature of transition zones between habitat types, and then link this information with studies of fragmentation effects (Brown 1998, Jacquez et al. 2000).

To improve the comparability of studies using geographic boundary analysis techniques, more work should be done to describe the effects of the many judgment calls required by the analysis process. Although the choice of what variables to measure is important in any study, the way in which variables are combined and typically given equal weights in multivariate techniques such as these makes the choice of variables particularly important (Fortin 1997, Hall and Maruca 2000). In addition, more research is needed on how to determine threshold levels for both the number of BEs included in a boundary, and the rules for joining adjacent BEs into larger units. Results for the LB-Slash site, where p-values for boundary cohesiveness and overlap shifted dramatically with different BE thresholds, provide strong evidence of the sensitivity of these techniques to threshold levels, and results are best interpreted with this sensitivity in mind.

The main challenge for future work with spatial methods of cluster analysis will be to provide better guidance on how to choose the number of clusters, especially when sites with different conditions are compared. Although the "best fit" method used here provides a good starting place (Milligan and Cooper 1985, Gordon 1999, Hall and Maruca 2001), the choice of number of clusters was still a challenge. In this study, some strong boundaries suggested by maps of understory characteristics and difference boundaries were not reflected in the cluster delineation. One example of this unsatisfying result can be seen in the north-west corner of the HB-Wishbone site, which was fairly strongly demarcated by subboundaries (Figure 5.1, lower left), but was included as part of the main cluster, cluster 1 (Figure 5.1, lower right). When I investigated very small numbers of cluster totals for this site (4-10), a cluster always outlined this area, while typically all of the rest of the clusters, besides a large "matrix" cluster, were only one or two grid-cells in size. As I examined larger cluster-totals, the clusters shown in Figure 5.1 were delineated, but as soon as the large, eastern portion of cluster type 2 emerged, the north-west corner cluster was no longer identified, up through at least cluster totals of

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40. In this case, inclusion of the "ghost cluster" would have strengthened the usefulness of the clusters for predicting bird distributions, as bird-occupancy means for cluster 1 would have increased due to the exclusion of this rarely occupied portion of the study area. In conclusion, the difference boundary detection and clustering tools used here are likely to be very useful, but offer many challenges in terms of standardization of application and most effective application.

An important next step in improving methods for evaluating the significance of boundaries, and similarities (overlap) between boundaries, is the development of more realistic null spatial models (Fortin and Jacquez 2000). The null model of complete spatial randomness that I used here as a basis for comparing sites was far from realistic, in that it inherently made the assumption that values measured in various grid-cells were independent. This assumption was most obviously incorrect for the bird data, as the scale of bird territories was larger than the 25 m grid-cells. The simplest new step to take in future analyses would be to create a null model that restricts the randomization of values during the Monte Carlo procedures (used for amassing null distributions) in a way that preserves an appropriate level of autocorrelation, which could be done by using a restriction length that is scaled to the territory size (Fortin and Jacquez 2000).

Incorporating understory characteristics into a spatially-explicit population model
One of the limitations of most spatially-explicit population models is that they require that habitats be represented as homogeneous cells (Villard et al. 1998). Working within this constraint, understory characteristics could be incorporated in a few different ways. First, if conditions were relatively uniform across sites, as was true at the LB-Slash site, the density (and reproductive success data) could be assigned at the stand level. Much of the variation in the LB-McNearney site was related to the fact that this site included parts of two management units, one of which was thinned more recently than the other, although some disturbances within these areas also contributed to the observed warbler distributional patterns. For LB sites, where browsing does not restrain understory growth, the suitability of the habitat could change with time in the model to simulate growth-processes following thinning. Within the two HB sites, the main source of vegetation variation was related to species composition (firs and hardwoods), with

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understory height variation also strongly linked to species composition, since most hardwoods were short due to browsing by deer. As the scale of the fir/hardwood pattern was fine relative to the scale at which these areas would likely be managed, an index that reflected the relative abundance of the two understory types, and the nature of the boundaries between them (e.g., roughly a straight boundary with a short total distance, or wavy, with many areas of mixing between the two types) might be a useful model parameter. For example, measures such as fractal dimension or edge density could be used as an index of the complexity of the border between habitats types at a given measurement scale (O'Neill et al. 1988, McGarigal and McComb 1995). This index could then be tested in terms of it's ability to predict the abundance of shrub-nesting birds, and if useful, could be used to group stands with similar characteristics for modeling purposes.

Another factor to consider when creating spatially-explicit population models is that vegetation is probably not the only factor determining within-patch distributions of various songbird species. Landscape-scale effects, past history, site-fidelity, and conspecific attraction (individuals preferentially selecting territories that are adjacent to those occupied by individuals of the same species, Stamps 1988) may all add additional layers of complexity to the modeling of bird habitat-relationships (Villard et al. 1998, Knick and Rotenberry 2000). Indeed, behavioral factors may prove to be very important in understanding black-throated blue warbler distributions. This species shows high breeding-site fidelity (Holmes et al. 1996, Chapter 3), and has fairly high rates of successful extra-pair copulations (Chuang-Dobbs et al. 2001), suggesting that having neighbors may improve male reproductive success. If applied at a larger scale than used here, spatial-analysis techniques, including boundary analysis, could be very useful for figuring out when the typically "clumped" distribution of songbirds represents a response to habitat conditions, and when observed patterns are not well explained by patterns in vegetation.

Conclusions

Typically, how species respond (at the territory scale) to variations in vegetation patterns is evaluated by collecting data within and outside of territories. These data are then

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compared, either as a set of distributions for individual vegetation variables (e.g., Jones and Robertson 2001), or through integration of variables with a principal components or ordination approach (e.g., Hunt 1998). Although helpful in understanding the typical composition of vegetation utilized by birds, these approaches do not incorporate the spatial patterns of habitat characteristics, which can be particularly important in heterogeneous habitats. In effect, these non-spatial approaches assume that habitat within territories is homogeneous, and may be particularly misleading if birds are selecting a territory that includes more than one distinct vegetation type. Although this "homogeneous area" approach facilitates the statistical detection of differences in habitat use through reduction of within-site variation, studies of homogeneous areas are not likely to provide generalizations applicable to forests that are patchy due to natural or management-related factors. A recent handbook of bird-study methods states that "there is little agreement among biologists on the methods, and even the scale, of vegetation data collection needed to correlate with bird abundance, habitat needs, distribution, and behavior" (Nur et al. 1999:7). With this thought in mind, it makes sense to continue to search for and develop new methods, such as geographic boundary analysis, that allow researchers to look in new ways at how factors such as within-site heterogeneity influence bird distributions.

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Table 5.1. Subboundary statistics for the understory vegetation and black-throated blue warbler boundaries. Significance values are one-tailed in the direction of boundary cohesiveness. Lengths and diameters are expressed in terms of the number of connected boundary elements.

	Number of subboundaries	Number of single BEs	Mean length	Maximum length	Mean diameter	Maximum diameter
Vegetation						
HB-Wish	94 p=0.001	55 p=0.001	1.8 p=0.001	7 p=0.11	1.8 p=0.001	6 p=0.16
HB-Wild	79 p=0.001	49 p=0.001	1.7 p=0.001	9 p=0.018	1.7 p=0.001	9 p=0.007
LB-McN	81 p=0.001	54 p=0.029	1.7 p=0.001	11 p=0.006	1.7 p=0.002	8 p=0.020
LB-Slash	41 p=0.001	20 p=0.002	2.1 p=0.001	8 p=0.096	2.1 p=0.001	8 p=0.042
Warblers						
HB-Wish	124 p=0.001	56 p=0.001	1.9 p=0.001	6 p=0.66	1.9 p=0.001	6 p=0.54
HB-Wild	80 p=0.001	30 p=0.001	2.3 p=0.001	9 p=0.086	2.3 p=0.001	7 p=0.16
LB-McN	101 p=0.001	55 p=0.001	1.9 p=0.001	8 p=0.14	1.9 p=0.001	8 p=0.063
LB-Slash (17% & 25%)	64, 65 p=0.001	38, 24 p=0.001	1.6, 2.3 p=0.026, p=0.001	3. 11 p=1.0, p=0.011	1.6, 2.2 p=0.018, p=0.001	3, 8 p=1.0, p=0.056

Table 5.2. Overlap statistics for difference boundaries in understory vegetation and black-throated blue warbler distributions. Significance values are one-tailed in the direction of boundary overlap. Distances (O_W, O_V, and O_{WV}) are expressed in meters.

	O_W	O_V	O_{WV}	O_E
HB-Wish	43 p=0.011	32 p=0.99*	39 p=0.20	31 0.92
HB-Wild	44 p=0.51	42 p=1*	43 p=1*	23 p=0.98*
LB-McN	35 p=0.003	27 p=0.91	31.4 p=0.067	37 p=0.44
LB-Slash	49, 49 p=0.20, p=0.092	30, 25 p=0.47, p=1*	40, 38 p=0.21, p=0.10	16, 25 p=0.61, p=0.98*

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Table 5.3. Vegetation characteristics for clusters within each of the four research sites. The mean frequency of black-throated blue warbler occupancy of each 25m grid cell within the various clusters is also included; this ranged from 0-4 (1998-2001) for the HB-Wishbone and LB-McNearney sites, and from 0-3 (1999-2001) for the HB-Wilderness and LB-Slash sites.

| Clusters	density (% area filled)	mode height (m)	range (m)	deciduous /coniferous (% decid)	bird frequency (# years)
HB-Wish					(max of 4)
1. N = 820	37 ± 0.78	1.9 ± 0.056	3.4 ± 0.85	37 ± 1.2	1.7 ± 0.047
2. N = 318	46 ± 1.3	0.74 ± 0.031	1.6 ±0.088	95 ± 0.45	1.2 ± 0.65
3. N = 56	29 ± 2.7	4.9 ± 0.31	6.6 ± 0.32	64 ± 4.9	1.1 ± 0.18
4. N = 21	17 ± 2.1	1.6 ± 0.36	5.4 ± 0.62	71 ± 4.6	0.095 ± 0.066
5. N = 13	11 ± 2.6	4.6 ± 0.53	7.2 ± 0.53	29 ± 8.7	1.2 ± 0.22
6. N = 6	70 ± 6.3	1.6 ± 0.50	5.3 ± 0.31	99 ± 0.83	1.3 ± 0.49
7. N = 6	48 ± 12	4.7 ± 0.33	6.8 ± 0.67	100 ± 0	0.33 ± 0.33
8. N = 2	60 ± 0	3.5 ± 0.50	5.9 ± 1.4	18 ± 2.5	4 ± 0
HB-Wild					(max of 3)
1. N = 720	39 ± 0.76	1.2 ± 0.042	2.4 ± 0.071	66 ± 1.2	0.92 ± 0.37
2. N = 227	47 ± 1.4	3.2 ± 0.11	4.9 ± 0.14	24 ± 1.6	1.6 ± 0.066
3. N = 12	80 ± 6.0	5.3 ± 0.58	6.6 ± 0.34	91 ± 3.0	2.3 ± 0.22
4. N = 8	13 ± 3.7	4.3 ± 1.0	7.0 ± 0.67	65 ± 14	0.25 ± 0.16
5. N = 7	64 ± 4.3	2.6 ± 0.43	4.2 ± 0.60	4.3 ± 1.3	0.29 ± 0.18
6. N = 6	8.3 ± 3.3	6.0 ± 1.2	4.3 ± 1.1	15 ± 13	0 ± 0
7. N = 5	59 ± 10	2.4 ± 0.93	5.4 ± 0.98	15 ± 4.5	1.6 ± 0.24
8. N = 2	75 ± 15	0.75 ± 0.25	1.3 ± 0.25	63 ± 28	2 ± 0
LB-McN					(max of 4)
1. N = 764	38 ± 0.72	1.4 ± 0.025	2.9 ± 0.69	98 ± 0.22	1.4 ± 0.043
2. N = 135	56 ± 2.0	4.1 ± 0.16	7.1 ± 0.15	99 ± 0.34	2.0 ± 0.10
3. N = 79	63 ± 2.0	2.6 ± 0.11	6.0 ± 0.17	99 ± 0.64	2.6 ± 0.15
4. N = 8	25 ± 0	6.5 ± 0.76	7.6 ± 0.55	91 ± 3.2	1.0 ± 0.32
5. N = 8	59 ± 6.1	6.3 ± 0.86	7.7 ± 0.44	73 ± 12	1.3 ± 0.45
6. N = 2	25 ± 0	1.0 ± 0	1.5 ± 0	45 ± 25	2 ± 0
LB-Slash					(max of 3)
1. N = 518	48 ± 0.94	1.4 ± 0.029	2.6 ± 0.061	98 ± 0.34	1.9 ± 0.044
2. N = 101	17 ± 1.1	0.84 ±0.077	1.4 ± 0.17	91 ± 2.4	1.1 ± 0.087
3. N = 10	21 ± 2.7	3.7 ± 0.62	7.5 ± 0.60	97 ± 1.3	0.20 ± 1.3
4. N = 6	15 ± 4.5	4.8 ± 1.2	6.9 ± 0.89	70 ± 12	0.5 ± 0.22
5. N = 2	60 ± 0	6.5 ± 1.5	7.8 ± 0.25	100 ± 0	2.0 ± 0

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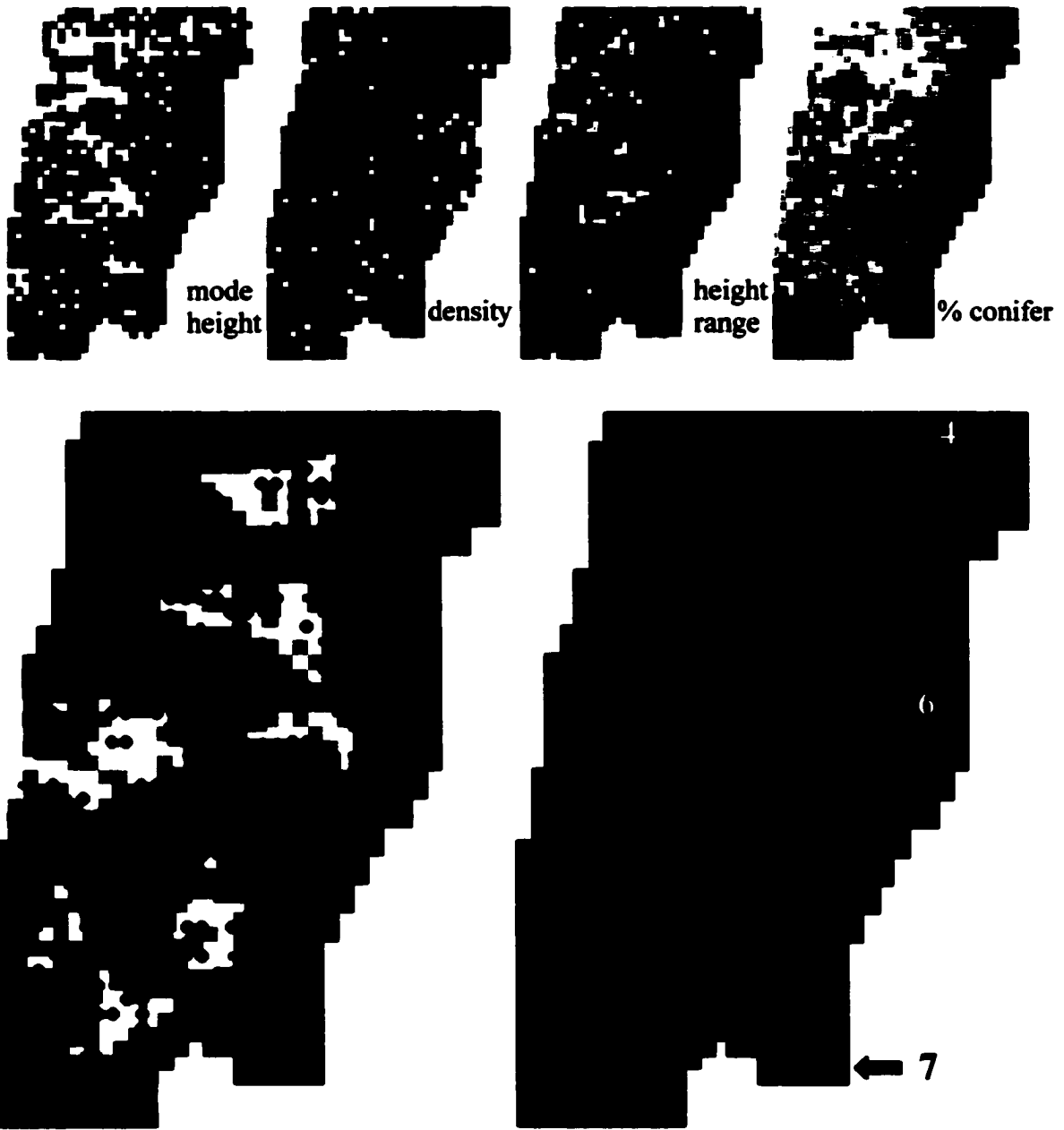
Figure 5.1. Boundary analysis results for the heavily-browsed Wishbone site. The four understory vegetation variables are shown across the top; for all, values go from dark (low) to light (high). The frequency of black-throated blue warbler use of each grid square is shown in the large lower left figure, with a range from 0 years (black) to 4 years (white). On the same figure, the difference boundaries are shown in red for warblers, and green for vegetation. The clusters identified for this site are shown in the lower right section, with vegetation characteristics corresponding to the cluster numbers shown in Table 5.3.
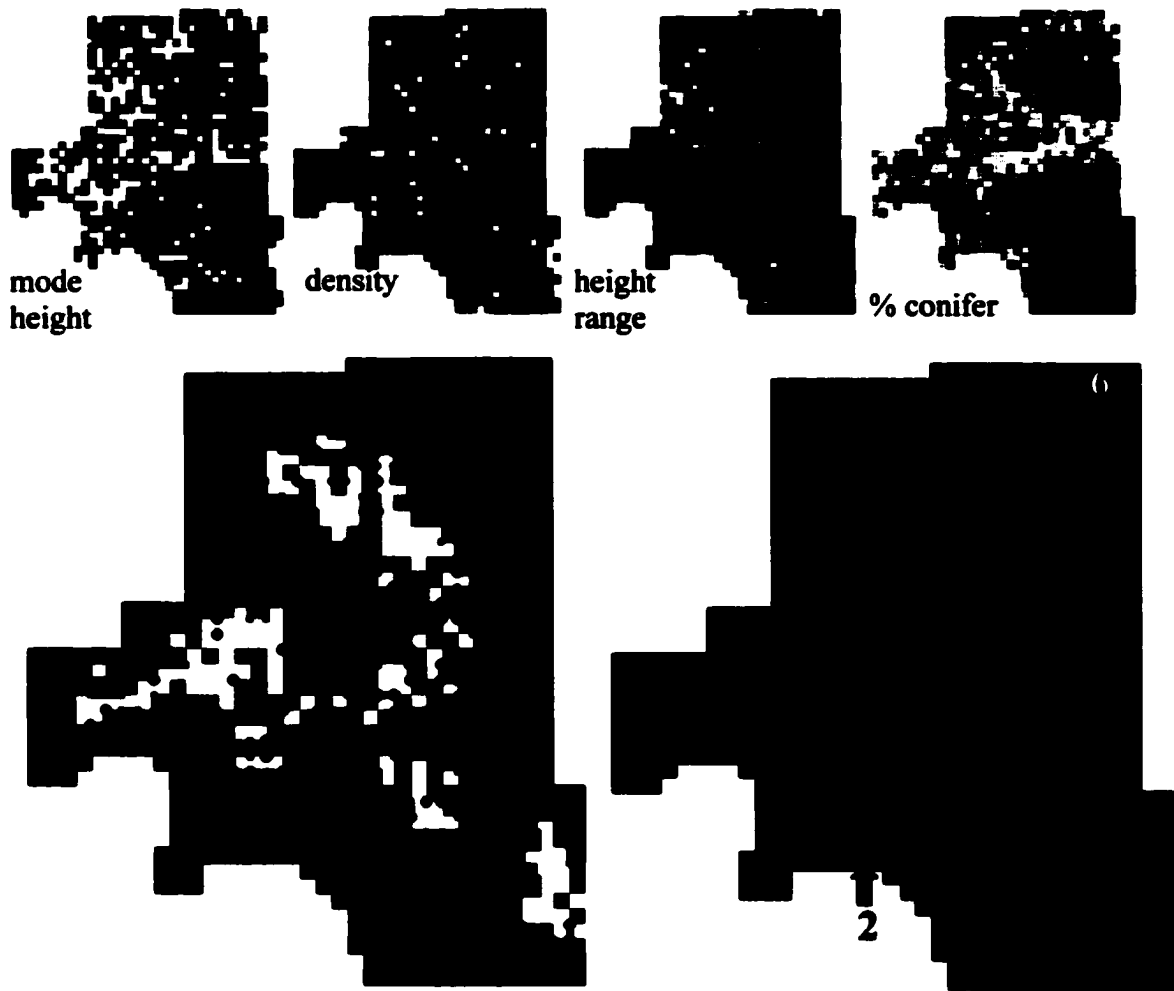
156

mode
height

density

height
range

% conifer

Figure 5.2. Boundary analysis results for the heavily-browsed Wilderness site. The four understory vegetation variables are shown across the top; for all, values go from dark (low) to light (high). The frequency of black-throated blue warbler use of each grid square is shown in the large lower left figure, with a range from 0 years (black) to 3 years (white). On the same figure, the difference boundaries are shown in red for warblers, and green for vegetation. The clusters identified for this site are shown in the lower right section, with vegetation characteristics corresponding to the cluster numbers shown in Table 5.3.

Figure 5.3. Boundary analysis results for the less-browsed McNearney site. The four understory vegetation variables are shown across the top; for all, values go from dark (low) to light (high). The frequency of black-throated blue warbler use of each grid square is shown in the large center figure, with a range from 0 years (black) to 4 years (white). On the same figure, the difference boundaries are shown in red for warblers, and green for vegetation. The clusters identified for this site are shown in the bottom figure, with vegetation characteristics corresponding to the cluster numbers shown in Table 5.3.
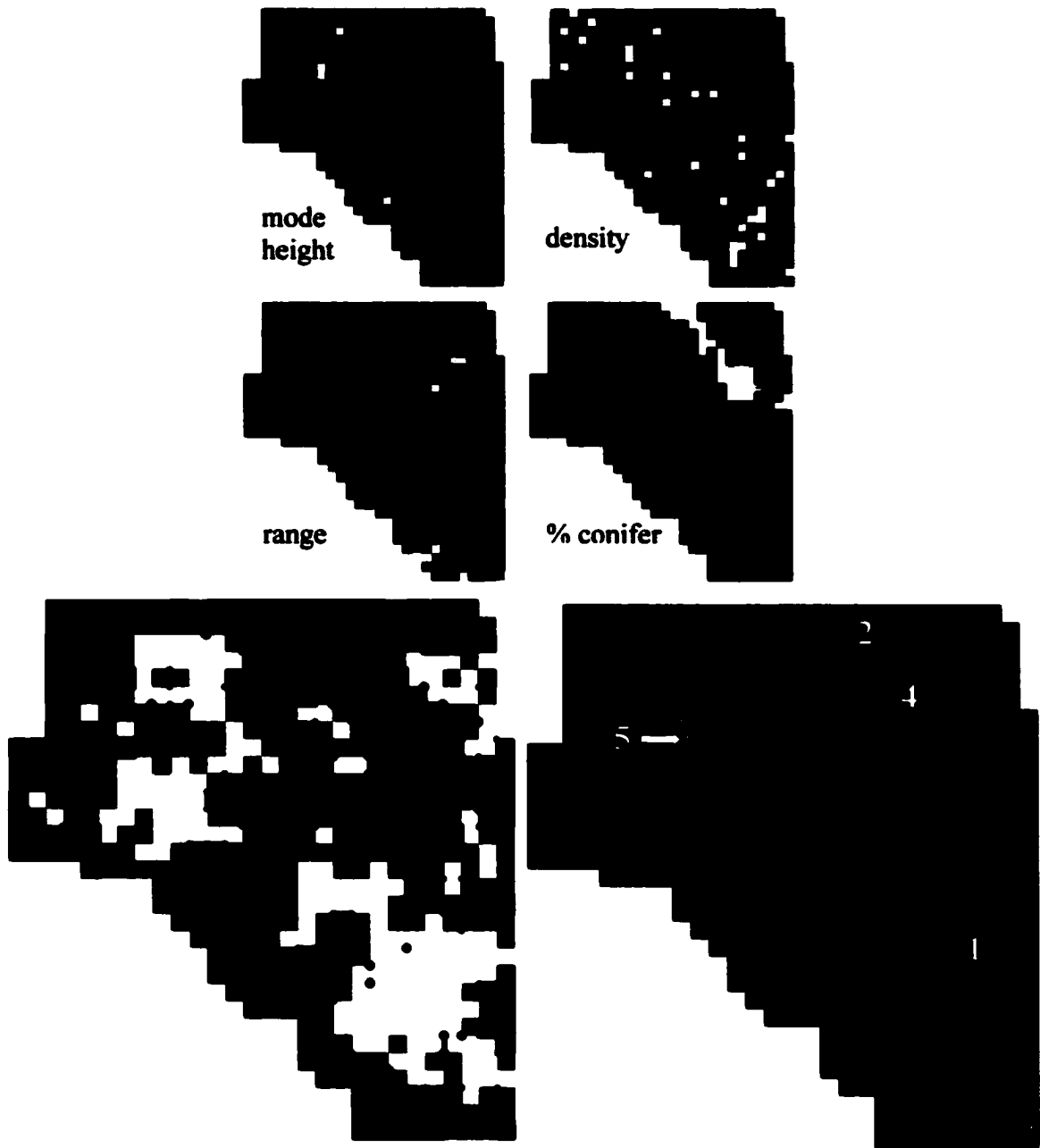
Figure 5.4. Boundary analysis results for the LB-Slash site. The four understory vegetation variables are shown across the top; for all, values go from dark (low) to light (high). The frequency of black-throated blue warbler use of each grid square is shown in the large lower left figure, with a range from 0 years (black) to 3 years (white). On the same figure, the difference boundaries are shown in red for warblers, and green for vegetation. The clusters identified for this site are shown in the lower right section, with vegetation characteristics corresponding to the cluster numbers shown in Table 5.3.
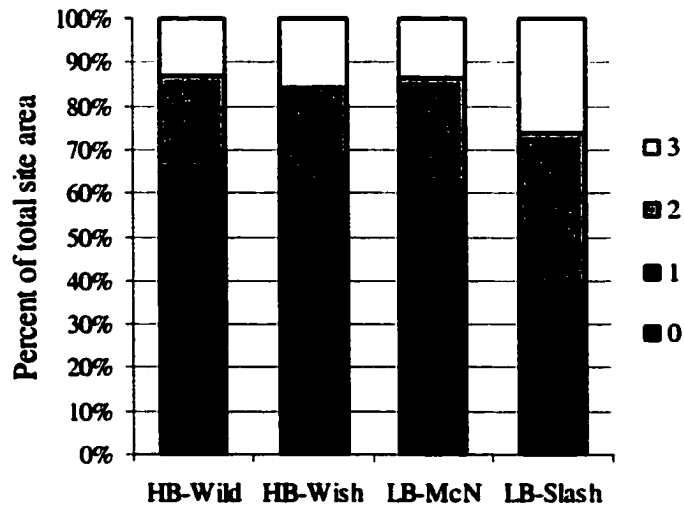
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Figure 5.5. Distribution of the years of black-throated blue warbler occupancy by percentage area for the four northern Michigan study sites, 1999 - 2001. Three years of data were used for all sites to permit between-site comparisons, with number of years of occupancy described by the shading pattern shown in the right-side key.

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CHAPTER VI

SUMMARY, AND MANAGEMENT SUGGESTIONS FOR PROTECTING SONGBIRDS IN THE HIAWATHA NATIONAL FOREST

Summary

- In heavily-browsed northern Michigan forests, balsam fir appear to supply "refuge" habitat for two shrub-nesting species, black-throated blue warblers (*Dendroica caerulescens*), and veeries (*Catharus fuscescens*) that prefer habitats with high shrub densities. Although when examined as a group, shrub-nesters were significantly less abundant in HB forests (which may be due to HB sites being near the southern range boundary for one shrub-nester, the Swainson's thrush), these two species maintained similar abundances across heavily-and less-browsed high-shrub density habitats, primarily because many of these HB habitat had high fir densities. Ground-nesting species, dominated numerically by the ovenbird, were most common where deer browse-pressure was high, regardless of whether forests had firs in the understory, were more-recently thinned (high shrub density), or had a closed canopy (low shrub density). Of the species that I observed, Rose-breasted grosbeaks and American redstarts appear to be the most sensitive to browse effects. Least flycatchers (*Epidomax minimus*) showed a strong avoidance of habitats with understory firs; together, these results suggest that any change in management to favor one of these neotropical migrant species is likely to reduce habitat available for another species in this potentially at-risk group. Overall, for most species that I detected, changes in understory and overstory density due to thinning seem likely to have stronger effects on bird distributions than browse intensity.

- Within Michigan forest sites with high shrub density, blue warbler density does seem to be a reasonable indicator of total reproductive output. Although even high-density populations in Michigan are likely low-density when compared to other populations, the quality of individual territories was high, as birds had high

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levels of reproductive success. As a result, a direct comparison of density alone between populations in different regions, especially those with higher rates of nest depredation, is likely to under-estimate the quality of Michigan forests for blue warbler populations.

- Local-scale vegetation heterogeneity appears to be a key factor influencing the location of blue warbler territories. Blue warbler territories at HB sites often occurred where patches of understory with different mode heights (e.g., 0.7 - 1.2 m, vs. 2 - 5 m) were adjacent. Heterogeneity with respect to vegetation height also seemed to influence distributions at the less-browsed McNearney site, although vegetation density alone was also a good predictor of territory distributions at both LB sites.

Scope of recommendations

The premise behind these recommendations is that it is likely that within the range of density levels typically seen in the Hiawatha National Forest (HNF), browsing by deer will reduce habitat quality for some migratory bird species, while improving quality for others with different resource needs. Browse-sensitive species may need special protection in order to persist, and there may be opportunities for managing browse-resistant plant species to provide additional habitat. In some cases, it may be beneficial to maintain some areas as heavily-browsed to promote species that survive and reproduce best in these types of habitats (McShea and Rappole 2000). As the managers at the HNF have little control over how deer are managed throughout Michigan's Upper Peninsula (U.P.), management suggestions and areas for future study focus on approaches that might be possible through landscape-scale forest management plans.

Long-term focus areas for research and management

Use a landscape-scale approach to manage both timber, and browse pressure
Ideas here follow those of McShea and Rappole (2000), who suggested focusing on managing vegetation, rather than managing deer. Their argument for managing

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landscapes is based on the following rationale: (1) deer densities are difficult to measure, especially when compared to measuring understory vegetation densities; (2) Deer management takes place at a larger scale than what most managers are trying to manage; and, (3) Birds respond to vegetation volume (although maybe not just vegetation characteristics), not deer densities. Through careful planning, it should be possible to concentrate deer in particular areas through taking a landscape-perspective on the selection of the location of management actions such as forest clearcutting or thinning, and selection of which areas will remain undisturbed (i.e., designated as being managed to promote old growth conditions). Besides providing a tool for focusing the effects of deer within a landscape, effects of timber management such as thinning will likely outweigh the effects of deer densities for most bird species (DeGraaf et al. 1991).

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A key question that needs to be addressed in these forests is: What are the goals for species management? A tempting answer may be that we want to manage for songbird population levels that are similar to those that would have been found in northern forests before European settlement of North America. However, the forests that are present now are likely to be very different in species composition and typical stand structure than what was present at that time. It is likely that many of the shrub dependent species like black-throated blue warblers and chestnut-sided warblers (*Dendroica pensylvanica*) were less common in pre-settlement forests, coming in after fire (chestnut-sided warbler) or occurring at low densities in the mature forests that had enough gaps to sustain areas of high shrub density (black-throated blue warbler). Also, many of these species may have utilized Canada yew (*Taxus canadensis*), a species that has become very rare in the region, presumably due to browsing by deer. So, in many cases there may be more of some species than were present before, and at least for now threats from brown-headed cowbirds (*Molothros ater*), brood parasites that are having major impacts on reproduction of songbirds in areas farther south (e.g., Robinson et al. 1995, Donovan et al. 1997), are not common in northern Michigan. I suggest the following ranked goals: (1) protect rare species for which this part of Michigan is an important part of the species' range; (2) provide habitat for common species that depend on typical Michigan forest habitats; and (3) look for opportunities to increase populations that may be particularly hard-hit by habitat loss in the fragmented Midwest.

Species with evidence for browse sensitivity

Of bird species in the HNF, Rose-breasted grosbeaks and American redstarts may be the most strongly negatively impacted by overabundant deer. Both of these species appear to tall hardwood saplings and small trees, which tend to be rare in heavily-browsed areas. While results for redstarts were not statistically significant, they do suggest a biological significant pattern of low abundance in heavily-browsed habitats. Redstarts showed a strong positive response to deer exclusion in Virginia forests (McShea and Rappole 2000), and have been found to require early successional forest conditions in New Hampshire's northern hardwood forests (Hunt 1996, 1998). In habitat with few firs,

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black-throated blue warblers and veeries are also likely to have lower densities where browse-pressure is high.

Species of special concern that might be more common with denser understory
Although close to their northern range limit in the UP, wood thrush are of particular conservation concern in Eastern and Midwestern forests, and are one of the three Partners in Flight priority species for this ecoregion (Robinson et al. 1995, Pashley et al. 2000). Wood thrush are likely to be more common in forests with dense, multi-layered understory vegetation and a closed canopy (Brewer et al. 1991), conditions not typically found together HNF's even-aged stands. Wood thrush had a significant positive response to removal of deer from Virginia oak-hickory forests (McShea and Rappole 2000), but a mixed, non-significant pattern in Massachusetts oak-pine forests (DeGraaf et al. 1991). Only a few wood thrush were observed during in this study, but this species might be more common under different management conditions. If particular "hotspots" for breeding wood thrush are found in northern forests, particular care should be taken to evaluate how both local and regional-scale management (e.g., activities that attract deer, such as clearcutting aspen) could alter important habitats.

Short term management suggestions

Include abundance of balsam fir in assessment of stands for possible thinning
In the heavily-browsed habitats, there was a strong relationship between the density of understory firs and the relative abundance of two species of concern, black-throated blue warblers and veeries. The fact that understory firs are visible in spring aerial photos (leaves off) suggests that assessment of fir abundance in particular stands could be one of the criteria used to select areas that will or will not be thinned in a particular thinning rotation. This could prevent many areas of high quality habitat for blue warblers and veeries from being thinned in the same year, which should help maintain populations, at least in the short term, even if browse levels remain high.

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Experiment with Canada yew reintroductions

Canada yew is missing from most of the HNF, but is likely to have provided habitat for shrub-nesters. A key question that could be addressed is whether yew is removed sequentially as deer are attracted to areas following thinning, and then is not able to recover after densities decrease. HNF interns could set up experiments to see if areas that are fairly isolated from management actions can support transplanted yew, or if deer densities even in those areas are too high.

Manage for lower nest predator populations

It may be possible to help protect songbirds in these forests by managing in a way that reduces populations of common nest predators, such as chipmunks. One factor likely to increase small mammals, especially chipmunks, is the presence of slash (branches, etc., left on the ground following thinning). So, tests could be done to assess the effects of leaving or removing slash on small mammal populations, and on bird nesting success.

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