Ecology and Management of Scrub-shrub Birds in New England: A Comprehensive Review

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Table of Contents

Executive Summary

- We conducted a review and synthesis of the literature pertaining to the ecology and conservation of scrub-shrub birds in New England.
- We identified 41 bird species that regularly breed in scrub-shrub habitats in New England. The composition of the scrub-scrub bird community varies substantially by geographic region.
- Scrub-shrub habitat is uncommon in New England and makes up roughly 12% of New England's land area. Most of this habitat (71%) is located in Maine. Southern New England has far less scrub-shrub habitat, and the overall amount of scrub-shrub habitat in New England is declining.
- Most (78%) of the scrub-shrub habitat in New England is regenerating forest created by logging, but the proportion of New England's forests in an early-successional stage (19%) is much lower than other regions of the eastern U.S.
- Twenty-one scrub-shrub bird species have shown long- or short-term declines in New England, and declining species outnumber increasing species by 3 to 1. These declines have become more pronounced in the past few decades, and are most severe in central and southern New England. Bird populations are relatively stable in the northern part of this region.
- Habitat use varies among species. Though most species (90%) will nest in clearcuts, some species occur only in other types of scrub-shrub habitats. Thus, no single type of management will accommodate all of the region's bird species.
- Many scrub-shrub birds show consistent patterns of changing abundance over successional stages in the first 20 years after logging, and nearly all scrub-shrub species disappear from

clearcuts by 20 years after logging, when the canopy closes and the understory is shaded out.

- Because of specificity to successional stages, scrub-shrub birds occupy an average of 50% of regenerating clearcuts up to year 20. Thus, estimates of scrub-shrub habitat based on forest inventories may be too high for many species.
- Most scrub-shrub birds avoid edges and, with a few exceptions, prefer larger (> 1-4 ha) patches of habitat.
- The few studies examining how landscape-level availability of scrub-shrub habitat affects avian abundances have found inconsistent results.
- Nest success rates vary among bird species and habitats, but there was little evidence for edge or area effects on nesting success.
- According to a meta-analysis, site fidelity rates of adult scrub-shrub birds are comparable to those of forest birds. Thus, scrub-shrub birds are not, as a group, “fugitive” species as asserted previously.
- All but 4 of New England’s 41 scrub-shrub birds winter south of New England, with winter species richness highest along the Gulf Coast of Texas and in Panama and Costa Rica.
- Most scrub-shrub birds winter in open, scrubby habitats similar to their breeding habitats. These habitats should be widely available due to logging, especially in the Neotropics. Six species, however, winter in mature forests, making them susceptible to tropical deforestation.
- Most scrub-shrub birds prefer scrubby, open habitats for stopover on migration.
- Based on our review of the literature, we make the following recommendations for managing scrub-shrub birds in New England: 1) Create more scrub-shrub habitat, especially in

southern New England. 2) Ensure that a variety of habitats, beyond just clearcuts, are available for birds. 3) To maximally benefit bids, patches of scrub-shrub habitat should be at least 1 ha in size and have regular shapes, avoiding irregular edges.

- More research is needed on several aspects of the ecology of scrub-shrub birds. Priorities for future research should include better monitoring and assessment of scrub-shrub habitats, estimating demographic parameters under a variety of ecological conditions, improved monitoring of bird populations, and determining impacts of landscape structure and configuration on birds.

Chapter 1. The New England Scrub-shrub Bird Community

Introduction

Scrub-shrub habitats in New England contain a diverse and varied breeding bird community. For instance, a shrubby power line corridor may hold Chestnut-Sided Warblers and Eastern Towhees. Clearcuts in coniferous forests may harbor White-throated Sparrows and Magnolia Warblers, and shrubby wetlands may have breeding Wilson's Snipe and Yellow Warblers. Some shrubland birds, like Golden-winged Warbler and Mourning Warbler, nest only in early-successional habitats and are rarely found in forests. Others, such as Northern Cardinal or Carolina Wren will breed in closed forests with a shrubby understory. To manage this diverse assemblage of birds and their habitats, it is important to know just what species would actually benefit from the creation of scrub-shrub habitat and which would not.

Here, we develop a list of core species breeding in New England shrublands. This list serves as a basis for the literature review and management recommendations that follow. The scope of this review is the six states of New England—Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine. As mentioned above, the scrub-shrub bird community varies substantially across this region, and we will emphasize these differences throughout this report.

Building the species list

What are the scrub-shrub birds of New England? This simple question proved surprisingly difficult to answer. For some ornithologists, the list would include all birds that *ever* use scrub-shrub habitats. Others might restrict the list to species that are *only* found in scrub. We sought a middle ground between these two extremes. Remsen (1994) suggested that species lists should be based on "core" species that are "characteristic" of their habitats. We agreed with Remsen and attempted to identify species that are typical of shrublands and would benefit from the creation of new habitat. By using this definition, we hoped to exclude species that are incidental in shrublands but to include those that regularly use such habitats. Conservation of these core species will depend in large part on scrub-shrub habitats.

As a starting point, we sought out expert opinions on which birds are characteristic of New England shrublands. We were able to find four independently created lists of birds breeding in early-successional habitats in this region (Peterjohn & Sauer 1993; DeGraaf & Yamasaki 2001; Hunter et al. 2001; Dettmers 2003). These "expert lists," developed for review papers or to analyze bird population trends by habitat, seemed a straightforward basis for our list. Unfortunately, the expert lists showed substantial disagreement over just what species breed in shrublands. All four lists included obvious species such as Brown Thrasher and Golden-Winged Warbler. At the same time, 45 bird species occurred on only one or two of the lists.

To resolve this confusion, instead of building our list directly from the expert lists, we chose to supplement the lists with a quantitative analysis of avian habitat usage. To this end, we conducted a meta-analysis of birds' habitat preferences across successional stages. Our goal was to determine the relative preference of each bird species for early- or late-successional habitats. This would provide quantitative data on birds' usage of scrub-shrub habitat and provide an additional source of data, beyond the expert lists.

For the meta-analysis, we located studies that compared the abundances of birds between early- and late-successional forests in the eastern United States or eastern Canada. To obtain sufficient sample sizes, we included studies from outside New England. All studies, however, took place in forest types (oak-hickory, northern hardwoods, or spruce-fir) found in New England. We located published studies using *Web of Knowledge* and *Biological Abstracts* as well as through papers' citations. To be included in the meta-analysis, a study had to compare avian abundances between early-successional and late-successional forests. For most studies, the early successional habitat was a recently logged area (the sole exception was Johnston & Odum [1956], in which the early-successional habitat was old fields). For clearcuts, we arbitrarily defined early-successional forest as less than 10 years post-logging, which is typically before the overstory closes and shades out the understory vegetation (DeGraaf & Yamasaki 2003). Late-successional forest had to be at least 40 years old. We excluded middle-successional stages, 10 to 40 years post-logging. Birds' usage of such forests, intermediate in structure between early and mature stages, does not provide insight into their relative preference for early-successional stages per se. We also excluded studies where the early-successional habitat was a group or selection cut less than 0.5 ha in size; such small patches often lack scrub-shrub birds due to area sensitivity (see Chapter 5). Finally, we excluded studies that did not did not distinguish between birds actually occurring in early-successional habitats and those found in adjacent forests.

Many bird species show preferences for different forest types (e.g. coniferous vs. deciduous) or forests of a specific age (e.g. 1-2 year-old forest vs. 5-7 year-old forest). If a study included a variety of forest types or stand ages, then preferences for distinct habitat types could mask differences between early- and late-successional habitats. To avoid such complications, for each species in each study we computed an Early Successional Index (ESI) according to the formula:

$$\text{ESI} = \frac{e}{e+l}$$

where e is the species' maximum abundance in any early-successional study site and l is the maximum abundance in any late-successional study site. Essentially, ESI is the relative abundance of birds in the "best" early-successional habitat versus the "best" late-successional habitat in any study. This can be thought of as the relative preference for early-successional habitat, smoothing over any preferences for distinct habitat types within successional stages. An ESI of 1 indicates that the birds occurred only in young forests while an ESI of 0 means that birds were found only in mature forests. In conducting the meta-analysis, we used a modified version of inverse variance weighting (Lipsey & Wilson 2001). We weighted ESIs by the sample size (the number of independent study sites) but not the within study standard error. This was necessary because, otherwise, ESIs of 0 or 1 would generate a standard error of 0 and, therefore, infinite weight.

We found 17 published studies that met our criteria (Table 1.1), and we estimated ESIs for 107 bird species. Mean ESIs by species had a J-shaped distribution (Figure 1.1). Approximately one-fourth of species evinced a strong preference for early-successional habitats, based on an ESI greater than 0.9. A species with an ESI of 0.9

Table 1.1. Studies included in the meta-analysis of habitat preferences of New England birds.

Study	Study location	Number of study sites
Burris & Haney 2005	Minnesota	4
Conner & Adkisson 1975	Virginia	5
Conner et al. 1979	Virginia	8
Costello et al. 2000	New Hampshire	18
DeGraaf et al. 1998	New Hampshire, Maine	20
Freedman et al. 1981	Nova Scotia	6
Germaine et al. 1997	Vermont	79
Hagan et al. 1997	Maine	355
Johnston and Odum 1956	Georgia	3
King & DeGraaf 2000	New Hampshire	20
Morgan and Freedman 1986	Nova Scotia	22
Probst et al. 1992	Michigan, Minnesota	17
Shugart & James 1973	Arkansas	4
Thompson & Fritzell 1990	Missouri	2
Thompson et al 1992	Missouri	18
Titterington et al. 1979	Maine	14
Yahner 1987	Pennsylvania	15

would be nine times more abundant in early-successional habitat than in mature forest. Most species, however, had intermediate ESIs, and the overall distribution was continuous, with no obvious cut point for separating out early-successional birds.

We used an iterative process to combine the results from the meta-analysis with the expert lists. The first step in this process was to create a candidate pool of species that could potentially be included in our final list. Species could become candidates by meeting one of two criteria: having an ESI > 0.5 or being on at least 3 of the 4 expert lists. We used an ESI of 0.5 as the cutoff because values greater than 0.5 indicate higher average abundance in early-successional habitat than in mature forest. Species that met both criteria, for the ESI and the expert lists, were automatically included in the final core list. The other species that met only one of the two criteria were evaluated on a case-by-case basis. We used accounts from the *Birds of North America* (BNA) series and the American Ornithologists' Union checklist (American Ornithologists' Union 1998) to determine whether or not these species regularly used scrub-shrub habitat. Where the evidence was uncertain, we erred on the side of including the species.

Twenty-nine species had an ESI greater than 0.5 and were on at least 3 expert lists; all of these species were included in our final core list (Table 1.2). Of these species, 27 had an ESI greater than 0.77, suggesting a strong preference for scrub-shrub habitats. Three species—Yellow Warbler, Willow Flycatcher, and Northern Bobwhite—were included on three or four expert lists but did

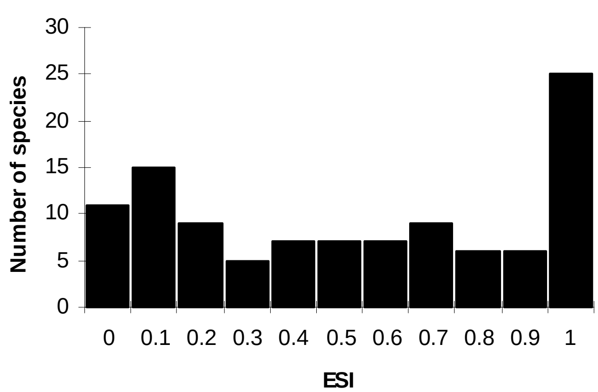


Figure 1.1. ESI scores (see text) for birds breeding in New England.

not appear in any of the studies in the meta-analysis. Expert assessments indicated that all three species are strongly attached to shrubby habitats, and we included all three in our final species list.

Three birds—Ruffed Grouse, Mourning Dove, and Carolina Wren—were found on three or four of the expert lists but had ESIs below 0.5. Ruffed Grouse had an ESI of 0.42. Grouse are often detected when drumming in poletimber stands or mature forests (Rusch et al. 2000). This may bias their ESI scores low, as the birds breed in scrub-shrub habitats, and shrubby openings are a requirement for their occurrence in forested landscapes (Dessecker & McAuley 2001). Thus, we included Ruffed Grouse on our final species list. Carolina Wren (ESI = 0.45) was included on the final list because it requires a dense shrubby layer for nesting and foraging (Haggerty & Morton 1995), and it's response to succession is similar to other scrub-shrub birds (Chapter 4). Mourning Dove (ESI = 0) was excluded from the final species list because of its low ESI and ability to breed in a wide variety of habitats (Mirarchi & Baskett 1994). While the dove can be found in shrublands, its conservation does not appear to be tied to this habitat.

Twenty-four species with ESI > 0.5 appeared on only one or two expert lists (Table 1.2, Table 1.3). Two woodpecker species, Northern Flicker and Hairy Woodpecker, were excluded on the basis of requiring large trees for nesting, a habitat feature often lacking in shrub habitats. Additionally, Northern Waterthrush was excluded on the basis of being a stream specialist. While waterthrushes use streams in shrubby habitats, they are not dependent on scrub-shrub habitats per se. We excluded Brown-headed Cowbird and Blue Jay from the species list because both birds are habitat generalists, and we could find no evidence suggesting that either is dependent on scrub-shrub habitats.

The meta-analysis identified a suite of birds that appeared to prefer scrub-shrub habitats (i.e. ESI > 0.5) but are more properly classified as birds of parklands, savannas, or open forests according to the AOU Checklist and BNA accounts (Table 1.3). These species are American Robin, Common Grackle, Chipping Sparrow, Eastern Kingbird, Eastern Bluebird, Baltimore Oriole, and Olive-sided Flycatcher. The fact that these spe-

Table 1.2. Core scrub-shrub bird species in New England and the criteria for their inclusion in this list. Scientific names are found at the end of this report.

Criteria for Inclusion	Species	Expert Lists: Dettmers[a]	Expert Lists: Peterjohn & Sauer[b]	Expert Lists: Hunter[c]	Expert Lists: DeGraaf & Yamasaki[d]	ESI[e]	n[f]
On 3 or 4 expert lists and ESI > 0.5	Northern Bobwhite	x	x			n/a	
	American Woodcock	x	x	x		1.00	1
	Alder Flycatcher	x	x	x	x	1.00	7
	Willow Flycatcher	x	x	x	x	n/a	
	White-eyed Vireo	x	x	x	x	0.80	4
	House Wren	x	x		x	1.00	1
	Gray Catbird	x	x	x	x	0.98	8
	Brown Thrasher	x	x	x	x	0.88	4
	Blue-winged Warbler	x	x	x	x	0.97	4
	Golden-winged Warbler	x	x	x	x	0.90	3
	Tennessee Warbler	x		x	x	0.93	3
	Nashville Warbler	x	x	x	x	0.77	5
	Yellow Warbler	x	x	x	x	n/a	
	Chestnut-sided Warbler	x	x	x	x	0.94	13
	Prairie Warbler	x	x	x	x	0.95	5
	Palm Warbler		x	x	x	0.78	1
	Mourning Warbler	x	x	x	x	0.95	9
	Common Yellowthroat	x	x	x	x	0.98	11
	Wilson's Warbler	x	x	x	x	0.88	1
	Yellow-breasted Chat	x	x	x	x	0.98	6
	Eastern Towhee	x	x	x	x	0.85	8
	Field Sparrow	x	x	x	x	0.97	6
	Song Sparrow	x	x		x	1.00	5
	Lincoln's Sparrow	x	x	x	x	1.00	1
	White-throated Sparrow	x	x	x	x	0.90	9
	Northern Cardinal	x	x		x	0.58	5
	Indigo Bunting	x	x	x	x	0.94	10
	American Goldfinch	x	x		x	0.97	8
	Wilson's Snipe				x	1.00	3
ESI > 0.5	Yellow-billed Cuckoo				x	0.57	4
	Whip-poor-will			x	x	0.71	2
	Ruby-throated Hummingbird				x	0.99	8
	Cedar Waxwing				x	0.69	6
	Magnolia Warbler			x	x	0.70	6
	Black-and-white Warbler			x		0.64	15
	Canada Warbler			x	x	0.61	8
	Dark-eyed Junco			x	x	0.60	6
	Rusty Blackbird			x	x	1.00	2
On 3 or 4 expert lists	Carolina wren	x	x		x	0.45	5
	Ruffed Grouse	x		x	x	0.42	2
Other (see text)	Northern Mockingbird	x			x	n/a	

[a]Dettmers (2003)

[b]Peterjohn & Sauer (1993)

[c]Hunter et al. (2001)

[d]DeGraaf & Yamasaki (2001)

[e]Early Successional Index, indicating preference for scrub habitat (see text)

[f]Number of studies used to estimate ESI

Table 1.3. Candidate species not included in the core list of New England scrub-shrub birds.

Species	Expert Lists[a]	ESI	n	Habitats[b]
Mourning Dove	3	0.00	2	"cultivated lands with scattered trees and bushes, open woodland, suburbs,and arid and desert country"
Hairy Woodpecker	0	0.58	9	"deciduous or coniferous forest, open woodland, swamps, well-wooded towns and parks"
Northern Flicker	0	0.85	9	"open woodland, open situations with scattered trees and snags"
Olive-sided Flycatcher	0	0.66	4	"taiga, subalpine coniferous forest, spruce bogs, burns, and mixed coniferous-deciduous forest with standing dead trees"
Eastern Kingbird	2	1.00	2	"open country with scattered trees and shrubs"
Blue Jay	0	0.66	9	"primarily forest (deciduous or mixed deciduous-coniferous), open woodland, parks, and residential areas"
Eastern Bluebird	1	1.00	4	"open deciduous, mixed, and pine woodland, and agricultural areas with scattered trees"
Hermit Thrush	2	0.52	8	"open coniferous and mixed coniferous-deciduous forest and forest edge, and dry sandy and sparse jack-pine, less frequently in deciduous forest and thickets"
American Robin	1	0.66	9	"coniferous and deciduous woodland and edge, parks and suburbs with lawns"
Northern Waterthrush	2	0.53	4	"thickets near slow-moving streams, ponds, swamps, and bogs"
Chipping Sparrow	1	0.82	4	"open coniferous forest (especially early second growth) and forest edge (especially pine), oak woodland, pine-oak association, and open woodland and parks"
Swamp Sparrow	2	1.00	1	"emergent vegetation around watercourses, marshes, bogs, and wet meadows"
Common Grackle	0	0.73	2	"partly open situations with scattered trees, open woodland (coniferous or deciduous), forest edge, and suburbs"
Brown-headed Cowbird	0	0.63	5	"woodland, forest (primarily deciduous) and forest edge"
Baltimore Oriole	0	0.60	2	"open woodland, deciduous forest, riparian woodland, orchards, and planted shade trees"

[a]Number of expert lists on which the species occurs
[b]Habitat description from AOU (1998)

cies were more abundant in early-successional than in mature forests points out a shortcoming in our meta-analysis procedure. The studies we reviewed compared abundances between early-successional and mature forests. If a species' preferred habitat was something altogether different, then the ESI could be misleading. The high ESI values for the above species were based on their avoiding mature, closed-canopy forests rather than actually preferring shrubby areas. All of those species are best classified as savanna and parkland birds. Similarly, we excluded Hermit Thrush from the final species list because it prefers edges, small openings, and mid-successional forests rather than scrub per se (Jones & Donovan 1996).

Ten additional species had ESI > 0.5 but were on fewer than three expert lists. All of these are relatively common in scrub-shrub habitats and do not appear to prefer some alternate habitat per the AOU Checklist and the BNA accounts. Thus we included Dark-eyed Junco, Canada Warbler, Cedar Waxwing, Black-and-white Warbler, Magnolia Warbler, Whip-poor-will, Yellow-billed Cuckoo, Rusty Blackbird, Ruby-throated Hummingbird, and Wilson's Snipe on our final species list. Of the remaining candidate species that appeared on at least one expert list, we included Northern Mockingbird in our final list. While we found no data on this species' habitat use in our meta-analysis, published accounts suggest a strong tie to scrub-shrub habitats.

Geographic Distribution

The final list of core scrub-shrub birds contains 41 species (Table 1.2). These species are not, however, distributed uniformly throughout New England. Ecologists divide New England into three physiographic provinces based on differences in climate, geology, and plant communities (Figure 1.2). The first province, Southern New England, includes Rhode Island, most of Connecticut, the eastern two-thirds of Massachusetts, coastal New Hampshire, and south-coastal Maine. Of the 41 shrubland bird species, 30 breed in Southern New England (Table 1.4). Several species, including White-eyed Vireo and Northern Bobwhite, reach their northeastern breeding limits in this region.

The second province, Northern New England, includes western Massachusetts and southern portions of New Hampshire, Vermont, and Maine. Thirty-two bird species breed in this area's shrublands, and several species reach their northern (e.g. Willow Flycatcher, Prairie Warbler, Northern Cardinal) or southern limits here (Wilson's Snipe, Alder Flycatcher) (Table 1.4). Finally, the third physiographic region in New England is the Spruce-Hardwood Forest. This area includes northern portions of Vermont, New Hampshire, and Maine and has 30 breeding species from our core list (Table 1.4). For boreal birds such as Wilson's Warbler and Rusty Blackbird, the Spruce-Hardwood Forest represents their only breeding areas in New England.

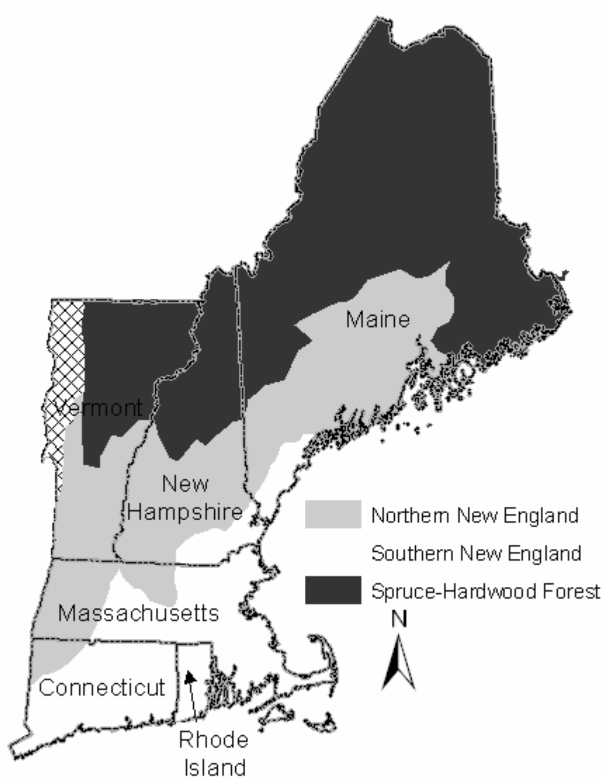


Figure 1.2. Physiographic provinces in New England, via Partners in Flight. Vermont includes small areas of two physiographic provinces (cross-hatched on the map) not discussed in this report.

After geographic location, the major source of variation in shrubland bird communities is position on the hydrologic gradient. Wetland habitats such as shrub swamps often contain a distinctive bird community including Yellow Warbler, Alder Flycatcher, and Wilson's Snipe (DeGraaf & Yamasaki 2001). In contrast, birds such as Northern Bobwhite, Whip-poor-will, and Brown Thrasher are most often associated with drier, upland habitats (DeGraaf & Yamasaki 2001). Thus, position along the hydrologic gradient may exert a strong influence on which bird species will occupy scrub habitats (see Chapter 4).

Geography and hydrology are only the most obvious factors generating variation in bird communities of early successional habitats. Numerous other features, from microhabitat structure to landscape configuration, influence bird communities and will be important when managing scrub-shrub bird habitat for birds. We elucidate these factors in detail in subsequent chapters of this report (see Chapters 4, 5).

Conclusion

Our list of New England scrub-shrub birds is, like any species list, somewhat arbitrary (see Remsen 1994). No doubt, some species that occasionally use scrub habitats have been left out, and some species included on the list will use other habitats. We believe, however, that we have erred on the side of inclusiveness in generating the list. Most importantly, we believe that it is highly unlikely that any bird whose conservation in New England depends on shrublands has been left off the list. The list should include all birds that will benefit substantially from the creation of new scrub-shrub habitat. Still, creating a more accurate list, based entirely on quantitative data, could be possible with better field data on habitat use.

Table 1.4. Core scrub-shrub bird species and their breeding distribution in physiographic regions of New England.

Species	Southern New England	Northern New England	Spruce-Hardwood Forest
Ruffed Grouse	x[a]	x	x
Northern Bobwhite	x		
Wilson's Snipe		x	x
American Woodcock	x	x	x
Yellow-billed Cuckoo		x	x
Whip-poor-will	x	x	x
Ruby-throated Hummingbird	x	x	x
Alder Flycatcher		x	x
Willow Flycatcher	x	s[b]	
White-eyed Vireo	x		
Carolina Wren	x		
House Wren	x	x	s
Gray Catbird	x	x	x
Northern Mockingbird	x	x	
Brown Thrasher	x	x	x
Cedar Waxwing	x	x	x
Blue-winged Warbler	x	s	
Golden-winged Warbler	x	x	
Tennessee Warbler			x
Nashville Warbler	x	x	x
Yellow Warbler	x	x	x
Chestnut-sided Warbler	x	x	x
Magnolia Warbler		x	x
Prairie Warbler	x	x	
Palm Warbler			x
Black-and-white Warbler	x	x	x
Mourning Warbler		x	x
Common Yellowthroat	x	x	x
Canada Warbler	x	x	x
Wilson's Warbler			x
Yellow-breasted Chat	s		
Eastern Towhee	x	x	s
Field Sparrow	x	x	
Song Sparrow	x	x	x
Lincoln's Sparrow			x
White-throated Sparrow		x	x
Dark-eyed Junco	x	x	x
Northern Cardinal	x	x	
Indigo Bunting	x	x	s
American Goldfinch	x	x	x
Rusty Blackbird			x
Total number of species	**30**	**32**	**30**

[a]Species found throughout region

[b]Species found in southern periphery of region

Collecting such data should be a future research priority.

We have not sub-divided the list of scrub-shrub birds into any categories or groups. All 41 species, however, are not necessarily equal in their conservation status. Because many species reach their range limits within New England, the distributions of breeding bird species vary substantially within this region. For some species, New England is critically important to global populations, and for others, New England represents only a tiny fraction of their overall breeding ranges and populations. Species also differ widely in their current population trends and conservation status (Chapter 3). Thus, inclusion on our list does not necessarily imply that all species are equally important or deserving of attention.

Chapter 2. Scrub-shrub Habitats

Introduction

Habitat availability is arguably the most important factor limiting bird populations (Newton 1998). As a result, managing birds requires understanding their habitats. For shrublands in New England, this is complicated, for two reasons. First, these habitats occur in several forms, and each type presents different management options. Second, scrub-shrub habitats have been in flux historically, changing in amount and location over time. These historical changes have significant implications for the current populations of scrub-shrub birds. Here, we describe New England's shrublands, including historical perspectives on habitat availability, recent changes in this habitat, and estimates of its current extent.

Defining scrub-shrub habitat

The first step towards understanding scrub-shrub habitats is to define exactly which plant associations are included in this term. In our literature review, we did not find a detailed yet general definition of this habitat type. Thus, we attempted to develop a broad definition that would encompass the habitat used by the entire bird community. For most of these species, the most important feature in habitat selection is leafy cover in the first 1 to 2 m above the ground (Chapter 4). Scrub-shrub birds vary widely in their responses to other habitat features such as canopy cover or herbaceous vegetation. The presence of saplings or shrubs is, however, universally important in habitat selection by these species. In general, this habitat will occur in areas with an open canopy. Thus, we define scrub-shrub habitat as areas with little or no tree canopy and dense shrubs and saplings within the first 2 m above ground.

Our definition of scrub-shrub habitat does not include several early-successional habitats that are sometimes included in discussions of scrub-shrub birds. First, we exclude grasslands because of their lack of woody vegetation. Management of grasslands generally involves excluding, not promoting, shrubs, and conservation of grassland birds in New England has been treated well elsewhere (e.g. Jones & Vickery 1997). Second, we exclude poletimber and other middle-successional forests. These densely stocked stands of trees often lack an understory, making them poorly suited for scrub-shrub birds (DeGraaf & Yamasaki 2003). Finally, we exclude Krummholz, the stunted forests of fir and spruce found just below treeline in New England mountains. Krummholz has a distinct bird community from lower-elevation shrublands (DeGraaf & Yamasaki 2001).

Scrub-shrub habitats in New England

The climate in New England promotes the growth of forests, so scrub-shrub habitat only occurs where edaphic factors or disturbances interrupt forest succession. Natural shrublands will not persist unless poor or hydric soils prevent trees from becoming established or growing tall (Latham 2003). Because poor soils and natural disturbances are uncommon in New England, naturally occurring early-successional habitats are uncommon. Today, most scrub-shrub habitats in this region are created by human activities, especially logging. In this section, we describe the naturally occurring and anthropogenic scrub-shrub habitats in New England.

Natural scrub-shrub habitats.

Of the naturally occurring scrub-shrub habitats in New England, the most abundant is **pitch pine-scrub oak** (PPSO). This community type occurs on sand plains, rocky ridges, and other xeric and nutrient-poor sites (Little & Garrett 1990). Due to poor soils, trees tend to be stunted and widely spaced, with extensive shrub growth in openings (Cryan 1985). The sandy soils on which PPSO occurs are often associated with glacial outwash, typically found in coastal areas (Parshall et al. 2003). PPSO habitats are fire-prone, with many fire-adapted plant species (Cryan 1985). Without fire or other disturbance, these habitats may develop a closed canopy, leading to the loss of understory vegetation and making the habitat unsuitable for scrub-shrub birds (Cryan 1985). Thus, management of PPSO often includes prescribed fire or logging to open the canopy and prevent trees from shading out understory vegetation. Since settlement, much of New England's PPSO has been lost to development or fire suppression (Noss et al. 1995).

Another natural source of scrub-shrub habitat is **beaver ponds**. Beavers thin overstory vegetation and encourage shrubby growth. Once abandoned by beavers, the ponds slowly dry out and become grassy or shrubby openings (Askins 2000). The actual type of vegetation present will depend on soils and the plant species available nearby to colonize the opening. Beaver meadows may be used by a variety of scrub-shrub birds (Grover & Baldassarre 1995; Edwards & Otis 1999). Trees can be slow to colonize beaver meadows, so scrub-shrub habitat may last longer there than in other types of forest openings (Remillard et al. 1987; Terwilliger & Pastor 1999).

Some **wetlands** harbor persistent scrub communities suitable for scrub-shrub birds. Shrub swamps in New England contain dense stands of alder, willow, red-osier dogwood, buttonbush, and spruce or maple saplings (Cowardin et al. 1979). Some bogs also have substantial shrub cover (especially ericaceous shrubs) over a mat of *Sphagnum* moss. In these habitats, poor, saturated soils inhibit tree growth and allow shrubby growth to persist. As discussed in Chapter 1, several scrub-shrub birds are largely restricted to these wetland habitats, including Wilson's Snipe, Alder Flycatcher, Lincoln's Sparrow, Palm Warbler, Yellow Warbler, and Rusty Blackbird. In this way, wetlands are different from other scrub-shrub habitats, which lack specialized scrub-shrub birds.

Finally, **treefall gaps and blowdowns** caused by wind and other disturbances create natural, though temporary, scrub-shrub habitats. In general, the opening created by a single fallen tree will be too small for most scrub-shrub birds to breed (Chapter 5). Larger gaps, more suitable for birds, can be created by wind, ice storms, tornadoes, tree pathogens, avalanches, and rock slides (Askins 2000; Lorimer & White 2003). As discussed below, the size and occurrence of treefall gaps vary with forest type across New England.

Anthropogenic scrub-shrub habitats.

While natural scrub-shrub habitats can be locally abundant, most shrublands in New England exist due to human activities. Of these, **silviculture** is by far the most important (see below). Removing the forest overstory releases the growth of herbs, shrubs, and seedling trees and creates scrub-shrub habitat (Thompson & DeGraaf 2001; DeGraaf & Yamasaki 2003). Different silvicultural treatments, however, result in the creation of different amounts and types of habitat. For birds, the most direct way to create scrub-shrub habitat is through even-aged management (Annand & Thompson 1997; Costello et al. 2000; King & DeGraaf 2000). This can include clearcutting, in which all trees are removed at once, and shelterwood or seed-tree harvests, which are done in two stages, with some mature trees left temporarily to aid in regeneration. Even-aged management creates relatively large, contiguous patches of early successional habitat, and nearly all scrub-shrub birds will breed in young clearcuts (Chapter 4).

In contrast, uneven-aged practices, such as single-tree and group-selection cuts, involve harvesting just a few trees at a time. The early-successional habitat thus created occurs in multiple small patches rather than a few large openings as in even-aged management (Thompson & DeGraaf 2001). Selection cuts are typically less than 0.5 ha in area (DeGraaf & Yamasaki 2003). In small group-selection or single-tree cuts, the surrounding tree canopy may block light from reaching the ground, inhibiting the growth of shrubs and seedlings. Thus, scrub-shrub habitat may not develop in very small openings (DeGraaf & Yamasaki 2003). Larger selection cuts, however, will receive full sunlight and may be similar to clearcuts in vegetation structure. For some scrub-shrub birds, group-selection cuts may be too small to be used for breeding (Chapter 5).

How long a treated area provides habitat for scrub-shrub birds will depend on three factors: the presence of advance regeneration, the size of the gap, and site fertility. Where the understory has many saplings, the trees will quickly grow to create a closed canopy and shade out the shrub layer (Thompson & DeGraaf 2001). In contrast, where few saplings are present, a dense growth of shrubs and seedlings can take hold and persist for several years (Askins 2001; DeGraaf & Yamasaki 2003). Site quality, as measured by site index, can also influence the persistence of scrub-shrub habitat. Compared to areas with a low site index, areas with a higher site index will experience more rapid growth of trees and shorter persistence of scrub-shrub habitat (DeGraaf & Yamasaki 2003). Finally, smaller openings tend to close up more quickly than larger openings because the canopies of surrounding trees can spread to shade a small gap but not a large one.

Other aspects of the way that trees are harvested can also affect the scrub-shrub habitat created. For instance, leaving snags in a clearcut may result in the development of a different bird community than might be present if all trees are harvested (Conner & Adkisson 1974; DeGraaf 1991). Partial harvests, in which 25 to 75% of basal area is removed and scattered, mature trees are retained, may still develop some scrub-shrub habitat in the understory (Annand & Thompson 1997; Rodewald & Yahner 2000). Forestry operations often use herbicides to favor conifers while suppressing herbaceous vegetation and hardwoods. This practice can reduce habitat suitability for some scrub-shrub birds while favoring others that prefer conifers or more open vegetation (McComb & Rumsey 1983; Santillo et al. 1989). Finally, planting trees can influence the type of early-successional forest that develops. Monocultures of planted conifers, for instance, may be attractive to Magnolia Warblers or Dark-eyed Juncos but eschewed by Yellow-billed Cuckoos (Chapter 4).

A second source of anthropogenic scrub-shrub habitat is **abandoned fields**. If left undisturbed, bare ground or grassland in New England will soon be colonized by shrubs and seedling trees, resulting in the creation of scrub-shrub habitat (Askins 2001). In the past, abandoned agricultural fields were the major source of early-successional habitat in New England (Hart 1968; see below). Now, however, few agricultural fields are being abandoned (Litvaitis 1993). Instead, old field succession occurs in habitats such as reclaimed strip mines and wildlife openings that are managed by mowing or burning. Woody species may take a few years to initially colonize an old field. Because, however, succession on old fields is slow, old fields often maintain their scrub-shrub community for decades before trees grow tall and dense enough to shade out the understory (Thompson & DeGraaf 2001; DeGraaf & Yamasaki 2003). Clearcuts, in contrast, lose their scrub-shrub habitat within 10-20 years after logging (Chapter 4).

Though both old fields and silvicultural openings provide scrub-shrub habitat, the two are quite different in structure (Lorimer 2001). Old fields tend to be more open, with a variety of shrubs, herbaceous vegetation, vines, and young trees (Askins 2001). Closure of these habitats can take decades. In contrast, logged areas rapidly sprout a dense layer of seedlings and shrubs (Thompson & DeGraaf 2001). Trees, under competitive pressure to avoid being out-shaded, grow quickly, and silvicultural openings are relatively short-lived (Askins 2001). Because of these differences in vegetation structure, old fields and silvicultural openings harbor somewhat different suites of scrub-shrub birds (Bulluck & Buehler 2006).

A third important category of anthropogenic scrub-shrub habitats is **utility rights-of-way** (Confer & Pascoe 2003). These corridors are often managed by controlling trees, which could interfere with power or communication lines. Shrubs and small trees, however, are generally free to grow, allowing scrub-shrub habitat to develop. Rights-of-way can vary in width, from less than 10 to over 100 meters, and some bird species prefer narrower or wider strips (Confer & Pascoe 2003; Chapter 5). These habitats are generally managed in one of two ways. First, trees and taller shrubs may be controlled by selective cutting or herbicide application, with other vegetation left intact. Alternatively, all vegetation may be cut every few years. Sites managed by cutting will generally be more open, while selective tree control creates denser stands of trees and shrubs. This difference in vegetation structure will impact the bird community (Confer & Pascoe 2003).

Finally, scrub-shrub habitat sometimes occurs in **forest edges**, field edges, hedgerows, and roadsides—areas that may be ignored by managers and allowed to undergo succession due to benign neglect. In general, these habitats are relatively small in area and occur in long, linear strips. They may, therefore, be suboptimal for birds that require large patches or avoid edges (Fink & Thompson 2006). Some researchers believe that scrub-shrub birds only occupy edge habitats when larger or higher-quality habitat patches are unavailable (Imbeau et al. 2003; Chapter 5).

Scrub-shrub Habitat in Pre-settlement Context

Scrub-shrub habitats in New England have a dynamic history, and understanding how these habitats have changed over time has significant implications for current management. Historically, scrub-shrub habitat in New England was created by natural disturbances such as storms, blowdowns, and insect outbreaks as well as by fires ignited by Native Americans (Askins 1998; Lorimer 2001). Historical ecologists have used a variety of information sources to recreate historical disturbance regimes in New England forests (Whitney 1994). This information can be used to estimate how much early-successional habitat existed in the past in this region (Lorimer 2001).

New England's moist and temperate climate makes forest the natural vegetation type throughout the region. Four different forest types occur in this region, distributed according to elevation, latitude, and, ultimately, climate (Westveld 1956; Smith 1979; DeGraaf & Yamasaki 2001). Oak-hickory forests, with a variety of oaks and hickories as well as tulip poplar and eastern white pine, predominate in southern New England. As discussed above, in sandy or rocky areas, pitch pine-scrub oak woodlands may develop. As one moves north or climbs in elevation, oak-hickory forests give way to northern hardwoods, consisting of birches, beech, maples, and hemlock. These forests predominate in central and northern New England. Finally, at high elevations and in northern New England, coniferous forests composed of spruce and fir occur. Disturbance regimes differ among these forest types, influencing the amount of early-successional habitat occurring under natural conditions (Lorimer 2001). Natural disturbances regimes for each of these forest types are described below.

Historically, severe weather events were probably the most common disturbance affecting New England forests. Major wind or ice storms could knock down mature trees over large areas, creating early-successional habitat (Askins 2000; Lorimer & White 2003). Because severe storms are more common near the coast, blowdowns occurred more often there than inland (Boose et al. 2001). Historical research has shown that the average area of a blowdown was typically less than 100 ha, though severe storms could occasionally produce disturbances larger than 3000 ha (Lorimer & White 2003).

Insect outbreaks causing tree mortality were another significant source of early-successional habitat in New England forests. Balsam fir, red spruce, eastern hemlock, and other conifers are susceptible to outbreaks of pests such as spruce budworm or hemlock looper (Lorimer & White 2003). These pests can kill mature trees in large numbers, and tree mortality can create scrub-shrub habitat (Matsuoka et al. 2001). Because insects tend to be species-specific in their effects, serious mortality that eliminated the canopy would only have occurred in monotypic stands of trees. Such stands do occur, however, in hemlock groves and high-elevation balsam fir forests, among other forest types. Historical accounts suggest that pest outbreaks could kill large number of trees over thousands of square kilometers (Lorimer & White 2003).

Many aspects of New England's presettlement fire ecology remain unresolved. Fires occurred regularly in parts of the region, and most were started by Native Americans to manage vegetation, to clear land for agriculture, or to promote populations of game animals (Lorimer & White 2003). Evidence from lake sediments suggests that fires were most common in pitch-pine woodlands (Parshall & Foster 2002; Parshall et al. 2003). Oak-hickory forests may have experienced fire often as well, but the exact frequency and distribution of fires is not known (Lorimer & White 2003). In contrast, fire was probably very rare in mature northern hardwoods and uncommon, though known to occur, in spruce-fir forests (Parshall & Foster 2002). These habitats are generally too wet to sustain fires except during droughts. One interesting finding from historical studies is that large tracts of early-successional forest created by blowdowns or insect outbreaks were fire-prone (Whitney 1994). Forest openings would dry in the sun, making their fuels flammable and leading to occasional fires. These fires would arrest the successional cycle and allow early-successional habitat to persist for a relatively long time in some areas (Latham 2003). Available evidence suggests that when fires occurred, they typically burned between 2 and 200 ha, with a maximum of 80,000 ha affected (Lorimer & White 2003).

Based on the areas impacted by natural disturbances and how often these disturbances occurred, ecologists have estimated the relative amount of early-successional habitat in presettlement forests of New England. In pitch pine-oak scrub, because of frequent fires, 10-31% of the area would have been young forest at any time (the range of the estimates is due to uncertainty in the return interval of fire) (Lorimer & White 2003). Oak-hickory forests experienced relatively frequent fires and wind damage and may have had a similarly large area of early successional forest. Runkle (1982) estimates that oak-hickory forests would naturally have 9.5% of their canopies open, though most of that area would have been small treefall gaps. Northern hardwoods, because of their resistance to fire and distance from the coast (mitigating storm damage), would have had only 1-3% of their area in an early successional stage (Lorimer & White 2003). Finally, 3-7% of spruce-fir forests would likely have been in an early successional stage (Lorimer & White 2003).

One important finding from historical studies of disturbance is that the frequency of a disturbance tends to be negatively related to the area affected (Seymour et al. 2002). Small disturbances, such as minor blowdowns or treefalls, occur relatively frequently. In contrast, disturbances that affect very large areas, such as hurricanes, occur much less often. In fact, the patch size of a disturbance increases as a geometric function of the return interval (Seymour et al. 2002). This means that the vast majority of disturbance events will impact small areas, and large disturbances will be rare. As a result, scrub habitats in New England would historically have occurred as many small patches with, perhaps, a few large ones (Lorimer & White 2003). Furthermore, scrub-shrub habitat would have shifted in location over time, as old patches grew into forests, and new patches were created by disturbance. Scrub-shrub birds may have evolved behavioral strategies for dealing with this shifting landscape of habitat patches (Chapter 7).

The scientific community is still debating the history of scrub-shrub habitats in New England. According to one view, natural disturbances and Native American agriculture created large amounts of early successional habitat before Europeans arrived (DeGraaf & Miller 1996; Latham 2003). Thus, the flora and fauna of scrub-shrub habitats have had a long tenure in New England, possibly extending back to just after glaciers retreated (Askins 2000). Another viewpoint holds that the presettlement landscape was heavily forested, with few openings (Motzkin & Foster 2002; Foster & Motzkin 2003). Accordingly, shrublands and other open habitats in New England are artifacts of forest clearing by European settlers, and the plants and animals of shrublands are recent immigrants from the Midwest that moved in as the landscape opened.

We believe that the origin of shrublands and the scrub-shrub bird community in New England is moot. In part, this is because selecting a historical baseline for management is problematic due to uncertainty over historical conditions and changes over time. Moreover, whether Native Americans, European settlers, or even Pleistocene megaherbivores are responsible, a large and diverse scrub-shrub bird community exists today in New England, and many of its members are declining and may soon be threatened with extirpation or extinction (Hunter et al. 2001; Dettmers 2003). Ultimately, the decision to conserve the scrub-shrub bird community will depend on whether or not we, as a society, want to continue to have these birds and their habitats in New England. Whether the habitats and the birds occur "naturally" is not relevant to the ultimate decision, and the academic argument over the origins of scrub-shrub habitat in New England is a distraction from the more pressing question of whether or not saving the scrub-shrub bird community will be worth the effort (see Lawton 1997).

Recent Changes in Scrub-shrub Habitat

European settlers arriving in New England encountered a heavily forested landscape (Hall et al. 2002). In part, this was due to massive epidemics that decimated Indian populations just before settlement, causing openings created by Indians to succeed to forest (Mann 2005). As New England was colonized between the 17th and 19th centuries, forests were largely cleared by settlers (Whitney 1994; Hall et al. 2002). The result was that New England's landscape changed from heavily wooded to mostly open with large areas of agriculture. By the mid-1800's, over 75% of the arable land in New England had been cleared (Litvaitis 2003). Massachusetts, for instance, was only 30% forested in 1830, versus 62% now (Hall et al. 2002). Not all deforested areas were used for agriculture. Homesteads typically included areas used for short-rotation fuelwood harvesting, creating significant amounts of early-successional habitat (Whitney 1994). Thus, the 19th century landscape in New England was generally open and probably contained a large amount of scrub-shrub habitat.

With a cool climate and rocky soils, conditions for farming were never good in New England. Thus, as the United States expanded westward, farmers in New England gradually gave up their farmsteads and moved west, where the environment was better suited for agriculture (Hart 1968). As a result, between the mid-1800's and the early 1900's, large areas of farmland were abandoned in New England. In Maine, for instance, an average of 13,000 ha of farmland were abandoned each year over that time period (Litvaitis 1993). Large areas of farmland were, therefore, allowed to undergo succession, creating a huge amount of early-successional habitat throughout New England. By the early 20th century, the amount of scrub-shrub habitat in New England was probably an all-time high (DeGraaf & Miller 1996).

By the 1940's, however, the wave of farmland abandonment had come to an end in New England (Litvaitis 1993). As a result, the rate at which new scrub-shrub habitat was being created declined dramatically. At the same time, previously abandoned farmland was succeeding to forest. Thus, the total amount of scrub-shrub habitat in New England began a decline that continues to this day (Litvaitis 1993). Since the 1950's, the total amount of early-successional forest has declined dramatically in southern New England (Figure 2.1). For instance, 26% of Massachusetts' timberland was early-successional in the 1950's, compared with 2% today, a decline of 97% (U.S. Forest Service 2006). In Rhode Island, young forest declined from 27% to 3% over the same time period. In contrast, Vermont and New Hampshire, with more active logging, have maintained more stable levels of early successional forest over the past few decades after earlier decreases (Figure 2.1). In Maine, early-successional forest has actually been increasing since the 1950's.

Most of the forested land in New England is privately owned. One worrisome trend for the future of early-successional habitats is that the number of forest owners in New England is increasing while average parcel sizes are decreasing (Brooks 2003). Owners of small forests are relatively unlikely to manage their holdings proactively, and using logging to create large tracts of early-successional habitat is not possible with small parcels (Kittredge et al. 1996). This may mean that in the future, fewer opportunities will exist to use silviculture to create habitat for scrub-shrub birds. The problem may be especially se-

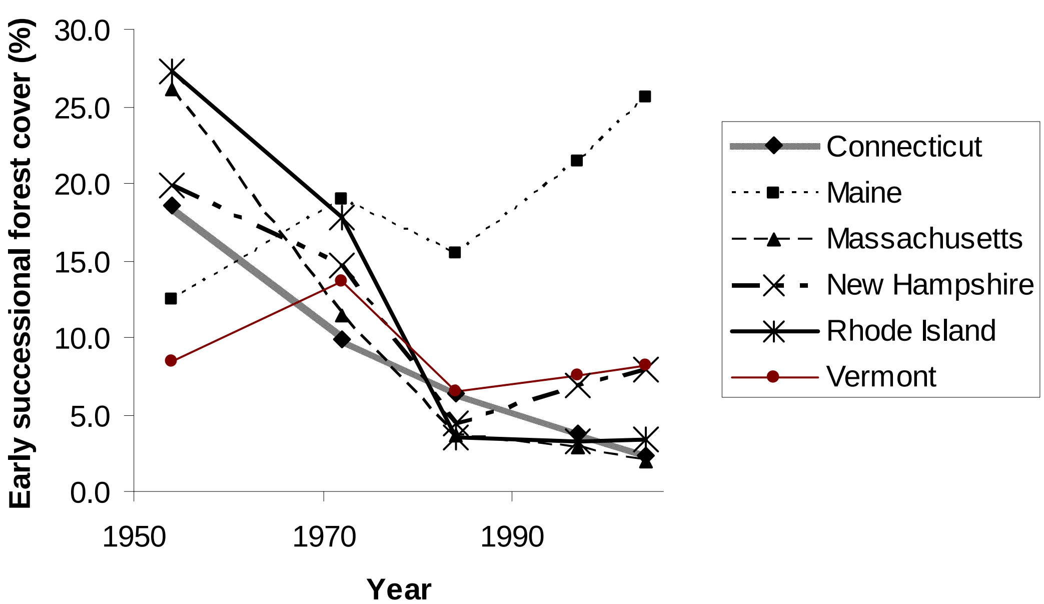


Figure 2.1. Cover of early-successional habitat in New England between the 1950's and the present, based on FIA data. Data shown are for productive timberlands only. Source: U.S. Forest Service (2006).

vere in southern New England, where forest parcels are even are smaller than in the north (Brooks 2003). Given the low availability of scrub-shrub habitat in southern New England, this trend is worrisome.

Current extent and distribution of scrub-shrub habitat in New England

Given the declines in early-successional forsest over the last several decades, how much habitat remains for scrub-shrub birds? We determined the current extent of scrub-shrub habitats in New England using two data sources, the Forest Inventory Analysis Program (FIA) and state gap analysis projects. The FIA is a survey of forest resources in the U.S. conducted by the U.S. Forest Service every 5-10 years (Smith et al. 2004). FIA data include total forest cover as well as the cover of early-successional woodlands, referred to as "seedling-sapling" (trees less than 12.7 cm in dbh but taller than 30.5 cm) or "nonstocked" (recently cutover forest or newly abandoned fields) (Trani et al. 2001).

The most recent FIA data show that 81% of New England is forested, ranging from 58% of Rhode Island to 90% of Maine (U.S. Forest Service 2006; Table 2.1). Those percentages include both early- and late-successional forests. Early-successional woodlands make up 18.6% of the region's forests and 15.1% of the total land surface (Table 2.1). Cover of early-successional forest, however, varies greatly from state to state. Scrub-shrub habitat is least abundant in Connecticut and Rhode Island. Massachusetts, New Hampshire, and Vermont have slightly more young forest. Finally, in Maine, with large areas managed for timber production, nearly one quarter of the land surface is early-successional stage forest. Compared to other parts of the eastern U.S., New England has relatively little young forest. Early-successional habitat makes up 24 to 31% (28% overall) of forests in the Great Lakes states and 20 to 38% (32% overall) of the Southeast.

Many scrub-shrub birds disappear from clearcuts within just a few years after logging, well before saplings reach 12.7 cm in dbh (DeGraaf 1991). Thus, the FIA's seedling-sapling class probably includes substantial areas that are too mature for scrub-shrub birds. As a result, the estimate that 18% of New England's forests are in an early-successional stage certainly overstates ac-

Table 2.1. Cover of forests and early successional habitats in New England. Source: U.S. Forest Service (2006).

				Area of early-successional forest (ha)			Cover of early-successional forest (%)		
State	Forest (ha)	Total area (ha)	Forest cover (%)	Seedling-sapling	Non-stocked	All young forest	Seedling-sapling	Non-stocked	All young forest
Connecticut	752,429	1,254,797	60.0	48,043	2,792	50,835	3.8	0.2	4.1
Maine	7,162,697	7,993,080	89.6	1,869,133	18,314	1,887,447	23.4	0.2	23.6
Massachusetts	1,265,049	2,030,545	62.3	115,081	0	115,081	5.7	0.0	5.7
New Hampshire	1,949,882	2,322,731	83.9	195,426	5,453	200,878	8.4	0.2	8.6
Rhode Island	155,951	270,635	57.6	10,198	0	10,198	3.8	0.0	3.8
Vermont	1,868,869	2,395,618	78.0	185,739	1,279	187,018	7.8	0.1	7.8
New England	13,154,877	16,267,407	80.9	2,423,620	27,838	2,451,458	14.9	0.2	15.1

tual habitat availability for scrub-shrub birds (Chapter 4). Furthermore, the FIA survey focuses on productive forests, which are generally found in forested landscapes. These data may not accurately estimate habitat availability for birds such as Northern Mockingbird that prefer open or agricultural landscapes.

A second source of information on scrub-shrub habitat extent is provided by gap analysis projects. These are state or regional efforts that use remote sensing to map cover of different vegetation types. According to the Maine Gap Analysis Project, shrub wetlands occupied approximately 2% of the total area, and early-successional forests made up approximately 13% (Krohn et al. 1998) (Table 2.2). Abandoned agricultural fields were estimated to be 0.4% of the state. The area of young forest reported in the Maine gap analysis project (12% of the total land area) is much lower than the FIA estimate (24%). As discussed above, this may be because the FIA data includes some older forests that the gap project did not identify as early-successional.

In the Southern New England Gap Analysis Project (for Massachusetts, Connecticut, and Rhode Island), forests were not separated into age classes; only natural scrub-shrub types were inventoried (Zuckerberg et al. 2004). Shrub wetlands made up 1% of the total area, and PPSO woodlands occupied 2.5% (Table 2.3). Because the latter habitat was not divided into age classes, the area reported certainly overestimates the amount of scrub-shrub habitat. "Corridors," presumably including utility rights-of-way, made up just 0.1% of southern New England. No gap analysis data were available for New Hampshire and Vermont.

To estimate the total amount of early-successional habitat in New England, we assumed that 50% of the FIA's seedling-sapling category is actually scrub-shrub habitat. This was based on the fact that the FIA estimate of early-successional habitat for Maine was roughly double the estimate from gap analysis data. In addition, scrub-shrub birds only occupy 50% of regenerating clearcuts up to age 20 (Chapter 4). We also assumed that the area of natural scrub-shrub habits in New Hampshire and Vermont is, proportionally, equal to that of Maine. We estimate that early successional habitats make up 12.1% (1,593,000 ha) of New England's land area. Seventy-one percent of New England's shrublands occur in Maine, which makes up just 49% of the region's total area. For all of New England, we estimate that 78% of scrub-shrub habitat is young forest created by silviculture, with the other 22% consisting of natural habitats. This highlights the importance of management in perpetuating the regional availability of scrub-shrub habitats.

Current amounts of scrub-shrub habitat might be similar to or even greater than historical levels (Litvaitis et al. 1999). The distribution of early successional habitat, however, has changed sub-

Table 2.2. Areas of scrub-shrub habitats in Maine from the Maine Gap Analysis Project. Source: Krohn et al. 1998.

Habitat Type	Area (km^2)	% of total[a]
Agricultural lands		
abandoned field	201.2	0.2
Forestlands		
clearcut	1,272.3	1.5
early regeneration	5,369.6	6.3
late regeneration	2,925.6	3.5
heavy partial cut[b]	1,536.1	1.8
Wetlands		
deciduous scrub-shrub	1384.1	1.6
coniferous scrub-shrub	156.3	0.2
Total	**12,845.2**	**15.2**

[a]Total area of Maine = 84,630 km^2.
[b]Forestland where greater than 50% of the canopy has been removed.

Table 2.3. Areas of scrub-shrub habitats in Massachusetts, Connecticut, and Rhode Island from the Southern New England Gap Analysis Project. Source: Zuckerberg et al. 2004.

Habitat Type	Area (km^2)	% of region[a]
Woodlands		
scrub oak dominant	205.0	0.6
60% pitch pine/40% scrub oak	89.5	0.3
pitch pine	537.3	1.5
Palustrine wetlands		
scrub or shrub marsh	338.5	0.9
shrub dominant with grass	33.9	0.1
Nonforest cover		
scrub/shrub and grassland mix	35.4	0.1
Total	**1,239.6**	**3.5**

[a]Total area of region = 35,634 km^2.

substantially since European settlement. Historically, scrub-shrub habitat would have been most common in pitch pine and oak-hickory forests, found mainly in southern New England and near the coast. Spruce-fir and northern hardwoods forests, found primarily in interior and northern New England, would have had far less. This pattern is essentially reversed today. Connecticut and Rhode Island have the least early-successional habitat in New England, and Maine, with its large-scale forestry operations, has the most (Brooks 2003). This shift in the location of scrub-shrub habitat has serious implications for bird populations in different parts of New England, as discussed in the next chapter of this report.

Chapter 3. Status and Trends of Scrub-shrub Bird Populations

Introduction

For over a century, scientists have been concerned about declining populations of migratory birds in North America (Peterjohn et al. 1995). Until recently, most concern was focused on birds that breed in forests (e.g. Whitcomb et al. 1981; Lynch & Whigham 1984; Wilcove 1985; Robbins et al. 1989b). More recently, however, ornithologists have recognized that species of early-successional habitats such as grasslands and shrublands are showing the most alarming trends (Askins 1993). Nationwide, 39% of scrub-shrub birds have declined in recent decades (Brawn et al. 2001). In contrast, only 20% of forest-breeding species are currently declining. In the eastern U.S., the situation is worse, with 70% of scrub-shrub species showing population decreases (Hunter et al. 2001). Of the 10 endangered songbirds in the continental U.S., 7 breed in scrub or other early-successional habitats (U.S. Fish & Wildlife Service 2006).

Scrub-shrub birds are evidently in conservation peril at a national level. Bird populations, however, can vary in trends from region to region. Compared to other parts of the eastern U.S., New England has little scrub-shrub habitat (Chapter 2). Furthermore, early-successional habitats in this region are rapidly being lost to development and forest succession. To assess the conservation status of scrub-shrub birds in New England and to determine what sort of management this community may need, we need quantitative data on scrub-shrub bird populations. Here, we use several sources of data including the Breeding Bird Survey, long-term field studies, American Woodcock survey, state endangered species lists, and priority rankings from Partners in Flight to describe the status and trends of this bird community. We also used recently developed techniques to estimate the population sizes of scrub-shrub birds in this region.

Population Trends from the Breeding Bird Survey

The Breeding Bird Survey (BBS) is an annual roadside count of birds in the United States and Canada (Sauer et al. 2005). The routes are permanent, and each is 39.4 km long with 50 bird-count stops spaced 0.8 km apart. Each route is surveyed once a year during June. Beginning at dawn, an observer conducts 3-minute point counts at each stop during a single morning. Over 2900 routes are monitored annually, and data extends back to 1966. This makes the BBS an excellent source of data on North American bird populations.

We analyzed BBS data for the six New England states to determine population trends for the 41 species of scrub-shrub birds listed in Chapter 1. We did this using the route regression method: for each species, we computed population trends on each route. Then, we averaged across routes to determine the overall population trajectory, which we present as annual percent change (e.g. -6% yr^{-1}). The analysis controls for the fact that on any route, counts may be conducted by different observers, with different skill levels, in different years. Trends' significance levels are based on the 95% confidence interval from 1000 bootstrapped trend estimates. One assumption of route regression is that population trends are linear for log-transformed data. We found that the log-linear model fit the data well for most species. Additional detail about route regression can be found in Geissler (1984), Geissler and Sauer (1990), and Thomas and Martin (1996).

BBS data were available for 40 years, from 1966 to 2005 (Sauer et al. 2005). Overall, 16 of 41 scrub-shrub birds species showed a significant decline while only 6 species increased (Figure 3.1; Table 3.1). Birds with the most alarming declines include Northern Bobwhite (-11% yr^{-1}), Eastern Towhee (-7% yr^{-1}), Field Sparrow (-5% yr^{-1}), and Brown Thrasher (-4% yr^{-1}). To put these numbers in perspective, a population declining at 4% annually would be reduced by 80% in 40 years. A decline of 11% per year translates to a 99% decrease over the same time period. Additionally, Yellow-Breasted Chat was present on 5 BBS routes in Connecticut prior to 1985 but disappeared completely thereafter. Chats are currently listed as state-endangered in Rhode Island and Connecticut. Annual counts for the scrub-shrub birds are presented in Appendix A.

To see how trends have changed over time, we split the 40-year period of the BBS into two halves, 1966 to 1985 and 1986 to 2005. Overall,

Table 3.1. Trends in scrub-shrub bird populations on BBS routes in New England by time period.

	1966 to 2005		1966 to 1985		1986 to 2006		
Species	Trend (% yr^{-1})[a]	*N*[b]	Trend (% yr^{-1})	*N*	Trend (% yr^{-1})	*N*	*Z*[c]
Ruffed Grouse	-0.1 ± 0.2	129	-0.9 ± 0.6	86	0.6 ± 0.4	96	1.88
Northern Bobwhite	-10.6 ± 2.4***	41	-9.4 ± 3.4**	34	-11.4 ± 2.8***	28	-0.45
Wilson's Snipe	0.8 ± 1.1	87	5.4 ± 1.8**	49	0.1 ± 0.8	79	-2.74**
American Woodcock	0.2 ± 0.2	76	2.2 ± 1.2	48	0.3 ± 0.5	34	-1.44
Yellow-billed Cuckoo	-1.8 ± 0.6**	81	-2.0 ± 1.3	58	1.0 ± 0.5	61	2.18*
Whip-poor-will	-0.6 ± 0.3*	66	2.1 ± 1.8	55	-2.9 ± 0.9**	26	-2.47*
Ruby-throated Hummingbird	0.6 ± 0.4	146	-0.7 ± 0.7	91	1.8 ± 0.7**	133	2.45*
Alder Flycatcher	0.0 ± 1.1	138	1.7 ± 1.5	92	-0.1 ± 0.6	129	-1.10
Willow Flycatcher	2.1 ± 0.5***	97	4.6 ± 1.1***	50	1.0 ± 0.9	87	-2.62*
White-eyed Vireo	0.6 ± 0.8	20	3.7 ± 1.9	18	3.6 ± 2.0	8	-0.01
Carolina Wren	4.5 ± 0.9***	49	1.8 ± 1.7	18	7.0 ± 2.3**	44	1.82
House Wren	-1.9 ± 0.5***	138	0.0 ± 0.5	104	-2.9 ± 0.5***	126	-4.05***
Gray Catbird	-0.1 ± 0.4	157	0.3 ± 0.5	121	-0.1 ± 0.5	147	-0.65
Northern Mockingbird	2.0 ± 0.8*	125	12.6 ± 1.7***	88	-4.9 ± 0.9***	107	-9.20***
Brown Thrasher	-4.2 ± 0.5***	138	-4.1 ± 1.7*	118	-0.7 ± 0.7	110	1.89
Cedar Waxwing	0.1 ± 0.6	160	4.5 ± 1.3***	121	-1.9 ± 0.8*	150	-4.16***
Blue-winged Warbler	-2.5 ± 0.7***	57	-0.3 ± 1.0	43	-3.4 ± 1.8	49	-1.49
Golden-winged Warbler	-0.6 ± 0.2**	28	-0.5 ± 0.6	22	-2.9 ± 1.4*	9	-1.62
Tennessee Warbler	-0.1 ± 1.2	66	14.6 ± 5.0**	34	-2.3 ± 1.0*	52	-3.34**
Nashville Warbler	-1.4 ± 0.6*	135	3.7 ± 1.1***	99	-1.3 ± 0.7*	118	-3.97***
Yellow Warbler	-0.2 ± 0.4	158	2.2 ± 0.7**	120	-2.3 ± 0.6***	149	-4.97***
Chestnut-sided Warbler	-1.9 ± 0.4***	158	-0.4 ± 0.6	121	-2.2 ± 0.8**	146	-1.82
Magnolia Warbler	3.5 ± 1.0***	127	4.2 ± 1.9*	89	4.3 ± 1.0***	112	0.03
Prairie Warbler	-1.7 ± 0.8*	68	0.3 ± 1.2	56	-2.2 ± 1.2	54	-1.46
Palm Warbler	3.9 ± 2.3	22	5.0 ± 15.4	3	5.1 ± 3.2	21	0.01
Black-and-white Warbler	-2.3 ± 0.7**	159	1.8 ± 1.2	120	-4.9 ± 0.5***	150	-5.25***
Mourning Warbler	1.3 ± 1.1	80	2.5 ± 1.7	40	0.6 ± 1.5	69	-0.84
Common Yellowthroat	-1.2 ± 0.3***	160	-0.2 ± 0.4	122	-0.8 ± 0.4*	151	-1.09
Canada Warbler	-1.6 ± 0.9	133	-1.8 ± 1.2	100	-0.4 ± 2.1	112	0.60
Wilson's Warbler	-0.1 ± 1.4	48	1.8 ± 3.4	25	1.8 ± 1.7	31	0.00
Yellow-breasted Chat	-0.9 ± 0.6	5	-1.7 ± 1.6	5	n/a		
Eastern Towhee	-6.7 ± 0.4***	122	-9.8 ± 0.8***	103	-3.5 ± 0.6***	106	6.21***
Field Sparrow	-4.8 ± 0.5***	133	-7.3 ± 0.7***	112	-2.8 ± 0.5***	102	5.36***
Song Sparrow	-1.8 ± 0.2***	160	-3.6 ± 0.6***	122	-0.7 ± 0.2**	151	4.49***
Lincoln's Sparrow	3.6 ± 2.7	37	1.3 ± 3.4	16	7.0 ± 3.7	30	1.12
White-throated Sparrow	-2.9 ± 0.4***	139	-4.1 ± 0.8***	105	-2.0 ± 0.6***	125	2.03
Dark-eyed Junco	1.2 ± 1.1	121	-2.3 ± 1.2	86	4.2 ± 2.1*	101	2.65*
Northern Cardinal	4.2 ± 1.0***	117	9.0 ± 1.9***	77	4.0 ± 0.6***	111	-2.55*
Indigo Bunting	-0.9 ± 0.6	144	0.8 ± 1.3	117	-1.7 ± 0.6**	124	-1.69
American Goldfinch	1.4 ± 0.5**	160	-4.3 ± 0.8***	122	3.6 + 0.5***	151	8.39***
Rusty Blackbird	0.9 ± 1.0	36	-3.6 ± 1.8*	23	3.8 ± 2.1	18	2.68*

[a]Estimated trend ± standard deviation based on 1000 bootstrap samples.
[b]Number of BBS routes used to estimate trend.
[c]*Z*-test statistic comparing trends between 1966-1985 and 1986-2005.
**P* < 0.05, ***P* < 0.01, ****P* < 0.001

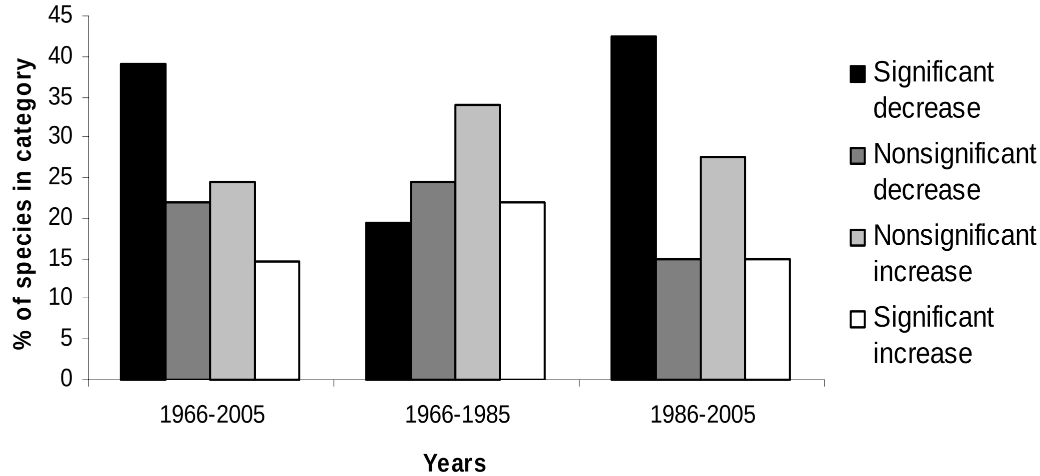


Figure 3.1. Summary of population trends for scrub-shrub birds on BBS routes in New England.

the bird community has fared significantly worse in the last 20 years than previously. Between 1966 and 1985, 8 species decreased significantly while 9 increased significantly. In contrast, between 1986 and 2005, 17 species declined significantly while only 6 increased (Figure 3.1; Table 3.1). For each species, we compared trends between the first and second halves of the BBS study period using two-group *z*-tests. Twenty species (50%) showed significant differences between the 1966-1985 and 1986-2005 periods (Table 3.1). Of these, 11 (55%) had a poorer trend in the later period.

Despite the overall declining trends, six species increased significantly in New England between 1966 and 2005, and one other increased in the last 20 years. Why have these species' populations grown while most scrub-shrub birds are declining? Four of these species—Willow Flycatcher, Carolina Wren, Northern Mockingbird, and Northern Cardinal—have been expanding their breeding ranges into New England and eastern Canada from the south since the 1940's (Beddall 1963; Norse 1985; David et al. 1990). These species may be responding to warmer temperatures in recent decades or the availability of bird feeders, which may aid winter survival (Brittingham & Temple 1988) (*note*: while Northern Mockingbird has shown an overall increase since 1966, this species has been declining rapidly since 1986). Two other increasing species, Ruby-throated Hummingbird and American Goldfinch, may also be responding to the proliferation of bird feeders. The remaining species with an increasing population is Magnolia Warbler. Given that this species is not well studied in New England, any suggestions as to why it is increasing would be speculative.

Regional Variation in Population Trends

Scrub-shrub bird communities and their habitats vary from north to south across New England (Chapters 1,2). In southern New England, forests are dominated by oaks and hickories, and the bird community is largely drawn from the deciduous forest biome. To the north, forests are composed of northern hardwoods and conifers, and bird species are typical of boreal forests. Habitat availability also differs across the region. Early-successional habitat is least abundant in southern New England and most common to the north (U.S.F.S. 2006). Historically, shrublands were more common to the south, but succession and development have eliminated most habitat there (Chapter 2). In contrast, forestry has created early-successional habitat in Vermont, New Hampshire, and especially Maine. Presumably, regional differences in bird communities and habitats could influence bird population trends. To determine how bird populations have fared in different parts of New England, we examined trends in the three physiographic provinces that make up the region (see Chapter 1 for map and discussion).

For the most recent 20 years of BBS data, trends differed widely between the northernmost province, the Spruce-Hardwood Forest, and the two southern provinces, Southern New England and Northern New England. In the two southern provinces, 41% and 50% of species, respectively, showed significant declines (Figure 3.2; Table 3.2). In contrast, in the Spruce-Hardwood Forest, just 12% of species declined over that same interval. Similar numbers of species showed increasing trends in all three regions. Thus, the scrub-shrub bird community appears to be in better condition in northern New England than further south.

Causes of Declines

Given the wide variety of factors that can affect bird populations, determining causes of population declines is difficult (Green 1995). For scrub-shrub birds in New England, however, declines are most easily explained by habitat loss. Regional trends in bird populations are completely consistent with recent changes in habitat availability. Massachusetts, Rhode Island, and Connecticut have lost the vast majority of their scrub-shrub habitats in the past 50 years, and bird declines have been most serious in this part of New England (Chapter 2). In contrast, early-successional habitat has actually increased recently in Maine, and bird populations there have been largely stable in the last 20 years.

Habitat loss, however, is not the only possible cause of decreasing bird populations. Intrinsic factors such as life-history traits or behaviors can predispose a species to decline (Reed 1999; Purvis et al. 2000; Reynolds 2003). For instance, species that winter in the tropics, where habitats are disappearing rapidly, may be more at risk than those that winter in the United States (Robbins et al. 1989b). For the scrub-shrub birds, we examined a few basic life-history characteristics to see if they could explain population trends. The variables that we examined were body size, migratory strategy (short- or long-distance), and nesting location (ground or tree/shrub).

Body size can be an important determinant of extinction risk (Gaston & Blackburn 1995; Bennett & Owens 1997; Owens & Bennett 2000). Larger species tend to require larger areas for breeding and, therefore, may disappear from fragmented landscapes. For a given area, larger species tend to have smaller populations than smaller species, making the larger species more vulnerable (Peters & Raelson 1984; Nee et al. 1991). For scrub-shrub birds in New England, we found no relationship between population trend and body size, as measured by mass (overall: r = -0.14, P = 0.39; 1966 to 1985: r = -0.13, P = 0.43; 1986 to 2005: r = -0.11, P = 0.51). Most of the scrub-shrub birds are small songbirds, so the inclusion of three large gamebirds—Northern Bobwhite, American Woodcock, and Ruffed Grouse—could bias these results. While Northern Bobwhites are declining rapidly, populations of the other two species are stable. Even after removing these three species from the dataset, body size and population trend were still uncorrelated.

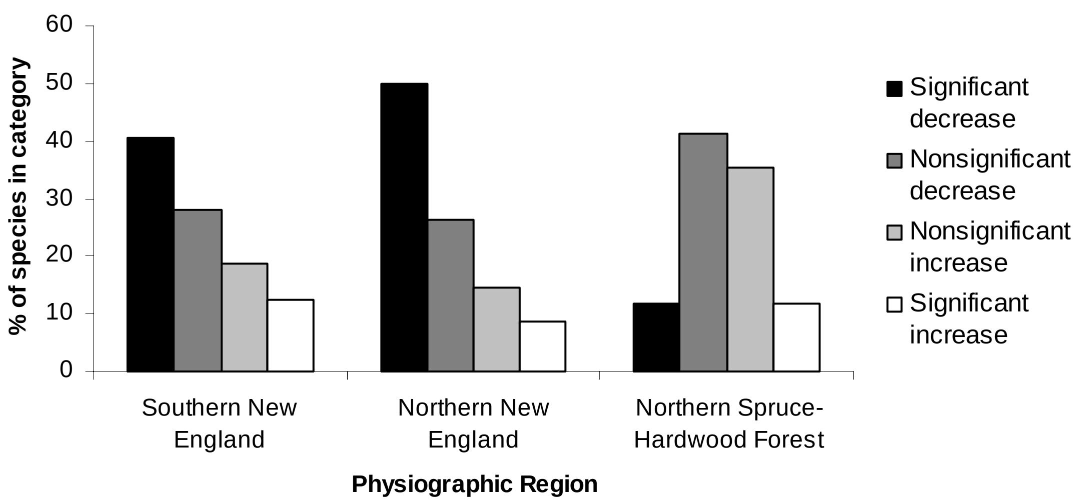


Figure 3.2. Summary of population trends for scrub-shrub birds on BBS routes by physiographic province. Data are from 1986-2005.

Table 3.2. Trends in scrub-shrub bird populations on BBS routes in New England by physiographic stratum. For stratum descriptions, see Chapter 1.

	Southern New England		Northern New England		Spruce-Hardwood Forest	
Species	Trend (% yr^{-1})[a]	*N*[b]	Trend (% yr^{-1})	*N*	Trend (% yr^{-1})	*N*
Ruffed Grouse	-0.9 ± 0.9	8	-0.1 ± 0.5	39	1.1 ± 0.7	47
Northern Bobwhite	-12.0 ± 1.8***	23				
Wilson's Snipe			-3.2 ± 0.9***	26	0.9 ± 0.9	46
American Woodcock	1.9 ± 1.4	8	-0.3 ± 0.7	10	0.4 ± 0.8	12
Yellow-billed Cuckoo	1.6 ± 0.9	34	0.2 ± 0.8	21		
Whip-poor-will	-4.4 ± 2.2*	12	-2.7 ± 1.3*	8	-3.3 ± 2.3	6
Ruby-throated Hummingbird	0.8 ± 0.7	32	1.2 ± 0.9	47	2.2 ± 1.1*	50
Alder Flycatcher	-1.1 ± 1.7	22	-0.5 ± 0.7	51	0.1 ± 0.9	53
Willow Flycatcher	1.4 ± 1.5	33	1.2 ± 1.3	34	-2.3 ± 2.1	16
White-eyed Vireo	3.2 ± 2.3	7				
Carolina Wren	7.1 ± 2.2**	36	1.1 ± 0.3***	7		
House Wren	-2.0 ± 0.7**	42	-4.3 ± 0.9***	48	-2.0 ± 0.7**	31
Gray Catbird	1.6 ± 0.6**	42	-1.9 ± 0.5***	51	-0.2 ± 1.5	49
Northern Mockingbird	-6.3 ± 1.2***	42	-3.6 ± 1.1**	39	-1.9 ± 1.6	22
Brown Thrasher	-3.9 ± 1.6*	37	0.2 ± 1.6	38	-0.3 ± 0.9	31
Cedar Waxwing	-1.7 ± 2.1	41	-3.0 ± 0.7***	51	-1.1 ± 1.5	53
Blue-winged Warbler	-3.5 ± 2.1	35	-2.4 ± 1.3	14		
Golden-winged Warbler			-4.0 ± 2.2	5		
Tennessee Warbler			-1.6 ± 1.2	8	-2.4 ± 1.1*	43
Nashville Warbler	-1.5 ± 0.7*	12	-4.2 ± 0.9***	50	-0.9 ± 0.8	53
Yellow Warbler	1.0 ± 0.9	42	-3.6 ± 0.6***	51	-2.1 ± 1.2	51
Chestnut-sided Warbler	-1.7 ± 2.8	37	-2.5 ± 0.7**	51	-2.1 ± 1.5	53
Magnolia Warbler	-0.1 ± 0.7	11	-2.2 ± 1.3	46	4.8 ± 1.2***	53
Prairie Warbler	-4.5 ± 1.4**	36	2.0 ± 1.5	16		
Palm Warbler					5.2 ± 3.4	20
Black-and-white Warbler	-2.5 ± 1.9	41	-4.0 ± 0.7***	51	-6.0 ± 0.9***	53
Mourning Warbler			-1.8 ± 1.5	18	0.8 ± 1.6	45
Common Yellowthroat	-2.2 ± 1.1*	42	-1.9 ± 0.4***	51	0.3 ± 0.6	53
Canada Warbler	-1.9 ± 0.6**	14	-2.6 ± 1.2*	46	0.3 ± 2.6	52
Wilson's Warbler					2.3 ± 1.9	28
Eastern Towhee	-2.7 ± 0.8***	42	-4.9 ± 0.9***	44	-1.5 ± 4.1	18
Field Sparrow	-4.0 ± 0.5***	37	-3.2 ± 0.8***	40	-0.6 ± 0.5	20
Song Sparrow	-1.4 ± 0.7	42	-0.9 ± 0.3**	51	-0.2 ± 0.4	53
Lincoln's Sparrow					7.0 ± 3.7	29
White-throated Sparrow	-3.2 ± 1.0**	16	-6.3 ± 1.0***	51	-1.3 ± 0.6*	53
Dark-eyed Junco	-2.9 ± 0.9***	8	-1.3 ± 1.0	38	4.9 ± 2.2*	52
Northern Cardinal	3.6 ± 0.5***	42	5.7 ± 1.4***	45	0.2 ± 1.0	19
Indigo Bunting	-1.0 ± 1.2	38	-2.9 ± 1.1**	47	-0.4 ± 0.6	35
American Goldfinch	6.4 ± 1.0***	42	3.4 ± 0.7***	51	3.0 ± 1.1**	53
Rusty Blackbird					3.8 ± 2.1	18

[a]Estimated trend (± 1 SD) based on 1000 bootstrap samples.

[b]Number of BBS routes used to estimate trend.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Past research has shown that birds that winter in the Neotropics may be more prone to decline than those that winter in the United States and Canada (Robbins et al. 1989b; Bohninggaese et al. 1993). This is likely because of deforestation and habitat loss in Central and South America. To determine how migratory behavior influences populations of scrub-shrub birds, we compared trends between birds wintering in the U.S. (short-distance migrants and residents) and those wintering in the Neotropics. We found no differences between Neotropical migrants and birds wintering in the U.S. for any of the three time periods we examined (Figure 3.3). Both groups included species with a wide range of increasing and decreasing populations. In contrast to forest-breeding birds, wintering in the tropics does not appear to predispose shrubland birds to decline. This is not surprising, as most scrub-shrub birds that winter in the tropics use a variety of scrub and second-growth habitats (Chapter 8). These habitats are widely available in Central and South America due to logging and abandonment of fields.

Finally, we examined how nesting location affected birds' population trends. Over half of New England's scrub-shrub birds (51%, n = 21) nest on the ground (DeGraaf & Yamasaki 2001), and research has shown that ground-nesting birds may experience higher nest predation than above-ground nesters (Martin 1993). Thus, the high proportion of ground nesters in shrublands could be a contributing factor in the community's overall decline. BBS data showed no significant differences between ground- and tree/shrub-nesters (Figure 3.4). In all time periods, ground nesters had slightly worse trends than tree- or shrub-nesters, but nesting location does not appear to be driving the overall declines in scrub-shrub birds.

Other Long-term Studies

Because the BBS is a roadside survey, the possibility exists that its results may be biased. In developing regions, roadsides are often the first areas to be developed, and habitats along roads may not be representative of the larger region (Keller & Scallan 1999; Lawler & O'Connor 2004). Furthermore, some birds may avoid roads (Van der Zande et al. 1980; Reijnen et al. 1995; Forman et al. 2002). Thus, BBS results may not necessarily reflect regional population trends. To supplement BBS data, we reviewed long-term

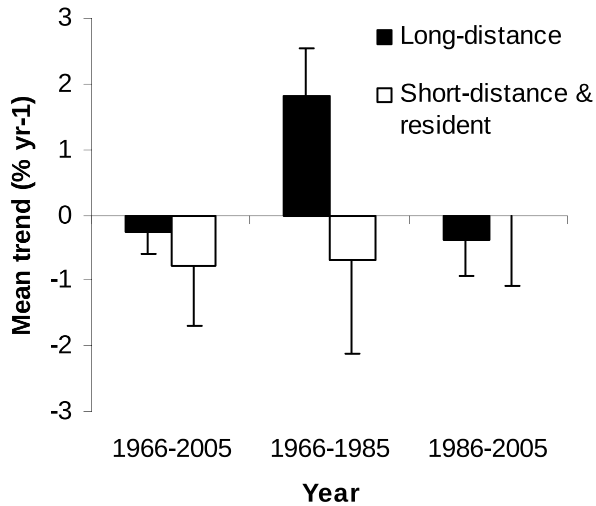


Figure 3.3. Population trends (mean ± SE) for scrub-shrub birds on BBS routes in New England, grouped by migratory behavior. Differences between groups were not significant (1966-2005: t = 0.53, P = 0.61; 1966-1985: t = 1.57, P = 0.13; 1986-2005: t = -0.30, P = 0.76).

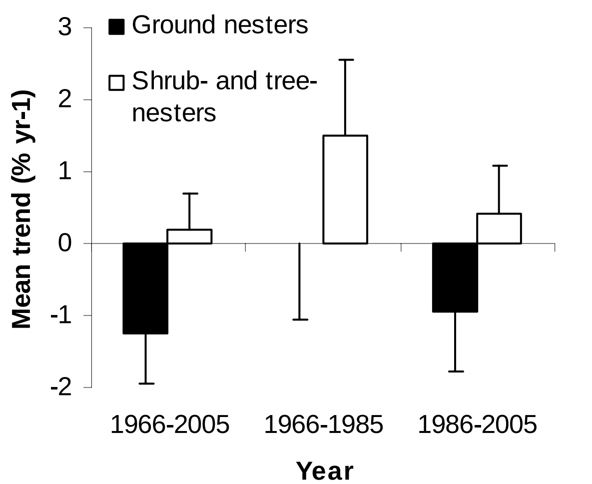


Figure 3.4. Population trends (mean ± SE) for scrub-shrub birds on BBS routes in New England, grouped by nest location. Differences between groups were not significant (1966-2005: t = -1.61, P = 0.12; 1966-1985: t = -0.96, P = 0.34; 1986-2005: t = -1.22, P = 0.23).

field studies of bird populations. We searched the literature for published long-term (> 10 yrs) studies on population trends of breeding or migrating scrub-shrub birds in New England. These studies generally assessed bird populations at different times in the same natural habitat, usually away from roads. Thus, these studies may provide a different perspective on population trends in scrub-shrub birds.

Two studies have examined trends in numbers of migrating birds in New England. While birds passing through the area may not necessarily be breeding in New England, they still can indicate regional trends. The first study, Hagan et al. (1992), examined populations of migratory birds at Cape Cod, Massachusetts from 1970 to 1988. They found significant declines for four scrub-shrub birds that also declined on BBS routes and significant increases for one species that also increased on the BBS. The only exception was Dark-eyed Junco, which increased on the BBS but decreased in Hagan et al.'s study.

In a second study, Hill & Hagan (1991) counted migrating birds in eastern Massachusetts between 1937 and 1989. As above, findings from this study corroborated BBS results. Six of seven species that declined in Hill & Hagan's study declined on the BBS, and two of three increasing species also increased on the BBS. One of the exceptions, Blue-winged Warbler, may have increased in Hill & Hagan's study as the warbler extended its breeding range to the north.

We also found two long-term studies of breeding birds in New England. In Connecticut, Askins & Philbrick (1987) reported that Canada Warbler disappeared from a forested study site between 1953 and 1976 while House Wren increased over the same period. Populations of several other scrub-shrub birds were relatively constant. During that time period, regional forest cover declined substantially. In New Hampshire, Holmes & Sherry (2001) found that Dark-eyed Juncos declined significantly between 1969 and 1998 on a forested site.

Overall, the above studies corroborate evidence from the BBS that scrub-shrub birds are declining in New England. These studies also show that some birds, especially Northern Cardinal and House Wren, are increasing in New England. Unfortunately, we could not locate any long-term studies of breeding birds in scrub-shrub habitat. This is likely because succession makes such habitats ephemeral; without management, such habitats would eventually become unsuitable for scrub-shrub birds. In forested habitats, long-term studies have produced compelling evidence of declines in forest birds (Wilcove 1988). No such studies, however, have been conducted in scrub-shrub habitat. Because long-term studies are invaluable as a source of data on bird populations, we hope that researchers will conduct such research in permanent scrub-shrub habitats such as bogs or shrub wetlands.

American Woodcock Survey Results

American Woodcock is a popular gamebird, so managers monitor woodcock populations to ensure that numbers are sufficient for hunting. Each year, the U.S. Fish and Wildlife Service conducts a Singing Ground Survey for breeding woodcock on road-based transects (Kelley & Rau 2006). These counts are similar to the BBS, except that the routes are shorter and less numerous, and surveys are conducted at dusk, when woodcock display. Between 1968 and 2006, the number of woodcock declined significantly in Maine, Massachusetts, Connecticut, and Rhode Island (Kelley & Rau 2006). No significant trends were observed in Vermont and New Hampshire. More recently, between 1996 and 2006, no significant trends have been observed for woodcock populations in any state. Thus, woodcock populations, appear to have stabilized in recent years after earlier declines. This is consistent with recent changes in the amount of scrub-shrub habitat in New England—steep declines followed by relatively constant levels more recently (Chapter 2). BBS data revealed no significant trends in woodcock populations for any time period, though sample sizes were small (Table 3.1).

Estimated Population Sizes

Population size is the most important factor determining whether a population will persist or go extinct (Lande 1988; Berger 1990; Renshaw 1991). Thus, population estimates can be useful for assessing conservation status and prioritizing species for management. We used recently developed methods to estimate populations for scrub-shrub birds in New England (Rosenberg & Blancher 2005). These estimates, however, come with significant uncertainty and should only be considered approximations (Thogmartin et al. 2006). The population estimates are sensitive to several assumptions used in the calculations, and the exact precision cannot be known for sure. Our estimates are based on average numbers of birds on BBS routes between 1996 and 2005 (Sauer et al. 2005).

Estimated populations of scrub-shrub birds in New England varied widely (Table 3.3). Species with the smallest estimated populations, below 10,000, include Northern Bobwhite, Rusty Blackbird, Whip-poor-will, Yellow-billed Cuckoo, and Golden-winged Warbler. All of these species reach their range limits in New England and, therefore, inhabit only a portion of the region. At the other end of the spectrum, species with estimated populations over 1,000,000 include Common Yellowthroat, American Goldfinch, and Cedar Waxwing. We found no correlation between estimated population size and population trend for the entire BBS period (r = -0.03, P = 0.84) or the most recent 20 years (r = 0.02, P = 0.92). Thus, species with small and large populations were equally likely to be declining.

Conservation Priorities

Another source of information on scrub-shrub bird populations is conservation assessments made by conservation organizations as well as state and federal government agencies. None of the scrub-shrub birds in New England are federally endangered, but the U.S. Fish & Wildlife Service considers several to be species of concern. These are species that, "without additional conservation actions, are likely to become candidates for listing under the Endangered Species Act" (U.S. Fish and Wildlife Service 2002). As of 2002, this list included Whip-poor-will, Golden-Winged Warbler, Prairie Warbler, and Canada Warbler. At the state level, Golden-winged Warbler is endangered in Massachusetts, and Yellow-breasted Chat is endangered in both Rhode Island and Connecticut. Species of concern include Dark-eyed Junco and White-throated Sparrow in Rhode Island and Mourning Warbler in Massachusetts.

Partners in Flight (PIF), a bird conservation organization, has ranked North American birds based on their conservation status at both the regional and continental levels (Rich et al. 2004). PIF assesses conservation status based on six factors that could potentially impact a species' risk of extinction: population size, area of breeding range, area of non-breeding range, threats to the breeding grounds, threats to the non-breeding grounds, and population trend. Based on these factors, seven of New England's scrub-shrub species are on PIF's North American Watch List, indicating high conservation need (Table 3.4). Golden-winged Warbler is in the most threatened category, in need of immediate action to halt declining populations. Six other Watch List species also require management to maintain or restore populations (Table 3.4). In addition, 13 other scrub-shrub birds are considered "stewardship" species due to their being restricted to only one biome (Table 3.4). These species could become threatened in the future and bear monitoring because of their limited ranges.

The above assessments are based on species' populations in all of North America. PIF also has identified species of conservation concern for the three physiographic regions of New England based on regional populations and conservation threats (Table 3.4) (Dettmers & Rosenberg 2000; Hodgman & Rosenberg 2000; Rosenberg & Hodgman 2000). American Woodcock and Canada Warbler are priority species in all three regions. Golden-winged Warbler, Prairie Warbler, Whip-poor-will, and Blue-winged Warbler are species of concern in two of the three regions.

Overall Assessment

The overall status of the scrub-shrub bird community in New England is poor. Currently, nearly three times as many species are declining as are increasing. Twenty-one of the forty-one bird species have show significant short or long-term declines, and twelve other species are of conservation concern, either locally or nationally. That leaves only eight species that are neither declining nor of concern. Some species, such as Northern Bobwhite and Yellow-breasted Chat, whose ranges barely extend into New England, may be on the verge of extirpation. The Golden-winged Warbler, with a tiny overall breeding range, is heading towards global extinction. Even some abundant and widespread species, such as Chestnut-sided Warbler and Eastern Towhee, are decreasing at alarming rates.

Conservation rankings for New England consistently identify other habitats, such as grassland or salt marsh, as being of higher priority (e.g.

Table 3.3. Population estimates for scrub-shrub birds in New England.

Species	Connecticut	Maine	Massachu-setts	New Hampshire	Rhode Island	Vermont	Total
Ruffed Grouse	2,000	43,000	4,300	4,300	200	10,700	64,400
Northern Bobwhite	14	100	1,500	100	100	0	1,800
Wilson's Snipe	0	219,500	0	44,200	0	175,000	438,700
American Woodcock	10,300	100,400	18,800	16,000	2,100	28,400	176,100
Yellow-billed Cuckoo	2,800	1,400	2,000	300	500	500	7,500
Whip-poor-will	1,600	2,300	500	500	200	200	5,400
Ruby-throated Hummingbird	16,700	97,700	20,800	30,900	2,300	42,700	211,100
Alder Flycatcher	7,500	490,900	14,000	99,800	700	136,100	749,000
Willow Flycatcher	12,700	10,200	13,800	2,900	2,100	27,200	68,900
White-eyed Vireo	10,500	1,200	0	0	1,200	0	12,900
Carolina Wren	35,000	800	79,600	300	11,400	1,500	128,600
House Wren	124,500	30,700	139,700	55,600	25,200	45,500	421,200
Gray Catbird	236,900	172,300	271,000	104,400	49,100	81,600	915,300
Northern Mockingbird	24,200	5,800	38,200	10,300	6,300	1,300	86,100
Brown Thrasher	1,200	4,900	1,700	1,600	300	3,200	12,800
Cedar Waxwing	110,900	960,200	192,200	313,900	21,600	286,000	1,884,800
Blue-winged Warbler	28,700	0	27,500	4,100	5,700	2,900	68,800
Golden-winged Warbler	0	0	0	200	0	3,400	3,700
Tennessee Warbler	0	20,400	0	300	0	1,200	21,900
Nashville Warbler	400	507,300	2,300	36,900	8	20,200	567,000
Yellow Warbler	158,300	462,400	159,100	110,600	27,700	184,400	1,102,500
Chestnut-sided Warbler	64,600	546,700	76,100	159,500	8,400	226,100	1,081,500
Magnolia Warbler	2,500	710,100	5,700	54,000	300	47,500	820,000
Prairie Warbler	5,500	3,700	20,300	4,800	2,500	900	37,700
Palm Warbler	0	33,500	0	0	0	0	33,500
Black-and-white Warbler	90,900	848,300	143,500	282,400	13,000	200,100	1,578,300
Mourning Warbler	100	78,300	400	3,100	0	18,300	100,200
Common Yellowthroat	185,000	1,680,000	348,300	406,100	41,200	556,800	3,217,500
Canada Warbler	3,000	90,100	6,200	13,100	300	15,200	127,900
Wilson's Warbler	0	23,000	0	300	0	500	23,800
Eastern Towhee	23,100	13,200	61,400	8,300	8,000	2,400	116,400
Field Sparrow	4,800	4,300	6,900	2,900	1,000	17,700	37,700
Song Sparrow	118,100	523,000	152,400	151,100	22,600	265,500	1,232,500
Lincoln's Sparrow	0	59,100	0	7,600	0	2,400	69,100
White-throated Sparrow	1,400	1,406,000	8,000	139,300	100	152,200	1,707,000
Dark-eyed Junco	3,400	183,400	15,700	24,000	100	38,400	265,000
Northern Cardinal	205,900	35,800	254,700	64,900	45,400	48,800	655,400
Indigo Bunting	21,100	38,800	27,000	51,900	3,300	76,600	218,600
American Goldfinch	278,800	1,008,500	492,000	386,800	69,100	395,100	2,630,200
Rusty Blackbird	0	5,000	0	100	0	100	5,200

Hodgman & Rosenberg 2000). These habitats are rare and do contain some imperiled species. Scrub-shrub habitats, however, have a much more diverse bird community with a greater number of rare and declining species. With 33 of 41 species in some sort of conservation difficulty, the New England's scrub-shrub bird is highly imperiled, and scrub-shrub community habitats should be of the highest priority in regional conservation planning. The succeeding chapters in this volume discuss critical habitat components and management options for this threatened bird community.

Table 3.4. National and regional species of conservation concern according to Partners in Flight.

Species	National Status	Southern New England	Northern New England	Northern Spruce-hardwood Forest
Golden-winged Warbler[a]	Immediate Action	x[c]	x	
Willow Flycatcher	Management			
Prairie Warbler	Management	x	x	
Gray Catbird	Management		x	
Canada Warbler	Management	x	x	x
Rusty Blackbird	Management			
Blue-winged Warbler	Management	x	x	
Alder Flycatcher	Stewardship[b]			
Carolina Wren	Stewardship			
Brown Thrasher	Stewardship			
Tennessee Warbler	Stewardship			
Nashville Warbler	Stewardship			x
Chestnut-sided Warbler	Stewardship		x	
Magnolia Warbler	Stewardship			
Palm Warbler	Stewardship			
Mourning Warbler	Stewardship		x	
Eastern Towhee	Stewardship	x		
Lincoln's Sparrow	Stewardship			
White-throated Sparrow	Stewardship			
Indigo Bunting	Stewardship			
American Woodcock		x	x	x
Whip-poor-will		x	x	
Yellow-breasted Chat		x		
Black-and-white Warbler		x		
Ruffed Grouse				x

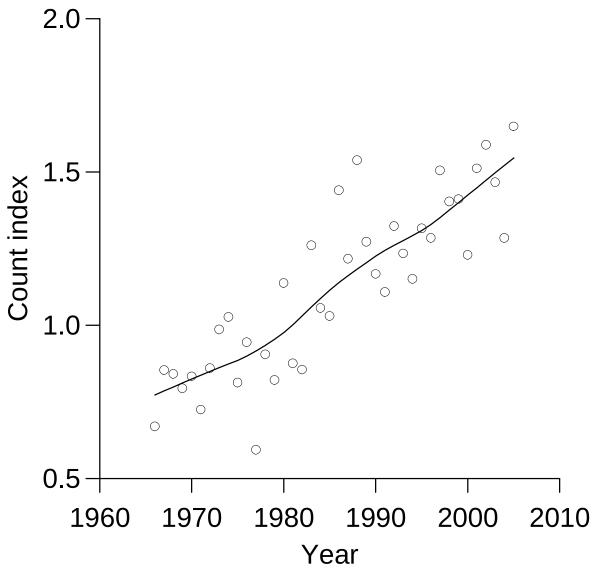
[a]Italics indicate national Watch List species

[b]Species not on the Watch List but in need of monitoring because of their restriction to a single biome.

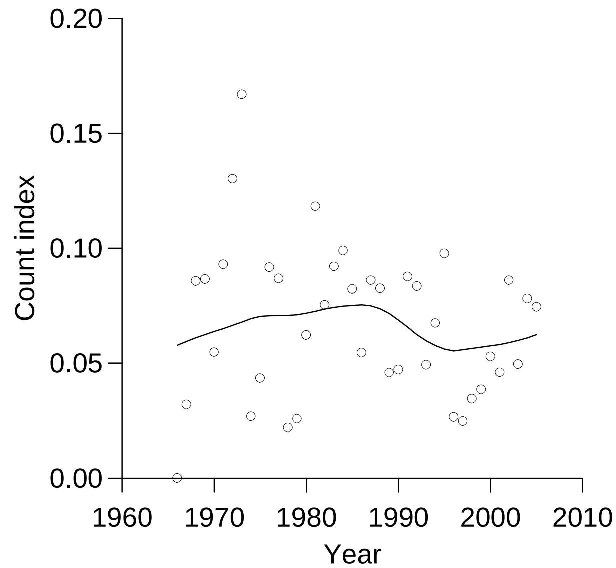
[c]Species of conservation concern for the given biogeographic province.

Appendix A. Annual counts of scrub-shrub birds in New England on BBS routes. Data are presented as the mean count per entire BBS route, each of which includes 50 3-minute point counts. Thus, an index of 25 indicates 0.5 birds per 3-minute count. Lines are LOWESS smooths with tension of 0.5. Note that scales on the y-axis differ among species.

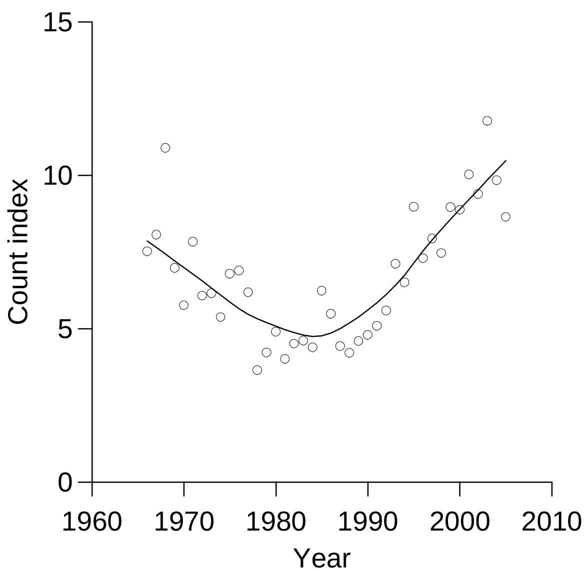
Alder Flycatcher



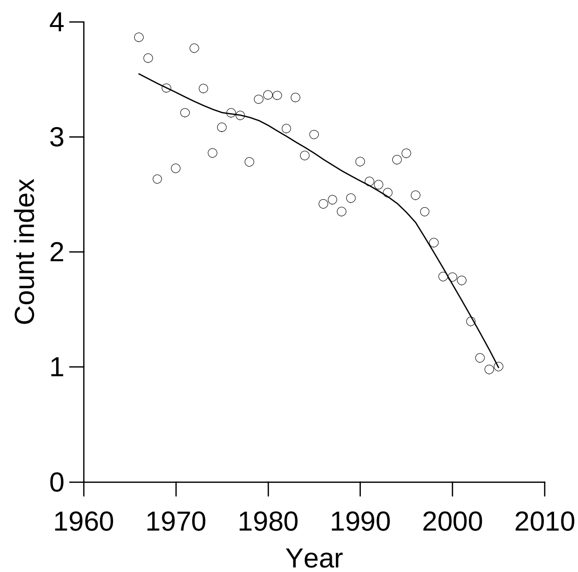
American Woodcock



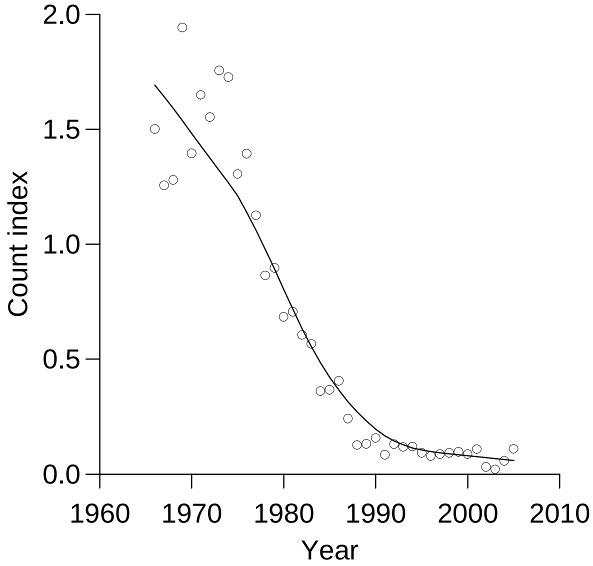
American Goldfinch



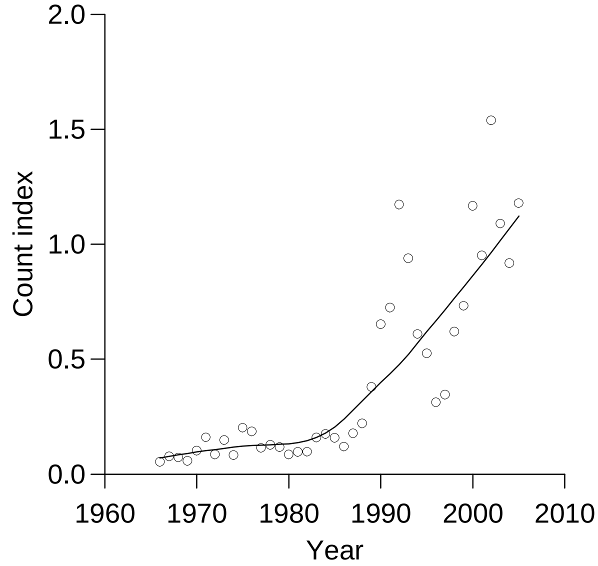
Black-and-white Warbler



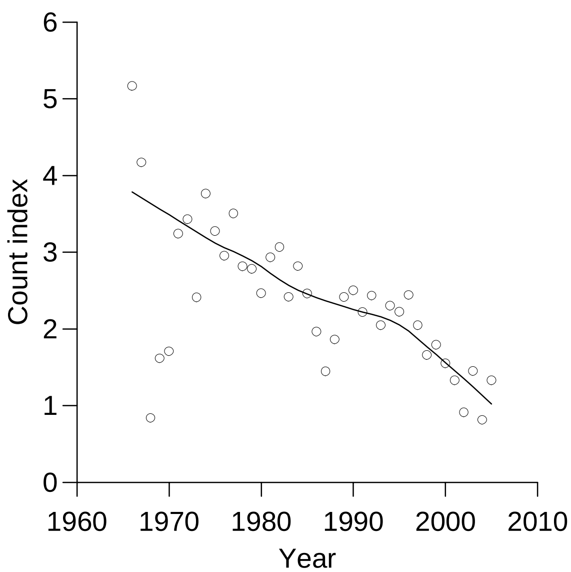
Brown Thrasher



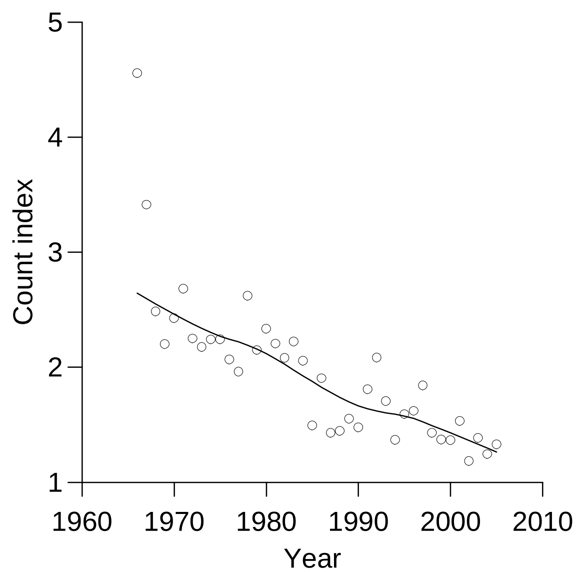
Carolina Wren



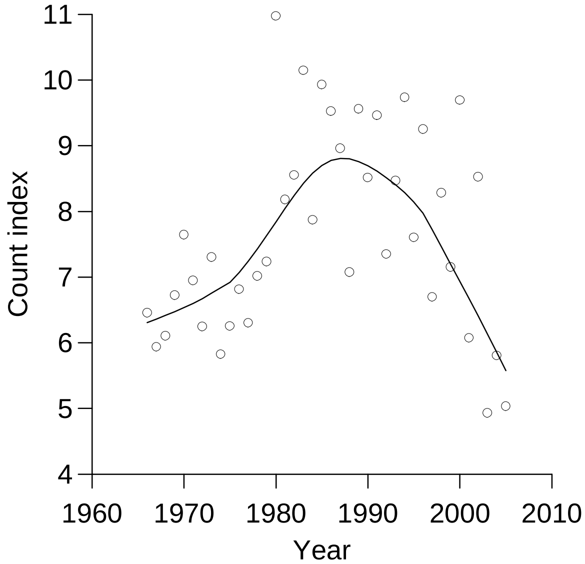
Blue-winged Warbler



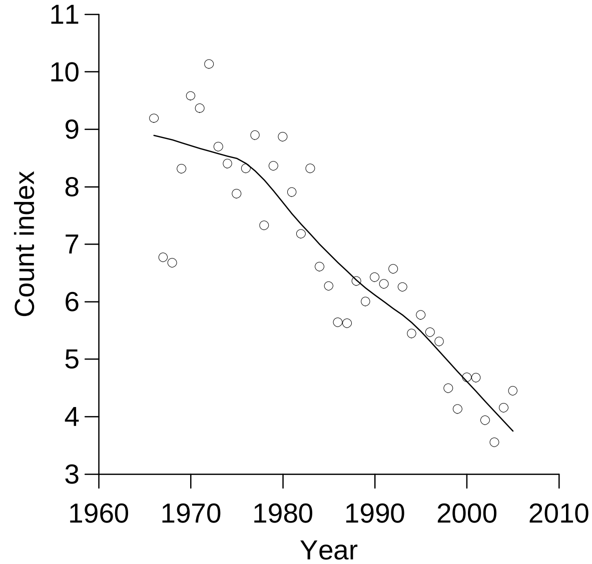
Canada Warbler



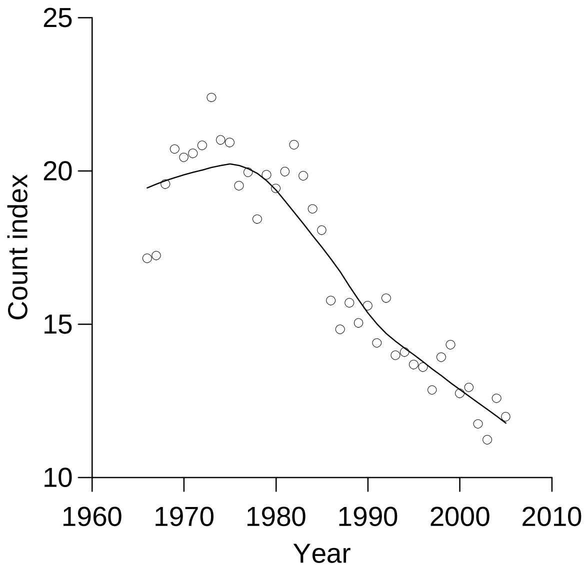
Cedar Waxwing



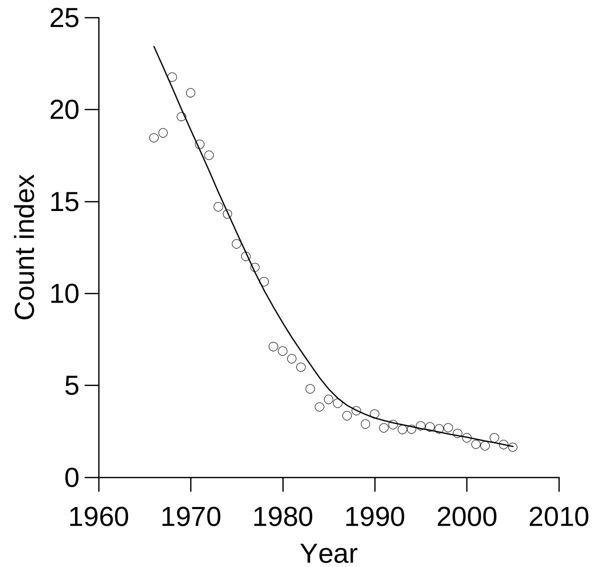
Chestnut-sided Warbler



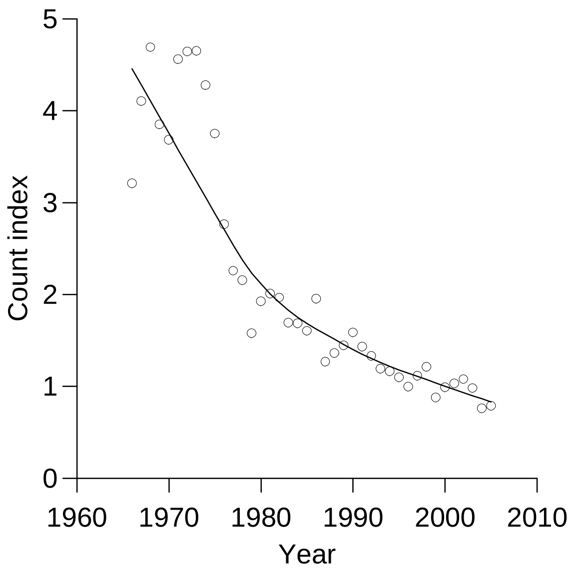
Common Yellowthroat



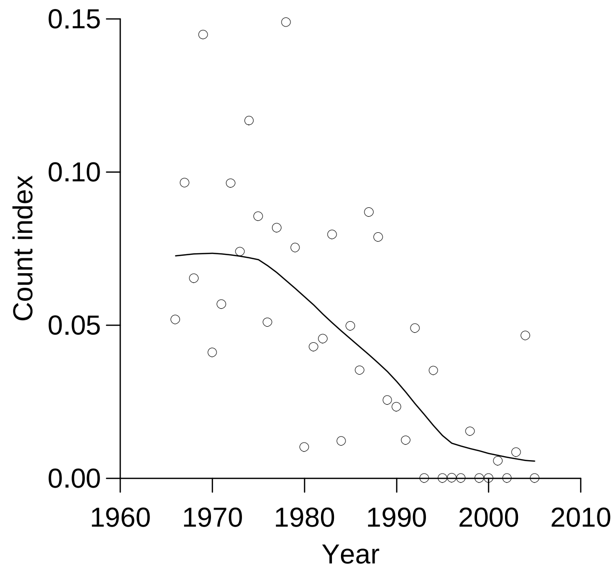
Eastern Towhee



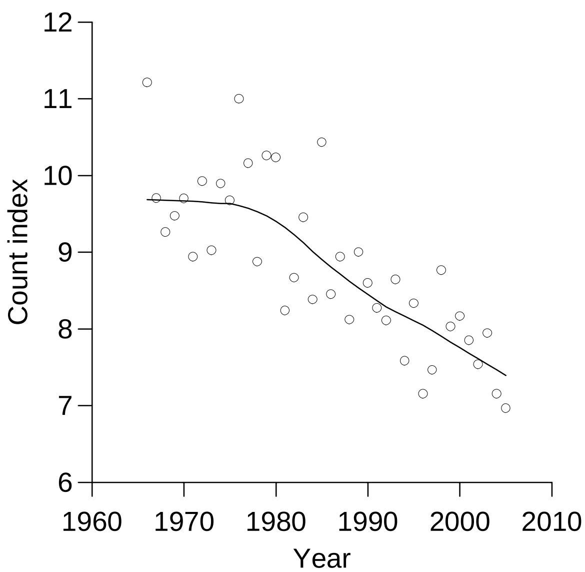
Field Sparrow



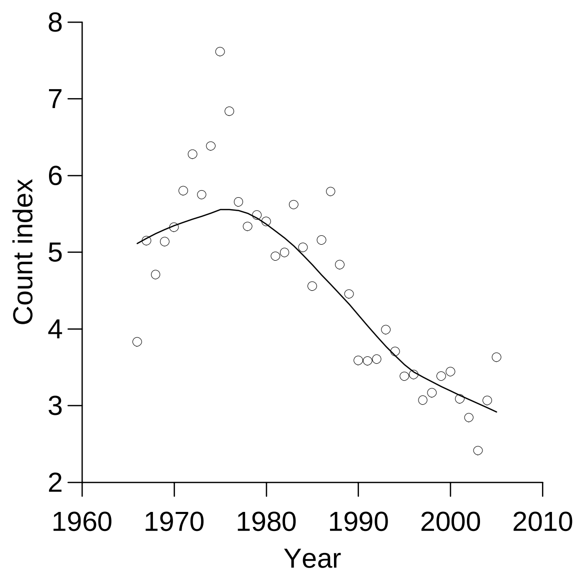
Golden-winged Warbler



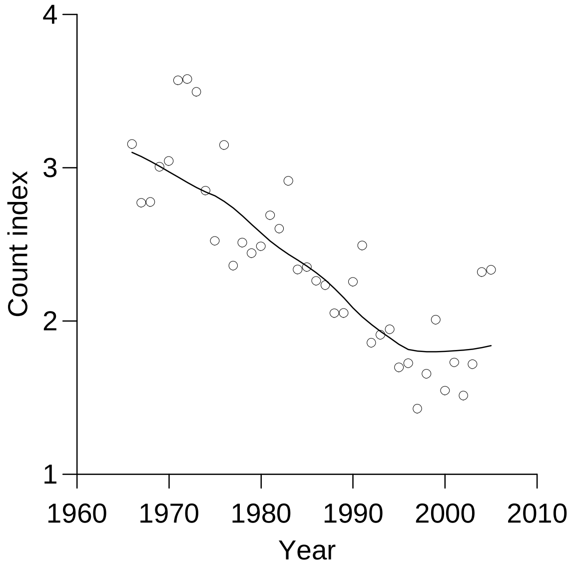
Gray Catbird



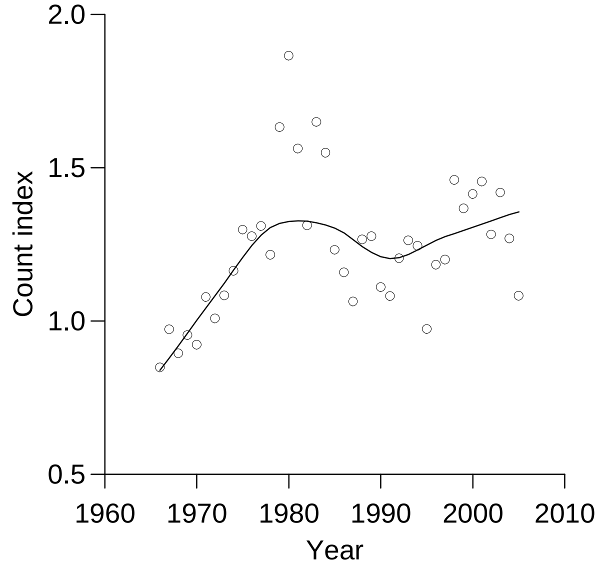
House Wren



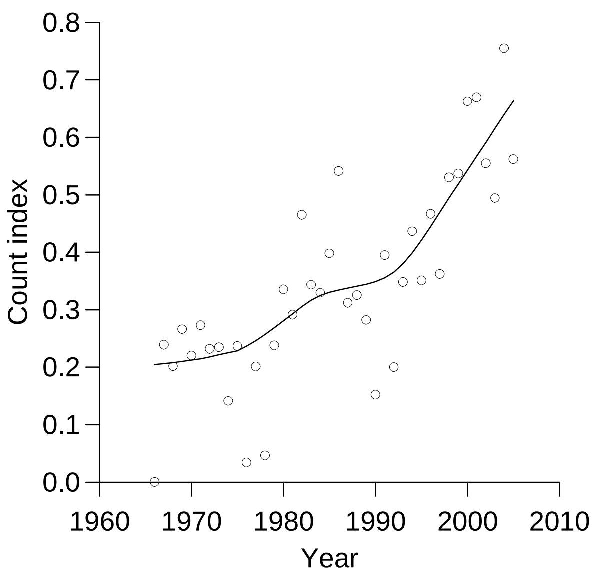
Indigo Bunting



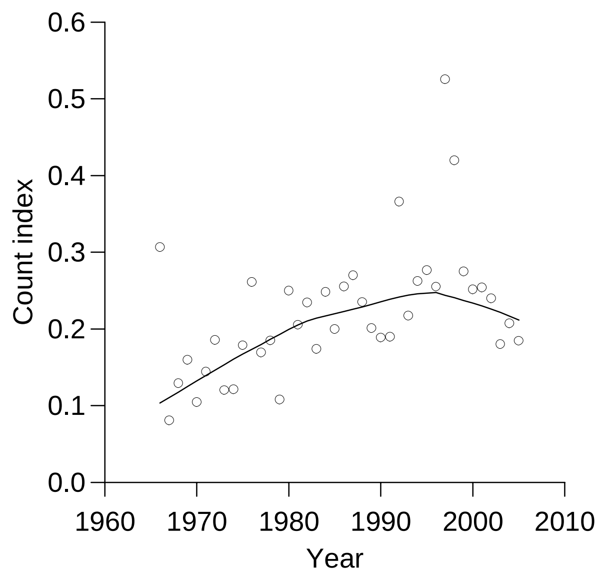
Magnolia Warbler



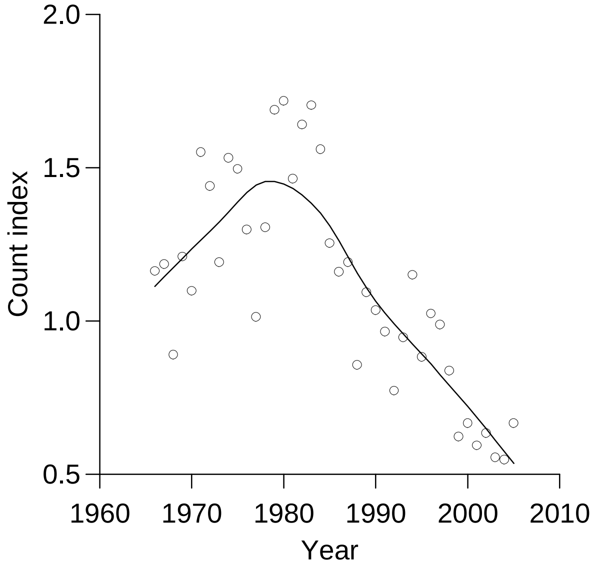
Lincoln's Sparrow



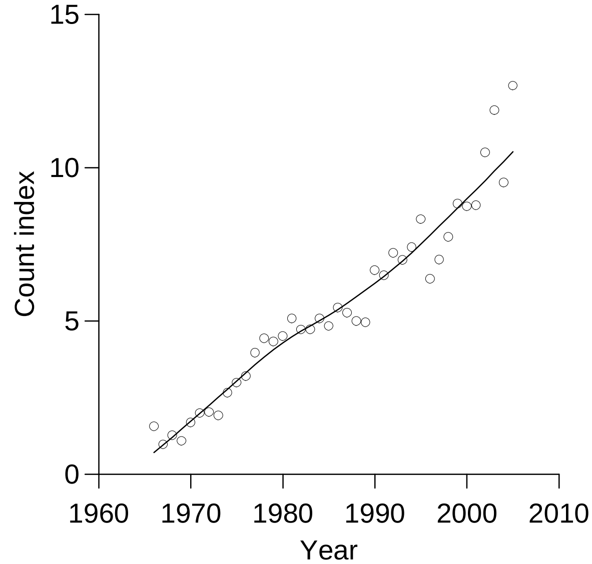
Mourning Warbler



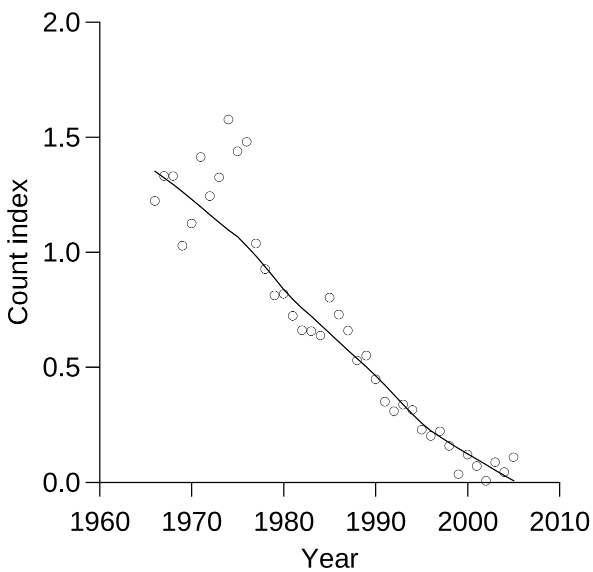
Nashville Warbler



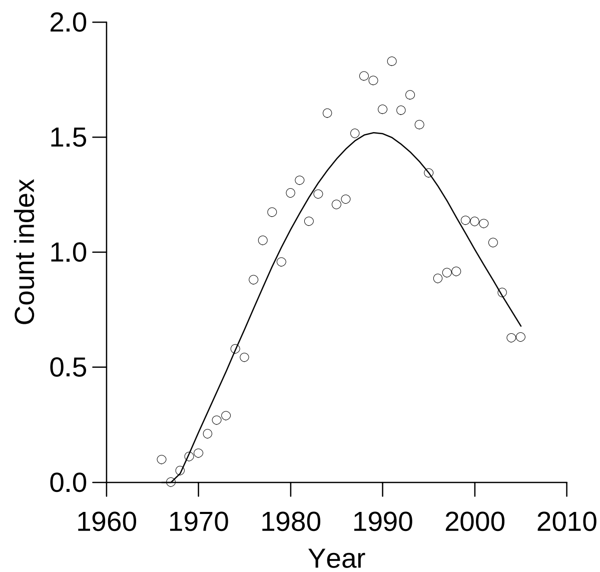
Northern Cardinal



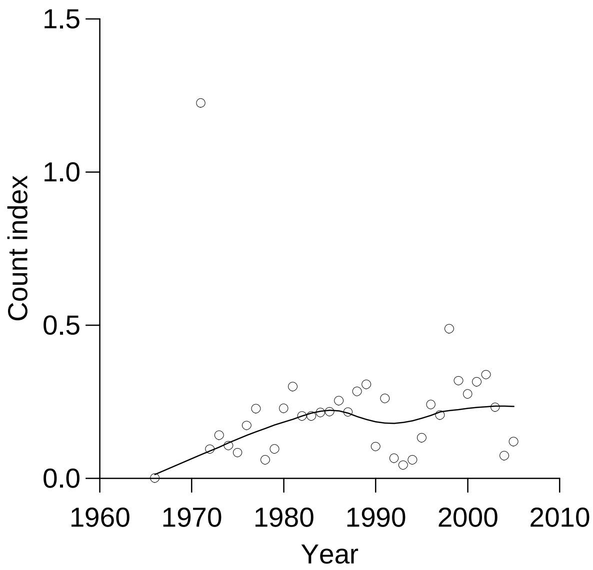
Northern Bobwhite



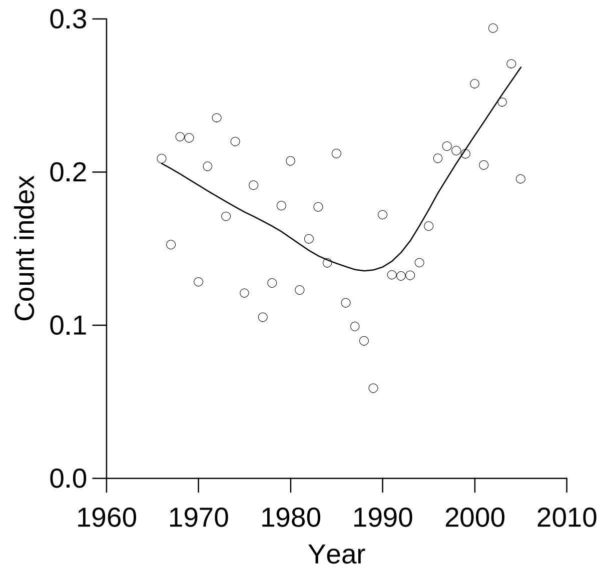
Northern Mockingbird



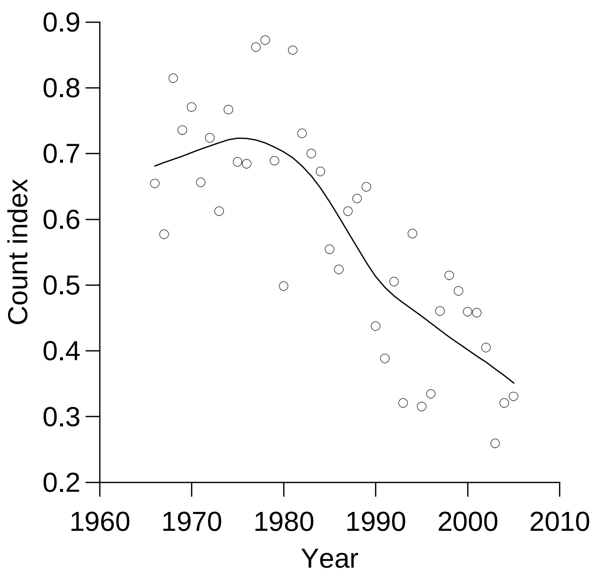
Palm Warbler



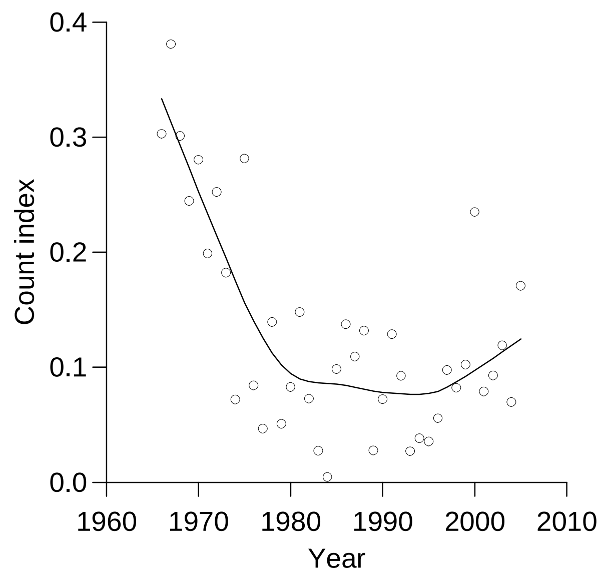
Ruby-throated Hummingbird



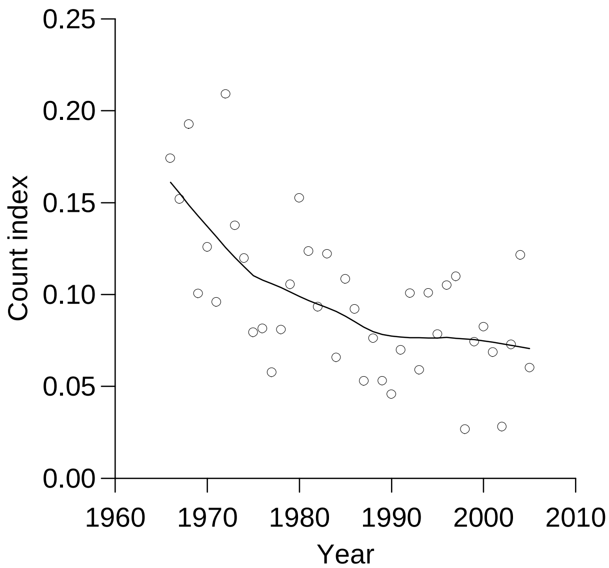
Prairie Warbler



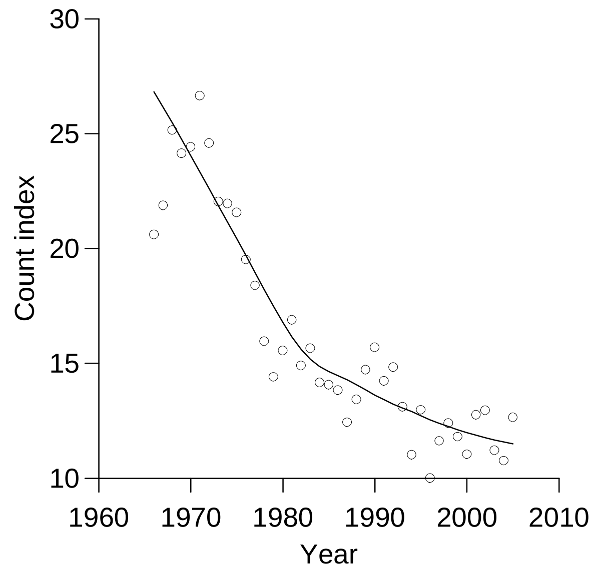
Rusty Blackbird



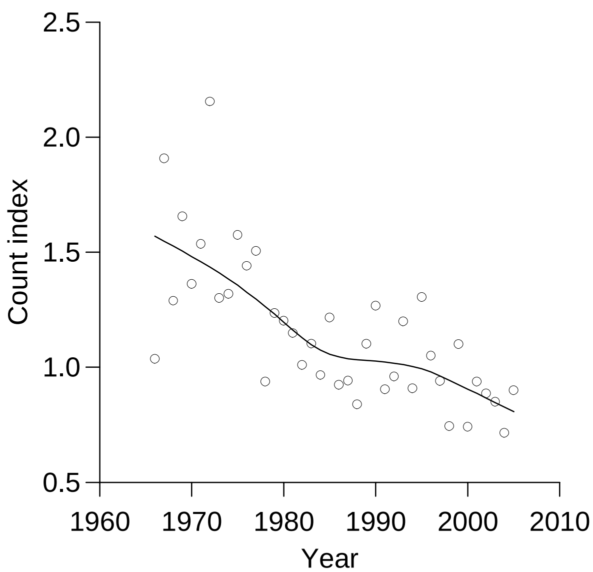
Ruffed Grouse



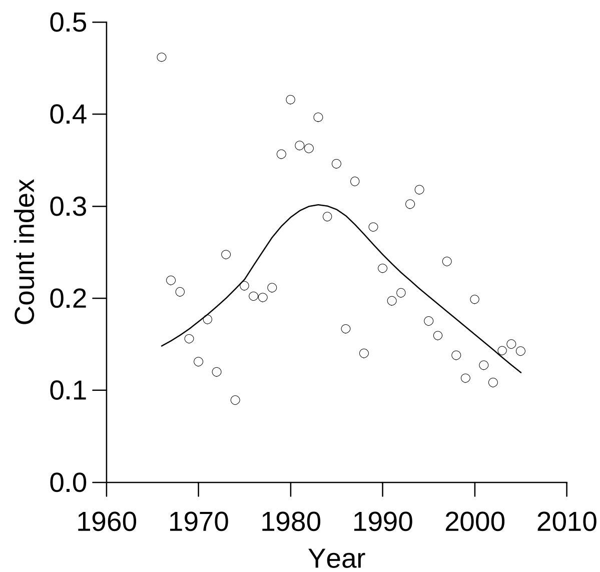
Song Sparrow



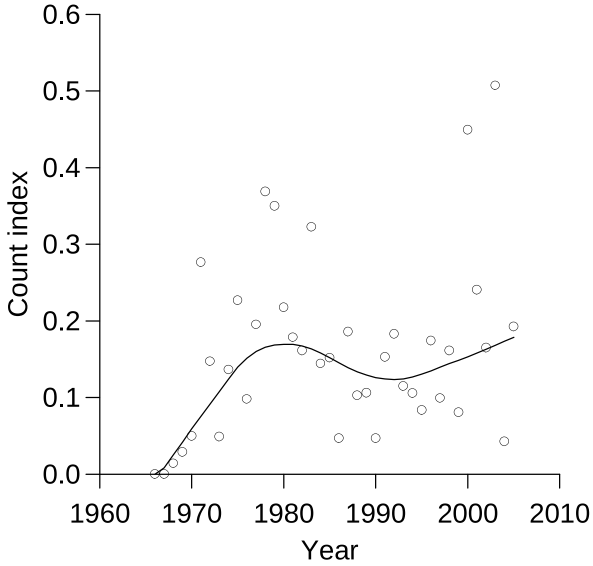
Dark-eyed Junco



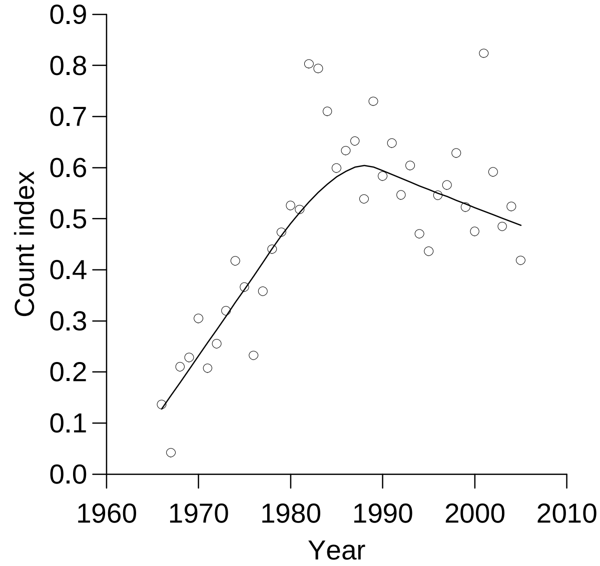
Tennessee Warbler



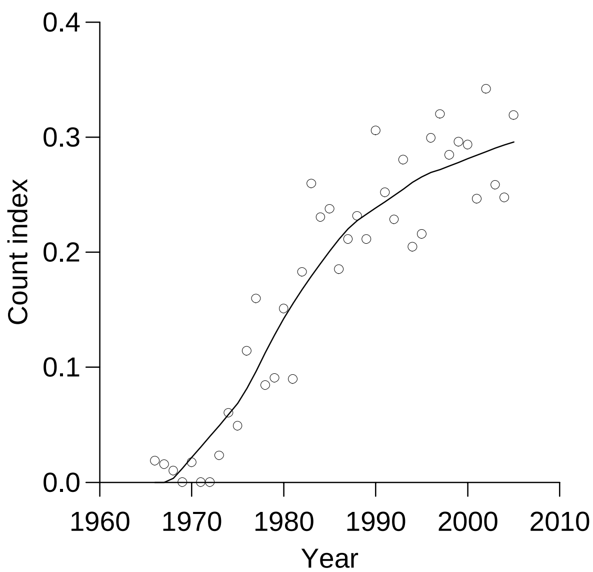
White-eyed Vireo



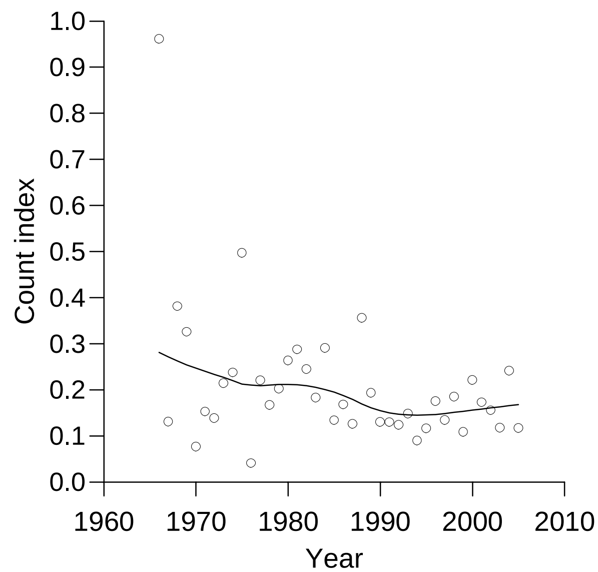
Wilson’s Snipe



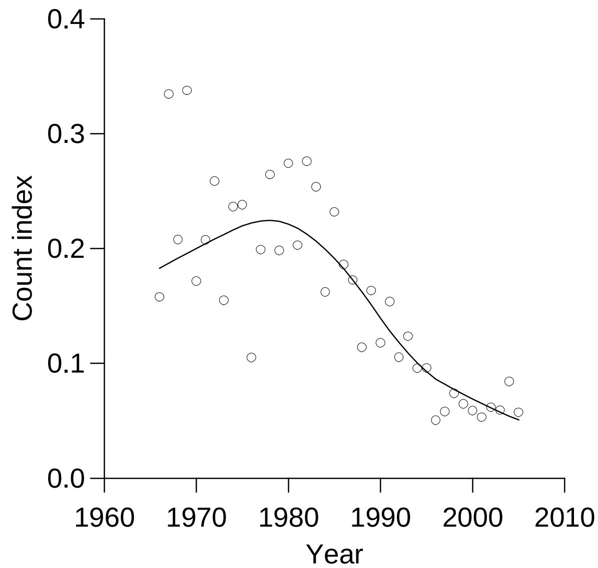
Willow Flycatcher



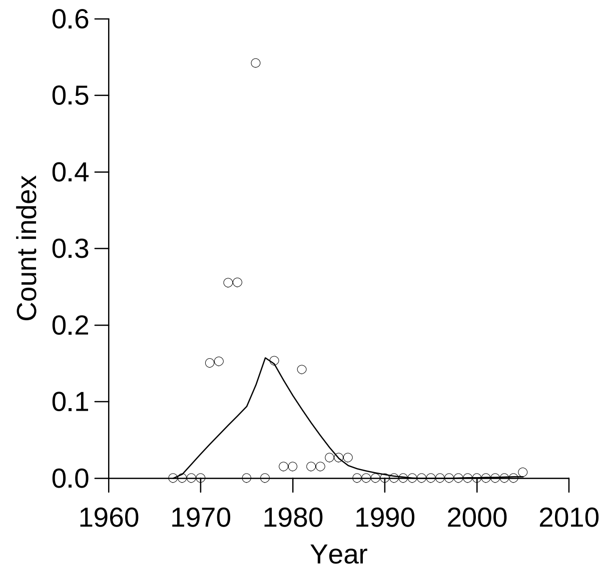
Wilson’s Warbler



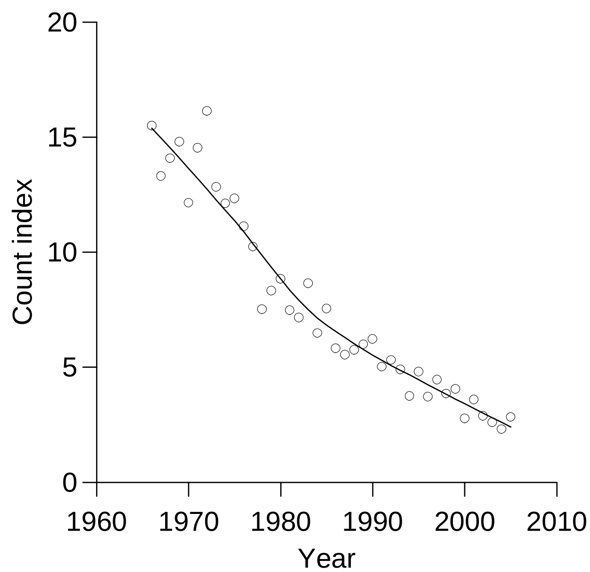
Whip-poor-will



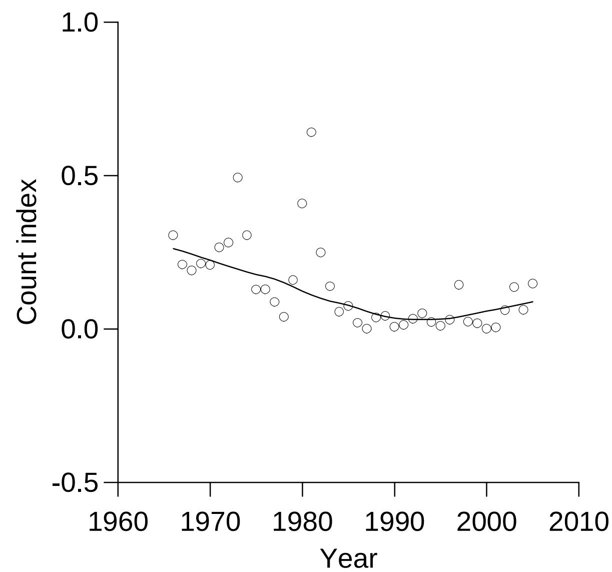
Yellow-breasted Chat



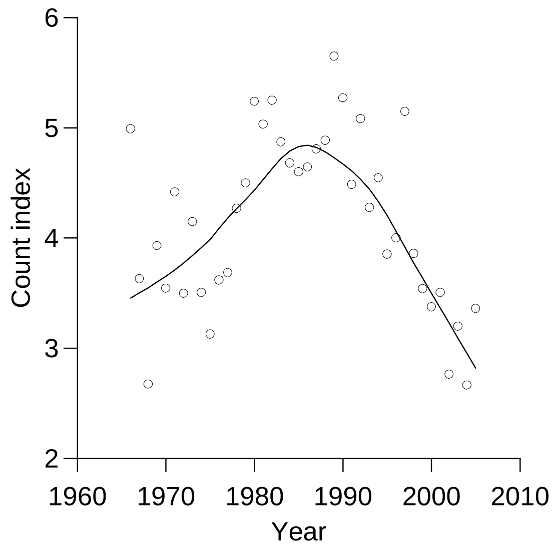
White-throated Sparrow



Yellow-billed Cuckoo



Yellow Warbler



Chapter 4. Habitat Selection

Introduction

Ecologists group scrub-shrub birds together because they all breed in scrubby, early-successional habitats with dense shrubs or sapling trees (Peterjohn & Sauer 1993; DeGraaf & Yamasaki 2001; Hunter et al. 2001). For management purposes, however, grouping these birds together may not be entirely justified; individual species have their own unique habitat preferences. Because scrub-shrub birds prefer different habitats, a one-size-fits-all management plan will not conserve this entire bird community. This is important, not only because of the diversity of scrub-shrub habitats in New England but also because habitats are dynamic and change over time due to succession. Managers can only ensure that the habitat needs of scrub-shrub birds are met if they understand which habitats individual species use. Several authors have described habitat usage by birds in qualitative terms (e.g. DeGraaf & Yamasaki 2001; the *Birds of North America* series). Here, we describe the habitat preferences of New England's scrub-shrub birds, with a focus on quantitative reviews of the published literature.

Usage of Different Habitat Types

When discussing habitat for scrub-shrub birds, ecologists have tended to treat all early-successional habitats as equivalent. In New England, over 75% of the existing scrub-shrub habitat, as well as nearly all habitat being created today, is regenerating forest created by logging (Chapter 2). Moreover, management prescriptions for creating additional scrub-shrub habitat generally focus on even-aged forest management, especially clearcutting (Thompson & DeGraaf 2001; Rodewald & Vitz 2005). To a great extent, "scrub-shrub habitat" has now become synonymous with "recently logged forests." The tendency to equate scrub-shrub habitat with logged areas may, however, be doing a disservice to some bird species. Shrublands come in a variety of forms (Chapter 2), and birds evince species-specific preferences for different scrub-shrub habitats (Bulluck & Buehler 2006; Fink et al. 2006). Some scrub-shrub birds, for instance, are primarily found in shrubby wetlands and bogs and avoid dry uplands. Other species prefer open landscapes and avoid clearings surrounded by forests. If logging does not provide habitat for all scrub-shrub birds, than other management methods will be necessary to conserve some species.

For purposes of this discussion, we divide scrub-shrub habitats in New England into seven categories: 1) regenerating clearcuts; 2) partial harvests involving retention of some overstory trees; 3) abandoned fields undergoing succession; 4) shrubby wetlands such as bogs and shrub swamps; 5) utility rights-of-way; 6) natural forest openings created by storms or insects; and 7) managed wildlife openings maintained in an early-successional stage by mowing or burning (see Chapter 2 for descriptions). We could not locate enough studies to include pitch pine-scrub oak woodlands in this analysis. Each of these habitat types has a distinct vegetative structure and floristic composition, features that are known to affect avian abundances. Thus, each of the above habitats will potentially host a different suite of scrub-shrub birds.

To provide better information about the habitat preferences of scrub-shrub birds, we surveyed the scientific literature for studies from eastern North America that listed bird species occurring in any of the seven habitats described above. We located published studies using *Web of Knowledge* and *Biological Abstracts* as well as through papers' citations. Ideally, we would have compared the relative abundances of individual species among habitats; however, differences in how researchers measured abundance (e.g. density via spot-mapping vs. presence-absence) made cross-study comparisons impossible. Also, we collected studies from a large geographic area, so we could not always know if a bird's absence from a study site was due to habitat preferences or the site's being near or beyond the edge of the species' geographic range. Instead, we simply recorded whether each species occurred in any study in a given habitat type and assessed the overall habitat breadth (the number of different habitats utilized) of each species. Because the habitats are not equally represented in our sample, our species lists for some habitats are certainly incomplete. These estimates of habitat usage should, therefore, be considered a minimum; several species on these lists are known to use habitats for which we could not find occurrences in our sample (see below).

Overall, we located 48 studies describing avian communities in the seven habitat types listed above (Table 4.1). The number of species recorded in each habitat type varied substantially, but this may have been an artifact of sampling effort. Habitats with more studies may have had more species simply because more locations were sampled (Gotelli & Colwell 2001). Thus, we used sample-based rarefaction to control for the number of studies in each habitat category (Colwell et al. 2004). After correcting for sample sizes, wetlands and wildlife openings appeared to have the greatest diversity of scrub-shrub birds, followed closely by clearcuts (Figure 4.1). Rarefied species richness was slightly lower for partial cuts, old fields, and rights-of-way. Species richness for natural gaps was the lowest of any habitat category.

Nearly all of New England's scrub-shrub birds (37 of 41 species) occurred in clearcuts (based on 19 published studies). The only species never observed in clearcuts were Northern Bobwhite, Willow Flycatcher, Northern Mockingbird, and House Wren. Given the large number of studies we found for this habitat, this is strong evidence that these four species avoid clearcuts. Of the four species, the first three typically inhabit open, non-forested landscapes while the House Wren is a cavity nester and may have avoided clearcuts due to a lack of cavity trees (see Appendix B). Partial harvests, in which the canopy is thinned but scattered mature trees are retained, had lower species richness than clearcuts. Rarefaction suggested that the differences in species richness between clearcuts and partial cuts were real and not merely a byproduct of sampling (Figure 4.1). The species that occurred in clearcuts but not partial cuts were American Woodcock, Brown Thrasher, Rusty Blackbird, Golden-Winged Warbler, Whip-poor-will, Wilson's Snipe, and Yellow Warbler. Given that many of these seven species are declining or of conservation concern (Chapter 3), clearcutting is likely to be a better management tool for scrub-shrub birds than partial cuts.

To determine how bird communities differed among habitats, we ordinated studies using principal coordinates analysis (Gotelli & Ellison 2004). Most of the variation in bird species composition (83%) was due to the geographic location of the studies. As expected, bird communities differed between northern and southern study sites (Chapter 1). After accounting for study location, we found a small effect of habitat type on bird community composition, explaining just 5% of the overall variation in the dataset. The small influence of habitat may be due, in part, to a lack of representation of some habitats in some regions. For instance, all five studies of old fields took place in the Southeast or Mid-Atlantic region. Thus, little is known about avian utilization of old fields in other areas. This highlights the need to conduct more research to describe scrub-shrub bird communities in varied habitats and regions.

Even with these limitations, individual species showed differences in their habitat usage. Three species occurred in only one habitat type: Rusty Blackbird (in clearcuts), Northern Mockingbird (old fields), and Willow Flycatcher (wetlands). Six other species occurred in only two habitat types (Table 4.1). Thus, nine species, 22% of New England's scrub-shrub birds, occurred in only one or two habitat types. Of the specialists, five used clearcuts, four used wetlands, and three were found in old fields. This emphasizes the importance of wetlands and old fields for scrub-shrub birds, a result that is even more compelling given the small number of studies we had for those habitats. In contrast, 15 bird species (37%) occurred in at least six of the seven habitat types.

These results show the importance of maintaining multiple habitat types, beyond just clearcuts, to conserve scrub-shrub birds (see Askins 2000). While most members of this bird community were found breeding in clearcuts at least once, a few species never occurred in logged areas. Moreover, because we used presence in any study as our measure of habitat usage, the results in Table 4.1 probably overestimate the importance of clearcuts. Yellow Warblers, for instance, bred in clearcuts in only 2 of 19 studies, even though all 19 studies took place within the species' breeding range. Regenerating clearcuts are used by many scrub-shrub species because they generally have dense cover of shrubs and saplings (Thompson & DeGraaf 2001). Other scrub-shrub habitats, however, may differ in structure. Old fields, for instance, tend to be more open and patchy in vegetation structure than clearcuts

Table 4.1. Habitats used by scrub-shrub birds, based on a literature review of published bird censuses in the East.

Species	Habitat Type							
	Wetland[a]	Clearcut[b]	Partial Cut[c]	Natural Gap[d]	Old Field[e]	Right-of-way[f]	Wildlife Opening[g]	Habitat Breadth[h]
Ruffed Grouse	x	x	x	x	x	X	x	7
Northern Bobwhite					x	x		2
Wilson's Snipe	x	x						2
American Woodcock	x	x			x		x	4
Yellow-billed Cuckoo		x	x		x	x		4
Whip-poor-will	x	x						2
Ruby-throated Hummingbird	x	x	x	x		x	x	6
Alder Flycatcher	x	x	x	x			x	5
Willow Flycatcher	x							1
White-eyed Vireo		x	x	x	x	x		5
Carolina Wren		x	x	x	x	x		5
House Wren	x				x			2
Gray Catbird	x	x	x		x	x	x	6
Northern Mockingbird					x			1
Brown Thrasher	x	x			x	x		4
Cedar Waxwing	x	x	x		x	x	x	6
Blue-winged Warbler	x	x	x		x	x	x	6
Golden-winged Warbler		x			x	x		3
Tennessee Warbler		x	x	x				3
Nashville Warbler	x	x	x	x			x	5
Yellow Warbler	x	x			x	x	x	5
Chestnut-sided Warbler	x	x	x	x	x	x	x	7
Magnolia Warbler	x	x	x	x			x	5
Prairie Warbler	x	x	x		x	x	x	6
Palm Warbler		x	x					2
Black-and-white Warbler	x	x	x	x	x	x	x	7
Mourning Warbler	x	x	x	x			x	5
Common Yellowthroat	x	x	x		x	x	x	6
Canada Warbler	x	x	x	x		x		5
Wilson's Warbler		x	x					2
Yellow-breasted Chat		x	x		x	x		4
Eastern Towhee	x	x	x	x	x	x	x	7
Field Sparrow	x	x	x		x	x	x	6
Song Sparrow	x	x	x		x	x	x	6
Lincoln's Sparrow	x	x	x					3
White-throated Sparrow	x	x	x	x			x	5
Dark-eyed Junco	x	x	x	x				4
Northern Cardinal	x	x	x		x	x	x	6
Indigo Bunting	x	x	x	x	x	x	x	7
American Goldfinch	x	x	x	x	x	x	x	7
Rusty Blackbird		x						1

[a]Based on: Grover & Baldassarre 1995, Brewer 1967, Martin 1960, Ewert 1982

[b]Rudnicky & Hunter 1993, Hagan et al. 1997, King & Collins 2005, Conner & Adkisson 1975, Maurer et al. 1981, Morgan & Freedman 1986, Bulluck & Buehler 2006, King & DeGraaf 2000, Costello et al. 2000, Tappe et al. 2004. Annand & Thompson 1997, Freedman et al. 1981, Thompson & Fritzell 1992, Yahner 1987, Niemi & Hanowski 1984, Titterington et al. 1979, Kerpez 1994, Simon et al. 2000, Conner et al. 1979

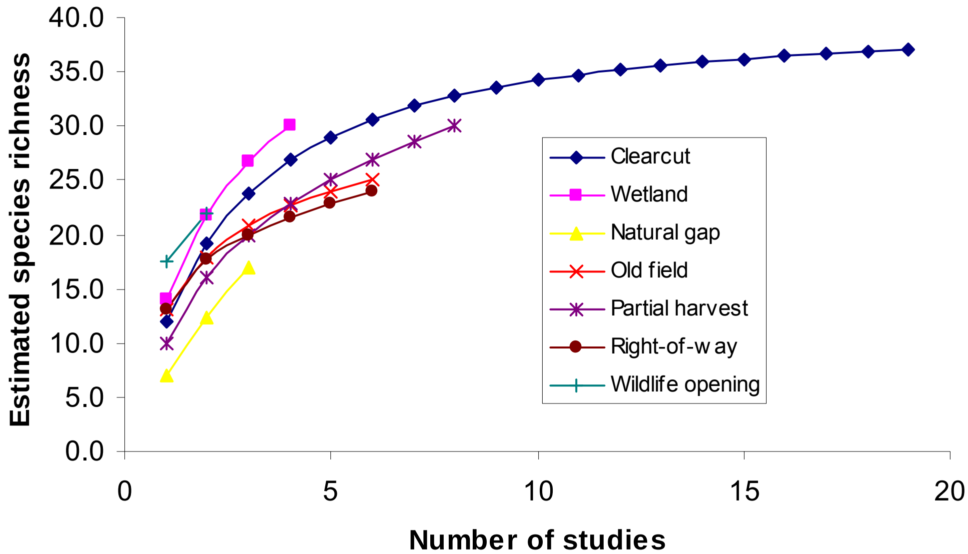


Figure 4.1. Rarefied species richness of scrub-shrub birds by habitat type. Data are expected richness of scrub-shrub birds based on subsamples of studies, as shown on the x axis.

(Askins 2001). Some scrub-shrub birds prefer such habitats (Appendix B). As an example, Bulluck & Buehler (2006) compared avian abundances in clearcuts, reclaimed mines, and power line rights-of-way. Several species preferred restored mines or rights-of-way over clearcuts. For instance, Golden-Winged Warblers were far more abundant in reclaimed mines than the other two habitats, and Song Sparrows reached their highest densities in power line rights-of-way. Similarly, Fink et al. (2006) found that several species differed in abundance between forest edges, clearcuts, and limestone glades. Thus, the distinct habitat preferences of individual bird species cause different scrub-shrub habitats to harbor different bird communities. If clearcuts have been overemphasized as habitat for scrub-shrub birds, then wetlands and old fields are the habitats most in need of additional attention from managers. Both of these habitat types harbor species that are essentially habitat specialists and avoid clearcuts. In addition, rarefied estimates of species richness were higher in wetlands than any other habitat.

For several habitat types, including managed wildlife openings, shrubby wetlands, and natural canopy gaps, bird communities remain poorly described. In particular, we found little information about habitat usage by birds of boreal forests, found in northern New England. Rusty Blackbirds, for instance, were found only in clearcuts in our review. This species, however, is generally an inhabitant of bogs and wetlands (Appendix B); we lacked information from such habitats in the range of this species. Future research should be aimed at documenting avian habitat usage in poorly sampled habitats and regions. In addition, compara-

<u>*Table 4.1 continued.*</u>

[c]Webb et al. 1979, King & DeGraaf 2000, Talbott & Yahner 2003, Hagan et al. 1997, Annand & Thompson 1997, Rodewald & Yahner 2000, Simon et al. 2000, Freedman et al. 1981

[d]Burris & Haney 2005, Greenberg & Lanham 2001, Prather & Smith 2003

[e]Butcher et al. 1981, Kricher 1973, Bulluck & Buehler 2006, Johnston & Odum 1956, Bay 1996, Shugart & James 1973

[f]Bulluck & Buehler 2006, Confer & Pascoe 2003, Yahner et al. 2003, Anderson et al. 1977, Yahner et al. 2002, Kroodsma 1982

[g]King & Collins 2005, Chandler 2006

[h]Total number of habitats used by the species.

tive studies that allow determination of relative densities in different habitats would also be useful to establish habitat preferences. To date, few such studies have been conducted (Bulluck & Buehler 2006; Fink et al. 2006).

Preferences for Habitat Structure and Composition

Birds' preferences for distinct habitat types are generally based on three factors: vegetation structure, plant species composition, and moisture/topographic position. Habitat structure is important because the vertical and horizontal distribution of foliage influences foraging opportunities and cover for nesting, roosting, and escaping predators (Hildén 1965). Birds, therefore, show species-specific preferences for taller or shorter vegetation, herbaceous groundcover, or an open or closed canopy, to name just a few possibilities (e.g. Anderson & Shugart 1974; Willson 1974). Plant species composition can also be important in habitat selection (e.g. Holmes & Robinson 1981; Wiens & Rotenberry 1981). Many birds specialize in foraging on or nesting in certain types of plants (e.g. Parrish 1995; Gabbe et al. 2002). Thus, whether a clearcut has deciduous or coniferous saplings can be important in determining which scrub-shrub birds are present. Similarly, for non-migratory birds, the presence of plants that provide food during winter can be the critical feature in habitat usage (Schroeder 1985). Finally, many bird species show distinct preferences for a specific topographic position: dry, upland habitats or low, wet areas (e.g. Janes 1985). Shorebirds such as American Woodcock and Wilson's Snipe, for instance, require moist or wet soil for foraging on earthworms and other soil-dwelling invertebrates (see Appendix B).

For managers, understanding habitat preferences is important because management activities can determine the type of habitat that exists at any location, the structure of the vegetation, and where on the landscape scrub-shrub habitat is located. All of these factors can influence the bird community. Planting seedlings or applying herbicide, for instance, can determine how many or what types of trees grow up in a clearcut (Wagner et al. 2004). Similarly, fire can be used to create a patchy vegetation structure, with open areas and scrubby patches intermingled, that may be preferred by some scrub-shrub birds (Price et al. 2003). In Appendix B, we describe habitat usage by scrub-shrub birds of New England based on a literature review. Because most scrub-shrub birds will use a variety of different habitat types and successional stages (see below), describing habitat preferences accurately is difficult. For each species, therefore, we have attempted to summarize the most salient features in their habitat usage at a general level. Habitat preferences can, however, vary geographically (Collins 1983; Vali et al. 2004). For managers interested in habitat usage by birds in a specific location, we suggest you also consult region-specific references such as breeding bird atlases.

Effects of Succession on Scrub-shrub Birds

Early-successional forests created by logging make up most of the scrub-shrub habitat in New England (Chapter 2). The U.S. Forest Service, in its Forest Inventory and Analysis (FIA) program, defines "seedling-sapling" forests as stands with trees up to 12.5 cm in dbh (Brooks 2003), and researchers have treated this size class as synonymous with scrub-shrub habitat. Treating clearcuts as a unitary habitat, however, type may be misleading. From the first growing season after trees are harvested, the vegetation in a clearcut changes rapidly due to succession. Thus, the type of habitat in a clearcut and the bird community present will largely be a function of the clearcut's age (DeGraaf 1991).

Successional changes in clearcuts typically follow a consistent pattern: initially, logged areas harbor dense, low vegetation including shrubs, saplings, and herbaceous plants released by removal of the canopy (Martin & Hornbeck 1989). In this stage, nearly all of the foliage is found within 1 m of the ground (Aber 1979). Over the next several years, the vegetation rapidly increases in height, and shrubs and saplings replace herbaceous vegetation (Martin & Hornbeck 1989). After roughly 10 years, fast-growing trees begin to form a canopy, shading the vegetation below (Aber 1979). This results in a decrease in the cover of understory shrubs and saplings. By the time the canopy closes completely, roughly 20 years after clearcutting, understory vegetation has almost completely disappeared, shaded out by a the dense overstory (Keller et al. 2003). With little or no understory vegetation, scrub-shrub habitat has effectively disappeared by this point in succession.

Understanding how successional changes in logged forests affect bird populations has important management implications. For instance, a bird that does not use clearcuts younger than 10 years old might best be managed using wildlife openings that are cut on longer rotations. Many wildlife openings, however, are cut or burned on much shorter schedules (Chandler 2006). Also, understanding birds' preferences for specific clearcut ages allows us to better estimate habitat availability for this community. Stands in the FIA's seedling-sapling class may be well over 20 years old (Loewenstein et al. 2000). If scrub-shrub birds prefer younger clearcuts, then current estimates of habitat availability for this community may be too high. Many studies have examined temporal changes in bird communities following logging. Because of differences in site index, climate, and plant species composition, individual clearcuts will vary in the pace of succession (Martin & Hornbeck 1989; Anderson et al. 2006). Thus, we felt that the best approach to understanding how bird populations change after logging was a meta-analysis, which would reveal general trends across studies.

The goal of the meta-analysis was to determine how populations of scrub-shrub birds change over time after logging. Data for the meta-analysis came from studies reporting the abundances of birds in clearcuts of defined age in eastern North America. All studies took place in forest types that occur in New England (oak-hickory, spruce-fir, and northern hardwoods; Smith 1979). To avoid confounding area sensitivity with habitat preferences, we used only studies in which clearcuts were at least 1 ha in size—this is the threshold for area sensitivity in many scrub-shrub species (Chapter 5). Because we were interested in the time period before closed canopies develop, eliminating scrub-shrub habitat, we used data from only the first 20 years following clearcutting. For studies reporting results from multiple sites of the same age, we averaged the abundances of each species across same-aged sites to create a single data point for each species and year. A few studies reported results averaged across clearcuts of a range of ages (e.g. 6-12 years post-cutting). For these studies, we used the midpoint of the age range as the age of the clearcut. We accounted for the imprecision of the age estimates by giving observations from these studies a lower weight in the meta-analysis than studies reporting exact ages (see below).

Studies used a variety of different methods to estimate avian abundances, and it was not possible to convert all results to the same measure. Instead, we transformed observations from each study to a 0 to 1 scale. For each species in each study, we assigned the maximum density in a clearcut of any age a value of 1 and transformed all other densities by dividing by the maximum density. This, however, caused one significant problem in that studies varied widely in the range of clearcut ages studied. For instance, hypothetical study A might include only 2- and 4-year-old clearcuts while study B includes clearcuts 2, 4, 6, 8, 10, and 15 years of age. If the species' abundance actually peaks at 10 years after logging, then combining results from studies A and B could result in biased conclusions. Study A did not include the year of the bird's peak abundance but would still show a transformed abundance of 1 in year 2 or 4. To overcome this problem, in our analyses we weighted studies by the number of separate years for which abundances were reported (results were essentially identical if we weighted studies by the range of years instead). Thus, in the above example, data from study B would be weighted three times as heavily as data from study A. Because studies with more years of observation already contribute more data to the dataset than studies with fewer years, our weighting scheme effectively minimizes the effect of smaller samples on the overall results. As discussed above, we weighted observations from studies that grouped clearcuts of multiple ages together 50% as much as those that reported results from clearcuts of specific ages.

Based on previous reports (DeGraaf 1991; Keller et al. 2003), we hypothesized that bird populations would show one of four patterns of changing density over time: 1) increase with clearcut age; 2) decrease with clearcut age; 3) initial increase followed by decrease; and 4) no change over time (constant density). To choose among these alternatives, we fit four types of regression curves to the combined data for each species: constant only, age (linear), age^2 (quadratic), and a full model including both linear and quadratic terms. These curve types are flexible enough to fit the four expected patterns of change over time. We compared the fits of the four functions using Akaike's Information Criterion, corrected for small sample size (AIC_c). Using AIC_c allowed us to determine the best model for each species, while accounting for the fact that model fit automatically increases with the number of parameters (Burnham & Anderson 2002). For each species, we only took data from studies where the species occurred at least once. To ensure that sample sizes were sufficient, we only analyzed data for species that occurred in at least two studies and for which we had at least six data points.

For each bird species, we used the best model, as indicated by AIC_c, to estimate the proportion of regenerating clearcuts, 0-20 years old, that would be occupied by each species. Essentially, we assumed that at the peak of the regression curve relating clearcut age to density, the species is at its maximum possible density in regenerating clearcuts. Lower densities, therefore, indicate unused habitat (i.e. vacant territories). If the age distribution of clearcuts is uniform up to year 20, then the area under the regression curve will be equal to the species' overall population as a proportion of the maximum density. Assuming, again, that lower densities indicate unused habitat, that proportion should be equivalent the proportion of clearcuts up to 20 years old that are suitable for the species. Take, for instance, a bird that only occurs in clearcuts 2, 3, and 4, years after cutting. If the bird has its peak density in year 3, and its densities are one-half of the peak value in years 2 and 4, then a total of only 10% of clearcuts up to age 20 would be occupied, 5% (1/20) for year 3 and 2.5% (0.5/20) for each of the other two years.

Overall, we found 11 studies (Table 4.2) that met our criteria for inclusion in the meta-analysis, and we analyzed successional patterns for 28 species. The studies included an average of 3.4 ± 1.9 years of data and a range (oldest clearcut – youngest clearcut) of 8.5 ± 5.8 years. For 13 species, the intercept-only model was the best, according to AIC analysis (Table 4.3). These species showed no obvious trend in abundance through succession (list in Table 4.4). For the other 15 species, the best model indicated changing abundance over time with succession. We placed these species into three groups based on how their populations changed over time since logging: 1) *Decreasers* (n = 6) peaked in density immediately after logging and decreased thereafter (Figure 4.2; Table 4.4). Regression models for decreasers generally predicted that they would disappear completely from clearcuts before year 20. 2) *Modal species* (n = 8) showed low density immediately after logging, increased for several years, and then decreased after roughly year 10 (Figure 4.3; Table 4.4). As with the decreasing species, the modal species were also predicted to disappear from clearcuts by approximately year 20. 3) *Increasers*' (n = 1) populations grew over succession. The only increaser in our sample was Black-and-white Warbler (Figure 4.4).

For the 15 species whose densities varied with clearcut age, the area under the age-density regression curve averaged 50 ± 5% of the maximum possible density (Table 4.5). Thus, the effective area of regenerating clearcuts used by these species is only one-half of the total area, assuming a uniform age distribution of clearcuts. Individual species varied widely in their occupancy of clearcuts up to age 20, from a low of just 9% for Wilson's Snipe to a maximum of 68% in Common Yellowthroat.

Decreasers, which peaked in abundance shortly after logging and then declined, generally included species that forage or nest near the ground (see Keller et al. 2003). These birds generally prefer areas with low vegetation and signifi-

Table 4.2. Studies used in the meta-analysis of successional changes in scrub-shrub bird populations.

Study	Study location	Years reported*
Hagan et al. 1997	ME	0-5, 6-20
Kerpez 1994	VA	1, 2
Yahner 1987	PA	1-3, 5-7
Titterington et al. 1979	ME	1-2, 3-5, 7-12
Morgan & Freedman 1986	NS	1, 2, 3, 5, 6, 8, 12, 20
Conner et al. 1979	VA	3, 10
Freedman et al. 1981	NS	3, 5
Keller et al. 2003	NY	2, 3, 4, 5, 6
Conner & Adkisson 1975	VA	1, 3, 7, 12
Probst 1992	MI, MN	1-3, 4-8, 8-12
Thompson et al. 1992	MO	1-10, 10-20

*Number of years after clearcutting; dashes indicate years grouped together.

Table 4.3. Results from meta-analysis of successional changes in bird populations following clearcutting. Results for each species are listed by AIC value, from lowest (best model) to highest (worst model).

Species	Model	K[a]	AIC_c[b]	ΔAIC_c[c]	Weight[d]
Ruffed Grouse	Intercept only	2	-23.77	0	0.55
n = 14[e]	Year	3	-21.99	1.79	0.22
	$Year^2$	3	-21.69	2.09	0.19
	Full model	4	-18.06	5.71	0.03
Wilson's Snipe	Full model	4	-25.15	0	0.45
n = 14	Year	3	-24.25	0.90	0.29
	Intercept only	2	-23.18	1.97	0.17
	$Year^2$	3	-22.15	3.00	0.10
Ruby-throated Hummingbird	Full model	4	-59.22	0	0.75
n = 25	Intercept only	2	-55.83	3.39	0.14
	$Year^2$	3	-54.60	4.62	0.07
	Year	3	-53.44	5.79	0.04
Alder Flycatcher	Intercept only	2	-35.16	0	0.39
n = 16	Full model	4	-35.16	0.01	0.38
	$Year^2$	3	-33.13	2.04	0.14
	Year	3	-32.29	2.88	0.09
Carolina Wren	Year	3	-19.46	0	1.00
n = 6	$Year^2$	3	-8.05	11.41	0.00
	Intercept only	2	-4.35	15.11	0.00
	Full model	4	5.33	24.79	0.00
Gray Catbird	Intercept only	2	-55.24	0	0.39
n = 25	$Year^2$	3	-54.76	0.49	0.30
	Year	3	-54.10	1.15	0.22
	Full model	4	-52.41	2.84	0.09
Brown Thrasher	Intercept only	2	-9.09	0	0.82
n = 8	$Year^2$	3	-4.60	4.49	0.09
	Year	3	-4.60	4.50	0.09
	Full model	4	4.71	13.81	0.00
Cedar Waxwing	Intercept only	2	-6.07	0	0.92
n = 6	$Year^2$	3	0.09	6.16	0.04
	Year	3	0.13	6.21	0.04
	Full model	4	30.05	36.13	0.00
Blue-winged Warbler	Intercept only	2	-3.18	0	0.98
n = 6	$Year^2$	3	5.83	9.01	0.01
	Year	3	6.47	9.65	0.01
	Full model	4	32.85	36.03	0.00
Golden-winged Warbler	Intercept only	2	-13.96	0	0.68
n = 10	Full model	4	-10.58	3.38	0.13
	$Year^2$	3	-10.44	3.52	0.12
	Year	3	-9.75	4.21	0.08
Nashville Warbler	Full model	4	-25.76	0	1.00
n = 8	Intercept only	2	-12.82	12.93	0.00
	$Year^2$	3	-9.07	16.68	0.00
	Year	3	-7.83	17.93	0.00

Table 4.3 continued.

Species	Model	K[a]	AIC_c[b]	ΔAIC_c[c]	Weight[d]
Chestnut-sided Warbler	Full model	4	-87.32	0	1.00
n = 30	Intercept only	2	-74.90	12.41	0.00
	$Year^2$	3	-74.89	12.43	0.00
	Year	3	-72.76	14.56	0.00
Magnolia Warbler	Intercept only	2	-27.23	0	0.59
n = 13	Year	3	-25.22	2.01	0.21
	$Year^2$	3	-24.46	2.77	0.15
	Full model	4	-22.39	4.84	0.05
Prairie Warbler	Intercept only	2	-11.36	0	0.75
n = 8	Year	3	-8.23	3.13	0.16
	$Year^2$	3	-6.89	4.47	0.08
	Full model	4	-3.49	7.88	0.01
Black-and-white Warbler	Year	3	-79.45	0	0.63
n = 26	Full model	4	-78.15	1.30	0.33
	$Year^2$	3	-74.29	5.16	0.05
	Intercept only	2	-60.55	18.90	0.00
Mourning Warbler	Full model	4	-54.69	0	0.44
n = 24	Intercept only	2	-53.60	1.09	0.25
	$Year^2$	3	-53.17	1.51	0.21
	Year	3	-51.82	2.87	0.10
Common Yellowthroat	Full model	4	-72.37	0	0.93
n = 26	$Year^2$	3	-66.65	5.71	0.05
	Year	3	-62.76	9.61	0.01
	Intercept only	2	-61.28	11.08	0.00
Canada Warbler	Full model	4	-52.82	0	0.66
n = 22	Intercept only	2	-50.57	2.25	0.22
	Year	3	-48.08	4.74	0.06
	$Year^2$	3	-47.92	4.90	0.06
Yellow-breasted Chat	Intercept only	2	-5.57	0	0.97
n = 6	Year	3	1.84	7.42	0.02
	$Year^2$	3	3.34	8.92	0.01
	Full model	4	24.33	29.90	0.00
Eastern Towhee	$Year^2$	3	-38.32	0	0.38
n = 17	Full model	4	-38.31	0.01	0.38
	Intercept only	2	-36.20	2.12	0.13
	Year	3	-35.91	2.41	0.11
Field Sparrow	Intercept only	2	-26.44	0	0.66
n = 13	$Year^2$	3	-23.61	2.83	0.16
	Year	3	-23.09	3.35	0.12
	Full model	4	-21.64	4.80	0.06
Song Sparrow	Year	3	-50.59	0	0.50
n = 21	Full model	4	-49.36	1.23	0.27
	$Year^2$	3	-48.42	2.17	0.17
	Intercept only	2	-46.30	4.29	0.06

Table 4.3 continued.

Species	Model	K[a]	AIC_c[b]	ΔAIC_c[c]	Weight[d]
White-throated Sparrow	Year	3	-74.89	0	0.46
n = 24	$Year^2$	3	-74.66	0.23	0.41
	Full model	4	-72.21	2.68	0.12
	Intercept only	2	-63.26	11.63	0.00
Dark-eyed Junco	Full model	4	-54.39	0	0.89
n = 18	Year	3	-50.00	4.40	0.10
	$Year^2$	3	-43.95	10.44	0.00
	Intercept only	2	-41.17	13.22	0.00
Northern Cardinal	Intercept only	2	-6.10	0	0.92
n = 7	$Year^2$	3	0.00	6.10	0.04
	Year	3	0.66	6.76	0.03
	Full model	4	11.06	17.16	0.00
Indigo Bunting	$Year^2$	3	-27.97	0	0.61
n = 12	Year	3	-26.43	1.55	0.28
	Full model	4	-23.42	4.56	0.06
	Intercept only	2	-22.78	5.19	0.05
American Goldfinch	Intercept only	2	-43.18	0	0.43
n = 21	$Year^2$	3	-42.26	0.92	0.27
	Year	3	-41.48	1.69	0.19
	Full model	4	-40.43	2.74	0.11
Rusty Blackbird	Intercept only	2	-16.67	0	0.74
n = 10	Year	3	-13.23	3.44	0.13
	$Year^2$	3	-12.99	3.68	0.12
	Full model	4	-7.38	9.29	0.01

[a]Number of parameters in model (including constant and error).
[b]Akaike's information criterion adjusted for small sample size.
[c]Difference between model AIC_c and the minimum AIC_c.
[d]Akaike weight indicating relative support for the model.
[e]Total number of observations used in meta-analysis.

cant herbaceous groundcover. For instance, cover of grasses and forbs is important in habitat selection for four of the six decreasers—Indigo Bunting, Dark-eyed Junco, White-throated Sparrow, and Song Sparrow (see Appendix B). The decline of these species with clearcut age is likely due to decreasing cover of herbaceous vegetation as woody plants grow during succession (Martin & Hornbeck 1989).

The modal species initially increased with clearcut age before eventually declining. During the first several years after clearcutting, vegetation height, foliage density, and overall leaf area increase each year (Keller et al. 2003). These variables may be important factors in habitat selection for modal species. Out of the eight modal species, seven either nest in the shrub layer or are foliage-gleaning insectivores, both of which would be expected to respond to increased shrub cover and leaf area. Nearly all of the modal species peaked in abundance around year 10. Around this time, fast-growing trees begin to form a canopy and shade out the understory vegetation (Aber 1979). Thus, foliage, which had previously been uniformly been distributed between the ground and the top of the vegetation, begins to be become concentrated in the canopy. Between 10 and 20 years after clearcutting, the developing canopy becomes taller and denser, and the understory vegetation decreases as a result (Keller et al.

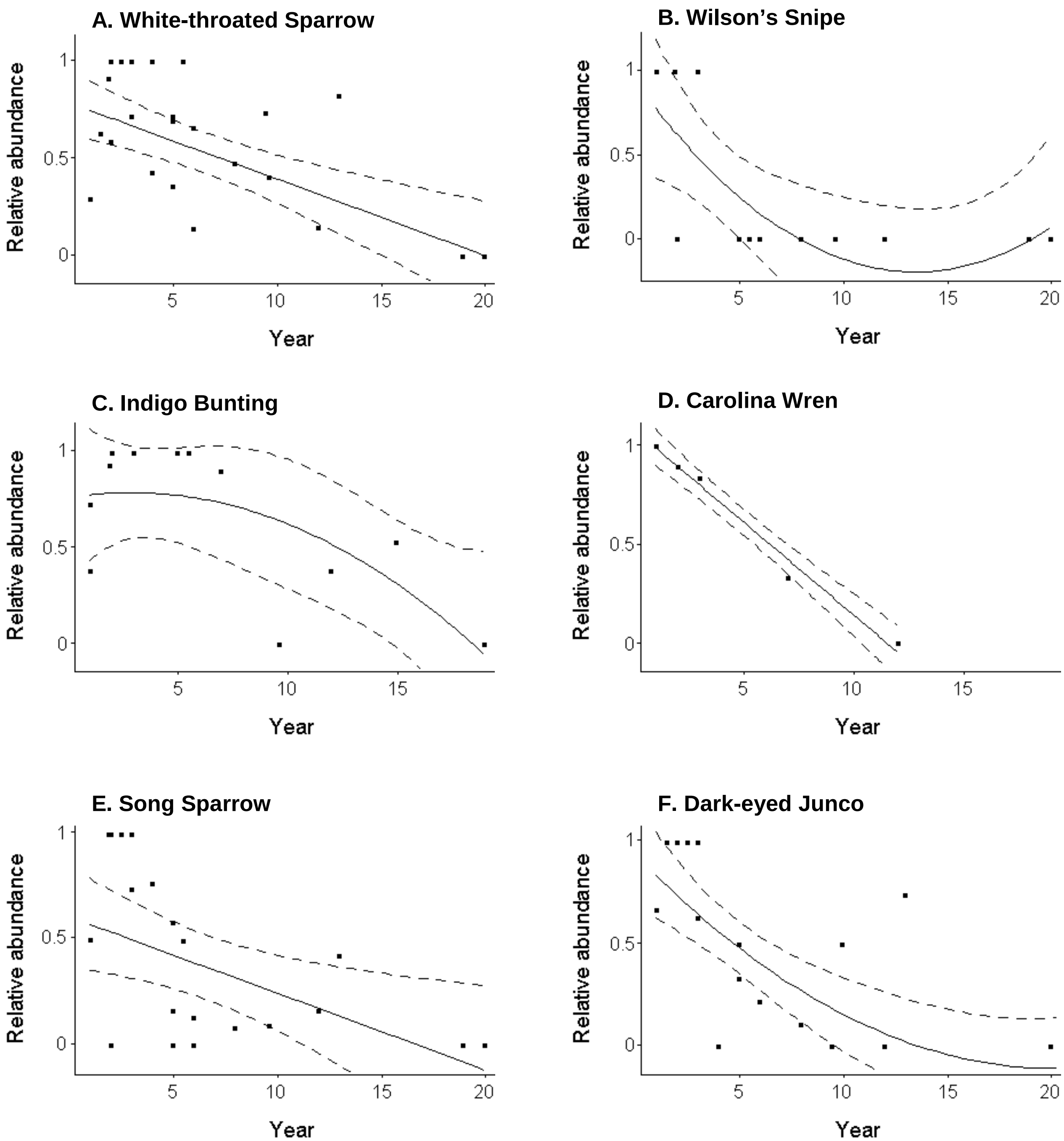


Figure 4.2. Abundances of decreasers in clearcuts as a function of time since logging. Data points are from a meta-analysis of successional changes in bird populations after logging. Regression curve (solid line) and 95% confidence intervals (dashed lines) are based on the best model according to AIC$_c$. Apparent lack of fit of some regression curves may be due to differential weighting of data points (see text for details).

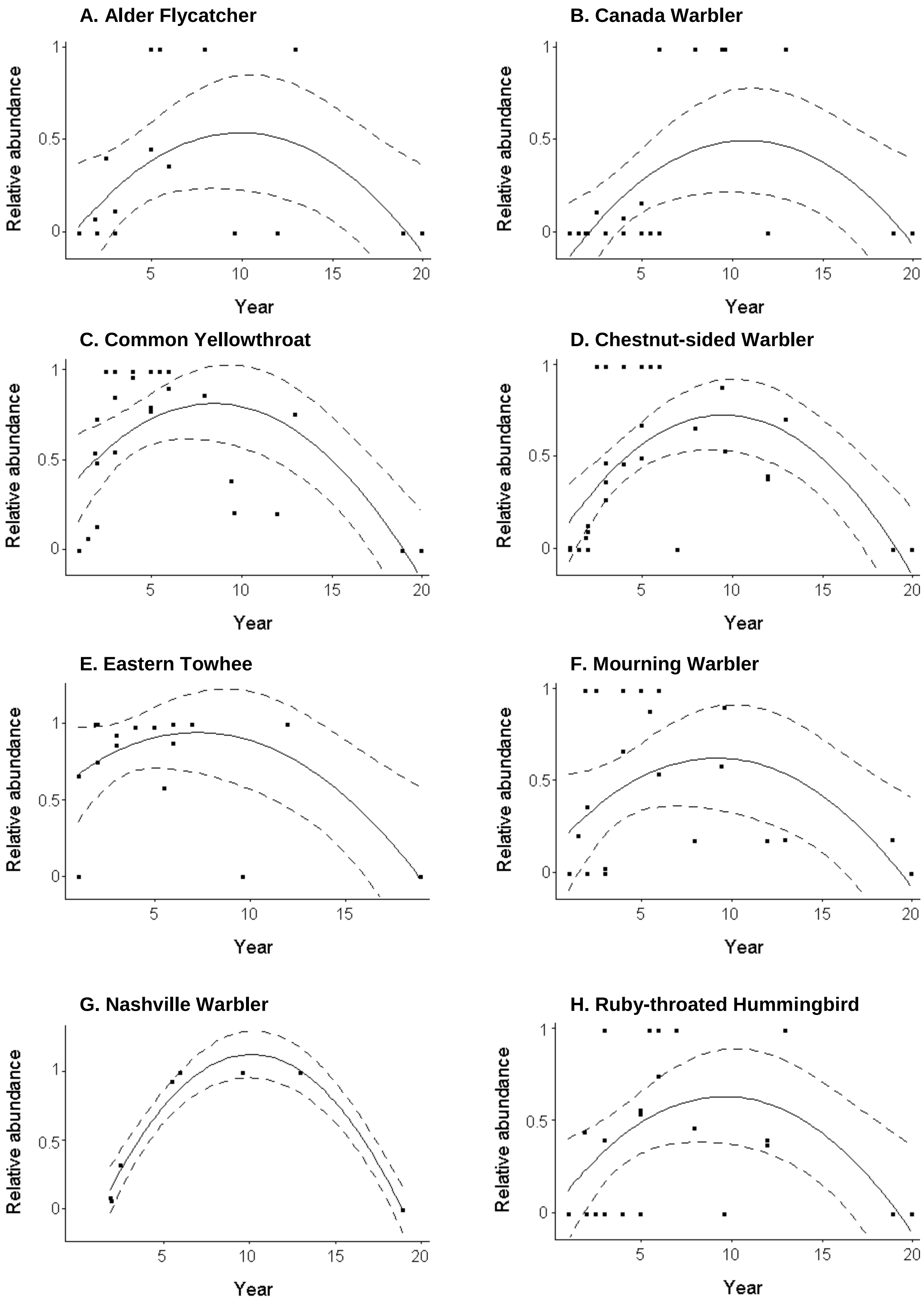


Figure 4.3. Abundances of modal species as a function of time since clearcutting. See Figure 4.2 for details.

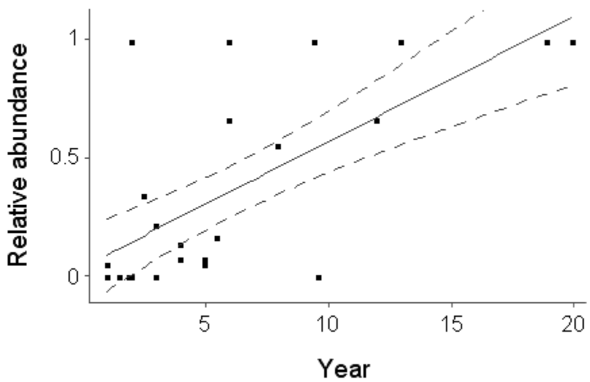


Figure 4.4. Abundance of Black-and-white Warbler in clearcuts as a function of time since logging. See Figure 4.2 for details.

Table 4.4. Summary of scrub-shrub birds' responses to succession.

Successional pattern	Species
Decrease	Wilson's Snipe
	Carolina Wren
	Song Sparrow
	White-throated Sparrow
	Dark-eyed Junco
	Indigo Bunting
Modal	Ruby-throated Hummingbird
	Alder Flycatcher
	Canada Warbler
	Nashville Warbler
	Mourning Warbler
	Chestnut-sided Warbler
	Common Yellowthroat
	Eastern Towhee
Increase	Black-and-White Warbler
No Response	Ruffed Grouse
	Gray Catbird
	Brown Thrasher
	Cedar Waxwing
	Blue-winged Warbler
	Golden-winged Warbler
	Magnolia Warbler
	Prairie Warbler
	Yellow-breasted Chat
	Field Sparrow
	Northern Cardinal
	American Goldfich
	Rusty Blackbird

Table 4.5. Occupancy of regenerating clearcuts, up to age 20, by scrub-shrub birds as a proportion of the maximum possible density.

Species	Proportion
Wilson's Snipe	0.09
Ruby-throated Hummingbird	0.64
Carolina Wren	0.13
Nashville Warbler	0.57
Chestnut-sided Warbler	0.63
Black-and-white Warbler	0.51
Mourning Warbler	0.67
Common Yellowthroat	0.68
Canada Warbler	0.55
Eastern Towhee	0.69
Song Sparrow	0.40
White-throated Sparrow	0.50
Dark-eyed Junco	0.25
Indigo Bunting	0.62

2003). Modal species, because they prefer areas with a dense layer of shrubs and saplings, decrease accordingly. Black-and-white Warbler was the only species that increased throughout succession. This species frequently forages on tree trunks and may, therefore, be less tied to the shrub/sapling layer than other birds in this community (Appendix B). Still, we include Black-and-white Warbler on our list of scrub-shrub birds because they are significantly more abundant in early-successional habitat than in forests (Chapter 1).

Several species showed no apparent response to successional change. For some of these species, sample sizes and statistical power may have been too low to detect change over time. For instance, Rusty Blackbird appeared in only two studies and only in 3-year-old clearcuts in each of those studies. While this could indicate a preference for young clearcuts, these data were too sparse for the best model to include the effect of year. With larger sample sizes, we would probably have detected responses to succession in this and other species. For other birds such as Cedar Waxwing or American Goldfinch, habitat selection is largely based on the presence of food plants (fruits for waxwings and forbs in the sunflower family for the goldfinch), and habitat structure is relatively unimportant. Finally, for some birds, all successional stages up to 20 years may be more or less equivalent, until the shrub layer begins to thin out around 15 years after harvest.

The responses of individual scrub-shrub birds to forest regeneration produce the broader, community-wide patterns of succession that have been well-studied in the past. Immediately after clearcutting, relative few bird species use clearcuts, and overall bird abundances tend to be low (May 1982; Helle & Mönkkönen 1990). The low vegetation present in a very young clearcut restricts usage to decreasers that forage or nest on the ground, such as Wilson's Snipe. As the vegetation grows taller, modal species that feed and nest in shrubs and small trees join the community. The overall density and diversity of birds peaks around year 10 in regenerating clearcuts, corresponding with the peak in foliage density (Helle & Mönkkönen 1990; Keller et al. 2003). Beyond year 10, as a tree canopy begins to develop and groundcover thins, the abundance and diversity of birds declines. Decreasers disappear first, followed shortly thereafter by birds that nest and forage in shrubs and saplings. Eventually, scrub-shrub birds are largely replaced by birds more typical of poletimber or mature forests. By year 20, the only scrub-shrub birds inhabiting clearcuts are increasers such as Black-and-White Warbler (DeGraaf 1991; Keller et al. 2003).

For managers, our findings have three major implications. First, frequently mowing, burning, or cutting vegetation in managed openings may eliminate habitat for birds that prefer more advanced successional stages (see also Chandler 2006; Zuckerberg & Vickery 2006). We found that densities of many birds peaked around 10 years after clearcutting, so the common practice of managing openings on shorter rotations may not allow habitat to develop sufficiently for these species to reach their potential populations. If managers are interested in maintaining populations of most birds in this community, then trees and shrubs should be allowed to grow for roughly 10 to 15 years before returning openings to an earlier successional stage. Second, specialization of scrub-shrub birds along a narrow portion of the successional sere means that only a portion of forests termed "early-successional" are actually suitable habitat for any one species. For many species, the actual area occupied may be less than half of the total area of regenerating clearcuts (Table 4.4). This suggests that recent assessments of habitat availability for scrub-shrub birds may be too optimistic because not all habitats will be used (Brooks 2003). Finally, because scrub-shrub birds generally disappear from clearcuts by 20 years after logging, the continued creation of new clearcuts is vital to the maintenance of bird populations. This is especially true given the fact that the majority of scrub-shrub habitat in New England is regenerating clearcuts (Chapter 2).

Conclusion

Many scrub-shrub birds are habitat specialists, restricted to distinct habitat types, areas with specific vegetation structure, or narrow time periods during forest succession. Moreover, because of specificity to successional stages, only a fraction of the early-successional forests formerly considered scrub-shrub habitat is actually suitable for many species.

Managing this bird community will require providing a variety of different habitat types and configurations; no one-size-fits-all strategy will meet the needs of all species. As a result, conservation strategies for scrub-shrub birds may be expensive, as the most cost-effective tool, clearcutting, will not provide habitat for the entire bird community. While logging will remain the most important source of scrub-shrub habitats, preservation of existing habitats such as shrubby wetlands and development of new habitats like wildlife openings and old fields allowed to undergo succession should be a high priority in managing this bird community. Old fields may be especially useful, as they can maintain scrub-shrub habitat without management for decades and may be used by many birds of conservation concern, including Blue- and Golden-winged Warblers and Northern Bobwhite (Chapter 9).

The habitat preferences of scrub-shrub birds are reasonably well understood on a small scale. How these birds respond to large-scale habitat configuration is, however, more of a mystery. We address the question of patch and landscape effects on scrub-shrub birds in the next chapter of this report.

Appendix B. Habitat preferences of scrub-shrub birds.

Descriptions are based on accounts in the *Birds of North America* series, DeGraaf & Yamasaki (2001), and the following: Burris & Haney (2005), Cade (1986), Cade & Sousa (1985), Chandler (2006), Confer & Knapp (1981), Confer & Pascoe (2003), Derleth et al. 1989, Dessecker & McAuley (2001), Hagan & Heehan (2002), King & DeGraaf (2000), Klaus & Buehler (2001), Marsi (1979), Mehlhop & Lynch (1986), Moore (1980), Morgan & Freedman (1986), Morimoto & Wasserman (1991), Niemi & Hanowski (1984), Probst et al. (1992), Santillo et al. (1989), Schroeder (1985), Scott et al. (1998), Sousa (1983), Thompson & Capen (1988), Titterington et al. 1989.

Alder Flycatcher – Dense, wet stands of shrubs and saplings with little or no tree canopy. Especially in wetlands such as bogs, swamps, and the margins of streams and lakes.

American Goldfinch – Open areas, with trees few or scattered if present. Most common in weedy areas with an abundance of composite flowers (especially thistles and dandelions) which provide food (seeds) and nest material.

American Woodcock – For feeding: low areas with moist, fertile soil; will use areas with some tree cover. For roosting and displaying: open fields and thickets of dense shrubs. Often associated with aspens, alders, and birches.

Black-and-white Warbler – Dense sapling- to pole-sized trees. Deciduous forests preferred. Will use mature, closed-canopy forests in some areas.

Brown Thrasher – Open areas with dense clusters of shrubs, preferably taller than 1 m. Dry habitats with deep litter cover (for feeding) preferred.

Blue-winged Warbler – Open areas with dense cover of herbaceous vegetation and patchy shrub/ sapling cover. Will use areas with some tall trees.

Carolina Wren – Most important feature is dense shrub cover. Canopy can be open or closed.

Canada Warbler – Areas with some canopy cover and moderate to high densities of shrubs/saplings. Groundcover of moss and coarse woody debris may be important.

Cedar Waxwing – Open areas with relatively few tall trees and many berry-producing shrubs. Availability of fruit may be the most important element in habitat selection.

Common Yellowthroat – Open areas with some shrub cover and dense cover of herbaceous vegetation. Generally found in moister areas and deciduous vegetation.

Chestnut-sided Warbler – Deciduous habitats with dense shrub cover. Tolerates moderate canopy closure.

Dark-eyed Junco – Dry areas with moderate to dense cover of shrubs and herbaceous vegetation. Will use areas with taller trees if canopy is somewhat open. Slash and coarse woody debris may also be important.

Eastern Towhee – Dry, open habitats with patchy to dense shrub cover and relatively few trees.

Field Sparrow – Open, grassy areas with low to moderate shrub cover. Generally tolerates trees only if small.

Gray Catbird – Dense, tall patches of shrubs/ saplings. Generally in deciduous habitats with a low or open canopy.

Golden-winged Warbler – Open areas with patchy shrub cover and dense herbaceous vegetation. Nearly always in areas with few or no tall trees.

House Wren – Open to moderately closed deciduous habitats. Nest boxes or cavity trees > 25 cm dbh must be present for nesting.

Indigo Bunting – Open areas with moderate to dense shrub cover and dense herbaceous vegetation. Will use forest edges and areas with some tall trees, used as song posts.

Lincoln's Sparrow – Wet situations with dense shrub cover. Especially bogs and sedge meadows. Avoids areas with dense stands of trees.

Magnolia Warbler – Coniferous habitats with moderate tree cover and a dense shrub/sapling layer.

Mourning Warbler – Open to moderately closed habitats with dense shrub cover.

Nashville Warbler – Moderately open areas with dense shrub cover and a dense herbaceous layer. Almost never in unbroken forest, but will use areas with small or scattered large trees.

Northern Bobwhite – Dry, open areas with dense shrub cover up to 2 m high. Significant areas of bare ground or litter cover are important for foraging. Seed-producing grasses and forbs are important for winter food.

Northern Cardinal – Almost any habitat with some dense shrub cover. Canopy can vary from open to completely closed.

Northern Mockingbird – Open areas with dense shrub cover for nesting and bare ground or short herbaceous vegetation for foraging. Prefers areas with some elevated perches for singing.

Palm Warbler – Wet habitats with dense shrub cover and coniferous vegetation. Especially in bogs or near water.

Prairie Warbler – Open areas with trees relatively few or small and some shrub cover. Generally in areas with little herbaceous groundcover.

Ruby-throated Hummingbird – Deciduous habitats with nectar-producing flowers. Will tolerate open or closed canopies and varied levels of shrub cover.

Rusty Blackbird – Wet areas with dense cover of shrubs and saplings, especially from 2 to 4 m high. Most common in swamps, bogs, and other wet habitats.

Ruffed Grouse – Areas with moderate canopy closure and dense shrub/sapling stands at least 1.5 m tall. Prefers deciduous and mesic situations, with aspens particularly important as a winter food source.

Song Sparrow – Tall, dense shrub/sapling cover with significant cover of herbaceous vegetation. Prefers relatively moist situations.

Tennessee Warbler – Open canopy with dense, low shrub cover and many young trees. Prefers moist areas such as swamps and bogs. May prefer conifers, though uses alders in some areas.

White-eyed Vireo – Areas with dense shrub cover, especially near the ground. Canopy coverage can vary widely but prefers deciduous vegetation.

Willow Flycatcher – Dense, patchy thickets, usually in drier areas than Alder Flycatcher.

Wilson's Snipe – Wet, open areas with variable shrub cover. Especially bogs and shrub swamps.

Wilson's Warbler – Wet, open areas with dense shrub cover and little or no tree cover. Especially in riparian areas and bogs.

Whip-poor-will – Generally in dry, open areas with sparse understory vegetation. Avoids dense stands of trees and frequently uses clearings for foraging.

White-throated Sparrow – Areas with dense shrub cover and significant herbaceous vegetation. Will use areas with significant tree cover. Prefers coniferous habitats but will use deciduous.

Yellow-breasted Chat – Open areas with dense, scattered shrubs. Generally avoids tall trees but will use open forests with dense understory.

Yellow-billed Cuckoo – Areas with dense shrubs or saplings. Uses areas with few trees as well as forests with scattered openings. Almost exclusively in deciduous habitats and often near water.

Yellow Warbler – Wet habitats with dense shrub cover less than 2 m high. Prefers deciduous vegetation and few or no trees. Especially common in willows and other hydrophytic shrubs.

Chapter 5. Patch and Landscape Ecology

Introduction

Researchers have long known that birds choose territories based on characteristics of the vegetation. Recently, however, ecologists have learned that conditions well beyond an animal's territory can affect habitat selection. In fact, habitat selection occurs at various scales, from the territory to the patch to the broader landscape surrounding a habitat (Cushman & McGarigal 2002). A bird's territory, for instance, may occupy just 1 ha. At a larger scale, that territory will be located in a patch—a contiguous area of habitat such as a woodlot or a field. And at an even larger scale, the woodlot or field will be located in a landscape that contains a variety of patches of different habitats. The organization and composition of habitats at these scales can profoundly impact the organisms living there (Turner 2005).

For birds, patch and landscape effects can manifest themselves in at least three different ways. First, many birds show area sensitivity, a tendency to avoid small habitat patches (Robbins et al. 1989a; Herkert 1994; Connor et al. 2000). Area-sensitive birds eschew isolated woodlots, small grasslands, or other habitat fragments. These species may require large, contiguous areas of habitat to persist. Second, some birds are less abundant near habitat edges, or ecotones, such as the border between a forest and a field (Parker et al. 2005). Finally, on a larger scale, some birds are sensitive to characteristics of the landscape. For instance, birds may be more abundant in landscapes that have more of their preferred habitat (Howell et al. 2000).

Much of what we know about landscape ecology has come from research on forest birds. Forest fragmentation—breaking large, contiguous forests into small, isolated patches—appears very harmful to forest birds (Robinson et al. 1995b). Many birds will not breed in small forest fragments, and birds nesting in small patches often experience high predation rates (Hoover et al. 1995; Roberts & Norment 1999). Similarly, birds that nest near forest edges, especially adjacent to agricultural fields, may suffer from high parasitism and predation rates (Gates & Gysel 1978; Manolis et al. 2000). As a result, creating or protecting intact, contiguous forests has become the primary management strategy for forest birds (Thompson 2005).

While the landscape ecology of forest birds is well understood, landscape impacts on scrub-shrub birds have received much less attention. A few studies have shown that scrub-shrub birds avoid small patches such as group-selection cuts (Annand & Thompson 1997; Costello et al. 2000). In some areas, public opposition to clearcutting is causing the practice to be curtailed and replaced by group-selection harvests (Askins 1994, 2001). Areas managed for scrub-shrub birds, such as wildlife openings, are often small and surrounded by forests (Overcash et al. 1989; Chandler 2006). If scrub-shrub birds are like forest birds in their responses to patch and landscape structure, then such small, scattered patches may not provide suitable habitat.

Understanding how scrub-shrub birds respond to habitat configuration on large scales is critical to developing effective management programs for these declining species. Here, we review the patch and landscape ecology of scrub-shrub birds. While the number of published studies in this area is small, we were able to conduct a meta-analysis of edge effects on the abundance of early-successional birds. We also synthesized the results from studies of how patch size and corridor width affect shrubland bird populations. Finally, we identify several areas in need of additional research.

Edge Effects

Despite earlier beliefs that edges can benefit game animals that require interspersion of different habitats (Leopold 1933), edges are now considered hostile landscapes for many songbirds. Weather conditions near edges may be more extreme than in habitat interiors (Saunders et al. 1991), so that forest edges, for instance, are warmer, windier, and drier than forest interiors (Chen et al. 1999). As a result, some bird species appear to avoid edges (Parker et al. 2005). When birds do nest near edges, they may experience high rates of nest predation (Batary & Baldi 2004). This may be because predators are more abundant or active along edges than in patch interiors (Chalfoun et al. 2002).

Most research on edge avoidance has been from the perspective of forest-breeding birds. In fact, scrub-shrub birds are often considered "edge species" in studies of forest fragmentation (e.g. Whitcomb et al. 1981; Freemark & Collins 1992). In landscapes that consist of only mature forest and open fields, scrub-shrub birds sometimes occur along forest edges. In such landscapes, however, the edges of woodlots may be the only areas with any scrub-shrub habitat. Still, this does not necessarily indicate a general affinity for ecotones (Imbeau et al. 2003), as scrub-shrub birds may have a different response to edges in actual scrub-shrub habitats such as clearcuts or old fields. How scrub-shrub birds use edge habitats has important implications for conservation of this bird community. The borders of clearcuts may be areas of high predator activity, and nest predation rates there can be high (King et al. 1998; Manolis et al. 2000; Flaspohler et al. 2001). For small patches of scrub-shrub habitat surrounded by forest, the entire patch may be subject to edge effects. Currently, the extent to which scrub-shrub birds are affected by edges is currently unknown. To address this research need, we conducted a meta-analysis to determine how scrub-shrub birds use edges and interiors of scrub-shrub habitats.

We began by conducting a literature search for studies comparing the abundances of birds in the interior and edge of scrub-shrub habitat. We searched for studies using *Biological Abstracts*, *ISI Web of Knowledge*, and the reference sections of studies we located. Because New England is heavily forested, forest is the habitat most likely to abut shrublands. Thus, we used studies where the habitat surrounding the early-successional habitat was mature forest. We only used studies from New England or from eastern North America in forest types found in New England. To avoid confounding edge effects with area sensitivity, we only included studies in which the scrub-shrub "interior" habitat was at least 1 ha in size. This should be below the threshold for area effects in scrub-shrub birds (see below). To ensure adequate sample sizes, we only analyzed data for species that occurred in two different studies and for which we had at least six data points.

Our response variable for the meta-analysis (the "effect size") was the standardized difference between the bird's abundance in the patch interior and the edge. For each species in each study, this was computed as $(d_i - d_e)/s$, where d_i is the bird's density in the interior, d_e is the density in the edge, and s is the pooled standard deviation (Lipsey & Wilson 2001). This is the difference between interior and edge habitats relative to the variation among replicates. Effect sizes greater than 0 indicate edge avoidance while negative effect sizes indicate attraction to edges.

Of the seven studies we reviewed, only four presented standard errors of density estimates. To estimate effect sizes for the three remaining studies (DeGraaf 1992; Kerpez 1994; Talbott & Yahner 2003), we had to estimate their standard errors. We assumed that the coefficients of variation for observations in those three studies were equal to those in the four studies that reported error levels. The average coefficient of variation (CV) for the studies that included standard errors was 69%. We assumed that each observation in the remaining studies had a CV of 69% as well, and then we calculated effect sizes accordingly. Results were robust to the CV estimate we used; even if our assumed CV was twice as high (138%) for studies without reported error levels, results were still significant for seven of the eight species that had significant edge effects with a CV of 69%.

All seven studies used in our analyses took place in recent clearcuts that bordered mature forest (Table 5.1). Overall, birds tended to avoid edges (mean effect size = 0.72 ± SE of 0.01). All 17 species that we analyzed had positive effect sizes, and 8 species' effect sizes were significantly different from zero, with two others nearly significant at $P = 0.06$ (Table 5.2). Furthermore, when analyzed by study, six of the seven studies showed significant avoidance of edges overall (Table 5.1). Thus, New England's scrub-shrub birds appeared to avoid edges.

The eight species that showed significant edge avoidance in the meta-analysis have previously been labeled as "edge species" in studies of forest fragmentation (Whitcomb et al. 1981; Freemark & Collins 1992). Some, such as Indigo Bunting, Field Sparrow, and Yellow-breasted Chat, have actually been termed "edge specialists" (Hansen & Urban 1992; Villard 1998). The results of our meta-analysis suggest that scrub-shrub birds generally avoid edges or are, at best, neutral towards them. This suggests that most scrub-shrub birds use forest edges only when more suitable habitats

Table 5.1. Studies used in the meta-analysis of edge effects on abundance of scrub-shrub birds.

Study	Study loc.	*N*[a]	Effect size[b] (mean ± SE)
DeGraaf 1992	NH	8	0.61 ± 0.04
Fink et al. 2006	MO	6	1.03 ± 0.14
Rodewald & Vitz 2005	OH	24	0.69 ± 0.02
Talbott & Yahner 2003	PA	20	0.91 ± 0.02
Yahner 1987	PA	6	0.01 ± 0.07
Elliott 1987	ME	8	0.78 ± 0.07
Kerpez 1994	VA	8	0.83 ± 0.10

[a]Number of study sites, including both edge and interior sites.
[b]The difference in abundance between patch edge and center, scaled by within-study standard deviation.

are unavailable in the landscape (Imbeau et al. 2003). This may be the case in agricultural landscapes that lack scrub-shrub habitat, forcing birds to utilize forest edges. Thus, when scrub-shrub birds breed in the edges of forest patches, it may be a case of lack of suitable habitat rather than a preference for edges.

Why some birds avoided edges was not revealed by the studies that we reviewed. One possibility is that habitat quality, as determined by vegetation structure or food availability, differs between interior and edge portions of openings. Rodewald and Vitz (2005), however, found that neither habitat structure nor food availability (arthropods and fruit) differed between edges and centers of clearcuts. Similarly, Shure & Phillips (1991) found that arthropod abundance in forest openings did not differ between patch centers and edges. Past research has shown that microclimate changes predictably as one moves from the edge to the center of a clearcut, the latter being sunnier, drier, and warmer than the edge (Godefroid et al. 2006). As a result, plant species composition and vegetation structure can differ between edges and centers of clearcuts (Minckler & Woerheide 1965). Finally, birds may be less abundant near edges because of passive displacement, restrictions on territory placement along edges (King et al. 1997).

The effects of edges on nest predation rates in scrub-shrub habitat are not clear (Chapter 6). Some predators may be attracted to clearcut-forest

Table 5.2. Results from meta-analysis of edge effects on abundances of scrub-shrub birds.

Species	Mean effect size[a]	95% confidence interval	*P*[b]	Number of studies
Ruffed Grouse	1.11	0.26 – 1.96	0.01	2
White-eyed Vireo	0.21	-0.55 – 0.97	0.59	2
Gray Catbird	0.71	-0.08 – 1.51	0.08	2
Cedar Waxwing	1.35	0.61 – 2.10	< 0.001	3
Blue-winged Warbler	1.35	0.54 – 2.16	0.001	2
Nashville Warbler	0.22	-0.66 – 1.11	0.62	3
Chestnut-sided Warbler	0.57	-0.06 – 1.21	0.08	4
Prairie Warbler	0.74	0.21 – 1.28	0.01	4
Black-and-white Warbler	0.29	-0.28 – 0.87	0.32	5
Common Yellowthroat	0.48	-0.02 – 0.97	0.06	5
Yellow-breasted Chat	1.46	0.80 – 2.12	< 0.001	3
Eastern Towhee	0.44	-0.07 – 0.95	0.09	5
Field Sparrow	1.07	0.52 – 1.62	< 0.001	5
White-throated Sparrow	1.04	-0.06 – 2.14	0.06	2
Dark-eyed Junco	0.87	-0.23 – 1.98	0.12	2
Indigo Bunting	1.03	0.50 – 1.56	< 0.001	5
American Goldfinch	1.17	0.48 – 1.87	0.001	4

[a]The difference in abundance between patch edge and center, scaled by within-study standard deviation.
[b]Based on a *Z* test.

borders by the variety of habitats or the high densities of prey available there. Snakes, for instance, use edges for thermoregulation because of the juxtaposition of sunlight and shade (Blouin-Demers & Weatherhead 2001). Limited evidence suggests that birds avoid areas with high predator densities (Fontaine & Martin 2006), and this could be another explanation for edge avoidance in scrub-shrub birds. At the same time, however, scrub-shrub birds can nest successfully along edges or in edge-dominated areas like group-selection cuts (Woodward et al. 2001; King & DeGraaf 2004). More research is needed to determine how predation and other factors affect birds' distributions within early-successional habitats.

Scrub-shrub birds vary in their willingness to breed in mature forests (Chapter 1). One might, therefore, expect birds that sometimes breed in forests would tolerate edges, as both habitats are similar in having some canopy cover. Likewise, species that do not breed in forests might avoid edges because of a preference for a more open canopy. We tested this prediction by comparing the Early Successional Index (ESI, see Chapter 1 for details) of scrub-shrub birds with our measure of edge avoidance from the meta-analysis. The ESI is an index of how abundant birds are in early-successional vs. mature forests. ESI varies from 0 to 1, with an ESI of 1 indicating that birds are found only in scrub-shrub habitat and an ESI of 0 indicating that birds are only found in forest. For the 15 species in the meta-analysis for which we had ESI estimates, we found no significant relationship between ESI and edge avoidance (Figure 5.1). Thus, willingness to breed in forests does not appear to be related to edge avoidance.

One caveat from our meta-analysis is that the seven studies differed in methodology as well as in the age and structure of the early-successional habitat. Still, when analyzed by study, all studies but one showed significant edge avoidance overall (Table 5.1). The exception, Yahner (1987), was unique in that it had only three study sites, and each differed in age and forest type, leading to high variation among replicates. The other six studies each found that the bird community tended to avoid edges. Thus, edge avoidance by scrub-shrub birds appears to be a general phenomenon in regenerating forests. Studies of this phenomenon in other habitats are needed.

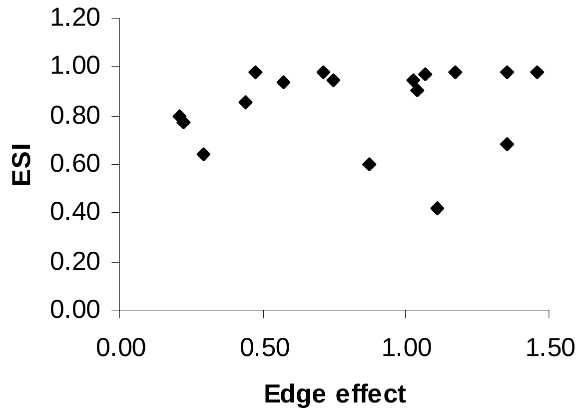


Figure 5.1. Relationship between Early Successional Index (ESI) and effect size from meta-analysis of edge effects. Higher values of ESI indicate higher abundance in early-successional habitat than in mature forest. Higher values of edge effect indicate lower abundance near edges than in centers of scrub-shrub patches. Results were not significant (r = 0.11, P = 0.66).

Area Sensitivity

In fragmented landscapes, animal densities often increase with patch size (Bender et al. 1998; Connor et al. 2000). This tendency, known as area sensitivity, is best described in forest birds, some of which will not breed in patches smaller than hundreds of hectares (Whitcomb et al. 1981; Lynch & Whigham 1984; Robbins et al. 1989a). In some regions, fragmentation of formerly extensive forests into small, isolated patches may be causing forest bird populations to decline (Robinson et al. 1995b). Whether or not scrub-shrub birds are area-sensitive is still uncertain. Addressing this question, however, has tremendous management implications. In forestry, uneven-aged management is gradually replacing even-aged strategies such as clearcutting (Askins 2001). Thus, the scrub-shrub habitat being created through forestry is increasingly likely to be in group-selection or single-tree cuts smaller than 0.5 ha. From the perspective of forest songbirds, isolated patches of that size would be far too small for most species, and nest success in such patches would probably be very low (e.g. Robbins et al. 1989a; Hoover et al. 1995). Knowing whether or not such small patches are suitable habitat for scrub-shrub birds is important for the future conservation of these species. To address this question, we reviewed the literature on how patch size affects the abundance of New England's scrub-shrub birds.

Because few studies have examined area effects on these birds, data were insufficient to conduct a meta-analysis. Instead, we have summarized the results of relevant studies in Table 5.3. Three studies, Annand & Thompson (1997), Costello (2000), and Kerpez (1994), compared avian abundances between group selection cuts (area ≤ 0.65 ha) and clearcuts (8-15 ha). In every instance but two, birds were more abundant in clearcuts than in group-selection cuts, and results were significant for 7 of 10 species in Annand & Thompson (Costello et al. did not report standard errors or *P* values). The exceptions were Ruby-throated Hummingbirds and Carolina Wren, both of which were more abundant in group cuts according to Kerpez (1994).

On a slightly larger scale, Rodewald & Vitz (2005) compared avian abundances in clearcuts of two size classes: 4-8 ha and 13-16 ha. All species except Eastern Towhee tended to be more abundant in larger patches; towhees preferred smaller patches. Results, however, were only significant for Yellow-breasted Chat. Overall, the five studies in Table 5.3 included 38 results for 21 species. In 34 of these comparisons, birds preferred larger patches of scrub-shrub habitat (sign test: $P < 0.0001$).

One area where results have been less clear is in studies of group-selection cuts of varying size. King and DeGraaf (2004) found that density of Chestnut-sided Warblers decreased with increasing cut size, from 0.15 to 0.69 ha. Kerpez (1994) found inconsistent responses of birds to the size of group-selection openings. Prairie Warblers, Black-and-white Warblers, and Eastern Towhees increased in density with opening size. Carolina Wrens, Indigo Buntings, and Ruby-throated Hummingbirds showed no obvious relationship with patch size. One problem with studying group-selection openings is that densities of birds are usually assessed based only on the size of the opening. If, however, birds are incorporating surrounding forests into their territories, as is likely with very small openings, then reported density estimates may be misleading.

A few other studies from forest types that do not occur in New England have examined area-sensitivity of scrub-shrub birds. In general, these studies agree with the results in Table 5.3. In Arkansas, Tappe et al. (2004) found that several scrub-shrub birds were more abundant in clearcuts 35-40 ha in size than in group-selection cuts of 0.5-2 ha. Like Annand & Thompson (1997), Tappe et al. found that Black-and-white Warbler, Carolina Wren, and Northern Cardinal had similar densities in clearcuts and group-selection cuts. On a smaller scale, Moorman & Guynn (2001) found that some scrub-shrub birds were more abundant in 0.26- and 0.5-ha openings than in smaller cuts. Krementz & Christie (2000), however, reported no obvious patterns of area-sensitivity for birds in South Carolina clearcuts between 2 and 57 ha in size.

While the number of studies is small, a few general patterns emerge from studies of area sensitivity in scrub-shrub birds. First, avian abundances are generally higher in clearcuts than in group-selection cuts. While a few species, such as Black-and-white Warbler or Carolina Wren, may use clearcuts and selection cuts in roughly similar numbers, 19 of 21 species had higher densities in clearcuts (Table 5.3). In fact, for species that occurred in both types of openings, densities averaged 10 times greater in clearcuts than in group-selection cuts (Table 5.3). Moreover, a few scrub-shrub birds did not use group-selection openings in any study. We conclude that clearcuts should be preferred over group-selection cuts when managing for scrub-shrub birds. Clearcuts can provide habitat for almost the entire bird community (with notable exceptions; see Chapter 4); only a few species use group cuts in significant numbers.

Second, beyond an area of 4 to 8 ha, increasing the size of clearcuts appears to have only modest effects on scrub-shrub bird populations. Rodewald & Vitz (2005) and other studies that looked across a range of clearcut sizes found weak tendencies for abundances to increase with patch size. Thus, on scales of 4 to 100 ha, scrub-shrub birds show less evidence of area sensitivity. Given the small number of studies to date, however, this conclusion remains tenuous until more research is conducted on how birds respond to patch size.

Proportionally, the differences between group cuts and clearcuts were far larger than those between clearcuts of varying size. Overall, this suggests a size threshold below which the birds do not occur and above which increasing patch size

Table 5.3. Summary of patch-size effects on scrub-shrub birds. Results in italics indicate greater abundance in smaller patches.

	Costello et al. 2000[a]	Annand & Thompson 1997[b]	Kerpez 1994[c]	Rodewald & Vitz 2005	King & DeGraaf 2004
Comparison	clearcuts vs. group-selection cuts	clearcuts vs. group-selection cuts	clearcuts vs. group-selection cuts	small (4-8 ha) vs. large (13-16 ha) clearcuts	group-selection cuts (0.19-0.65 ha)
Ruby-throated Hummingbird			*only found in group cuts*		
Alder Flycatcher	only found in clearcuts				
White-eyed Vireo		42x more abundant in clearcuts ($P < 0.001$)		1.5x more abundant in larger patch ($P = 0.19$)	
Carolina Wren		1.3x more abundant in clearcuts ($P = 0.14$)	*2.0x more abundant in group cuts*		
Cedar Waxwing	only found in clearcuts				
Blue-winged Warbler		29x more abundant in clearcuts ($P < 0.001$)		1.5x more abundant in larger clearcuts ($P = 0.19$)	
Chestnut-sided Warbler	3.0x more abundant in clearcuts				*abundance decrased with patch size ($r = -0.5$)*
Prairie Warbler		only found in clearcuts ($P < 0.001$)	12x more abundant in clearcuts	1.3x more abundant in larger patch ($P = 0.39$)	
Black-and-white Warbler	only found in clearcuts	1.2x more abundant in clearcuts ($P = 0.35$)	1.1x more abundant in clearcuts		
Mourning Warbler	2.0x more abundant in clearcuts				
Common Yellowthroat	3.7x more abundant in clearcuts			2.0x more abundant in larger patch ($P = 0.37$)	
Canada Warbler	only found in clearcuts				
Yellow-breasted Chat		25x more abundant in clearcuts ($P < 0.001$)		2.0x more abundant in larger patch ($P = 0.05$)	
Eastern Towhee		18.9x more abundant in clearcuts ($P < 0.001$)	1.8x more abundant in clearcuts	*1.9x more abundant in smaller patch ($P = 0.14$)*	
Field Sparrow		only found in clearcuts ($P = 0.003$)	only found in clearcuts	1.6x more abundant in larger patch ($P = 0.47$)	
Song Sparrow	only found in clearcuts				
White-throated Sparrow	19x more abundant in clearcuts				
Dark-eyed Junco	8.5x more abundant in clearcuts				
Northern Cardinal		1.4x more abundant in clearcuts ($P = 0.43$)			
Indigo Bunting	only found in clearcuts	1.8x more abundant in clearcuts ($P = 0.001$)	2.0x more abundant in clearcuts	1.1x more abundant in larger patch ($P = 0.67$)	
American Goldfinch	only found in clearcuts				

[a]Clearcuts: 8-12 ha; group-selection cuts: 0.13-0.65 ha

[b]Clearcuts: size not given; group-selection cuts: 0.2-0.4 ha

[c]Clearcuts: 4.9-11.3 ha; group-selection cuts: 0.12-1.1 ha

has relatively little influence on abundance. For the few species, like Black-and-White Warbler or Carolina Wren, that regularly use group-selection cuts, the threshold size for occurrence may be very small. For other species, the threshold probably lies somewhere between 1 and 4 ha, larger than any group-selection cut. Unfortunately, little research has been conducted on area sensitivity in openings between 1 and 4 ha in size, so determining exactly where this threshold occurs is difficult to know. Thus, we suggest that to benefit scrub-shrub birds, clearcuts should be a minimum of 1 ha in size.

Why do many species avoid small patches of scrub-shrub habitat? Several explanations are possible. One possibility is that area sensitivity is due to edge avoidance. Larger patches have more core area and are less subject to edge effects while small patches are essentially all edge. For instance, a circular 1-ha group-selection cut has a radius of just 56 m, so 98.7% of the patch area would be within 50 m of the surrounding forest. This is well within the range that edge effects are thought to occur (Batary & Baldi 2004). Thus, a simple explanation for birds' avoiding small patches is that they prefer to nest away from edges. A simple model of edge effects shows that core habitat, > 50 m from any edge, initially increases rapidly with patch size but shows diminishing returns thereafter. This is analogous to the manner in which bird densities appear to respond to patch size (Figure 5.2). The link between area sensitivity and edge avoidance is supported by the fact that species that appear to lack area sensitivity—Eastern Towhee, Black-and-white Warbler, and White-eyed Vireo—also did not avoid edges in our meta-analysis (see Table 5.2). Thus, edge avoidance provides a potential explanation for area sensitivity in scrub-shrub birds.

Other possible causes of area sensitivity involve characteristics of the patches themselves. The smallest group-selection cuts may simply be too small to contain the territory of even one pair of birds (Costello et al. 2000). Furthermore, because of shading from surrounding trees, small patches may not develop the dense woody vegetation preferred by most scrub-shrub birds (Phillips & Shure 1990). Food for songbirds—insects and fruit—may also be more abundant in larger openings (Shure & Phillips 1991; DeGraaf & Yamasaki 2003). For species that aggregate their territories, larger patches may be better because they can hold more territories (Ward & Schlossberg 2004; Bourque & Desrochers 2006). Finally, larger patches tend to have a wider variety of microhabitats (Hart & Horwitz 1991). Habitat specialists, therefore, may be more likely to find suitable habitat in a larger patch that a smaller patch.

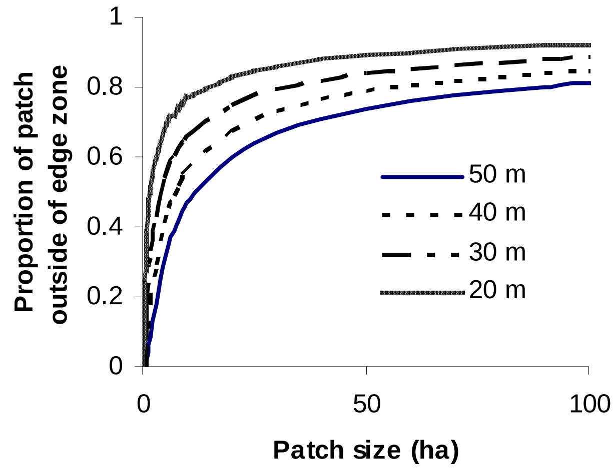


Figure 5.2. Proportion of a patch unaffected by edge effects for given distances over which edge effects are hypothesized to occur. Patches are assumed to be square in shape.

Our conclusions about area sensitivity in scrub-shrub birds come with two caveats. First, patch size can affect avian nesting success independently of abundance (Brawn & Robinson 1996). Thus, the fact that birds prefer larger clearcuts does not necessarily mean that larger patches are better habitats for breeding. Because of birds' high dispersal rates, abundance and nesting success are largely decoupled in bird populations (Vickery et al. 1992; Brawn & Robinson 1996). In Chapter 6, we review the factors that affect nesting success of scrub-shrub birds. Second, data on area sensitivity are available for fewer than half of New England's scrub-shrub birds. Additional research in this area is clearly needed, especially for birds of northern New England.

Right-of-Way Width

Utility rights-of-way can be important habitats for scrub-shrub birds (Confer & Pascoe 2003). These corridors are often maintained in an early-successional stage to prevent vegetation from interfering with utility lines (Chapter 2).

Thus, unlike the transient habitats of old fields or clearcuts, scrub-shrub habitat in rights-of-way can be essentially permanent (Askins 1994). Many scrub-shrub birds breed in shrubby rights-of-way, and avian densities there can be quite high (e.g. Kroodsma 1982; Meehan & Haas 1997; Yahner et al. 2002; Confer & Pascoe 2003).

Because most of New England is forested, utility corridors are usually surrounded by forest. Thus, rights-of-way are essentially long, narrow "islands" of scrub-shrub habitat. Assuming that the habitat within the right-of-way is appropriate, the key variable determining whether or not corridors are suitable for scrub-shrub birds is corridor width. As discussed above, many scrub-shrub birds avoid edges and small patches of habitat. Thus, one might expect birds to avoid narrow corridors because of the close proximity of surrounding forests. Exactly how wide corridors must be for New England's scrub-shrub birds to occur is not known. This question, however, is important for management. In New England, new utility corridors are likely to be developed in the near future; therefore, opportunities may exist to build corridors in ways that benefit birds, such as by aggregating rights-of-way together. Here, we review the literature on the effects of right-of-way width on scrub-shrub bird populations.

While numerous studies have described bird communities in rights-of-way, little quantitative data exists on how corridor width affects bird populations. In fact, we located only three studies addressing this question (summarized in Table 5.4). Kroodsma (1982) found that no scrub-shrub species evinced a significant relationship between corridor width and density in Tennessee. In New York, Confer & Pascoe (2003) found that scrub-shrub birds generally occurred more often in wider corridors. The only exception was Chestnut-sided Warbler, which was found less frequently in wider rights-of-way. Finally, King et al. (unpublished manuscript) found that several species were more abundant in corridors wider than 35 m than in narrower rights-of-way.

Overall, the three studies showed very little agreement in how individual species respond to the width of utility rights-of-way. As an example, Kroodsma (1982) found that densities of Prairie Warblers and Field Sparrows were unaffected by corridor width while Confer & Pascoe (2003) found that both species were more likely to occur in wider rights-of-way. In fact, in almost every case in which a species appeared in more than one study, there was a difference in results across studies. Such disagreement suggests that differences in methodology or habitat structure may have influenced the results from one or more of these studies. Kroodsma (1982), for instance, found that vegetation variables were much better predictors of avian densities than corridor with.

Another difference among the three studies is the range of rights-of-way widths studied (Table 5.4). King et al. found quadratic or modal responses to corridor width for some species, so studies that only examined a portion of the potential range of widths could have produced misleading results. The narrowest corridor studied by Kroodsma (1982) was 43 m wide. If birds only avoid the narrowest corridors, Kroodsma's study design would not have detected such a preference.

Clearly, much additional research is needed on how scrub-shrub birds use utility corridors. Studies have shown that birds can nest successfully in rights-of-way (Confer & Pascoe 2003). In fact, corridors can be population sources for some species (King & Byers 2002). At the same time, however, wider rights-of-way may be harmful to birds breeding in surrounding forests (Askins 1994). Thus, a trade-off will exist between providing habitat for scrub-shrub birds and those of surrounding forest. As a result, understanding just how wide corridors need to be for scrub-shrub birds is an important research goal.

Landscape Composition

While patch size and proximity to edge can affect bird populations, landscape composition at much larger scales can also be important. For instance, the abundance of some forest songbirds increases with forest cover on scales up to 100 km^2 (Trzcinski et al. 1999; Lee et al. 2002; Magness et al. 2006). Whether or not scrub-shrub birds are responsive to these sorts of landscape effects is not well understood. Several factors, however, suggest that landscape composition could be important to scrub-shrub birds. First, landscapes with more scrub-shrub habitat could be preferred because birds would have more locations to choose among for breeding sites, allowing them to choose a higher-quality territory (Badyaev et al. 1996). Second, birds often move between patches within the breeding season

Table 5.4. Summary of effects of right-of-way width on scrub-shrub birds.

	Kroodsma 1982	Confer & Pascoe 2003	King et al. unpublished ms.
Range of widths	43 – 100 m	20 – 110 m	15 – 78 m
Northern Bobwhite	no effect of width		
White-eyed Vireo	no effect of width		
Carolina Wren	no effect of width		
Gray Catbird		prefers wider corridors	inconsistent across years
Blue-winged Warbler		no effect of width	
Yellow Warbler		prefers wider corridors	
Chestnut-sided Warbler		prefers narrower corridors	prefers wider corridors
Prairie Warbler	no effect of width	prefers wider corridors	prefers wider corridors
Common Yellowthroat	no effect of width		prefers wider corridors
Yellow-breasted Chat	no effect of width		
Eastern Towhee	no effect of width		prefers narrower corridors
Eastern Towhee		no effect of width	
Field Sparrow	no effect of width	prefers wider corridors	prefers wider corridors
Song Sparrow		no effect of width	
Northern Cardinal	no effect of width		
Indigo Bunting	no effect of width		prefers corridors ~50 m wide
American Goldfinch		prefers wider corridors	

(Chapter 7). After a failed nesting attempt, for instance, birds may move to a new location where odds of nesting successfully could be greater (Jackson et al. 1989). Thus, birds may prefer landscapes with more habitat and, therefore, more opportunities for dispersal. Finally, landscapes with more suitable habitat will generally have less edge and larger patches (Hargis et al. 1998). These factors, as discussed above, could make such landscapes preferred by scrub-shrub birds. Here, we review findings from studies of how scrub-shrub birds respond to larger-scale landscape features.

We found few studies that examined landscape effects on this bird community. Two studies reported the obvious finding that landscapes with forest openings had more scrub-shrub birds than landscapes that were essentially all closed-canopy forest (Buford & Capen 1999; Drapeau et al. 2000). This comes as no surprise, given that most scrub-shrub birds have much higher abundances in early-successional habitats than in mature forest (Chapter 1).

Better information on the landscape ecology of scrub-shrub birds comes from two studies that sampled birds in varied locations and then determined how the broader landscape affected local abundance. In an industrial forest in Maine, Hagan et al. (1997) found that the abundances of Nashville Warbler, Palm Warbler, Mourning Warbler, Alder Flycatcher, Gray Catbird, and Magnolia Warbler increased with the amount of early-successional habitat within 1 km of a site. In contrast, Chestnut-sided Warbler and Black-and-white Warbler preferred landscapes with less scrub-shrub habitat.

Chandler (2006) found that the amount of early-successional habitat in the landscape had little influence on birds of wildlife openings in New Hampshire. Song Sparrows preferred more diverse landscapes, with a variety of successional stages intermingled, and White-throated Sparrows were more abundant in landscapes with more edge. The overall amount of early successional habitat, however, was not important for any species. This suggests that birds in New Hampshire were colonizing patches independently of the presence of additional scrub-shrub habitat in a landscape. The differences in the results of Chandler (2006) and Hagan et al. (1997) may be due to the landscapes they studied. Hagan et al. (1997) worked in an industrial forest landscape, with large areas of clearcut and regenerating forest. In contrast, Chandler (2006) studied managed openings in an extensively forested landscape. Birds in the industrial forest may have had more habitat available and more opportunity to select habitats in a preferred landscape setting. Birds in the heavily forested New Hampshire study area may have had little habitat available and little opportunity to choose landscapes of a particular composition.

One important question raised by these results is the relative importance of landscape and local-scale factors. Are birds selecting habitat based primarily on the structure of vegetation in a territory, the size or shape of a patch, or the composition of habitats on the landscape level? MacFaden & Capen (2002) found that microhabitat structure predicted bird densities better than landscape structure for seven of nine scrub-shrub birds. For the other two species, the two scales were roughly equally predictors. Hagan & Meehan (2002) reported similar results; six of seven species' distributions were better predicted by local habitat than by landscape conditions. In contrast, Chandler (2006) found that four of six scrub-shrub birds had stronger associations with landscape composition than with microhabitat structure. The latter study, however, was conducted solely in scrub-shrub habitat. The other two studies were conducted in forests of varying successional stages and, therefore, may have been more likely to emphasize local-scale factors that distinguished mature and early-successional forests. These results suggest that landscape structure and composition influence habitat selection in scrub-shrub birds, but clearly, more research is needed in this field.

Conclusion

For scrub-shrub birds, characteristics of the breeding patch and the surrounding landscape clearly affect habitat usage. We found that scrub-shrub birds generally avoid edges where early-successional habitat abuts mature forest. Furthermore, most scrub-shrub birds avoid very small openings such as those created by group-selection harvests. Above a certain critical patch size, however, most birds appear to show relatively small responses to increasing patch size. Based on the limited data available to date, the minimum patch size for most species is approximately 1 ha. Finally, landscape context has variable impacts on scrub-shrub birds. In some studies, some species prefer landscapes with more early-successional habitat. Other studies, however, have found that birds are largely unaffected by surrounding patches. Moreover, vegetation and habitat structure at smaller scales are usually better predictors of habitat usage for scrub-shrub birds than landscape patterns. All of these conclusions are based on relatively small numbers of studies, and additional research in this field is sorely needed.

Chapter 6. Factors Influencing Reproductive Success

Introduction

Ornithologists frequently use bird abundance as a measure of habitat quality or conservation status. In doing so, we assume that places with high bird densities or stable populations are good habitats. Birds, however, are highly vagile and often disperse widely from one year to the next (May 1981; Weatherhead & Forbes 1994). Because they move so freely, birds can be abundant in places where reproduction is poor due to predators, parasites, or other limiting factors (Vickery et al. 1992; Brawn & Robinson 1996). In fact, birds are sometimes even attracted to poor habitats, creating "ecological traps" that may harm populations (Schlaepfer et al. 2002). In other cases, competition or crowding may force birds to breed in low-quality habitats where reproductive success is low (Newton 1998). Because of the potential disconnect between avian abundance and productivity, bird counts alone are not sufficient to assess avian populations and habitats. To accurately evaluate a bird community's conservation status and to make recommendations for management, one needs data on reproductive success as well. Here, we review factors affecting the reproductive success of scrub-shrub birds in New England.

Our review addresses two questions. First, how well are scrub-shrub birds reproducing? For birds that breed in forests and grasslands of the East and Midwest, areas subject to high rates of nest predation and parasitism by Brown-headed Cowbirds, poor reproduction is a likely cause of recent population declines (Wilcove 1985; Robinson et al. 1995b). Given that many scrub-shrub birds are declining in New England (Chapter 3), whether or not these birds are producing enough young to make up for annual mortality is an important question. To determine how well scrub-shrub birds are reproducing, we compiled results from studies that reported nest success rates for these species. The second question we address is what limits the reproductive success of scrub-shrub birds? In general, avian nesting success depends on multiple factors including predators, parasites, food, the microhabitat around the nest, and the configuration of the surrounding landscape (Newton 1998). Understanding the relative importance of these influences on nest success is necessary to manage bird populations. This is especially important for vegetation features that can potentially be manipulated through habitat restoration or management (Burhans et al. 2002). To this end, we have reviewed the evidence for local and landscape-level influences on avian nest success in scrub-shrub birds.

Nest Success Review

The best measure of avian reproductive success is fecundity, the number of fledglings raised by each pair of birds over an entire breeding season. Because, however, measuring season-long fecundity is difficult, most researchers simply measure nest success, the proportion of nests that fledge young. This does not always correlate with fecundity, but nest success is, by far, the most widely used metric of reproduction in scrub-shrub birds. To determine general trends in the reproductive success of scrub-shrub birds, we compiled results from studies reporting their nest success rates. Few such studies have taken place in New England, so we used data from all studies occurring in scrub-shrub habitat in eastern North America. In analyzing the data, we separated studies of precocial gamebirds, which do not have a nestling period, and altricial species, whose young remain in the nest for several days. Some studies reported daily survival rates (Mayfield estimates) while others reported the simple proportion of nests fledging young. As expected, simple estimates of nest success were slightly higher than Mayfield estimates, but results of our analyses were similar regardless of whether or not we separated these two methods. Thus, we combined them for analysis.

Researchers have reported nest success rates for three precocial gamebirds that are part of New England's scrub-shrub avifauna (Table 6.1). When summarized across studies, nest success for these species was 0.56 for Ruffed Grouse (range: 0.41 – 0.63; n = 5 studies) and 0.31 for Northern Bobwhite (range: 0.18 – 0.44; n = 5). In a summary of 4 studies, Keppie and Whiting (1994) reported nesting success in American Woodcock of 0.58. The relatively high nest success of Ruffed Grouse may not be indicative of overall reproductive success, as young grouse have very high mortality rates (Tirpak et al. 2006).

For altricial scrub-shrub birds, we found 38 studies describing the nest success of 22 species. Average nesting success in these studies was 0.43 ± standard error of 0.02 (Table 6.2). The studies that we reviewed spanned a wide range of time periods, from the 1930's to the present, but nest success in our sample did not change with time ($r = -0.03$, $P = 0.78$). Individual species varied widely in their overall rates of nest success (range: 0.10 – 1.00; Table 6.3), and a few species, such as Northern Cardinal, Prairie Warbler, and Yellow-breasted Chat had especially low nest success rates. One factor that can affect nest success is nest location; ground nesters typically experience higher nest predation rates than birds that nest in trees and shrubs (Martin 1993). We found, however, no significant differences in the nest success of ground-nesting ($\bar{x} = 0.44 \pm 0.04$) and shrub-nesting species ($\bar{x} = 0.42 \pm 0.03$; $P = 0.71$) in our sample of scrub-shrub birds.

The key question raised by these results is whether or not observed levels of nest success are sufficient to keep populations of scrub-shrub birds stable or growing. Because birds can produce multiple clutches over a breeding season, high predation rates do not necessarily indicate low productivity (Pease & Grzybowski 1995). At the same time, high nesting success may not lead to high productivity if few young fledge per nest (Schmidt & Whelan 1999b). To estimate season-long productivity, however, one needs detailed demographic data (Pease & Grzybowski 1995), and those data are not available for most scrub-shrub birds. One exception is a study of Chestnut-sided Warblers nesting on rights-of-way, in which season-long fecundity was more than enough to compensate for annual mortality (King & Byers 2002). In general, however, conclusions about what the nest success rates we observed mean for bird populations would be speculative.

Our review of nest success rates come with several caveats. First, the studies included in our review took place in a variety of habitats and landscapes throughout the East. Few of these studies took place in New England, and most studies gave no information about landscape context, an important potential confound (Donovan et al. 1995; Robinson et al. 1995b). Thus, whether or not these studies are indicative of avian nest success in New England is difficult to know. Moreover, we found nesting data for only 25 of 41 scrub-shrub birds. Thus, we have no information on nest success for roughly one-third of this bird community, and several other species have only one or two published estimates. Clearly, more research is needed on the reproductive success for New England's scrub-shrub birds.

Factors Influencing Nest Success

Nest predators

Predators are responsible for the vast majority of nest failures in birds, and nest predation can

Table 6.1. Results from studies of nest success of precocial scrub-shrub birds in eastern North America.

Species	Nest success	Method[a]	Nests[b]	Location	Reference
Northern Bobwhite	0.34	simple	863	Illinois	Klimstra & Roseberry 1975
Northern Bobwhite	0.18	simple	1725	Georgia	Simpson 1976
Northern Bobwhite	0.44	simple	157	Missouri	Burger et al. 1995
Northern Bobwhite	0.34	simple	34	North Carolina	Puckett et al. 1995
Northern Bobwhite	0.23	simple	766	Tennessee	Dimmick 1974
Ruffed Grouse	0.63	simple	234	central Appalachians	Tirpak et al. 2006
Ruffed Grouse	0.46	simple	27	Wisconsin	Small et al. 1996
Ruffed Grouse	0.61	simple	1431	New York	Bump et al. 1947
Ruffed Grouse	0.51	Mayfield	41	Michigan	Larson et al. 2003
Ruffed Grouse	0.59	simple	22	Minnesota	Maxson 1978
American Woodcock	0.58	simple	403	review of 4 studies	Keppie & Whiting 1994

[a]Method of calculating nest success. Simple = proportion of nests fledging young; Mayfield = daily predation rate extrapolated over the entire nesting period.
[b]Number of nests used to estimate nest success.

Table 6.2. Results from studies of nest success of altricial scrub-shrub birds in eastern North America.

Species	Nest success	Type	Nests	Location	Reference
Yellow-billed Cuckoo	0.17	Simple	6	Indiana	Nolan 1963
Alder Flycatcher	0.37	Simple	19	Michigan	Hofslund 1959
Willow Flycatcher	0.40	Simple	91	Ohio	Holcomb 1972
Willow Flycatcher	0.65	Simple	92	Michigan	Walkinshaw 1966
House Wren	0.52	Simple	77	Ontario	Belles-Isles & Picman 1986
Gray Catbird	0.37	Mayfield	25	New York	Dhondt et al. 2007
Gray Catbird	0.30	Simple	10	Minnesota	Hanski et al. 1996
Gray Catbird	0.43	Simple	7	Michigan	Hofslund 1959
Gray Catbird	0.48	Simple	23	Pennsylvania	Yahner 1991
Gray Catbird	0.69	Simple	22	Michigan	Zimmerman 1963
Northern Mockingbird	0.44	Simple	108	Louisiana	Joern & Jackson 1983
Cedar Waxwing	0.41	Mayfield	25	New York	Dhondt et al. 2007
Cedar Waxwing	0.42	Mayfield	23	Minnesota	Hanski et al. 1996
Cedar Waxwing	0.55	Simple	11	Michigan	Lea 1942
Cedar Waxwing	0.21	Mayfield	n/a	New York	Murphy et al. 1997
Cedar Waxwing	0.77	Simple	60	Michigan	Putnam 1949
Blue-winged Warbler	0.51	Mayfield	7	Missouri	Annand & Thompson 1997
Golden-winged Warbler	1.00	Simple	4	Pennsylvania	Yahner 1991
Tennessee Warbler	0.92	Simple	13	Quebec	Holmes 1998
Yellow Warbler	0.76	Mayfield	18	Minnesota	Hanski et al. 1996
Yellow Warbler	0.63	Simple	8	Michigan	Hofslund 1959
Chestnut-sided Warbler	0.57	Mayfield	77	New Hampshire	Chandler 2006
Chestnut-sided Warbler	0.59	Mayfield	16	Minnesota	Hanski et al. 1996
Chestnut-sided Warbler	0.44	Simple	9	Minnesota	Hanski et al. 1996
Chestnut-sided Warbler	0.67	Simple	6	Pennsylvania	Yahner 1991
Chestnut-sided Warbler	0.83	Simple	86	Massachusetts	King & Byers 2002
Chestnut-sided Warbler	0.80	Mayfield	217	New Hampshire	King et al. 2001
Prairie Warbler	0.10	Mayfield	10	Missouri	Annand & Thompson 1997
Prairie Warbler	0.15	Simple	55	Indiana	Nolan 1963
Prairie Warbler	0.24	Simple	400	Indiana	Nolan 1978
Common Yellowthroat	0.29	Simple	7	Minnesota	Hanski et al. 1996
Common Yellowthroat	0.55	Simple	38	Michigan	Hofslund 1959
Common Yellowthroat	0.33	Simple	12	Minnesota	Hofslund 1959
Common Yellowthroat	0.57	Simple	7	Pennsylvania	Yahner 1991
Yellow-breasted Chat	0.18	Mayfield	37	Missouri	Annand & Thompson 1997
Yellow-breasted Chat	0.34	Mayfield	42	Missouri	Burhans & Thompson 1999
Yellow-breasted Chat	0.11	Simple	19	Indiana	Nolan 1963
Yellow-breasted Chat	0.42	Mayfield	49	Kentucky	Ricketts & Ritchison 2000
Yellow-breasted Chat	0.22	Simple	68	Indiana	Thompson & Nolan 1973
Eastern Towhee	0.19	Mayfield	41	West Virginia	Bell & Whitmore 2000
Eastern Towhee	0.33	Simple	6	Indiana	Nolan 1963
Eastern Towhee	0.52	Simple	25	Pennsylvania	Yahner 1991
Field Sparrow	0.10	Simple	147	Illinois	Best 1978
Field Sparrow	0.30	Mayfield	484	Missouri	Burhans et al. 2002
Field Sparrow	0.42	Simple	97	Michigan	Evans 1978
Field Sparrow	0.29	Mayfield	46	North Carolina	Fretwell 1968
Field Sparrow	0.29	Simple	42	North Carolina	Fretwell 1968

Table 6.2 continued

Species	Nest success	Type	Nests	Location	Reference
Field Sparrow	0.27	Simple	33	Indiana	Nolan 1963
Field Sparrow	0.38	Mayfield	81	Missouri	Thompson et al. 1999
Field Sparrow	0.38	Simple	593	Michigan	Walkinshaw unpub.
Field Sparrow	0.65	Simple	23	West Virginia	Wray et al. 1982
Field Sparrow	0.60	Simple	5	Pennsylvania	Yahner 1991
Song Sparrow	0.24	Mayfield	10	Minnesota	Hanski et al. 1996
Song Sparrow	0.52	Simple	147	Ohio	Nice 1937
Song Sparrow	0.39	Simple	76	Ohio	Nice 1937
White-throated Sparrow	0.50	Simple	62	Ontario	Knapton et al. 1984
Northern Cardinal	0.15	Mayfield	n/a	Ohio	Filliater et al. 1994
Northern Cardinal	0.10	Simple	10	Indiana	Nolan 1963
Indigo Bunting	0.31	Mayfield	16	Missouri	Annand & Thompson 1997
Indigo Bunting	0.39	Mayfield	60	West Virginia	Bell & Whitmore 2000
Indigo Bunting	0.26	Mayfield	519	Missouri	Burhans et al. 2002
Indigo Bunting	0.40	Simple	5	Michigan	Hofslund 1959
Indigo Bunting	0.20	Simple	10	Indiana	Nolan 1963
Indigo Bunting	0.25	Mayfield	46	Missouri	Thompson et al. 1999
American Goldfinch	0.43	Mayfield	67	New York	Dhondt et al. 2007
American Goldfinch	0.63	Simple	8	Michigan	Hofslund 1959
American Goldfinch	0.40	Simple	88	Ohio	Holcomb 1969
American Goldfinch	0.47	Simple	45	Wisconsin	Knight & Temple 1988
American Goldfinch	0.45	Simple	192	Ontario	Middleton 1979
American Goldfinch	0.34	Simple	32	Ontario	Middleton 1979
American Goldfinch	0.74	Simple	31	Ontario	Middleton 1979
American Goldfinch	0.33	Simple	24	Indiana	Nolan 1963
American Goldfinch	0.60	Simple	35	Michigan	Walkinshaw 1939

seriously limit reproduction success (Ricklefs 1969; Martin 1992, 1993). In fact, nest predation has become a conservation issue for birds breeding where anthropogenic disturbance has increased numbers of nest predators (e.g. Wilcove 1985; Robinson 1992; Crooks & Soulé 1999). No systematic research has been conducted on nest predators in scrub-shrub habitat in New England. This region, however, contains a diverse assemblage of animals likely to prey upon the nests of scrub-shrub birds. Research in forests of New England has found that common nest predators include hawks, crows, jays, squirrels, chipmunks, and various small mammals (King & DeGraaf 2006). Elsewhere in the eastern U.S., weasels, raccoons, skunks, and Brown-headed Cowbirds are important nest predators; these species are widespread in New England as well (DeGraaf & Yamasaki 2001). Finally, in warmer parts of New England, snakes may be important nest predators.

Because the predator community includes animals with a wide range of habitat preferences and home range sizes, predicting their abundance in different scrub-shrub habitats is difficult (Fisher & Wilkinson 2005). Studies of these species' habitat usage often show inconsistent or contradictory results (Kirkland 1990). Despite these difficulties, we did identify a few important trends in nest predator communities for scrub-shrub habitats. Compared to mature forests, early-successional woodlands tend to have few arboreal mammals or carnivores but high densities of small mammals (Kirkland 1977; King et al. 1998; Fisher & Wilkinson 2005). Changes during forest succession can also affect predator communities. New clearcuts and recently abandoned fields have the highest densities of small mammals such as

Table 6.3. Mean nest success rates of altricial scrub-shrub birds from published studies listed in Table 6.2.

Species	Nest success	SE	N
Yellow-billed Cuckoo	0.17		1
Alder Flycatcher	0.37		1
Willow Flycatcher	0.52	0.13	2
House Wren	0.52		1
Gray Catbird	0.45	0.07	5
Northern Mockingbird	0.44		1
Cedar Waxwing	0.47	0.09	5
Blue-winged Warbler	0.51		1
Golden-winged Warbler	1.00		1
Tennessee Warbler	0.92		1
Yellow Warbler	0.69	0.07	2
Chestnut-sided Warbler	0.65	0.06	6
Prairie Warbler	0.16	0.04	3
Common Yellowthroat	0.44	0.07	4
Yellow-breasted Chat	0.25	0.06	5
Eastern Towhee	0.35	0.10	3
Field Sparrow	0.37	0.05	10
Song Sparrow	0.39	0.08	3
White-throated Sparrow	0.50		1
Northern Cardinal	0.13	0.03	2
Indigo Bunting	0.30	0.03	6
American Goldfinch	0.49	0.05	9

Peromyscus mice, but their abundances typically decline over time as forests regenerate (Pearson 1959; Kirkland 1977; Fisher & Wilkinson 2005).

Another frequently reported trend is that potential nest predators are abundant along forest edges. In New Hampshire, for instance, Blue Jays and squirrels were more common along forest edges than in clearcut interiors (King et al. 1998). High populations of snakes, chipmunks, mice, crows, and other nest predators have also been found near forest edges (Forsyth & Smith 1973; Blouin-Demers & Weatherhead 2001; Chalfoun et al. 2002). Fencerows and power-line rights-of-way may be heavily used by small mammals as well (Johnson et al. 1979; Wegner & Merriam 1979).

In other respects, however, factors determining the abundance of nest predators are poorly understood. One example is the effect of patch size on nest predators. In South Carolina, *Peromyscus* mice were equally abundant in clearcuts ranging from < 6 ha to > 25 ha in size (Yates et al. 1997). In contrast, a study in Missouri found higher mouse densities in clearcuts (3-12 ha) than in group-selection cuts (< 0.6 ha) (Fantz & Renken 2005). Finally, in North Carolina, *Peromyscus* abundance decreased with increasing patch size (Buckner & Shure 1985). Thus, the general effect of patch size on small mammal abundances remains unresolved. Other potential effects on predator communities, such as plant species composition, landscape configuration, and position on the moisture gradient are all largely unknown for scrub-shrub habitats.

For birds, the abundances of nest predators are only important to the extent that they indicate nest predation rates. A few studies from forested habitats have shown correlations between abundances of nest predators and nest predation rates (Sieving & Willson 1998; De Santo & Willson 2001; Schmidt & Ostfeld 2003). Whether or not this holds true in scrub-shrub habitat is not known. Future research should focus on determining the relative abundance of nest predators in different types of scrub-shrub habitats and determining how well numbers of nest predators predict nest predation rates. With this knowledge, managers could potentially maintain or restore habitats where birds might be expected to have high nesting success.

Patch and Landscape Effects

Patch and landscape characteristics have significant impacts on the distribution and abundance of scrub-shrub birds (Chapter 5). For birds, patterns of abundance at the patch and landscape level are often correlated with nest predation. Forest birds, for instance, generally avoid small, isolated woodlots where nest predation rates are high (Wilcove 1985; Brawn & Robinson 1996). In scrub-shrub habitat, researchers have tested three different types of patch effects on avian nest success—proximity to edge, patch shape, and patch size.

Most scrub-shrub birds avoid nesting near edges, where early-successional habitat abuts forest (Chapter 5). Is this because nesting success is reduced near forest edges? The few published studies on this subject suggest that proximity to a forest edge has little or no effect on nesting success of scrub-shrub birds (Table 6.4). The only study reporting a negative effect of edges on nest success is Burhans et al. (2002), in a study of In-

Table 6.4. Summary of landscape effects on nesting success of scrub-shrub birds.

Effect Tested	Reference	Location	Species	Result
Edge distance	King et al. 2001	New Hampshire	Chestnut-sided Warbler	no effect of edge distance on nest success
	Chandler 2006	New Hampshire	Chestnut-sided Warbler	no effect of edge distance on nest success
	Burhans et al. 2002	Missouri	Indigo Bunting	nests farther from forest edge more likely to fledge young
	Weldon & Haddad 2005	South Carolina	Indigo Bunting	no effect of edge distance on nest success
	Woodward et al. 2001	Missouri	Indigo Bunting	no simple effect of distance to edge on predation rate
			Yellow-breasted Chat	no simple effect of distance to edge on predation rate
			Field Sparrow	no simple effect of distance to edge on predation rate
			Prairie Warbler	no simple effect of distance to edge on predation rate
			Northern Cardinal	no simple effect of distance to edge on predation rate
Patch Shape	Chandler 2006	New Hampshire	Chestnut-sided Warbler	nest success decreased with patch shape complexity
	Weldon & Haddad 2005	South Carolina	Indigo Bunting	nest success higher in rectangular patches than winged patches
Patch Area	King et al. 2001	New Hampshire	Chestnut-sided Warbler	no difference in nest success between group cuts and clearcuts
	King & DeGraaf 2004	New Hampshire	Chestnut-sided Warbler	no effect of group cut area on nest success
	Chandler 2006	New Hampshire	Chestnut-sided Warbler	no effect of wildlife opening area on nest success
	Rodewald & Vitz 2005	Ohio	White-eyed Vireo	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Blue-winged Warbler	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Prairie Warbler	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Yellow-breasted Chat	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Common Yellowthroat	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Eastern Towhee	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Field Sparrow	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts
			Indigo Bunting	age ratios (HY:AHY) did not differ between small (4-8 ha) and large (13-16 ha) clearcuts

digo Buntings. Nest success in old fields was higher away from forest edges than near them. Two other studies of Indigo Buntings, however, found no effect of edge proximity on nesting success (Woodward et al. 2001; Weldon & Haddad 2005). Tests of edge effects in other scrub-shrub birds have also reported negative results (Woodward et al. 2001; Chandler 2006), though King et al. (2001) reported a marginally significant elevation of predation rates near forest edges (Table 6.4).

The lack of edge effects on nest success is inconsistent with the high abundance of nest predators along forests edges (see above). A potential explanation for this discrepancy comes from studies of how patch shape influences nesting success. For a given patch area, patches with a more complex shape will have a more edge and less core habitat (Temple 1986). Two studies examining how the shape of a scrub-shrub patch influences nest success found that birds nesting in more complex patches, with more edge, had lower nest success than those nesting in patches with simpler shapes (Weldon & Haddad 2005; Chandler 2006). This suggests that the relationship between distance to edge and nest success may be more complex than the largely negative results described above. Rather, the influence of edges on nesting success may only be noticeable on the scale of the entire patch. Edge density at this larger scale may, therefore, be more important than distance to edge per se (see Donovan et al. 1997).

Another important characteristic of the landscape for scrub-shrub birds is patch size. Most scrub-shrub birds avoid the smallest patches, especially group-selection cuts or openings less than 1 ha in size (Chapter 5). As with edge distance, however, our review found that patch size has little effect on the nesting success of scrub-shrub birds (Table 6.4). Of four studies testing for area effects, none found significant differences in nest success for birds breeding in different-sized patches. This was true across a wide range of patch sizes, from group cuts of less than 1 ha (King & DeGraaf 2004) to clearcuts of 4-8 or 13-16 ha (Rodewald & Vitz 2005). While the number of studies in this area is small, patch size appears to have little effect on nest success of scrub-shrub birds.

Microhabitat

The vegetation and habitat features immediately surrounding a nest can have significant effects on avian nesting success. Many predators locate nests visually, so nest concealment can sometimes predict nest success (Martin 1992). Also, individual tree and shrub species provide different amounts of cover for nests, so the type of plant in which a nest is placed can affect predation rates (e.g. Schmidt & Whelan 1999a; Borgmann & Rodewald 2004). Finally, nests placed in more heterogeneous habitats may be more difficult to locate than those in more homogenous vegetation (Bowman & Harris 1980). Understanding how the microhabitat affects nesting success is important because vegetation can be managed relatively easily to manipulate nesting cover for birds (Martin 1992). For these reasons, we reviewed studies examining the effects of microhabitat on the nesting success of scrub-shrub birds.

We located several studies addressing this question. The results, however, were quite variable, and no general patterns were apparent. In fact, several studies actually reached contradictory conclusions. For instance, Ruffed Grouse in the southern Appalachians had higher nest success in areas with higher basal area and canopy cover (Tirpak et al. 2006), but in Michigan vegetation had no effect on grouse nest success (Murphy et al. 1997). For Field Sparrow, Evans (1978) reported higher nest success in red cedars than other nest substrates, but Best (1978) found that no vegetation measure predicted nest success. In a third study height above ground was the only consistent predictor of nest success (Burhans et al. 2002). These results suggest that the effects of vegetation on nesting success of scrub-shrub birds are species- and location-specific and difficult to generalize. These results parallel findings for birds in other habitats, which have also been somewhat equivocal. Even experimentally adding or removing vegetation around nests often has little effect on predation rates (Howlett & Stutchbury 1996; Peak 2003; Remeš 2005).

Habitat type

A sizeable literature exists on the habitat preferences of scrub-shrub birds (see Chapters 4 and 5). At the same time, researchers have paid less attention to whether or not avian reproductive success varies with habitat type (see Martin 1992).

Given the wide variety of scrub-shrub habitats, including old fields, forest edges, clearcuts, and bogs, understanding the nest success of birds in these habitats is important for management. We compared the nest success rates of birds in different habitats based on our review of such studies, above (Table 6.2). Sample sizes were only sufficient to compare nest success in three habitats: logged areas (clearcuts and shelterwood cuts), old fields, and wetlands. Of the three habitats, nest success was consistently highest in shrubby wetlands (Figure 6.1), with old fields having the lowest nest success and clearcuts intermediate (ANOVA: $F_{2,31} = 13.4$, $P < 0.001$). These results, however, need to be viewed with some caution because the studies differed greatly in bird species composition, geographic location, and landscape context. Nonetheless, the possibility remains that habitat may have a significant effect on avian nesting success.

A better approach to understand how nest success differs by habitat is to study different habitats in the same geographic area, focusing on the same species. Unfortunately, we were only able to locate a few comparative studies of this type. Fink et al. (2006) compared nesting success of birds in clearcuts and glades (naturally occurring shrublands) in Missouri but found that differences between habitats were species-specific. In Massachusetts, avian nesting success was similar in re-

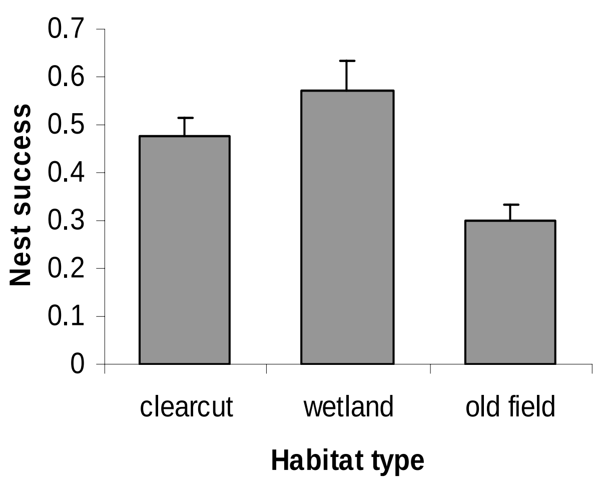


Figure 6.1. Nest success of altricial scrub-shrub birds in three habitat types. Results are based on studies listed in Table 6.2.

cent clearcuts and wildlife openings managed as scrub-shrub habitat (King & Collins, unpub. data). In Illinois, Indigo Buntings had higher nest success on gradual, natural edges and in forest-interior sites than on abrupt, anthropogenic edges or forest-exterior sites (Suarez et al. 1997). For Yellow-breasted Chats, nesting success rates were equivalent in old fields, shrubby clumps, and fencerows (Ricketts & Ritchison 2000). Clearly, more research is badly needed on this subject to determine which habitat types are most valuable for scrub-shrub birds. This information could aid managers seeking to determine how to manage the land for scrub-shrub birds.

Brown-headed Cowbirds

Brown-headed Cowbirds are brood parasites that lay their eggs in the nests of other birds (Friedmann 1929). Female cowbirds often remove eggs from nests, and nestling cowbirds have high food demands. As a result, brood parasitism can significantly reduce the reproductive success of cowbird hosts (Robinson et al. 1995a). Some birds have evolved defenses against brood parasitism, but many others readily accept cowbird eggs and young (Peer et al. 2005). Cowbirds are a conservation problem in areas where they are abundant or where hosts lack defenses against cowbirds (Robinson et al. 1995a). New England is near the edge of the cowbird's breeding range, and cowbirds are relatively uncommon in most of this region (Sauer et al. 2005). Published studies from New England generally show very low rates of brood parasitism for scrub-shrub birds (King & Byers 2002; Chandler 2006). Most such studies, however, are from heavily forested regions. Because cowbirds prefer to forage in open fields, they are most common in areas with agricultural fields or suburban lawns (Thompson 1994; Robinson et al. 1995a; Gates & Evans 1998). We have little information on brood parasitism rates in more open landscapes of southern New England, where cowbirds are locally abundant (Sauer et al. 2005). Theoretically, cowbirds could be a problem for this bird community because several species are preferred cowbird hosts (Table 6.5). Thus, more information is needed to determine whether or not brood parasitism is significantly affecting reproduction of scrub-shrub birds in New England.

Table 6.5. Frequency of brood parasitism by Brown-headed Cowbirds for scrub-shrub birds, based on the Birds of North America series and reflecting parasitism levels in areas where cowbirds are common.

Species	Frequency of parasitism[a]
Ruffed Grouse	never
Northern Bobwhite	never
Wilson's Snipe	never
American Woodcock	never
Yellow-billed Cuckoo	occasional
Whip-poor-will	never
Ruby-throated Hummingbird	never
Alder Flycatcher	frequent
Willow Flycatcher	frequent
White-eyed Vireo	frequent
Carolina Wren	frequent
House Wren	never
Gray Catbird	rejector
Northern Mockingbird	occasional
Brown Thrasher	rejector
Cedar Waxwing	occasional
Blue-winged Warbler	frequent
Golden-winged Warbler	frequent
Tennessee Warbler	never
Nashville Warbler	occasional
Yellow Warbler	frequent
Chestnut-sided Warbler	frequent
Magnolia Warbler	occasional
Prairie Warbler	frequent
Palm Warbler	occasional or never
Black-and-white Warbler	frequent
Mourning Warbler	occasional
Common Yellowthroat	frequent
Canada Warbler	frequent
Wilson's Warbler	frequent
Yellow-breasted Chat	frequent
Eastern Towhee	frequent
Field Sparrow	frequent
Song Sparrow	frequent
Lincoln's Sparrow	frequent
White-throated Sparrow	uncommon
Dark-eyed Junco	frequent
Northern Cardinal	frequent
Indigo Bunting	frequent
American Goldfinch	frequent
Rusty Blackbird	occasional or never

[a]Never = <1% of nests; occasional = 1-20%; frequent = >20%; rejector = species removes cowbird eggs.

Other factors

Numerous other factors can limit the reproductive success of birds. These include food availability, weather, parasites, pesticides or other pollutants, the availability of mates, and competition with other bird species. Unfortunately, almost no information is available on the impacts of these factors on New England's scrub-shrub birds. Research elsewhere, however, has shown that these limiting factors can reduce avian nesting success in certain situations (Newton 1998). Because scrub-shrub birds have rarely been the focus of the in-depth, detailed studies necessary to elucidate these factors, their importance is simply unknown for this bird community. Gathering more information on these factors should be an important research priority.

Conclusion

Fifteen years ago, Martin (1992) bemoaned the lack of basic information on avian nesting success and the factors controlling it. Since that time, substantial gains have been made in understanding the reproductive ecology of some birds, especially those of forests and grasslands. For scrub-shrub birds in New England, however, our knowledge has advanced little. Thus, our primary conclusion from this review is that much more research on the reproductive success of scrub-shrub birds is needed. While we were able to find data for a few species and environmental conditions, data were largely insufficient for most species and potential limiting factors. As a result, we lack information to determine whether or not reproduction is limiting scrub-shrub populations. Research is needed in several areas, including identifying nest predators, patch and landscape effects on nest success, habitat-specific demography, and rates of cowbird parasitism. Given the importance of reproduction for the long-term viability of any bird population, this is potentially the most critical research need for scrub-shrub birds in New England.

Chapter 7. Movement and Dispersal

Introduction

Of the 41 scrub-shrub birds breeding in New England, 37 are migratory. They spend the winter in the southern United States, the Caribbean, or Central and South America. Given their ability to move long distances, these birds can disperse to new breeding sites among years, often quite distant from their previous locations. Such movements complicate efforts to understand avian population dynamics and might make managing bird populations more difficult. Because birds can disperse to new breeding areas, the birds nesting at any location may be immigrants from distant populations (Robinson et al. 1995; Trine 1998). Thus, the numbers of birds breeding at a site could be affected by the productivity of populations well outside the area under management.

For scrub-shrub birds, these dynamics are further complicated by the fact that the habitats used are largely ephemeral. Owing to succession, some scrub-shrub birds will use regenerating forests for only a few years, and within 20 years after logging, nearly all scrub-shrub birds will have vanished (Chapter 4). As a result, in heavily forested areas like New England, scrub-shrub habitats probably exist in a "shifting mosaic" of patches. Each year, older areas of scrub become unsuitable due to succession while new patches are created by logging or other disturbances. Thus, the total area of scrub-shrub habitat may be relatively constant while the locations of suitable patches change from decade to decade. This has led some to suggest that scrub-shrub birds are "fugitive" species that move more freely among patches between years and show less fidelity to previous breeding sites than birds of more static habitats (Hutchinson 1951; Lent & Capen 1995).

Despite the possibility that dispersal behavior in scrub-shrub birds is qualitatively different from that of other birds, there has been no synthesis of the movements and dispersal of these bird species. Addressing this question is, however, important for conservation. If scrub-shrub birds are fugitive species, with high vagility and low site fidelity, then populations in any location will be open (strongly influenced by recruitment of birds from other sites). This could make tracking population sizes difficult, as they might be expected to fluctuate widely from year to year, independent of a site's quality. On the other hand, if scrub-shrub birds are not fugitive species and instead return to their previous breeding sites, then populations will be more closed (dependent on local reproduction for new recruitment). This would make managing populations easier but could pose risks because closed populations could be liable to extirpation if reproductive success or survival is low. Here, we review and synthesize studies on the site fidelity and movements of New England's scrub-shrub birds.

Are scrub-shrub birds fugitive species?

Changing breeding sites frequently could be adaptive for an animal if habitats only remain suitable for a short time period. Because scrub-shrub birds occupy highly ephemeral habitats, they might be expected have higher dispersal rates and lower site fidelity than birds breeding in more stable habitats. As a result, scrub-shrub birds have been characterized as "fugitive species" (Lent and Capen 1995). Hutchinson (1951) developed the concept of fugitive species to describe a group of copepods (tiny crustaceans) that are excellent colonizers of disturbed habitats but compete poorly with other copepod species. These species only occur in newly created bodies of water and disappear once other species, presumably stronger competitors, arrive. Fugitive species sacrifice competitive ability for high rates of dispersal, allowing them to reach newly created habitats before stronger competitors arrive (Levin & Paine 1974). According to Hutchinson, fugitive species have four characteristics: 1) they appear early in succession; 2) they become extinct before succession reaches the climax; 3) they are poor competitors; and 4) they are frequent dispersers, "forever on the move" (Hutchinson 1951:575).

For scrub-shrub birds, criteria 1 and 2 are obviously true—most of these species disappear well before forests mature (Chapter 4). Criterion 3, competitive ability, remains a poorly studied area. The fact that scrub-shrub birds disappear at roughly the same time that mature-forest birds begin to colonize a site is evidence only of the possibility of competition (Wiens 1989). To our knowledge, no study has tested whether or not competition restricts scrub-shrub birds to early-successional habitats.

We tested Hutchinson's fourth criteria for fugitive species, high vagility, using published data on scrub-shrub birds. Numerous studies have examined site fidelity, the tendency to return to former breeding sites, in scrub-shrub birds. Thus, we conducted a meta-analysis of the site fidelity rates of scrub-shrub birds to determine how frequently they disperse. To understand how the site fidelity levels of scrub-shrub compare to birds of more stable habitats, we also assessed the return rates of forest birds. Under the fugitive species hypothesis, forest birds would be expected to have higher site fidelity rates owing to greater competitive abilities and more stable habitats.

We conducted a literature search for studies in which researchers individually marked adult birds during the breeding season and counted returning birds during one or more subsequent years. We searched for studies using *ISI Web of Knowledge*, Biological Abstracts, and references cited in the literature. We also used unpublished data cited in the *Birds of North America* series. We searched for studies of both scrub-shrub birds and forest-breeding birds found in New England (per DeGraaf & Yamasaki 2001). For studies that followed marked cohorts for multiple years, we restricted analyses to the first year of returns to avoid pseudoreplication. Because the number of studies was limited, we used all studies of scrub-shrub birds from any part of their breeding ranges. In birds, the sexes tend to differ in their site fidelity rates (Clarke et al. 1997), and the studies we reviewed included either only males or both sexes. As a result, estimates of site fidelity rates for individual species may have been biased by how many studies of that species included females. To overcome this bias, we used mixed models to estimate the site fidelity rates for each species, controlling for sex. Because studies with larger sample sizes produce more reliable results, we weighted studies based on the number of birds marked (Lipsey & Wilson 2001).

Overall, we located 55 studies reporting site fidelity rates. Males had higher site fidelity rates than females in every species for which we had data on both sexes ($t_{21} = 5.69$, $P = 0.0001$). After controlling for sex differences, site fidelity rates for scrub-shrub birds were similar to those of forest birds. The mean return rate was 38 ± 4% for scrub-shrub birds (based on 66 separate data points and a total of 9476 marked birds) and 33 ± 4% for forest birds (53 data points; 3081 marked birds). The mixed model showed no significant difference in the site fidelity of forest and scrub-shrub birds ($F_{1, 105} = 1.77$, $P = 0.19$). Individual scrub-shrub birds showed substantial variation in their return rates (Table 7.1). For most scrub-shrub birds, estimated return rates were greater than 30%, though Cedar Waxwing and Yellow-breasted Chat had return rates below 10%.

These results do not support the hypothesis that scrub-shrub birds are, as a group, fugitive species. Return rates for scrub-shrub birds were similar to those of forest birds and also similar to those of several other passerine species reviewed in Greenwood & Harvey (1982). Thus, scrub-shrub birds do not follow a strategy of frequent dispersal, as suggested by Lent & Capen (1995).

Why would scrub-shrub birds follow return to previous breeding sites if such sites grow unsuitable after a few years due to succession? First, dispersing to a new breeding site may impose costs on a bird (Beletsky & Orians 1989; Bensch & Hasselquist 1991). Given the limited availability of scrub-shrub habitats, searching for a new territory will require time and energy and potentially expose birds to predation (Yoder et al. 2004). Even when a new breeding site is found, birds immigrating to new areas may be relegated to lower-quality territories by dominant individuals (Ward & Weatherhead 2005). Conversely, returning to a previously used site may confer advantages of site dominance (Bruinzeel & van de Pol 2004). For scrub-shrub birds, returning to a previous site that is decreasing in quality due to succession may be safer than trying one's luck elsewhere. Second, even for species that prefer specific stages of succession, regenerating clearcuts provide suitable habitat for roughly 10 years (see Chapter 4). This time is significantly longer than the lifespans of most small passerines (Klimkiewicz et al. 1983). Thus, returning to previously used habitat may be a viable strategy if the habitat is likely to remain suitable through a bird's expected lifespan. Interestingly, one group of birds that appears to follow the fugitive species strategy is grassland breeders on the Great Plains (Jones et al. 2007). These birds may have evolved a strategy of frequent dispersal and low site fidel-

Table 7.1. Results of meta-analysis of site fidelity rates of scrub-shrub birds. Site fidelity rates are marginal means from a mixed model.

Species	Site Fidelity Rate (%, ± SE)	Datasets	Birds marked	Sources*
Scrub-shrub Birds				
Whip-poor-will	54 ± 30	2	24	1
Willow Flycatcher	54 ± 16	4	1497	2, 3
White-eyed Vireo	47 ± 21	1	74	4
House Wren	32 ± 16	5	4095	5 – 7
Gray Catbird	23 ± 17	5	387	8 – 10
Cedar Waxwing	1 ± 20	4	108	11 – 14
Blue-winged Warbler	24 ± 20	4	106	15 – 17
Golden-winged Warbler	66 ± 40	1	11	17
Yellow Warbler	23 ± 11	1	137	18
Prairie Warbler	36 ± 18	2	160	19
Common Yellowthroat	55 ± 27	1	32	20
Wilson's Warbler	43 ± 18	7	156	21, 22
Yellow-breasted Chat	7 ± 24	2	47	23
Eastern Towhee	18 ± 19	2	129	8
Field Sparrow	47 ± 18	5	193	24 – 27
Song Sparrow	30 ± 17	3	442	28, 29
Lincoln's Sparrow	36 ± 18	2	208	30
White-throated Sparrow	30 ± 17	4	307	31, 32
Dark-eyed Junco	47 ± 18	3	149	33, 34
Northern Cardinal	27 ± 25	1	42	8
Indigo Bunting	60 ± 16	2	1172	35
Forest Birds				
Eastern Wood-Pewee	21 ± 35	1	9	36
Acadian Flycatcher	47 ± 16	4	89	37, 38
Great-crested Flycatcher	8 ± 25	1	21	36
Red-eyed Vireo	41 ± 16	2	98	36, 39
Ruby-crowned Kinglet	0 ± 23	1	27	40
Swainson's Thrush	37 ± 17	2	n/a	41
Hermit Thrush	35 ± 16	2	109	42
Wood Thrush	48 ± 13	5	n/a	36, 43, 44
Black-throated Blue Warbler	36 ± 13	4	436	45, 46
American Redstart	26 ± 13	4	493	45, 47
Worm-eating Warbler	24 ± 51	1	4	36
Ovenbird	34 ± 13	16	908	36, 42, 48 - 53
Louisiana Waterthrush	27 ± 39	2	7	36, 54
Kentucky Warbler	17 ± 25	1	22	36
Hooded Warbler	49 ± 13	4	441	55, 56
Scarlet Tanager	49 ± 51	1	4	36
Rose-breasted Grosbeak	0 ± 51	1	4	36

*(1) Cink 2002; (2) Sedgwick 2004; (3) Sedgwick 2000 (2 studies); (4) Hopp et al. 1999; (5) Drilling & Thompson 1988; (6) Kendeigh 1937; (7) Baldwin & Bowen 1928; (8) Leck et al. 1988 (9) Darley et al. 1977; (10) Johnson & Best 1980; (11) Brugger et al. 1994; (12) Witmer et al. 1997; (13) Putman 1949; (14) Mountjoy & John 1987; (15) Canterbury et al. unpublished; (16) Gill et al. 2001 (2 studies); (17) Murray & Gill 1976; (18) Yezerinac et al. 1996 (19) Nolan 1978; (20) Roberts 1971; (21) Stewart et al. 1977 (2 studies); (22) Ammon & Gilbert 1999; (23) Thompson & Nolan 1973; (24) Fretwell 1968; (25) Carey et al. 1994; (26) Best 1977; (27) Nelson 1992; (28) Weatherhead & Boak 1986; (29) Nice 1937; (30) Ammon 1995; (31) Knapton et al. 1984; (32) Lowther & Falls 1968; (33) Ketterson et al. 1992; (34) Ketterson & Nolan 1985; (35) Payne & Payne 1990; (36) Robinson 1992; (37) Fauth & Cabe 2005; (38) Walkinshaw 1966; (39) Cimprich et al. 2000; (40) Ingold & Wallace 1994; (41) Evans Mack & Yong 2000; (42) Hartley 2003; (43) Roth & Johnson 1993; (44) Trine 1998; (45) Sherry & Holmes 1992; (46) Holmes et al. 1996; (47) Lemon et al. 1996; (48) Bayne & Hobson 2002a; (49) Bayne & Hobson 2002b; (50) Burke & Nol 2001; (51) Porneluzi 2003; (52) Roberts 1971; (53) Hann 1937; (54) Robinson 1990; (55) Howlett & Stutchbury 2003

ity due to interannual fluctuations in habitat quality caused by bison, fire, or drought (Andersson 1980).

While most scrub-shrub birds had relatively high site fidelity, two species may have met the criteria for fugitive species. Cedar Waxwing showed average return rates of just 1% across 3 studies. This species chooses its breeding habitats based on the availability of fruit, its primary food (Witmer et al. 1997). Because areas with fruits are patchily distributed and may vary in location from year to year, waxwings wander widely in search of suitable habitat. At the same time, however, waxwings are non-territorial and have large home ranges, meaning that birds that do return to former breeding sites may be hard to detect (Witmer et al. 1997). Yellow-breasted chats also showed extremely low site fidelity, 7% according to Thompson & Nolan (1973). This result is difficult to reconcile with the chat's natural history, which is similar to other warblers that show much higher site fidelity rates. A recent study in Ohio found that approximately 60% of chats returned to previous breeding sites, suggesting that Thompson & Nolan's data may have been an aberration (S. Larner, pers. comm.).

For managers, the relatively high site fidelity of scrub-shrub birds is a benefit. Birds should be expected to persist in sites where they breed successfully. Thus, conventional management prescriptions—restoring and maintaining habitat and controlling nest predation and brood parasitism—should be effective in building healthy populations. For species like Cedar Waxwing that wander widely, management will be much more difficult because the birds may breed in different places each year.

Return rates of birds are actually the product of two parameters: a bird's propensity to return to previous nesting sites and its survival over the winter (Lebreton et al. 1992). Knowing annual survival rates of scrub-shrub birds would be extremely useful because of their relevance for conservation; low annual survival could doom a population to extinction even if reproductive rates were high (Pulliam 1988). Unfortunately, disentangling survival rates and site fidelity is difficult because birds cannot be followed individually over their annual migrations (Martin et al. 1995). When a bird does not return to its former breeding site in spring, one cannot know if it has died or simply dispersed to a new breeding location. Thus, in terms of annual survival rates, the only conclusion that we can make based on current data is that return rates of scrub-shrub birds are similar to those of birds of mature forests. Low survival rates are probably no more or less of a problem for scrub-shrub birds than for forest birds. Clearly, more research on survival rates of scrub-shrub birds is needed.

Natal philopatry of scrub-shrub birds

While adult scrub-shrub birds generally show relatively high site fidelity, the same may not be expected of yearlings, returning to the breeding grounds for the first time. This is because selective pressures on dispersal of young birds may be different from those of adults (Weatherhead & Forbes 1994). Yearlings that breed where they were hatched could end up pairing with one of their parents or another close relative, resulting in inbreeding and reduced fitness (Brown & Brown 1998; Shutler et al. 2004). At the same time, however, young birds that disperse to a new breeding site may suffer from the same disadvantages—unfamiliarity with the terrain and relegation to poor sites—experienced by dispersing adults (Pärt 1994; Hansson et al. 2004). For scrub-shrub birds, the issue is complicated by succession, which can cause habitat suitability to decline over time (Chapter 4). Thus, breeding where a bird was hatched could be disadvantageous because habitat quality will be likely to decline over the bird's lifetime. A better strategy in such cases could be to disperse to a younger, more suitable site that will provide breeding habitat for a longer period of time. Kirtland's Warblers appear to follow this strategy, with yearlings preferring sites younger than those where they were reared (Walkinshaw 1983).

The rate at which young scrub-shrub birds return to their natal sites has significant conservation implications. If birds return at high rates, then populations will be dominated by birds produced locally. This could result in populations being relatively isolated from one another so that a population's persistence would depend on the production of new young. In contrast, if few birds return to their natal sites, then populations would be more open, and the number of breeders at any site would depend on birds' immigrating from elsewhere (May 1981). In such situations, the number of breeders at any site may depend on how well birds reproduce elsewhere in their ranges.

To better understand the population dynamics of scrub-shrub birds, we reviewed studies of natal philopatry in these species. We collected studies in which birds were banded as nestlings or fledglings and their returns were measured in the following breeding season. The average rate of natal philopatry for 12 species studied was 4.0 ± 1.5% (Table 7.2). Out of a total of 19,622 birds marked in these studies, only 754 returned to breed at their natal sites. The highest levels of site fidelity were just 17% for Willow Flycatcher and 12% for a partially migratory population of Dark-eyed Juncos. In several studies, no marked young returned at all. These include Eastern Towhee (n = 29 banded young; Leck et al. 1988), White-throated Sparrow (n = 65; Knapton et al. 1984), and Gray Catbird (n = 32; Johnson & Best 1980).

In a larger review of natal philopatry by birds, Weatherhead & Forbes (1994) found return rates roughly as low as ours for birds of non-scrub habitats ($\bar{x}$= 3.9%). Thus, the tendency of young birds to disperse to new breeding sites, distant from where they hatched, is apparently widespread in passerines, not specific to scrub-shrub birds. For this bird community, the main effect of low natal philopatry is that recruitment of new birds to breeding sites will depend upon production of young elsewhere (May 1981). To date, little is known about just how widely young migratory birds disperse (Robinson & Morse 2000). The scale of this dispersal has major implications for future populations of scrub-shrub birds. If, for instance, Brown Thrashers hatched in New England generally disperse within this region, then New England's populations would be isolated at the regional scale. As a result, we could not count on thrasher production in other regions to augment New England's declining populations. On the other hand, if birds disperse into New England from other regions, then even if thrashers reproduce poorly in New England, populations could be maintained by immigrants from elsewhere (Pulliam 1988). Some initial evidence suggests that young migratory songbirds can disperse very long distances between natal and breeding sites (Graves et al. 2002; Hobson et al. 2004). In general, however, no firm conclusions can be made about the range over which birds disperse. This is an active area of research (Webster et al. 2002; Donovan et al. 2006).

Within season movements of scrub-shrub birds

So far, our discussion of avian dispersal has focused on interannual movements. Birds, however, can also make movements within the breeding season, dispersing to a new territory between nesting attempts. For instance, Darley et al. (1971) found that between 21 and 43% of Gray Catbirds switched breeding territories during the breeding season. Most of these birds moved to new sites within a few hundred meters of their former territories. Similarly, Nolan (1978) reported several instances of Prairie Warblers' switching territories in the middle of the breeding season. Many of the movements in Nolan's study

Table 7.2. Natal philopatry rates for scrub-shrub birds.

Species	Site fidelity rate (%)	Birds marked	Sources
Willow Flycatcher	16.8	1476	Sedgwick 2000, 2004
House Wren	2.4	13674	Drilling & Thompson 1988; Kendeigh 1937
Gray Catbird	4.7	85	Johnson & Best 1980; Leck et al. 1988
Brown Thrasher	2.0	392	Haas 1995
Cedar Waxwing	0.0	42	Mountjoy 1987
Chestnut-sided Warbler	2.3	219	King, unpublished data
Common Yellowthroat	1.2	85	Hofslund 1959
Eastern Towhee	0.0	29	Leck et al. 1988
Song Sparrow	0.7	146	Weatherhead & Boak 1986
White-throated Sparrow	0.0	65	Knapton et al. 1984
Dark-eyed Junco	12.5	795	Nolan et al. 2002
Indigo Bunting	5.4	2544	Payne 1991

were apparently triggered by nest failures; birds may have moved to new territories to avoid having their subsequent nests depredated by the same predators as previously (Jackson et al. 1989). Other within season movements of birds involve temporary forays into other birds' territories or unoccupied habitats (Stutchbury et al. 2005). For males, these birds may be opportunities to obtain extra-pair copulations with females besides their social mates.

How might within-season movements of scrub-shrub birds influence habitat selection? Many scrub-shrub birds prefer to settle in larger patches of habitat or in landscapes with more habitat (Chapter 5). Breeding in such areas would make it relatively easy for birds to switch to a new territory nearby. Conversely, living in a small, isolated patch might limit a bird's ability to switch territories during the breeding season. Isolation could mean that a bird would have to travel a long distance and use valuable time to find a new territory. In some forest birds, males inhabiting small fragments will travel to nearby fragments to seek extra-pair copulations (Norris & Stutchbury 2001; Fraser & Stutchbury 2004). For these birds, a series of small patches located near one another may be the functional equivalent of a large patch. This may explain why some forest birds use forest fragments located near other patches but eschew isolated fragments (Lynch & Whigham 1984; Askins et al. 1987). In the only study of isolation effects on scrub-shrub birds to date, Chandler (2006) found that isolation did not affect abundances of birds breeding in small wildlife openings. Clearly, more research on this subject is needed. Management of scrub-shrub birds could be more effective if we understood the effects of isolation on habitat usage. If scrub-shrub birds treat adjacent small patches as if they were one large patch, then a group of small cuts could be just useful as a large clearcut. Accordingly, in areas where large clearcuts are not a viable silvicultural practice, a number of smaller clearcuts (but not group-selection cuts—see Chapter 5) located near one another could be just as beneficial for these birds. If, however, scrub-shrub birds do not treat nearby patches as connected, then a cluster of small patches would not be an effective substitute for a large cut.

Conclusion

Though researchers have suggested that scrub-shrub birds are fugitive species, we found that site fidelity rates of adult birds were similar to rates of forest birds. Furthermore, site fidelity rates for young birds, returning for their first breeding season, were extremely low. In this sense, the population dynamics of scrub-shrub birds appear similar to those of forest birds. The management implications of these dynamics are that providing high-quality habitat where birds can nest successfully is likely the best way to ensure a persistent, viable population. Because, however, young birds can disperse widely, local populations of scrub-shrub birds may be impacted by conditions elsewhere in their ranges.

One of the most critical areas for future research on scrub-shrub birds is survival rates. Without estimates of annual survival rates, we cannot know whether or not scrub-shrub bird populations are sources (producing more young each year than are needed to compensate for deaths) or sinks (not producing enough young to compensate for deaths). Survival estimates are available for only a few scrub-shrub species, and in most cases those estimates come from the western U.S., making their applicability to New England questionable. Of particular need is a method that avoids the confound between site fidelity and survival. For instance, Sillett & Holmes (2002), estimated annual survival for a migratory warbler by separately estimating survival during summer, winter, and migration. Similar studies for scrub-shrub birds would be invaluable for conservation.

Chapter 8. Winter and Migration

Introduction

Most songbirds breeding in the United States and Canada migrate south each fall, avoiding the cold temperature and food shortages that characterize temperate winters (Gauthreaux 1982). Of New England's 41 scrub-shrub birds, only 4 species remain on the breeding grounds through the winter; the remaining 37 species migrate to warmer areas (Table 8.1). Most of the migrants (23 species) spend the winter in the Neotropics—Mexico, Central and South America, or the West Indies. The other 14 species are short-distance migrants and winter in the eastern or southeastern United States.

While this report focuses on New England, no discussion of avian ecology would be complete without including winter and migration. The significance of migratory behavior is that managing New England's scrub-shrub solely on the breeding grounds may not be sufficient for conservation. Even if high-quality breeding habitat were abundant in New England, bird populations might still decline if conditions on the wintering grounds or along migratory routes were poor. Some research suggests that habitat availability on the wintering grounds is the key factor limiting bird populations (Rappole & McDonald 1994; Sherry & Holmes 1996). Deforestation in Central and South America has been severe and may be causing declines in populations of some scrub-shrub birds (FAO 2007). Mortality of birds during migration due weather or collisions with structures may also impact on bird populations (Erickson et al. 2001; Newton 2006). If migration and winter are limiting times for populations of scrub-shrub birds, than management on the wintering grounds might be the most effective way to bolster populations (Sherry & Holmes 1995). Here, we review what is known about the ecology of New England's scrub-shrub birds on the wintering grounds and in migration.

Summer versus winter limitation of bird populations

The question of whether conditions on the breeding or wintering grounds limit bird populations has been controversial in ornithology (Rappole & McDonald 1994; Sherry & Holmes 1995; Latta & Baltz 1997). Breeding season factors such as nest predation and habitat fragmentation are widely viewed as the leading candidates for why many Neotropical migrants are declining (Wilcove 1985; Robinson et al. 1995b). Some researchers, however, believe that the wintering grounds may have a greater impact on bird populations, for several reasons. First, the breeding season in New England lasts only 3 or 4 months, so birds spend most of the year at their wintering sites. Thus, conditions at those sites may be more important for population persistence than those on the breeding grounds (Rappole 1995). Second, deforestation is proceeding rapidly in many parts of the Neotropics, meaning that wintering habitats are disappearing in some areas (FAO 2007). Third, birds appear to compete for habitat on the wintering grounds, as evinced by territorial behavior (Rappole & Warner 1980; Neudorf & Tarof 1998; Koronkiewicz et al. 2006). In some birds, habitat limitation forces some individuals to "float," living inconspicuously among territory holders without holding a territory (Stutchbury 1994; Koronkiewicz et al. 2006). Floaters may survive at lower rates than territory holders (Newton 1998). Finally, habitat quality and availability on the wintering grounds can have direct effects on bird populations and their growth rates. Birds forced to winter in low-quality habitats, where food is limited, may have low survival rates (Brown et al. 2002; Studds & Marra 2005; Johnson et al. 2006). More significantly, birds that winter in low-quality sites may have to delay their departure for the breeding grounds, resulting in lower breeding-season reproductive success than birds that winter at high-quality sites (Marra et al. 1998; Norris et al. 2004).

These factors suggest but do not prove that winter habitat limits numbers of breeding birds. Resolving the issue of summer vs. winter limitation of bird populations is significant for conserving scrub-shrub birds. For a bird population limited by winter habitat, adding more breeding habitat may have little effect on overall breeding populations (Sutherland 1996). Similarly, birds limited by breeding habitat availability may not respond to changes in winter habitat. Thus, understanding whether or not scrub-shrub birds are

Table 8.1. Wintering locations of scrub-shrub birds. Species in italics are primarily Neotropical migrants; others are residents or short-distance migrants.

Species	Winter Range
Ruffed Grouse	resident
Northern Bobwhite	resident
Wilson's Snipe	e. U.S., Mexico, Central Ameica, West Indies, n. South America
American Woodcock	se. U.S.
Yellow-billed Cuckoo	e. South America
Whip-poor-will	Florida, U.S. Gulf coast, e. Mexico, n. Central America
Ruby-throated Hummingbird	s. Mexico, Central America
Alder Flycatcher	n. and c. South America
Willow Flycatcher	Central America
White-eyed Vireo	Florida, se. U.S. coast, e. Mexico, n. Central America
Carolina Wren	resident
House Wren	se. U.S., Mexico
Gray Catbird	e. and se. coast of U.S., e. Mexico, Central America, w. West Indies
Northern Mockingbird	resident
Brown Thrasher	se. U.S.
Cedar Waxwing	resident
Blue-winged Warbler	Caribbean slope of Central America & Mexico
Golden-winged Warbler	s. Central America, n. South America
Tennessee Warbler	s. Mexico, Central America, n. South America
Nashville Warbler	s. Mexico
Yellow Warbler	Mexico to n. S. America
Chestnut-sided Warbler	Central America
Magnolia Warbler	s. Mexico, Central America, West Indies
Prairie Warbler	Florida, West Indies
Palm Warbler	se. U.S. coast, West Indies
Black-and-white Warbler	se. U.S., Central America, West Indies, n. South America
Mourning Warbler	s. Central America, n. South America
Common Yellowthroat	se. U.S., West Indies, Central America, Mexico
Canada Warbler	n. S. America, mainly near the Andes
Wilson's Warbler	Mexico, Central America
Yellow-breasted Chat	s. Mexico, Central America
Eastern Towhee	se. U.S.
Field Sparrow	se. U.S.
Song Sparrow	se. U.S.
Lincoln's Sparrow	s.-central U.S., Mexico
White-throated Sparrow	e. U.S.
Dark-eyed Junco	se. U.S.
Northern Cardinal	resident
Indigo Bunting	Mexico, Central America, West Indies
American Goldfinch	se. U.S.
Rusty Blackbird	e. U.S.

limited in winter or summer has major management implications. Below, we review some of the factors influencing winter populations of scrub-shrub birds.

Wintering locations

To conserve the non-breeding habitats of New England's scrub-shrub birds, conservationists need to know where these species winter. In particular, identifying areas where many species co-occur could make management more efficient by targeting efforts in areas with high numbers of scrub-shrub birds (Margules & Pressey 2000). As a coarse approach to the question of wintering locations, we used geographic information systems to overlay the winter ranges of 35 scrub-shrub birds that migrate south from New England each winter. We divided North and South America into an 80 x 80 km grid and counted the number of species that winter in each cell. The winter species richness ranged from 0 to 20 (Figure 8.1). Areas with the highest diversity include Panama, Costa Rica, and the Gulf Coast of Texas. Other areas of high species diversity include the Gulf and Atlantic Coasts of the southeastern U.S. (including Florida), eastern Mexico, and remaining areas of Central America. The islands of the Caribbean had slightly lower numbers of species. Species richness of wintering birds was generally low away from the coasts in the United States and in South America.

While our map identified potentially important wintering locations for scrub-shrub birds, the results should be viewed with some caution. The map was based on species' entire winter ranges, but geographic ranges can include some areas where a species is not present (Rondinini et al. 2005). Thus, our analysis certainly includes some areas where each species does not occur. This means that actual species richness in some grid cells may be lower than what is shown in Figure 8.1. In general, however, the patterns of species richness shown on the map should hold true even if the use of geographic ranges overstates the occurrences of individual species (Rondinini et al. 2005).

Another shortcoming of the above analysis is that geographic ranges do not reveal exactly where birds that breed in New England spend the winter. In some species, birds from different breeding populations winter in distinct locations. For instance, Black-throated Blue Warblers winter throughout the Caribbean, but populations on western islands tend to come from the northern part of the breeding range and vice versa (Rubenstein et al. 2002). For scrub-shrub birds little is known about connections between wintering and breeding populations. Thus, we do not know exactly which areas to prioritize for conserving New England's scrub-shrub species. This is a problem because many scrub-shrub birds have large breeding and wintering ranges. For instance, Black-and-white Warblers breed throughout the eastern United States and southern Canada, and they winter from northern Mexico and Florida south to northern South America. Where Black-and-white Warblers that breed in New England spend the winter is not currently known. Migratory connectivity, however, is an active area of research, and we hope to have better answers to the question of where New England's scrub-shrub birds winter in the near future.

Winter habitats

Closely related to the issue of wintering locations is the question of which habitats scrub-shrub birds utilize during the non-breeding season. In the Neotropics, wintering scrub-shrub birds are most abundant in open, scrubby habitats (Lynch 1992; Petit et al. 1992; Rappole et al. 1995; Siegel & Centeno 1996; Smith et al. 2001). In Table 8.2, we have summarized the habitats that scrub-shrub birds commonly occupy in winter. These birds can be found in a variety of scrubby habitats, from pastures to forests with open canopies. Thus, for most of New England's scrub-shrub birds, breeding and non-breeding habitats are relatively similar.

One of the striking features of avian migration is that some species shift habitats completely between the breeding and non-breeding seasons. At least six scrub-shrub birds—Canada Warbler, Magnolia Warbler, Golden-winged Warbler, Blue-winged Warbler, Chestnut-sided Warbler, and Whip-poor-will—winter in mature forests in the Neotropics (Petit et al. 1995). Most of these species are almost never found in closed-canopy forests during the breeding season (Chapter 4). Past research has found that birds that winter in forests may be declining due to tropical deforestation (Robbins et al. 1989b). To test this hypothesis for scrub-shrub birds, we used Breeding Bird

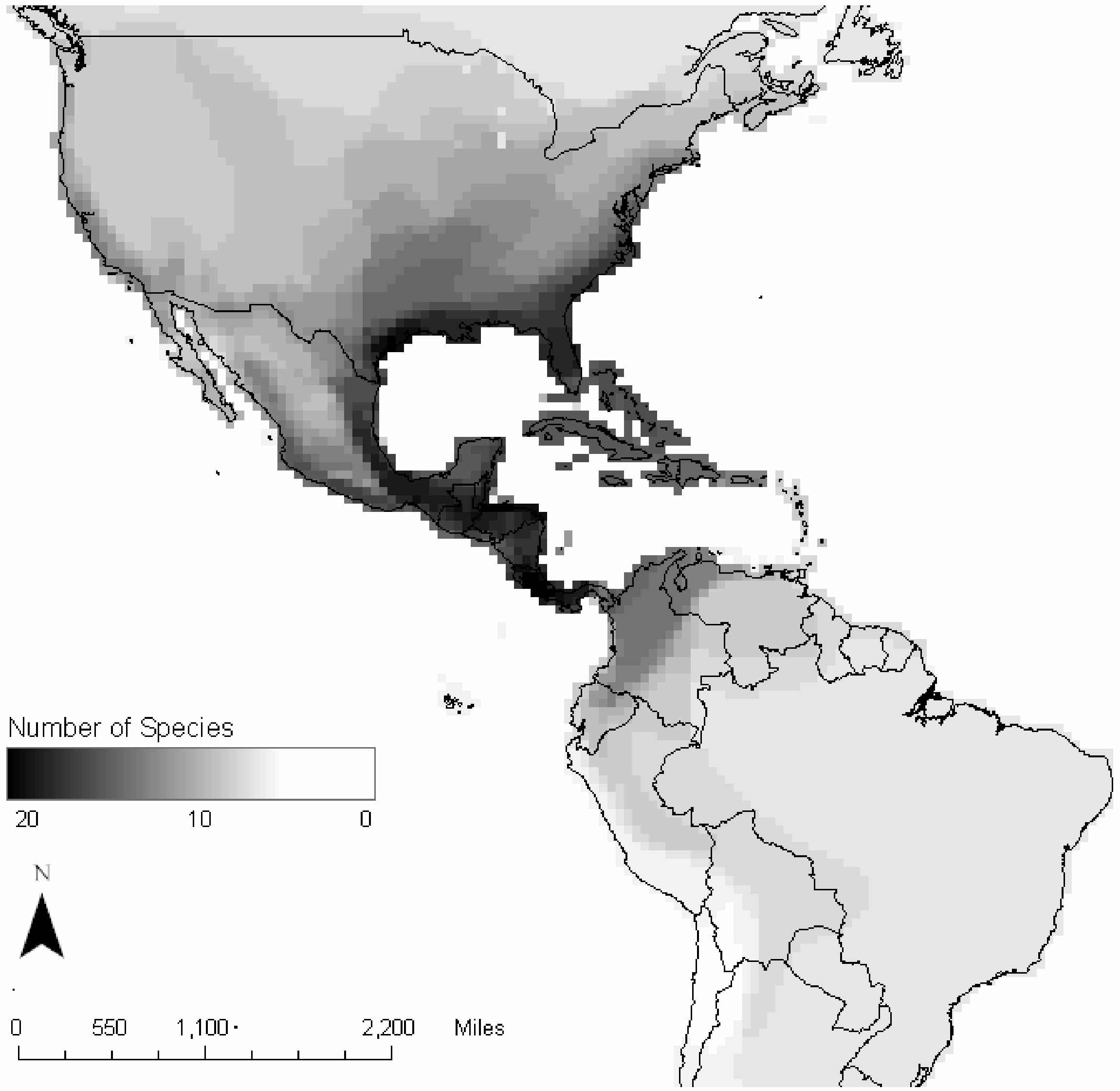


Figure 8.1. Species richness of New England's scrub-shrub birds in winter. Winter ranges are based on maps from NatureServe (Ridgely et al. 2005).

Survey data to compare population trends for the six forest-wintering species with those for Neotropical migrants wintering in shrublands (see Chapter 3 for details). While trends were slightly lower for the forest-wintering birds ($\bar{x}$ = -1.26% year^{-1}) than for other Neotropical migrants ($\bar{x}$= -0.05% year^{-1}), the difference was not significant (P = 0.40).

At a very general level, we predict that habitat availability for scrub-shrub birds should be high because they utilize second-growth forests and other disturbed habitats. Logging of tropical forests has created scrub-shrub and open habitats in regions that were largely forested until recently (Rappole 1995). Research on the breeding grounds has shown that many scrub-shrub birds are actually habitat specialists, preferring specific plant associations or successional stages (Chapter 4). Aside from general preferences for early-successional or open habitats (e.g. Lynch 1992; Rappole et al. 1995; Smith et al. 2001), little information is available on exactly which habitat types these birds prefer in winter. Because we lack detailed information on avian habitat preferences in winter, we cannot make quantitative conclusions about habitat availability. Clearly, we

Table 8.2. Habitats used in winter by migratory scrub-shrub birds. Habitats are summarized from information in the Birds of North America series.

Species	Winter Habitat
Wilson's Snipe	varied wet habitats - marshes, swamps, fields
American Woodcock	forests for roosting; fields and scrub for foraging
Yellow-billed Cuckoo	varied - scrub, forest, riparian
Whip-poor-will	woods and scrub
Ruby-throated Hummingbird	varied - forest, second growth, citrus groves
Alder Flycatcher	wet second growth, scrub
Willow Flycatcher	wet second growth, scrub
White-eyed Vireo	varied - second growth to forest
House Wren	second growth, thickets, scrub
Gray Catbird	generally in scrub, but also uses forests
Brown Thrasher	scrub, thickets
Blue-winged Warbler	humid and semihumid forest and forest edge, second growth
Golden-winged Warbler	canopy of woodland
Tennessee Warbler	second growth, forest edge, open forest
Nashville Warbler	open forests, gardens
Yellow Warbler	varied - wooded, open, scrubby habitats
Chestnut-sided Warbler	varied - old and young forest, coffee, scrub
Magnolia Warbler	varied - all wooded habitats, scrub to forest
Prairie Warbler	second growth, forest edge, open forest
Palm Warbler	varied – wooded, open, scrubby habitats
Black-and-white Warbler	varied - early successional to mature forest
Mourning Warbler	scrubby, wet, open habitats
Common Yellowthroat	varied - open forest, second growth, scrub
Canada Warbler	forest undergrowth, scrub, forest edge, coffee
Wilson's Warbler	mostly in forests, also second growth, scrub
Yellow-breasted Chat	scrub, second growth, open forest with dense understory
Eastern Towhee	scrub, second growth, open forest with dense understory
Field Sparrow	old fields, forest edges
Song Sparrow	field edges, old fields, second growth
Lincoln's Sparrow	forests
White-throated Sparrow	scrub, thickets, hedgerows - places with dense cover
Dark-eyed Junco	second growth, old fields, suburbs
Indigo Bunting	grasslands, agricultural fields, second growth, towns
American Goldfinch	varied - open, weedy areas, feeders
Rusty Blackbird	varied wet habitats - forests, scrub, marsh

need more information about what habitats these birds use to make more detailed assessments of habitat availability and whether or not winter habitats are limiting.

One problem with studying habitat preferences in winter is that birds may use sub-optimal habitat types if high-quality habitats are saturated or locally unavailable (Sherry & Holmes 1996). Simply because birds use a habitat does not guarantee that the habitat is actually suitable. Thus, understanding avian survival rates in different habitat types is an important research need. Research with forest birds has shown that birds survive in winter at different rates in different forest types (Sherry & Holmes 1995). As discussed above, scrub-shrub birds winter in a variety of habitats, but almost nothing is known about their habitat-specific survival rates. Research in this area is needed to understand how to manage winter populations of scrub-shrub birds.

Because we know so little about habitat usage by scrub-shrub birds, we cannot offer specific recommendations on strategies for conserving winter populations, nor can we determine with any confidence whether or not winter habitats may be limiting breeding populations. Gathering knowledge on how scrub-shrub birds use different habitats during winter should be a high priority for future research. The well-studied winter ecology of American Redstarts and Black-throated Blue Warblers could serve as a model for future research on scrub-shrub species (see Sherry & Holmes 1996; Marra et al. 1998; Rubenstein et al. 2002; Sillett & Holmes 2002).

Migration

Migratory birds spend up to three months each year in passage, and migration can be a time of high energy demands and vulnerability to predators (Moore et al. 1995). For adult songbirds, mortality is higher during migration than at any other time of year (Sillett & Holmes 2002). Thus, migration constitutes a critical time, both for birds themselves and for conservationists interested in preserving bird populations. Two aspects of avian migration are most important for management: ensuring stopover habitats are available and preventing avian mortality due to collisions with structures.

Birds may travel hundreds or thousands of miles on their migratory journeys, but they make the journey in stages (Moore et al. 1995). Long flights create a huge demand for energy, so birds must stop at least once per day to feed and refuel before the next leg of the journey (Klaassen 1996). For birds to complete their migration in a timely manner, they need stopover habitats where they can be safe from predators but find enough food to rapidly gain weight (Mehlman et al. 2005). Conservationists are increasingly concerned that development and habitat fragmentation are reducing the quantity and quality of stopover habitats, making an inherently perilous journey even more difficult for some migrants (Moore et al. 1995).

Most birds use a variety of habitats during migration, selecting stopover sites based on cover and food availability (Moore et al. 1995). As a result, some migrating birds will utilize habitats quite different from their typical breeding sites. Scrub-shrub birds, however, tend to use stopover habitats that are similar to their breeding sites—open-canopied, with dense vegetation within a few meters of the ground. For instance, Parnell (1969) found that migrating Common Yellowthroats, Prairie Warblers, Yellow-breasted Chats, and Yellow Warblers were all more abundant in thickets than in forested habitats. Similarly, Rodewald & Brittingham (2004) found that migrating scrub-shrub birds like Gray Catbird and Indigo Bunting were most abundant in young clearcuts and avoided mature forests. Compared with forest-breeding birds, scrub-shrub birds are more narrow and consistent in selecting stopover sites (Power 1971) .

Unfortunately, understanding the stopover ecology of scrub-shrub birds does not make managing their migration easy. Migration occurs across huge spatial scales and lasts several months each year. Moreover, for landbirds numbers of birds visiting stopover sites can vary greatly from year to year due to weather, birds' physiological conditions, and resource availability (Mehlman et al. 2005). Thus, identifying individual sites or specific reserves for migrants might be counterproductive since such sites may not be used consistently. Instead, a better strategy for conserving scrub-shrub birds on migration might be to ensure that scrub-shrub habitats are widely available throughout the eastern U.S, especially along the coasts or at other sites where migrants are known to congregate (Mehlman et al. 2005). Because the availability of stopover sites can affect the number of birds that successfully complete migration, the abundance of scrub-shrub birds in New England may be, in part, a function of how widely available scrub-shrub habitats are to the south of this region.

One other difficulty in dealing with migration is the high mortality of migrating birds due to collisions with structures such as windows, communication towers, and power lines. Ornithologists estimate that over 100 million birds die in collisions with windows each year in the U.S., and several million more are killed by flying into communication towers (Erickson et al. 2001). These numbers are large enough that they could be contributing to declines in some populations. We bring up this point not to suggest that scrub-shrub bird populations are definitely affected by these collisions but merely to show that some aspects of scrub-shrub bird conservation will not be soluble by management on the breeding grounds.

Non-migratory Birds

Only four scrub-shrub birds—Northern Bobwhite, Ruffed Grouse, Northern Cardinal, and Carolina Wren—are completely non-migratory and spend the winter on the breeding grounds. For two other birds, Cedar Waxwing and Northern Mockingbirds, migration is not well understood; both species may wander in the winter or remain on the breeding grounds (Witmer et al. 1997). Non-migratory birds may still move short distances to suitable wintering habitats that provide food and cover. Cardinals, for instance, may move from their breeding territories to areas with bird feeders or abundant fruit (Laskey 1944). Ruffed Grouse use mature male aspen trees as a food source in winter and may move from breeding areas to stands of aspen during the fall (Dessecker & McAuley 2001). Unlike true migrants, movements of resident birds in winter are facultative and, when they occur, likely to be short (Rusch & Keith 1971). Thus, conservation of these species requires that breeding and winter habitat both be available within a relatively small area.

Conclusion

Whether migratory and winter habitats are limiting the total populations of scrub-shrub birds is not known but could have great significance for conservation. If winter habitat is limiting populations, than management on the breeding grounds, as discussed in the previous chapters of this report, may be insufficent to bolster populations. This is a critical important area for future research, as the efficacy of management actions on the breeding grounds will depend on the adequacy of wintering and stopover habitats.

Chapter 9. Management and Research Recommendations

Scrub-shrub birds are clearly declining in New England. Due to the severity of the declines and the number of species affected, we recommend that scrub-shrub birds receive the highest priority for conservation and management. In order to facilitate these efforts, we conclude this report with recommendations for the management of scrub-shrub birds in New England based on our literature review. Our ability, however, to make detailed recommendations is hampered by a lack of information on some aspects of the ecology of scrub-shrub birds. Thus, in addition to management recommendations, we have also identified key research needs for these species. We hope that this chapter will serve as a springboard both for improved management of this bird community and for new research that will improve future management efforts.

Management Recommendations

1) Provide more habitat, especially in southern New England.

Several lines of evidence suggest that habitat loss is the primary cause of bird population declines in New England (Chapters 2, 3). If the loss of scrub-shrub habitat continues, birds like Northern Bobwhite and Golden-winged Warbler could be extirpated from New England within the next few decades. Thus, the conservation of these species will require providing more scrub habitat, particularly in Massachusetts, Connecticut, and Rhode Island. We estimate that in these three states, with dense human populations and relatively little silviculture, scrub-shrub habitat occupies just 4.8% of the total area (Chapter 2). Given that this estimate is based on forest inventory data from the last complete survey in the late 1990's, the current amount of habitat is probably even lower. Furthermore, creation of new habitat has decreased relative to previous decades due to increasing development and parcelization (Brooks 2003) as well as the disruption of natural disturbance regimes (Lorimer & White 2003). Habitat-creation projects on state-owned lands provide only 1,000-2,000 ha per year in each state, a few hundredths of one percent of the total land area (Oehler 2003). Given that creation of new scrub-shrub habitat is lagging behind habitat loss, new efforts to create early-successional habitat will be necessary to stabilize bird populations.

How much additional habitat would be needed to maintain stable bird populations? DeGraaf et al. (1992) suggested that in a healthy forested landscape, approximately 10% of the land should be in early-successional stages. The problem with such a simple rule of thumb, however, is that it is not based on a quantitative model of bird populations. While such targets may sound appealing, they may not be accurate and could, if implemented, be insufficient to conserve the target species or overestimate the habitat needed and waste scarce time and money (Soule & Sanjayan 1998).

As an alternative to simple rules of thumb, Partners in Flight (PIF), a bird conservation consortium, has developed population targets for North American birds based on their recent population trends (Rich et al. 2004). For instance, birds that are declining rapidly have a population target of a 50% increase within 30 years. Birds with relatively stable populations have maintaining current populations as their target. These continental goals are then scaled down to physiographic regions (Chapter 1), and density estimates for each species are used to determine exactly how much habitat is needed to meet the population target (Rich et al. 2004). For scrub-shrub birds in the Northeast, PIF calls for adding substantial areas of new habitat (Dettmers & Rosenberg 2000; Hodgman & Rosenberg 2000; Rosenberg & Hodgman 2000).

While the general approach used by PIF is an improvement over simple rules of thumb, their population goals are also problematic. PIF's regional population targets are based on continental-scale trends in bird populations. For many birds, population trends differ between New England and elsewhere in North America (Sauer et al. 2006). As a result, PIF population targets for New England may not be appropriate for bird populations in this region.

In general, estimating the area or number of individuals necessary to conserve a population is difficult, and we lack ecological information needed to make the necessary calculations (Soule

& Sanjayan 1998; Tear et al. 2005). Thus we suggest that setting explicit targets for habitat or bird populations would be premature for scrub-shrub birds in New England. Instead, any conservation goal for this community should include halting the current population declines. Stopping the ongoing declines is a simple and measurable standard for conserving this bird community. Exactly how much habitat would be needed to stabilize populations of scrub-shrub birds is unknown. At this point, and for the foreseeable future, any additional habitat is certain to benefit scrub-shrub birds.

2) Ensure that a variety of scrub-shrub habitats are represented

Scrub-shrub habitats occur in a variety of forms that differ in habitat characteristics (Chapter 2) and bird communities (Chapter 4). Thus, ensuring that all of these habitat types are represented in New England. Habitats besides clearcuts are especially important; clearcuts are not used by all scrub-shrub birds, and species richness there is lower than in wetlands and wildlife openings (Chapter 4). Here, we provide recommendations for management of these different habitat types for scrub-shrub birds.

Silvicultural treatments. Silviculture is a simple and cost-effective method to provide high quality scrub-shrub habitat (Thompson & DeGraaf 2001; DeGraaf & Yamasaki 2003). One benefit of using silviculture as a management technique is that revenues from timber harvests can offset the costs of habitat creation Because it produces larger patches of scrub-shrub habitat, even-aged management is far more effective for the creation of scrub-successional habitat than uneven-aged management (see below). Regenerating clearcuts are suitable for scrub-shrub birds for no more than 20 years after treatment (Chapter 4), so clearcuts older than this age should not be included in the development of habitat management goals. Furthermore, even-aged management should not be practiced where the deleterious effects of logging on other forest values, such as water quality, old growth, or aesthetics, would be unacceptable.

Old fields. When left undisturbed for several years, old fields will develop scrub-shrub habitat due to succession. In fields with clonal shrubs such as dogwood and alder, tree growth may be suppressed for decades, resulting in a long-term, stable scrub community (Tefft 2006). Initially, old fields should require little management, as trees and shrubs slowly colonize the habitat. Eventually, however, due to succession, old fields will gradually lose their scrub-shrub habitat. For managers, arresting old-field succession in an early stage will eventually require some sort of disturbance (Tefft 2006) (see next section).

Wildlife openings. Wildlife openings are small cleared areas in forested landscapes and are maintained in an early-successional state through mowing or burning every few years (Overcash et al. 1989). Wildlife openings can be created by modifying or maintaining any type of early-successional habitat, including old fields, clearcuts, log landings, or orchards. Several options are available for maintaining openings. For small numbers of trees, cutting followed by selective spraying with herbicides can be effective (Payne & Bryant 1994). For larger stands of trees, using a mower, hydroaxe, or "Brontosaurus" may be required (Hill 2006). Prescribed fire can also be used to control woody plants (Simmons 2006). Because habitat selection in most scrub-shrub birds is based on habitat structure rather than plant species composition, there is not likely to be a need for planting individual plant species (Chapter 4).

How frequently an opening is disturbed has a major influence on the vegetation. Frequent disturbance will result in a shrubland with less woody and more herbaceous vegetation (Chandler 2006). In contrast, long rotation times will result in an opening dominated by shrubs, vines, and saplings. In practice, most wildlife openings utilize short intervals, often less than 5 years, with the purpose of promoting populations of game animals (Overcash et al. 1989; Chandler 2006). While some scrub-shrub birds prefer significant herbaceous cover, densities of many scrub-shrub birds do not peak until a tall, thick cover of shrubs and saplings has developed (Chapter 4). Disturbing openings every few years does not allow this dense cover to develop. Thus, some birds may benefit from much longer rotation intervals between mowing or burning than are typically utilized in wildlife openings. Because each species of scrub-shrub bird has unique habitat preferences, there is no simple answer to the question of which rotation time is best. One option may be to stagger the rotation schedule and lengthen rotations to 10 years to ensure that all successional stages are represented.

Utility rights-of-way. Rights-of way (ROWs) beneath electrical and communications lines are occupied by a variety of scrub-shrub birds (Chapter 4). Management methods that maintain a substantial amount of shrub cover, such as selective tree removal, herbicide application, or grazing, should be favored over methods that result in grassy conditions (Confer & Pascoe 2003). Although these habitats account for only a small proportion of New England's shrublands (Chapter 2), ROWs create conditions similar to old fields, a habitat that is underrepresented in New England. Thus, this habitat should receive similar priority for management.

Pitch pine-scrub oak (PPSO) woodlands. PPSO forests are naturally pyrogenic and probably evolved with frequent fires (Parshall & Foster 2002; Parshall et al. 2003). When managed with regular burning, PPSO woodlands provide habitat for a diverse assemblage of scrub-shrub birds (Grand & Cushman 2003). When fire is suppressed, however, shade-tolerant, mesophytic trees may invade, replacing the PPSO community with a more typical hardwood forest (Cryan 1985). Maintaining PPSO woodlands in a state suitable for scrub-shrub birds requires regular management, through fire or mechanically thinning the vegetation. Prescribed fire, however, is considered the best management technique for maintaining PPSO habitat because it returns nutrients to the soils and leads to dense regrowth of pitch pines and other shrubs (Buchholz 1983). PPSO woodlands that become degraded due to lack of fire and invasion of fire-intolerant species can be restored through logging and reintroducing fire or other regular disturbances (Ammann 2000).

S*hrub wetlands.* Bogs, beaver ponds, and shrub swamps are characterized by high bird species richness, and several scrub-shrub birds appear to be specialized to such habitats (Chapter 4). Thus, these habitats are worthy of significant attention from managers. In general, naturally occurring shrub swamps are only flooded during a portion of the year and may be replaced by other vegetation types in permanent impoundments or where the hydrologic regime is altered (Thompson & Sorenson 2000). If time and money are available, shrub swamps can be established on wet sites. Species such as alder and willows can be propagated by cuttings, and several other shrub species establish readily from seeds. Additional information on shrub wetland management can be found in Wheeler et al. (1995) and Harker et al. (1999); however, management of these wetlands will generally depend on protection of these habitats and the disturbance agents (e.g. flood regimes) that create them.

3) Consider patch size and shape

Our review showed that scrub-shrub bird are less abundant near edges and in small patches (see Chapter 5). Thus, managers should attempt to provide large habitat patches and avoid creating patches with irregular shapes or unnecessary edges. Although exact size thresholds have yet to be identified, patches less than 1 ha are unsuitable for most scrub-shrub birds. We, therefore, recommend that scrub-shrub patches be a minimum of 1 ha in size, and 2-4 ha if possible, to benefit this bird community. Patches larger than this may have slightly higher bird densities, but the returns generally diminish beyond 4 ha (Chapter 5).

In addition, scrub patches with simple shapes should be favored over complex or irregular ones which have greater edge density. Not only do most scrub-shrub birds avoid edges, but edge density has a negative effect on avian nesting success (Chapter 5). Thus, patches should have simple shapes such as rectangles or circles, avoiding complex shapes with indentations and irregular borders.

Larger patches can be created by consolidating smaller patches or by utilizing even-aged silvicultural techniques such as clearcutting or shelterwood cuts (DeGraaf & Yamasaki 2003). Uneven-aged management creates only small patches of scrub-shrub habitat and should not be used as a management technique for scrub-shrub birds. Techniques such as group-selection or single-tree logging have been promoted as an option to maintain relatively intact forests (DeGraaf et al. 2005). The small openings these methods create, however, are of little benefit for scrub-shrub birds in New England because few birds will breed in them. Similarly, wildlife openings are often less than 1 ha in size (Overcash et al. 1989; Chandler 2006). These habitats would be more valuable for scrub-shrub birds were they significantly larger.

Research and Monitoring Needs

Our review has summarized what is known about the ecology and management of scrub-shrub birds. Throughout this review, however, we have been hampered by gaps in knowledge of the ecology of scrub-shrub birds. To help guide future researchers interested in this bird community, we list below the most important needs for future research on this community. The topics listed below define a research agenda that could significantly aid in the conservation and management of scrub-shrub birds.

Measuring habitat availability

Understanding habitat use and availability is critical for prioritizing conservation actions and designing management practices. Surprisingly, even basic measures of shrubland availability are unavailable in many parts of New England. We, therefore, recommend that the area of different scrub-shrub habitats in New England be estimated using aerial photography or satellite imagery. Because of the dynamic nature of these habitats, these measurements should be made on a regular, continuing basis to determine how habitat availability is changing over time. Measuring habitat availability on the wintering grounds of scrub-shrub birds would also be useful for conservation.

Population monitoring

Recent concern about the status of scrub-shrub birds resulted from long-term monitoring programs such as the Breeding Bird Survey. We recommend continued support for these monitoring efforts. We also suggest that further monitoring programs be designed to address the shortcomings of roadside surveys. The species at greatest risk in New England, such as Northern Bobwhite and Golden-winged Warbler, should get particular attention, with monitoring focused on their breeding populations.

In addition, measurement of long-term population trends in “permanent” scrub-shrub habitats such as pitch-pine scrub-oak woodlands, shrub swamps, or even ROWs would help to reveal how populations are changing in the absence of successional changes in habitats or anthropogenic disturbance.

Demography

Estimates of basic demographic parameters are necessary to understanding population viability. For most scrub-shrub birds and their habitats, this information is lacking. To rectify this situation, we recommend that estimates of survival rates, fecundity, and nest success of scrub-shrub birds be provided in a variety of habitats and landscape contexts. In addition, estimating survival rates and determining the effects of cowbird parasitism should be priorities.

Landscape ecology

Finally, we recommend further research into the effects of patch and landscape configuration on scrub-shrub birds. Important factors to be studied include the effects of habitat configuration and availability at the landscape level, as well as the effects of landscape context (i.e. forested vs. agricultural vs. suburban/developed). We need to understand how these landscape variables affect both avian abundances and reproductive success. Finally, we need information on how patch isolation affects the occupancy and persistence of avian populations in scrub-shrub habitat.

Understudied species

Managing scrub-shrub birds will only be possible if we understand their ecology and what factors limit their populations. We, therefore, recommend efforts to provide better information about the breeding biology, habitat preferences, and demography of poorly studied scrub-shrub birds. In the scrub-shrub bird community, the species that are most poorly known are found in boreal forests of northern New England. These include Rusty Blackbird, Tennessee Warbler, Mourning Warbler, Nashville Warbler, Palm Warbler, Canada Warbler, and Lincoln’s Sparrow.

Conclusion

Overall, the scrub-shrub bird community in New England is in need of immediate conservation attention. Declining bird populations and shrinking amounts of habitat will create a serious challenge for managers. Nonetheless, populations of most scrub-shrub birds are still large enough that they can be stabilized and even recovered with appropriate management. Acting soon, however, is critical.

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Scientific Names of Plants and Animals Discussed in the Text

Scrub-shrub Birds

Ruffed Grouse	*Bonasa umbellus*
Northern Bobwhite	*Colinus virginianus*
Wilson's Snipe	*Gallinago delicata*
American Woodcock	*Scolopax minor*
Yellow-billed Cuckoo	*Coccyzus americanus*
Whip-poor-will	*Caprimulgus vociferus*
Ruby-throated Hummingbird	*Archilochus colubris*
Alder Flycatcher	*Empidonax alnorum*
Willow Flycatcher	*Empidonax traillii*
White-eyed Vireo	*Vireo griseus*
Carolina Wren	*Thryothorus ludovicianus*
House Wren	*Troglodytes aedon*
Gray Catbird	*Dumetella carolinensis*
Northern Mockingbird	*Mimus polyglottos*
Brown Thrasher	*Toxostoma rufum*
Cedar Waxwing	*Bombycilla cedrorum*
Blue-winged Warbler	*Vermivora pinus*
Golden-winged Warbler	*Vermivora chrysoptera*
Tennessee Warbler	*Vermivora peregrina*
Nashville Warbler	*Vermivora ruficapilla*
Yellow Warbler	*Dendroica petechia*
Chestnut-sided Warbler	*Dendroica pensylvanica*
Magnolia Warbler	*Dendroica magnolia*
Prairie Warbler	*Dendroica discolor*
Palm Warbler	*Dendroica palmarum*
Black-and-white Warbler	*Mniotilta varia*
Mourning Warbler	*Oporornis philadelphia*
Common Yellowthroat	*Geothlypis trichas*
Canada Warbler	*Wilsonia canadensis*
Wilson's Warbler	*Wilsonia pusilla*
Yellow-breasted Chat	*Icteria virens*
Eastern Towhee	*Pipilo erythrophthalmus*
Field Sparrow	*Spizella pusilla*
Song Sparrow	*Melospiza melodia*
Lincoln's Sparrow	*Melospiza lincolnii*
White-throated Sparrow	*Zonotrichia albicollis*
Dark-eyed Junco	*Junco hyemalis*
Northern Cardinal	*Cardinalis cardinalis*
Indigo Bunting	*Passerina cyanea*
American Goldfinch	*Carduelis tristis*
Rusty Blackbird	*Euphagus carolinus*

Other Birds

Spruce Grouse	*Falcipennis canadensis*
Wild Turkey	*Meleagris gallopavo*

Cooper's Hawk	*Accipter cooperii*
Red-tailed Hawk	*Buteo jamaicensis*
Mourning Dove	*Zenaida macroura*
Black-billed Cuckoo	*Coccyzus erythropthalmus*
Hairy Woodpecker	*Picoides villosus*
Northern Flicker	*Colaptes auratus*
Olive-sided Flycatcher	*Contopus cooperi*
Eastern Wood-Pewee	*Contopus virens*
Yellow-bellied Flycatcher	*Empidonax flaviventris*
Acadian Flycatcher	*Empidonax virescens*
Least Flycatcher	*Empidonax minimus*
Great-crested Flycatcher	*Myiarchus crinitus*
Eastern Kingbird	*Tyrannus tyrannus*
Warbling Vireo	*Vireo gilvus*
Philadelphia Vireo	*Vireo philadelphicus*
Red-eyed Vireo	*Vireo olivaceus*
Blue Jay	*Cyanocitta cristata*
American Crow	*Corvus brachyrhynchos*
Winter Wren	*Troglodytes troglodytes*
Ruby-crowned Kinglet	*Regulus calendula*
Blue-gray Gnatcatcher	*Polioptila caerulea*
Eastern Bluebird	*Sialia sialis*
Veery	*Catharus fuscescens*
Swainson's Thrush	*Catharus swainsonii*
Hermit Thrush	*Catharus guttatus*
Wood Thrush	*Hylocichla mustelina*
American Robin	*Turdus migratorius*
Northern Parula	*Parula americana*
Cape May Warbler	*Dendroica tigrina*
Black-throated Blue Warbler	*Dendroica caerulescens*
Kirtland's Warbler	*Dendroica kirtlandii*
Bay-breasted Warbler	*Dendroica castanea*
Cerulean Warbler	*Dendroica cerulea*
American Redstart	*Setophaga ruticilla*
Worm-eating Warbler	*Helmitheros vermivorum*
Ovenbird	*Seiurus aurocapilla*
Northern Waterthrush	*Seiurus noveboracensis*
Louisiana Waterthrush	*Seiurus motacilla*
Kentucky Warbler	*Oporornis formosus*
Connecticut Warbler	*Oporornis agilis*
Hooded Warbler	*Wilsonia citrina*
Scarlet Tanager	*Piranga olivacea*
Chipping Sparrow	*Spizella passerina*
Vesper Sparrow	*Pooecetes gramineus*
Fox Sparrow	*Passerella iliaca*
Swamp Sparrow	*Melospiza georgiana*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Common Grackle	*Quiscalus quiscula*

Brown-headed Cowbird	*Molothrus ater*
Orchard Oriole	*Icterus spurius*
Baltimore Oriole	*Icterus galbula*
Other animals	
Beaver	*Castor canadensis*
Raccoon	*Procyon lotor*
Gray squirrel	*Sciurus caroinensis*
Red Squirrel	*Tamiasciurus hudsonicus*
Chipmunk	*Tamias* spp.
Spruce Budworm	*Choristoneura fumiferana*
Hemlock Looper	*Lambdina fiscellaria*
Plants	
Pitch Pine	*Pinus rigida*
Eastern White Pine	*Pinus strobus*
Spruce	*Picea spp.*
Red Spruce	*Picea rubens*
Fir	*Abies spp.*
Balsam Fir	*Abies balsamea*
Eastern Hemlock	*Tsuga canadensis*
Alder	*Alnus* spp.
Willow	*Salix* spp.
Red-osier dogwood	*Cornus sericea*
Buttonbush	*Cephalanthus occidentalis*
Maple	*Acer* spp.
Oak	*Quercus* spp.
Scrub Oak	*Quercus ilicifolia*
Scrub Oak	*Quercus prinoides*
Hickory	*Carya* spp.
Tulip Poplar	*Liriodendron tulipifera*
Birch	*Betula* spp.
American Beech	*Fagus grandifolia*