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DO THE SIZE AND LANDSCAPE CONTEXT OF FOREST OPENINGS INFLUENCE THE ABUNDANCE AND BREEDING SUCCESS OF SHRUBLAND SONGBIRDS IN SOUTHERN NEW ENGLAND?

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Abstract

Early successional birds have declined in the northeastern United States due to the regeneration of forest on abandoned farm fields and the suppression of natural disturbances that once provided appropriate habitat. These species have become increasingly dependent on early successional habitats generated by such activities as timber harvesting. Recent approaches of timber harvesting, which range from single tree harvesting to clearcutting, create forest openings of different sizes and configurations embedded in landscapes with different land use patterns. To assess the importance of forest openings created by timber harvesting for shrubland birds, we surveyed birds on 50-m radius plots in 34 harvest sites (0.5 – 21 ha). We collected data on multi-scaled habitat variables ranging from plot-level vegetation characteristics to land use patterns within 1 km of each study site. We also monitored mating and nesting success of Blue-winged Warblers (*Vermivora pinus*) in 10 forest openings.

The abundance of most shrubland species was influenced by plot-level habitat variables, such as tree density and vegetation height, rather than shrubland area or the composition of land uses in the surrounding landscape. Only Eastern Towhees (*Pipilo erythrophthalmus*) were more frequent in survey plots in larger forest openings. In contrast, neither abundance nor reproductive activity of Blue-winged Warblers was correlated with the size of the forest opening. Their abundance was negatively related to vegetation height, however. Only 54% of the territorial male Blue-winged Warblers in forest openings were mated. We documented relatively low nest success rates of 21.1% during the egg laying and incubation nest stages, but increased success rates during the

later stages of nest development.

Our results indicate that even small forest openings with low vegetation provide habitat for Blue-winged Warblers and other shrubland birds. The overall reproductive rate of territorial male Blue-winged Warblers in forests openings was low during the two years of the study, however. Further studies are needed to assess the long-term value of this type of habitat for sustaining shrubland bird populations.

Keywords: early successional birds, shrubland birds, Blue-winged Warbler, clearcuts, habitat fragmentation, landscape context, area sensitivity

1. Introduction

Forestry in southern New England is increasingly dominated by uneven-aged management characterized by selective cutting of individual trees or small groups of trees (DeGraaf *et al.*, 1992). Single-tree and group selection harvesting is also becoming more common on both public and private land in many other regions in eastern North America in response to public concerns about the visual and environmental impacts of clearcuts, especially the problems of soil erosion, stream sedimentation, and degradation or loss of habitat for forest species. Ironically, many declining species in eastern North America depend on early successional woody habitats such as regenerating forest, and these species generally benefit from even-aged management techniques that create large expanses of open habitat (Hunter *et al.*, 2001, Dettmers, 2003). An important question for forest managers is whether these species can also use the smaller openings that are created as a result of new methods and regulations for timber harvesting.

Numerous studies have documented that recent clearcuts support a diversity of birds that are "shrubland specialists" (species that are restricted to low, woody vegetation) (Conner and Adkisson, 1975; Webb *et al.*, 1977; Crawford *et al.*, 1981; Hagan *et al.*, 1997; Yahner, 1997). These species are rare or absent in mature forests, so they depend upon some sort of disturbance, such as fire, windstorms, severe flooding, or logging, to generate low, woody habitat (Askins, 2002). Shrubland species are also generally rare or absent in the small openings in forests created by single-tree and group selection harvesting (Annand and Thompson, 1997; Rodewald and Smith, 1998: Robinson and Robinson, 1999; Costello *et al.*, 2000; Moorman and Guynn, 2001). These small openings are colonized by only a few species of shrubland specialists and forest-edge species along with species such as the Hooded Warbler (*Wilsonia citrina*) that are best characterized as canopy gap specialists (Annand and Thompson, 1997; Germaine *et al.*, 1997). Canopy gap specialists generally are associated with mature forests, not extensive open habitats, because they are often concentrated in small, shrubby openings created by tree falls. Thus, different harvesting methods favor different sets of bird species.

Another approach to reducing the negative environmental effects of even-aged management is to shift from large clearcuts to small clearcuts (including patch cuts in the 0.5 – 2 ha range). This approach has been adopted in state forests in Connecticut, where clearcuts are generally no larger than 4 ha (10 acres). Compared to large clearcuts, small clearcuts reduce problems with soil erosion and stream sedimentation while still favoring regeneration of commercially important oaks (which grow better in open, sunny conditions (Meadows and Stanturf, 1997)). If these small clearcuts provide habitat for shrubland birds, then they may be preferable to individual or group selection cuts in regions where conservation of shrubland species is a high priority. The pressing question is how large an opening is needed to provide appropriate and productive habitat for shrubland birds. Rudnicky and Hunter (1993) addressed this question by surveying bird populations in standardized plots in clearcuts with a wide range of areas (2 - 112 ha) in Maine. When they included all of their sites in the analysis, they found that the frequency of occurrence of particular species was not related to clearcut area. When the analysis was limited to clearcuts ≤ 20 ha, however, many species showed positive trends in frequency of occurrence as clearcut area increased, suggesting that these species may be sensitive to clearcut area for small clearcuts. In a mist-net study of regenerating clearcuts in longleaf pine forests in South Carolina, Krementz and Christie (2000) carefully standardized sampling effort for all of their measures of bird abundance and productivity. They found no relationship between area of clearcuts and either abundance or productivity (as measured by juvenile: adult ratios) of scrub-successional birds for clearcuts that ranged in area from 3 to 57 ha. In contrast, Rodewald and Vitz (2005) found weak evidence that several species of shrubland birds were less frequent in mist net samples from small clearcuts than in samples from large clearcuts. They found stronger evidence that shrubland birds tended to avoid the area near the forest edge, which would tend to reduce densities in small or irregularly shaped clearcuts. Thus, the limited number of studies that address this question do not provide a clear answer about whether the area of habitat patches should be an important management concern.

The distribution and abundance of early successional birds is potentially determined not only by vegetation characteristics and the area of forest openings, but also by the amount and pattern of early successional habitats in the surrounding landscape (Lichstein *et al.*, 2002). Habitat selection by birds often occurs at multiple spatial scales, and may be influenced by habitat variables both within and surrounding habitat patches (Cody, 1985). Although a substantial amount of research has focused on the landscape-scale effects of habitat selection in birds of mature forests, not much is known about the importance of surrounding landscape features in explaining shrubland bird distributions.

The objectives of this study were to 1) determine the minimum area of early successional habitat required by different species of shrubland specialists, 2) test whether the size of openings is related to reproductive success by monitoring the mating and nest success of the Blue-winged Warbler (*Vermivora pinus*), a shrubland specialist, and 3) analyze the relative importance of habitat characteristics in explaining bird distributions at three spatial scales (i.e., plot, patch, and landscape scales). Our broader goal was to determine whether small clearcuts provide suitable habitat for a diversity of early successional birds, and, if so, whether their value for these species diminishes if the clearcuts are too small or if they are too isolated from other early successional habitat.

2. Methods

2.1 Study Areas

Study sites consisted of 34 forest openings located in the Nehantic, Pachaug, Cockaponset, Salmon River, and Meshomasic state forests in southeastern Connecticut. These clearcuts, deferment cuts, shelterwood cuts, and wildlife openings were created and managed by the Connecticut Department of Environmental Protection. All study sites were openings dominated by low, woody vegetation surrounded by mature forest. They ranged in size from 0.6 – 21 ha and had been created by harvests during the preceding three to 11 years. We avoided group selection cuts (which are <0.6 ha) because previous studies showed that these primarily support mature-forest and canopy-gap specialists rather than shrubland species, and thus are different from larger openings (Costello *et al.*, 2000). Adjacent study sites were separated from one another by at least 10 m of forest. The greatest distance between study sites was 61 km. The average distance from other forest openings (including other study sites) was 235 m, and all study sites were at least 100 m from powerline rights-of-way or other shrubby openings.

2.2 Abundance and reproductive success of birds

In 1997, we determined densities of breeding shrubland songbirds on 50-m, fixed-radius circular plots (Bibby *et al.*, 2000) near the center of each forest opening. Each survey plot was visited once during the early breeding season (28 May to 13 June) and once during the late breeding season (16 June to 7 July), with a separation of at least three weeks between visits. We conducted surveys between 0530 and 0930 Eastern Daylight Time (EDT). Surveys began two minutes after arriving at the site and lasted for 10 min. We did not survey birds during inclement weather, such as rain or high wind (>15 km/hr)

(Vickery *et al.,* 1994). Locations and movements of all individual birds were noted for the first and second halves of the observation period. We used the maximum number of individuals of a particular species recorded during the 10-min observation periods during the two visits as a measure of relative abundance for each study area.

We conducted spot-mapping and nest searches to assess the reproductive success of Blue-winged Warblers in a total of 10 openings with comparatively low, woody vegetation. In 1998, we surveyed five clearcuts ranging in size from 0.7 – 16.7 ha. In 1999, we surveyed five different openings ranging in size from 0.6 – 7.2 ha. Each site was visited at least once per week between 20 May and 17 July. We used the following methods to assess reproductive activity of Blue-winged Warblers within each study area: (1) spot mapping of individual breeding territories (Robbins, 1970), (2) recording male mating success (i.e., whether a male was associated with a female at least once during the breeding season), (3) recording direct evidence of nesting activity (i.e., carrying nest material, fecal sacs, or food), and (4) locating and monitoring nests to determine nesting success. These measures were used to determine rates of mating success, nesting activity, and nest success for each Blue-winged Warbler territory.

2.3 Vegetation Surveys

In conjunction with the bird surveys conducted in 1998, we performed vegetation surveys in each bird survey plot. We used the line-intercept method to determine plant species composition and percent cover of different plant species (Brower and Zar, 1977). A 25-m transect was set up in a random compass direction from the center of each bird survey plot. We recorded the linear distance of the transect covered by each plant species, including all foliage that physically touched or overlay the transect (Brower and Zar, 1977). Total intercept lengths were used to estimate percent cover for each plant species. At 1-m intervals we recorded the ground cover as leaf litter, dead wood, herb, bare ground, grass, or other. To determine the average canopy height, we recorded the maximum vegetation height at 5 m intervals along the transect using a meter stick or a rangefinder and clinometer. In addition, we recorded the numbers of live trees and snags with > 25 cm diameter at breast height (dbh) within the 50-m-radius survey plot.

We implemented an alternative vegetation sampling method that emphasizes vertical vegetation structure for use in the study of reproductive success in Blue-winged Warblers. A vertical profile of foliage density was determined at 20 random points within each Blue-winged Warbler territory. At each point, the number of contacts between living vegetation and a pole was recorded for the following height intervals: 0 – 0.25 m, 0.25 – 0.5 m, 0.5 – 1.5 m, 1.5 – 3.0 m, 3.0 – 6.0 m, 6.0 – 8.0 m, and > 8.0 m (Morimoto and Wasserman, 1991). This permitted a comparison of the vegetation profiles in different Blue-winged Warbler territories.

2.4 Patch and landscape characteristics

We used aerial photographs (1995-1996; American Reprograpaphics, Denver, CO) to determine the area of the forest opening and land use patterns in the region around the study area. We calculated the total area of residential developments, farmland, and clearcuts within 1 km of the periphery of each study site. In addition, we measured a number of proximate landscape features including distances to the closest house, farm, clearcut, road, and powerline corridor within 1 km of the study site.

2.5 Statistical Analyses

To summarize information on habitat variables, we used separate principal component analyses (PCA) at three different spatial scales. Five variables (percent cover of trees, shrubs and herbs; tree density; and average canopy height) were used for the plot-level scale, 3 variables (area of opening, time since final harvest, and distance around perimeter/area of opening) were used for the patch-level scale, and six variables (total area [ha] of residential developments and clearcuts within 1 km of the site; distances [m] to nearest residence, road, powerline, and clearcut) were used for the landscape-level scale. We analyzed landscape variables within a radius of 1 km assuming that this distance would reflect (within an order of magnitude) dispersal distances from natal to breeding areas for young songbirds and as a measure of the immediate landscape context surrounding each study site. Natal dispersal distances are not known for Blue-winged Warbler, but averaged 1.13 km for Prairie Warbler (Nolan, 1978: 463), which is another shrubland specialist.

By performing separate PCAs for the three different spatial scales, we maintained a sample to variable ratio of at least 3:1 (McGarigal *et al.*, 2000). Data for each variable were checked for normality using Q-Q plots in SPSS (Version 10), and transformed if necessary to approximate normality. Transformed variables were used in PCA for tree, shrub and herb cover (arcsine); canopy height and tree density (ln); and clearcut and residential area (square root).

Factor scores from the three principal component analyses were used as independent variables for multiple regression analyses of the abundance of particular bird species and for the overall abundance of groups of ecologically similar species. We completed separate regression analyses for shrubland specialists (species largely restricted to low, woody vegetation), shrubland generalists (species found both in low, woody vegetation and other habitats), and mature-forest species (Table 1). We also analyzed the relationship between Brown-headed Cowbird abundance and the abundance of snags that had been retained in forest openings during timber harvests to enhance habitat for cavity-nesting birds and other wildlife. Female cowbirds use high perches to search for host nests (Norman and Robertson, 1975), so openings with numerous snags may provide better breeding habitat for cowbirds than openings with few or no snags.

Differences in mating success and nesting activity were compared at two spatial scales, among individual bird territories (n = 28) and forest openings (n = 10). Our null hypotheses were that mating success, nesting activity and nest success rates are the same in forest openings regardless of their area and do not differ between territories regardless of vegetation structure. Spot mapping of individual bird territories allowed us to document male mating status and nesting activity on individual territories.

We used a general linear model (GLM) function in R to perform a logistic regression to determine whether foliage density influenced mating success and nesting activity in individual territories (Hosmer and Lemeshow, 1989; R Development Core Team, 2004). In the GLM model, mating success (e.g., a territory without mate = 0, a territory with a mate = 1) and nesting activity (e.g., a territory with no evidence of nesting = 0, a territory with evidence of nesting = 1) is provided as a binary dependent variable and the foliage density categories were used as explanatory variables. We used Pearson product-moment correlation analysis to determine if any of the foliage density variables were highly correlated; only uncorrelated variables were entered into the GLM model.

Multiple regression analyses and Fisher's Exact Tests were used to test the effects of forest opening area and age of the opening (time since final harvest) on mating success and nesting activity (R Development Core Team, 2004). Study sites were also re-classified into sites ≤ 4 ha and sites > 4 ha to allow for the use of the Fisher's Exact Test to test for differences in the number of territories with evidence of mating or nesting in small and large forest openings. This classification separates very small openings (0.6 – 2.2 ha) that potentially could accommodate only one or two Blue-winged Warbler territories from larger openings (4.1 – 16.7 ha) that potentially could accommodate more territories. (According to Canterbury et al. [1995, as cited in Gill *et al*., 2001], the average territory size for Blue-winged Warblers was 1.1 ha in a study area in Ohio.) We set an a priori significance level of $\alpha = 0.05$ and a marginal significance level of $0.10 > P > 0.05$ for these analyses.

Nests were considered successful if at least one fledged young was observed or if the nest was found empty between visits and the nestlings were sufficiently well developed to assume successful fledging. We assumed predation or nest failure when eggs or nestlings too young to have fledged disappeared. We developed three candidate models to estimate stage-specific daily survival probabilities for three different nest stages (Stanley, 2000; 2004). The nest stages included egg laying (begins with the laying of first egg and ends with incubation), incubation (begins with the onset of incubation and ends with hatching), and nestling (begins with hatching and ends when the nestlings fledge) (Stanley, 2004). All models allowed for the joint estimation of stage-specific survival probabilities for all three nest stages including egg laying (ρ_0), incubation (ρ_1), and nestling (ρ_2) stages, even when the exact time of nest failure is unknown (Stanley, 2004). The first model was the global model and estimated separate survival probabilities for all nest stages (ρ_0, ρ_1, ρ_2), the second model assumed equal survivorship in the egg laying and incubation stages ($\rho_0 = \rho_1, \rho_2$), and the third model assumed constant survivorship throughout the entire nesting period ($\rho_0 = \rho_1 = \rho_2$). The third model is equivalent to calculating nest success using the traditional Mayfield method (Mayfield, 1961; Mayfield, 1975) and Johnson's (1979) formula to calculate standard deviations. For all models, we specified an egg laying stage of 4 days, incubation period of 11 days, and a nestling period of 9 days (Will, 1986). Maximum-likelihood parameter estimates and standard errors were obtained using SAS PROC NLIN (SAS Institute, 1989) (see Stanley [2004] for program details). We evaluated model performance by calculating the AIC_c value for each model (Hurvich and Tsai, 1989; Burnham and Anderson, 2002).

3. Results

3.1 Relative abundance of Different Species in Openings

The most abundant species of birds on survey plots in 34 forest openings were three shrubland generalists (Gray Catbird [*Dumetella carolinensis*], Eastern Towhee [*Pipilo erythrophthalmus*], and Common Yellowthroat [*Geothlypis trichas*]) and two shrubland specialists (Chestnut-sided Warbler [*Dendroica pensylvanica*] and Blue-winged Warbler) (Table 1). Another shrubland specialist, the Prairie Warbler (*Dendroica discolor*), was infrequent at these sites. Brown-headed Cowbird was the most abundant bird at these sites if both males and females are counted (Table 1), but these counts included large numbers of males in highly conspicuous flocks. Female cowbirds are a better measure of cowbird abundance and impact on host populations because they have discrete (albeit overlapping) home ranges (Lowther, 1993) during the breeding season, and they lay eggs in the nests of other species. The abundance of female cowbirds was relatively low (Table 1). [**INSERT TABLE 1]**

Several species of birds typically associated with closed-canopy forests or forest with canopy gaps (Black-and-white Warbler [*Mniotilta varia*], Wood Thrush [*Hylocichla mustelina*], Veery [*Catharus fuscescens*], Great Crested Flycatcher [*Myiarchus crinitus*], American Redstart [*Setophaga ruticilla*], and Red-eyed Vireo [*Vireo olivaceus*]) were recorded in forest openings (Table 1). Most of these species were infrequent in openings, but Black-and-white Warblers were fairly common.

3.2 Relationship between Habitat Variables and Bird Distributions

Using principal component analysis, we were able to reduce the number of habitat variables for use in multiple regression analysis from 14 to 5. The first two principal components for plot-level variables accounted for 70% of the variance in the original variables, the first principal component for patch-level variables accounted for 68% (the second component was excluded because there were only 3 original patch-level variables and the first component accounted for most of the variance), and the first two principal components for landscape-level variables accounted for 59% (Table 2). When used as independent variables in multiple regression analysis, some of these principal components were significantly related to the abundance of particular species of birds. We completed regression analyses for all species that were detected in ≥15 sites (Table 3). Blue-winged Warbler, Chestnut-sided Warbler, Common Yellowthroat, and Eastern Towhee were all significantly more abundant at sites with lower tree density and lower vegetation height. Eastern Towhees were also significantly more common in larger openings. The only species that was significantly related to principal components for landscape variables was Gray Catbird, which was more abundant in openings closer to residential areas and farther away from other clearcuts (Table 3**). [INSERT TABLE 2]**

We included counts for both males and females in regression analyses of Brown-headed Cowbirds because of low sample sizes when females were considered separately. Although including conspicuous groups of male cowbirds probably exaggerates the relative abundance of cowbirds compared to that of territorial songbirds, male and female cowbirds probably occur in similar habitats along powerlines because males visit these sites primarily to mate with females. Cowbirds were most abundant at sites with lower vegetation height, higher shrub cover, and lower tree cover (Table 3). A separate linear regression also showed that cowbirds were detected significantly more frequently in forest openings with higher densities of snags ($F=18.5$, $DF=32$, $P<0.001$).

When shrubland specialists were considered as a group, the total abundance was greatest at sites with higher shrub density, lower tree cover, lower tree density, and lower canopy height (Table 3). There were no significant relationships for patch-level or landscape-level principal components. Shrubland generalists were most frequent at plots in larger openings, with lower tree density, greater distance to the nearest clearcut, and a greater area of residential development within 1 km (Table 3). The frequency of forest birds showed no significant relationship with the any of the principal component variables (Table 3).

[INSERT TABLE 3]

3.3 Territory-level Differences in Mating Success and Nesting Activity

In the summers of 1998 and 1999, we documented 28 Blue-winged Warbler territories in 10 study sites. A territory was considered potentially productive if we recorded a female at least once during the breeding season (mating success) or we recorded direct evidence of nesting (nesting activity). Over both years, 15 territories (54%) showed evidence of female occupancy and 10 territories (28%) showed evidence of nesting. We used foliage density data to determine whether vegetation density at particular heights influenced mating success and nesting activity. The pole vegetation method produced a relative density of foliage within 8 separate height classes: 0 – 0.25 m, 0.25 – 0.5 m, 0.5 – 1.5 m, 1.5 – 3.0 m, 3.0 – 6.0 m, 6.0 – 8.0 m, and > 8.0 m (Morimoto and Wasserman, 1991). Pearson product-moment correlation analysis found no significant correlations between any of these foliage density categories so all eight categories were used as explanatory variables in the GLM. Territories were characterized by relatively low, dense foliage, with 88% of the foliage heights < 3 m.

Our GLM analyses suggested that foliage density had a limited influence on the probability of mating success and nesting activity on different territories. None of the densities for particular foliage heights were significant predictors of mating success at the 0.05 significance level. The density of vegetation between two height categories, 0 – 0.25 m (1.26 ± 0.74 S.E., $P = 0.088$) and 6.0 – 8.0 m (4.68 ± 2.82 S.E., $P = 0.096$), were marginally significant and positively correlated with mating success. Foliage density also was not a significant predictor of nesting activity. None of the foliage height categories were significant predictors of nesting activity at the 0.05 significance level. The density of vegetation between 0 – 0.25 m (0.94 ± 0.55 S.E., $P = 0.087$) was marginally significant and positively correlated with the probability of nesting activity. Our findings indicate that foliage density and height were not important factors in mating success or nesting activity in Blue-winged Warblers in forest openings.

3.4 Patch-level Differences in Mating Success and Nesting Activity

Mating success and nesting activity were aggregated to the site (habitat patch) level to represent the proportion of territories with evidence of mating or nesting. At the patch-level our effective sample size was limited to 10 study sites. Patch area had no effect on the proportion of territories with mates (-0.07 ± 0.087 S.E., $P = 0.415$) or on the proportion of territories with evidence of nesting (-0.16 ± 0.096 S.E., $P = 0.140$). Similarly, patch age (time since harvest) had no effect on the proportion of territories with mates (-0.05 ± 0.058 S.E., $P = 0.369$) or on the proportion of territories with evidence of nesting (-0.069 ± 0.064 S.E., $P = 0.325$). When sites were reclassified into small patches (≤4 ha; n = 6) and large patches (>4 ha; n = 4), small patches supported significantly fewer territories (2.0 ± 0.63 S.E.) than did large patches (4.5 ± 0.50 S.E.) (*P*

= 0.0147). Patch area was not significantly correlated with mating success (P = 0.710), however, but was a significant predictor of nesting activity (P = 0.026), with the proportion of territories with evidence of nesting higher in small patches (0.67 ± 0.19 S.E.) than in large patches (0.18 ± 0.11 S.E.) (Figure 1). Our results suggest that mating success and nesting activity of Blue-winged Warblers were not strongly influenced by the age of the forest opening, but that nesting activity was significantly higher in smaller openings within the range of variability in our sample (Figure 1).

[INSERT FIGURE 1]

3.5 Nest Survival Rates

Despite extensive nest searches in ten openings, we were able to document and follow only eight Blue-winged Warbler nests. This limited sample size was primarily a result of the relatively low number of pairs that attempted to nest within the study sites. Given such a limited sample size, we were unable to test effects between sites, and all nest data were pooled for analysis. We documented a mean clutch size of 3.56 (± 0.18 S.E.) eggs. None of the nests were parasitized by cowbirds. The second model, in which the daily survival probabilities for the egg laying and incubation stages were assumed to be equal ($\rho_0 = \rho_1, \rho_2$), had the lowest AIC_c value (AIC_c =12.52) when compared to the global (AIC_c = 13.62) and the constant survivorship model (AIC_c =16.27). We chose the second model as the best model because it minimizes information loss. This model assumes a constant survival probability in the egg laying and incubation stages, which may be appropriate for our data because of the limited sample size and small number of nests observed in the egg-laying stage. The second model produced stage-specific survival probabilities of 21.1% (± 0.18 S.E.) for the egg laying and incubation stage and 100% (± 0.00 S.E.) for the nestling stage. Although the third model was the least supported of all three models, we calculated a nest success rate of 42.7% to allow for comparison with past studies that used the Mayfield method.

4. Discussion

4.1 Importance of habitat area and vegetation structure to shrubland birds

The abundance of shrubland specialists in forest openings was related to vegetation structure rather than to the extent of continuous early successional habitat at a study site or to surrounding land use patterns. Two common shrubland specialists, Blue-winged Warbler and Chestnut-sided Warbler, were most abundant on study plots dominated by relatively low vegetation with few trees. When considered as a group, shrubland specialists were most abundant at sites with low vegetation, few trees, and a high density of shrubs. Within the range of forest openings we studied (0.6 – 21 ha), none of the common shrubland specialists displayed a significant relationship between abundance (average number per survey plot) and forest opening size, indicating that they occupy even very small clearcuts. Openings created by timber harvesting that are smaller than our smallest site (0.6 ha) are classified as individual or group selection cuts rather than clearcuts. These generally support relatively few shrubland specialists (Robinson and Robinson, 1999; Costello *et al.*, 2000, Moorman and Guynn, 2001). The minimum recorded territory areas are 0.3 ha for Blue-winged Warbler (Gill *et al.*, 2001) and 0.4 ha for Chestnut-sided Warbler (Richardson and Brauning, 1995), so it is not surprising that these species were infrequent or absent in individual and group selection cuts.

In contrast to shrubland specialists, the occurrence of some shrubland generalists appears to be influenced by the size and landscape context of the forest opening. Shrubland generalists as a group were most frequent in plots in larger forest openings, with lower tree density, greater distance to the nearest clearcut, and more residential area within 1 km. The abundance of the two most frequent shrubland generalists was related to patch or landscape level variables. Eastern Towhee is the only species we analyzed that was more abundant in larger openings, and Gray Catbird was more abundant at sites closer to residential areas and farther from other clearcuts, so these two species may drive the pattern for the entire group of shrubland generalist species. Abundance of another common shrubland generalist, Common Yellowthroat, was significantly related only to vegetation characteristics.

Among species that are usually classified as mature-forest birds, only Black-and-white Warblers were observed frequently enough in forest openings to permit multiple regression analysis. The abundance of this species was not significantly related to the habitat variables we measured. The frequent detection of this species in shrubby openings was surprising because previous studies in various parts of its breeding range showed that this species was strongly associated with mature, closed canopy forests rather than early successional forest (Kricher, 1995). However, Hagan *et al.* (1997) and Costello *et al.* (2000) reported that Black-and-white Warblers were more abundant in clearcut regeneration plots than in mature-forest plots, indicating that this species may be associated with early successional habitat as well as mature forest. We found no evidence of nesting by Black-and-white Warblers in forest openings, however. The Black-and-white Warbler, like the Wood Thrush (Anders *et al.*, 1998), might nest in mature forests and feed in shrubby openings during certain periods of the breeding season, but this requires further study.

We could not find clearcuts >21 ha in southeastern Connecticut (an example of the current shift to smaller-scaled silvicultural practices), so we were unable to test the hypothesis that very large clearcuts support a higher density of shrubland specialists. When Rudnicky and Hunter (1993) surveyed birds in clearcuts in eastern Maine that ranged in size from 2 to 112 ha, they found no relationship between the frequency of occurrence of particular species on survey plots and the area of the opening, indicating that larger clearcuts do not provide more favorable habitat. Interestingly, they found that there was a relationship between frequency of occurrence and clearcut area for many species if only sites <20 ha (which happens to be the size range for our study) are considered. They provide few details, however, and the bird species composition of openings in their northern coniferous forest sites differs from that of the deciduous forest openings we studied. Two species that were frequently detected in both studies, the Chestnut-sided Warbler and Common Yellowthroat, do not show a consistent negative relationship between frequency and clearcut area in clearcuts <20 ha in Maine (Figure 3 in Rudnicky and Hunter, 1993), which is consistent with our results.

The lack of a relationship between the abundance of shrubland specialists on survey plots and the area of habitat patches or the composition and configuration of surrounding landscapes contrasts with the pattern for mature-forest birds in the same region of eastern North America. The abundance of many mature-forest bird species on survey plots tends to be highly correlated with forest area and with the amount and configuration of forest cover in the surrounding landscape (Askins *et al.*, 1987; Robinson *et al.*, 1995; Villard *et al.*, 1999). This difference in sensitivity to the composition and configuration of preferred habitats may reflect adaptations to different patterns of habitat availability for early successional and late successional species during most of their evolutionary history. In eastern North America, mature deciduous and boreal forests frequently occurred in large, unbroken stretches, while shrubby early successional patches occurred in small, isolated patches created by windstorms, fires, beaver activity and severe flooding along rivers and streams (Askins, 2001). Consequently, early successional species may be adapted to colonize and reproduce successfully in small, isolated habitat patches that are a product of more stochastic and spatially restricted disturbance regimes. This general pattern of landscape insensitivity for shrubland species may be less frequent in those shrubland birds that can exploit a greater breadth of resources (i.e., shrubland generalists). Also, many species among both open grassland and mature forest breeding birds tend to be area-sensitive and are similar in that they have evolved to depend on extensive habitats that are influenced by a number of landscape-scale abiotic and biotic factors. In contrast, shrubland specialists that depend on more stochastic, small-scale disturbances to generate appropriate habitat may not be influenced as much by patterns of habitat availability and disturbance at landscape scales, as our results indicate. Once bird assemblages in enough habitats in different parts of the world have been studied, this hypothesis can be tested by determining whether there is a consistent relationship between sensitivity to habitat fragmentation and historical patterns of habitat continuity.

4.2 Breeding Success of a Shrubland Specialist

Blue-winged Warblers are considered shrubland specialists because they typically breed in early-to mid-succession habitat (Confer and Knapp, 1981; Will, 1986; Buckelew and Hall, 1994; Gill *et al.*, 2001). Although their territories are characterized by a mosaic of dense herbs, shrubs, and trees, their breeding habitats are typically dominated by low-growing herbs and shrubs (Confer and Knapp, 1981; Gill *et al.*, 2001). Consequently, forest management techniques that promote early-successional habitat, such as clearcuts and shelterwood cuts, may produce optimal breeding areas. In our study, although 28 territories were characterized by short dense vegetation rarely exceeding 3 m in height, we did not find a significant relationship between reproductive success and vegetation height or foliage density. This was surprising considering that only 28% of Blue-winged Warbler territories showed evidence of nesting. The nest success rate of 21.1% during the egg laying and incubation stages (41.2% assuming $\rho_0 = \rho_1 = \rho_2$) is also relatively low compared to other studies of this species (Gill *et al.*, 2001), including a study in clearcuts and shelterwood cuts where the nest success rate was 51% (Annand and Thompson, 1997). These findings suggest that, although Blue-winged Warblers become established in artificial forest openings, their reproductive success may not be optimal and is not affected by the structural characteristics of these openings as long as the vegetation remains low. The reproductive success rates of other species nesting in clearcuts in Missouri and Illinois (Annand and Thompson, 1997; Morse and Robinson, 1999) are even lower than the rate we documented for Blue-winged Warblers in

Connecticut. In contrast, nest success was much higher (60 – 99% of nests fledged ≥ 1 young) in clearcuts in New Hampshire (King *et al.*, 2001). Comparison of the results of these studies suggests that nest success in clearcuts may be higher in heavily forested regions with relatively little agricultural or suburban habitat (King *et al.*, 2001), but this requires more study.

Brown-headed Cowbirds were frequent in the forest openings we studied. Although they did not parasitize any of the Blue-winged Warbler nests we monitored, they could potentially reduce the reproductive success of this species and other shrubland specialists. Like many of the shrubland specialists that they parasitize, they were most frequent at sites with low, dense vegetation and live trees. Their abundance increased with the density of snags on survey plots, so snags left in clearcuts to enhance wildlife habitat may have a negative effect on nesting success of songbirds. This relationship should be studied more thoroughly.

The size and age (time since harvest) of the forest opening may affect the reproductive success of Blue-winged Warblers. Robinson and Robinson (1999) found that Blue-winged Warblers were more likely to be found in larger clearcuts than in smaller group cuts in southern Illinois. However, we found that the abundance of Blue-winged Warblers was similar on survey plots in clearcuts of different sizes, and we found no significant effect of forest opening size on Blue-winged Warbler reproductive activity within the range of sizes we were studying (0.6 to 16.9 ha). We did, however, find a general trend of higher mating success and nesting activity within smaller forest openings (< 4 ha) (Figure 1). This general trend could be an artifact of a relatively low number of study sites, however, especially with respect to larger sites (n = 4).

4.3 Conclusions

We found high densities of shrubland birds in small clearcuts and shelterwood cuts, including species such as Blue-winged Warbler, Chestnut-sided Warbler, and Eastern Towhee that have shown long-term population declines in southern New England (Dettmers and Rosenberg, 2000). All of the species detected frequently enough to analyze with regression analysis were found in both small and large clearcuts and shelterwood cuts, and only the Eastern Towhee showed a significant tendency to occur more frequently in larger openings. This supports the conclusions of previous studies that indicate that the density of shrubland birds generally does not increase with clearcut area (Rudnicky and Hunter, 1993; Krementz and Christie, 2000). The evidence from distribution of shrubland birds in clearcuts of different sizes suggests that small clearcuts provide appropriate habitat, and there is no need to create larger areas of continuous early successional habitats for these species. One caveat, however, is that two shrubland species that tend to be missing in small shrubland openings, the Yellow-breasted Chat (*Icteria virens*) and Golden-winged Warbler (*Vermivora chrysoptera*) (Thompson and Nolan, 1973; Confer, 1992), were not detected in our study areas. Both of these species were once common in southern New England but are now almost extirpated (Dettmers and Rosenberg, 2000).

Even if the abundance of shrubland birds is similar on survey plots in small and large openings, we cannot be certain that the habitat quality is similar without assessing reproductive success. Our results for mating success and evidence of nesting in Blue-winged Warblers did not indicate that larger forest openings represent better breeding habitat. In fact, males in smaller openings tended to have higher mating success and rates of nesting. However, the low average rates of mating success and nesting activity of Blue-winged Warblers in forest openings during the two years of our study suggest that these forest openings (both small and large) are relatively poor breeding habitat. We were unable to test whether nest success was influenced by the area of the forest opening due to a limited sample of nests. Nest failures were due to predation and were more likely to occur during the early stages of nesting (i.e., egg laying and incubation). A longer-term study should reveal whether the rate of nest success is consistently low for Blue-winged Warblers in clearcuts. Also, although none of the Blue-winged Warbler nests we monitored were parasitized by cowbirds, the high density of cowbirds in clearcuts is a cause of concern for this species and other declining shrubland birds. The higher abundance of cowbirds in clearcuts with more snags, which are frequently left after timber harvesting to provide wildlife habitat, indicates that the effect of isolated snags on cowbird density and activity should be studied.

Clearcuts are an ephemeral habitat for Blue-winged Warblers, Chestnut-sided Warblers, Common Yellowthroats, and Eastern Towhees. The abundance of each of these species is greatest at sites with low vegetation and few trees, so they decline as low, woody vegetation grows into closed-canopy forest. Consequently, stable regional populations of these species depend on a continual production of new forest openings as old openings undergo succession. These openings may also be important feeding areas for some forest bird species, particularly Black-and-white Warbler.

In conclusion, small forest openings support populations of several species of shrubland birds. Unlike other bird species and guilds, the abundance and occupancy of shrubland specialists in forest openings does not appear to be heavily influenced by the area of the habitat patch (as long as the patch accommodates a breeding territory) or the landscape context. Habitat selection for many shrubland specialists appeared to be determined by plot-scale characteristics including vegetation structure and tree density. The low reproductive rate in Blue-winged Warblers in our study sites, however, indicates that more information on reproductive rates of shrubland birds in small clearcuts will be needed before we can conclude that they provide productive, long-term habitat for these birds.

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Table 1. Abundance (mean number of individuals per survey plot) for species detected in 34 forest openings in Connecticut. Some species were grouped according to their association with a restricted range of habitats: open shrubland ("shrubland specialist"), the shrub layer in habitats with both open and closed tree canopies ("shrub generalist"), and closed-canopy forest ("forest specialist").

Species	Scientific Name	Breeding Habitat Group	Mean	SD
Brown-headed Cowbird (males and females)	*Molothrus ater*		1.35	1.55
Gray Catbird	*Dumetella carolinensis*	Shrubland generalist	1.32	0.98
Chestnut-sided Warbler	*Dendroica pensylvanica*	Shrubland specialist	1.12	0.81
Eastern Towhee	*Pipilo erythrophthalmus*	Shrubland generalist	1.00	0.85
Blue-winged Warbler	*Vermivora pinus*	Shrubland specialist	0.79	0.77
Common Yellowthroat	*Geothlypis trichas*	Shrubland generalist	0.53	0.66
Black-and-white Warbler	*Mniotilta varia*	Forest specialist	0.50	0.51
Cedar Waxwing	*Bombycilla cedrorum*		0.41	1.21
Wood Thrush	*Hylocichla mustelina*	Forest specialist	0.29	0.52
Prairie Warbler	*Dendroica discolor*	Shrubland specialist	0.26	0.57
Eastern Tufted Titmouse	*Baeolophus bicolor*		0.21	0.48
Veery	*Catharus fuscescens*	Forest specialist	0.21	0.41
Northern Cardinal	*Cardinalis cardinalis*		0.18	0.46
Hooded Warbler	*Wilsonia citrina*	Shrubland generalist	0.18	0.39
American Redstart	*Setophaga ruticilla*	Forest specialist	0.15	0.36
Black-capped Chickadee	*Poecile atricapilla*		0.15	0.36
Brown-headed Cowbird (females)	*Molothrus ater*		0.15	0.36
Great Crested Flycatcher	*Myiarchus crinitus*	Forest specialist	0.15	0.36
Baltimore Oriole	*Icterus galbula*		0.15	0.36
Red-eyed Vireo	*Vireo olivaceus*	Forest specialist	0.15	0.36
American Goldfinch	*Carduelis tristis*		0.12	0.48
Blue Jay	*Cyanocitta cristata*		0.12	0.33
American Robin	*Turdus migratorius*		0.12	0.33
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Shrubland generalist	0.09	0.29
Mourning Dove	*Zenaida macroura*		0.09	0.38
Pileated Woodpecker	*Dryocopus pileatus*	Forest specialist	0.06	0.24
Scarlet Tanager	*Piranga olivacea*	Forest specialist	0.06	0.24

Turkey Vulture	*Cathartes aura*		0.06	0.24
Yellow-throated Vireo	*Vireo flavifrons*	Forest specialist	0.06	0.24
American Crow	*Corvus brachyrhynchos*		0.03	0.17

Table 2. Results of three separate principal component analyses at different spatial scales: plot scale (variables sampled within the 100-m diameter survey plot), patch scale (variables associated with the forest opening), and landscape scale (variables associated with the region within 1 km of the study site). Factor scores are shown for each independent variable for principal components that explain a high percentage of the variance.

	Plot 1	Plot 2	Patch 1	Landscape 1	Landscape 2
Percent of variance explained	47	23	68	39	20
Plot PCA					
Percent tree cover	-0.96	0.05			
Percent shrub cover	0.83	0.17			
Percent herb cover	0.54	-0.23			
Tree density	0.27	0.88			
Canopy height	-0.62	0.50			
Patch PCA					
Clearcut area			-0.97		
Clearcut age			0.42		
Distance around perimeter/area			0.96		
Landscape PCA					
Regional clearcut area				-0.78	0.44
Regional residential area				0.65	0.12
Distance to nearest residence				-0.48	-0.46
Distance to nearest road				0.10	0.81
Distance to nearest powerline				0.60	0.26
Distance to nearest clearcut				0.83	-0.23

Table 3. Relationships between principal components and abundance of particular species in forest plots. Components are shown for three separate principal components at different spatial scales: plot scale (first 2 components), patch scale (first component), and landscape scale* (first 2 components).

Species	Model (P)	R^2	Plot 1	Plot 2	Patch 1	Landscape 1	Abundance increases with:
Gray Catbird	0.032	0.34				0.001 (+)	smaller distance to houses, greater distance from other clearcuts
Black-and-white Warbler	0.92						
Blue-winged Warbler	0.03	0.34		0.037 (-)			lower tree density, lower vegetation (veg.) height
Chestnut-sided Warbler	0.047	0.32		0.034 (-)			lower tree density, lower veg. height
Common Yellowthroat	0.01	0.29		0.006 (-)			lower tree density, lower veg. height
Brown-headed Cowbird	0.004	0.45	<0.001 (+)				higher shrub cover, lower tree cover and veg. height
Eastern Towhee	0.013	0.39		0.034 (-)	0.005 (-)		larger habitat patch, lower tree density and veg. height
Habitat groups							
Shrubland specialists	0.001	0.42	0.019 (+)	0.001 (-)			higher shrub density, lower tree cover, lower tree density
Shrubland generalists	0.04	0.34		0.006 (-)	0.037 (-)	0.039 (+)	larger patch size, lower tree density, greater distance to clearcut, lower area of clearcuts and larger amount of housing nearby
Forest species	0.87						

*Landscape Principal Component 2 is not shown because there were no significant relationships.

Caption

Figure 1. Blue-winged Warblers were generally more successful in finding mates and establishing nests in smaller forest openings (≤ 4 ha) than in larger forest openings (> 4 ha). Although mating success was not significantly different in either small or larger forest openings ($\alpha = 0.05$), the general trend was similar to that for nesting activity, which was significantly greater in small forest openings.