Research Article

Area Requirements and Landscape-Level Factors Influencing Shrubland Birds

H. PATRICK ROBERTS,[1] *Department of Environmental Conservation, University of Massachusetts, 204 Holdsworth Hall, Amherst, MA 01003, USA*

DAVID I. KING, *U.S. Forest Service Northern Research Station, University of Massachusetts, 201 Holdsworth Hall, Amherst, MA 01003, USA*

ABSTRACT Declines in populations of birds that breed in disturbance-dependent early-successional forest have largely been ascribed to habitat loss. Clearcutting is an efficient and effective means for creating early-successional vegetation; however, negative public perceptions of clearcutting and the small parcel size typical of private forested land in much of the eastern United States make this practice impractical in many situations. Group selection harvests, where groups of adjacent trees are removed from a mature forest matrix, may be more acceptable to the public and could provide habitat for shrubland birds. Although some shrubland bird species that occupy clearcuts are scarce or absent from smaller patches created by group selection, some of these smaller patches support shrubland species of conservation concern. The specific factors affecting shrubland bird occupancy of these smaller patches, such as habitat structure, patch area, and landscape context, are poorly understood. We sampled birds in forest openings ranging 0.02–1.29 ha to identify species-specific minimum-area habitat requirements and other factors affecting shrubland birds. We modeled bird occurrence in relation to microhabitat-, patch-, and landscape-level variables using occupancy models. The minimum-area requirements for black-and-white warblers (*Mniotilta varia*), common yellowthroats (*Geothlypis trichas*), chestnut-sided warblers (*Setophaga pensylvanica*), eastern towhees (*Pipilo erythrophthalmus*), and gray catbirds (*Dumetella carolinensis*) were ≤0.23 ha, whereas indigo buntings (*Passerina cyanea*) and prairie warblers (*S. discolor*) required openings of 0.56 ha and 1.11 ha, respectively. Notably, prairie warblers were more likely to occur in openings closer to large patches of habitat such as powerline corridors, even if those openings were small in size. We concluded that, despite their inability to support the entire suite of shrubland species, small forest openings can provide habitat for several species of conservation concern if proper attention is given to promoting suitable microhabitat, patch, and landscape characteristics. © 2017 The Wildlife Society.

KEY WORDS area-sensitivity, early-successional, forest opening, group selection harvest, landscape, occupancy models, shrubland birds.

Many bird species that breed in early-successional vegetation are currently experiencing population declines in eastern North America (Askins 1993, Hunter et al. 2001, Sauer et al. 2014). These negative trends are in part attributed to the loss of required disturbance-dependent early-successional vegetation (Litvaitis 1993, Askins 2001, Thompson and Degraaf 2001, King and Schlossberg 2014), which has primarily declined as a result of the maturation of second-growth forests in the eastern United States (Foster et al. 2002). Early-successional forests are declining at a rate of approximately 2.5% per year and are currently near historical lows across much of the northeastern United States such as in Massachusetts where upland shrublands make up only 2.8% of the landscape (King and Schlossberg 2014). Disturbances

such as windthrow, wildfire, beaver (*Castor canadensis*) activity, and flooding, which once naturally sustained these ephemeral habitats (Brawn et al. 2001, Lorimer 2001, Lorimer and White 2003), have largely been suppressed by humans (DeStefano and Deblinger 2005, Spetich et al. 2011). As a result, state agencies (Oehler et al. 2006, King and Schlossberg 2014) and conservation organizations such as Partners in Flight (Rosenberg et al. 2016) now consider maintaining disturbance-dependent shrublands a conservation priority in the northeastern United States.

In an effort to support shrubland bird populations, land-managing agencies and organizations employ prescribed fire, mowing, and silviculture. Schlossberg and King (2015) recently assessed the extent and origin of shrublands in Massachusetts and concluded that nearly half of indigo bunting (*Passerina cyanea*) and field sparrow (*Spizella pusilla*) populations were supported by deliberate management efforts by government or non-governmental organizations. This suggests that anthropogenic efforts to create and

maintain early-successional vegetative cover are important. Developing a better understanding of shrubland bird responses to these management strategies will facilitate more effective management and conservation of these species.

Recent research indicates that permanent openings created for wildlife support a wide range of shrubland bird species (Chandler et al. 2009a, King et al. 2009a, Smetzer et al. 2014) and may be more effective than traditional silvicultural practices for certain species (Smetzer et al. 2014). However, the maintenance of wildlife openings, which typically requires mowing or burning at regular intervals, is expensive (Thompson and DeGraaf 2001, Oehler 2003), making widespread use of wildlife openings impractical. Silviculture presents a useful alternative for creating early-successional vegetation because the costs can be offset by timber revenue.

Silviculture currently plays an important role in supporting shrubland bird populations, creating about 78% of the early-successional forest in New England (Schlossberg and King 2007). Several studies indicate that clearcutting is an effective approach for creating shrubland bird habitat (Annand and Thompson 1997, Costello et al. 2000, King and DeGraaf 2000, Perry and Thill 2013). However, the majority of woodlots in southern New England are <3.6 ha in size (Butler et al. 2007) and clearcutting, especially under such circumstances, elicits strong public opposition (Gobster 2001). As a result, silviculture in New England has shifted toward uneven-aged strategies (Trani et al. 2001) where only a portion of managed stands are removed during harvests. Of uneven-aged-practices, only group selection harvest, in which groups of adjacent trees are removed from a mature forest matrix (Smith et al. 1997), creates shrubland suitable in structure for shrubland-obligate birds (Annand and Thompson 1997). However, patches created by group selection harvest (typically <1.0 ha) are too small to support some area-sensitive shrubland bird species (Costello et al. 2000, Alterman et al. 2005). Nevertheless, small forest openings still support some shrubland bird species less sensitive to patch area that are of regional concern (Costello et al. 2000) and it is possible that group selection could enable managers to contribute to bird conservation on sites where creating large patches of early-successional forest is not practical. The precise minimum-area requirements of these species have not been established and thus the conservation value of small forest openings is not clear.

Although the landscape-level characteristics required by mature forest birds have been identified (Robinson et al. 1995, Howell et al. 2000), the landscape-level needs of shrubland birds are less clear (Schlossberg and King 2007). Some studies report significant relationships between avian abundance and landscape composition (Hagan et al. 1997, Lichstein et al. 2002), whereas others have reported limited (Askins et al. 2007, Chandler et al. 2009b), or no (Chandler 2006) relationship with composition. Furthermore, juxtaposition with larger patches of habitat appears to increase occupancy of smaller patches by shrubland birds (Buffum and McKinney 2014). These findings suggest that landscape conditions may influence patch suitability for many shrubland-obligate species

and highlights the need for considering landscape context and habitat juxtaposition when developing management guidelines.

Our goal was to investigate and describe the potential for small forest openings created by group selection to support shrubland birds. Our objectives were to identify species-specific minimum-area requirements for shrubland birds capable of occupying these openings and identify additional microhabitat-, patch-, and landscape-level factors that can promote occupancy of shrubland-associated species within small forest openings.
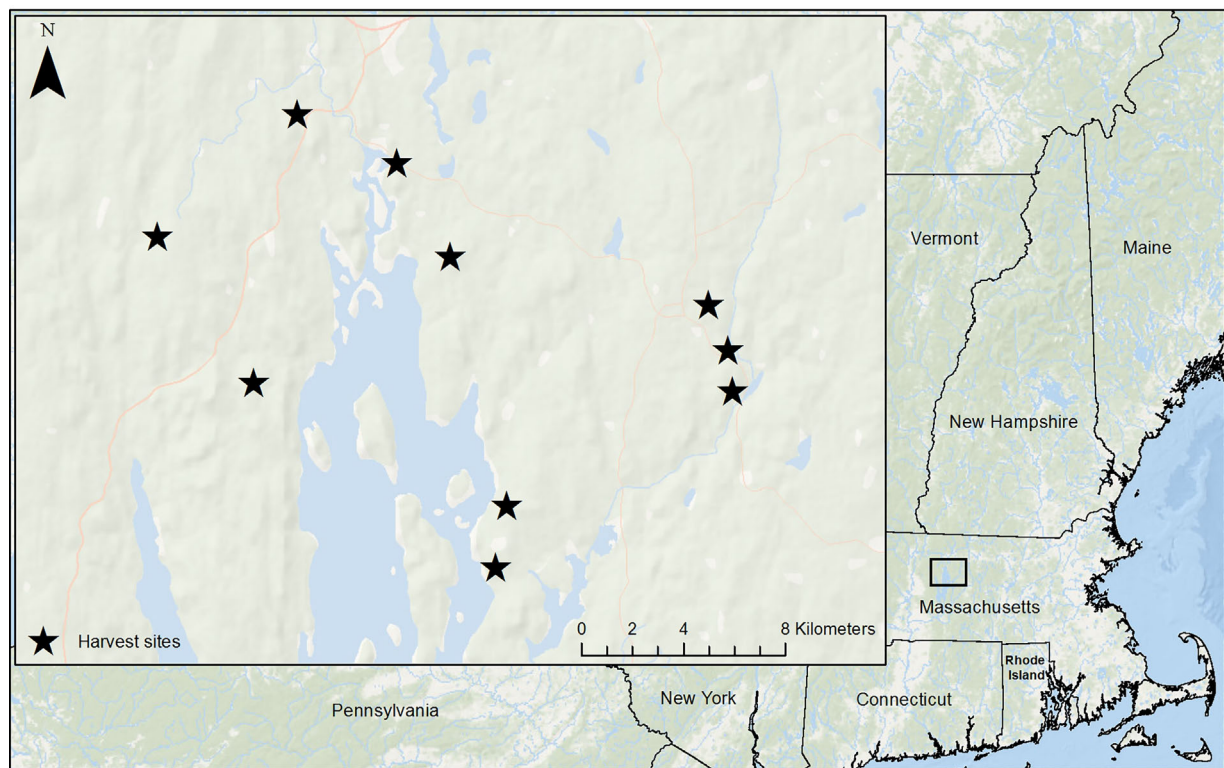
STUDY AREA

We conducted this study during 2014 and 2015 in Franklin and Worcester counties, western Massachusetts, USA (42.46°N, 72.32°W; Fig. 1). The study area was approximately 57,000 ha, over 90% forested with <5% human development, and dominated by transitional hardwoods, consisting primarily of red maple (*Acer rubrum*), red oak (*Quercus rubra*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*). Forest openings contained seedlings and saplings of adjacent tree species, principally birches (*Betula* spp.), red maple, white pine, as well as *Rubus* spp., mountain laurel (*Kalmia latifolia*), and numerous fern species. Elevation at study sites ranged approximately 185–380 m. Annual mean precipitation and temperature (at nearby Barre Falls Dam, Massachusetts) were 1,191 mm and 7.3°C, with means of 105 mm/month and 16.3°C during the field season (i.e., May–Jul; National Oceanic and Atmospheric Administration 2017).

METHODS

We randomly selected openings to study from a list of 146 candidate openings within the study area, 90 openings in 2014 and 104 in 2015. Openings ranged from 0.02 ha to 1.29 ha and had been harvested between 2006 and 2010. Forest openings in this study were created by group selection harvests, with the exception of 2 openings, which were the product of harvests where only a single opening was created. We conducted surveys at 10 harvest sites (Fig. 1), which were each comprised of between 1 and 40 openings. The average edge-to-edge nearest-neighbor distance between openings within harvest sites was 43 ± 18 m (SD). To ensure openings represented the entire range of opening sizes, we randomly chose openings from 4 bins representing different size ranges (0–0.14 ha, 0.15–0.27 ha, 0.28–0.49 ha, and $\geq$0.5 ha). We added 14 smaller openings in 2015 in addition to those sampled the previous year to fully capture the lower range in opening sizes.

Bird and Microhabitat Surveys

We surveyed birds 3 times per year from late May to early July with 10-minute, 50-m radius point counts (Ralph et al. 1995) at the center of each opening. We commenced surveys 15 minutes after sunrise and continued until 1100 hours. We conducted surveys only on days with low wind (<5 on the Beaufort scale) and no precipitation. We alternated the order

Figure 1. Map of study area in western Massachusetts (42.46°N, 72.32°W), USA. Black stars indicate timber harvest sites where we conducted bird surveys in forest openings in 2014 and 2015. The number of forest openings per harvest site ranged from 1 to 40.

in which we surveyed points to minimize bias due to time of day. We recorded wind speed (Beaufort scale) and cloud cover before each survey. We recorded location, sex, and detection method of all birds noted during point counts on scaled orthoimagery. We assumed birds singing, but not seen, were males. We did not record sex for non-sexually dimorphic species that we identified by sight only. At least 2 different technicians visited each survey point each year to reduce observer bias (Ralph et al. 1995). We did not include birds flying above the surrounding mature forest canopy or detected outside of the 50-m radius in the analysis. Surveys did not disturb birds and complied with accepted guidelines (Fair et al. 2010).

We measured microhabitat characteristics relating to vegetation structure and composition at 20 random locations within each opening using random bearings and distances (1–25 m) and starting from point count locations. We recorded species and maximum height of the plant species in contact with a vertical pole within 4 height classes: <0.5 m, 0.5–1.39 m, 1.4–2.9 m, and ≥3.0 m (Martin et al. 1997). We did not measure trees because we encountered few within openings.

Patch and Landscape Metrics

For each opening, we measured 2 patch-level metrics (area and shape index) and 2 landscape-level metrics (% of the surrounding landscape that was shrubland [PLAND] and the distance to the nearest large patch of shrubland). We calculated area, shape index, and PLAND using

FRAGSTATS, version 4 (McGarigal et al. 2012) and ArcGIS version 10.2.1 (Environmental Systems Research Institute, Redlands, CA, USA). To facilitate analysis in FRAGSTATS, we first created shapefiles delineating shrubland boundaries using ArcGIS, which we then rasterized using a 3-m cell size. Shape index quantifies patch shape complexity by dividing the perimeter of a patch by the minimum possible perimeter of a patch equal in area. This eliminates bias associated with using the perimeter-to-area ratio metric on patches that vary in size. We chose to examine patch shape in addition to area because there is evidence that it is an influential factor for shrubland birds (Weldon and Haddad 2005, Shake et al. 2012). We calculated PLAND using a specified search-radius from the centroid of each opening. Because the scale at which birds respond to their surroundings is largely unknown, we calculated PLAND at 100-m, 200-m, 300-m, 400-m, and 500-m scales. We did not examine radii >500 m because this scale adequately represented the group selection harvests in this study and there was little shrubland outside of harvested areas. Initially, we considered 3 additional FRAGSTATS metrics (proximity index, core area, and core area index) for inclusion in models, but these measures were either skewed with too many outliers (proximity index) or redundant with measures we employed (core area and core index with shape index). We measured the distance to the nearest large patch using ArcGIS. We defined large patches as any powerline corridor with shrubland vegetation >50 m wide or patches of shrubland >5 ha in area. Patches of this size are large enough

to accommodate even the most area-sensitive birds in this area (King et al. 2009*a,b*).

Statistical Analysis

We related shrubland bird occupancy to environmental variables using occupancy models that allow the incorporation of detection probability, which reduces bias associated with imperfect detection (MacKenzie et al. 2002, 2006). This framework uses replicated point counts to estimate detection probability (Thompson 2002). Occupancy models are valid under the assumption of closure where no immigration, emigration, and mortalities occur (Royle and Dorazio 2008). We considered this assumption fulfilled given territoriality and the relatively short amount of time allowed between replicate counts (≤ 10 days; Smetzer et al. 2014).

We restricted the analysis to males that were detected inside openings and to species that occurred in $\geq 10\%$ of openings. We related occupancy and detection probability to respective covariates using a logit link. We considered variables with $r > 0.5$ closely correlated. Because patch area was of primary concern to this study, we removed any variables that were closely correlated with area, leading us to remove PLAND at the 100-m scale. We also removed variables describing the amount of forb, fern, grass, and needleleaf vegetation because they were correlated with the amount of broadleaf vegetation, which we hypothesized was likely more important for the majority of the species in this study. Measurements of PLAND for the 200-m, 300-m, 400-m, and 500-m scales were highly correlated, but we retained them because we chose only the best predictive scale for inclusion in the model selection process. We scaled all continuous variables with mean $= 0$ and standard deviation $= 1$ to promote model convergence. The final set of predictor variables considered in models included percent broadleaf vegetation, median vegetation height, and coefficient of variation (CV) of vegetation height at the microhabitat level, area and shape index at the patch level, and distance to the nearest large patch of shrubland and PLAND at the landscape level. Detection covariates included observer, date, time, wind speed, and cloud cover.

We employed an information-theoretic approach to determine best-performing model(s) (Burnham and Anderson 2002). We used Akaike's Information Criterion adjusted for overdispersion and small sample sizes ($QAIC_c$) to compare models (Burnham et al. 2011). Prior to model selection, we assessed fit of the data by conducting a goodness-of-fit bootstrap (1,000 bootstraps) of models containing all detection and occupancy covariates for each species (MacKenzie and Bailey 2004) using the AICcmodavg package (Mazerolle 2015) in the R software environment, version 3.1.1 (R Version 3.1.1, http://r-project.org/, accessed 25 Jan 2014). This produced overdispersion parameters ($\hat{c}$), which we used to inflate standard errors and influence the subsequent selection of models (MacKenzie and Bailey 2004). We assigned all species with $\hat{c} \leq 1$ a value of 1 (Mazerolle 2015).

To begin the model selection process, we first determined best detection covariates for predicting occupancy for each species, which we subsequently included in all candidate models. We did this by fitting all subsets of detection covariates while including all occupancy variables. We retained detection covariates that were in models that performed better than a null model with a $\Delta QAIC_c \leq 2$ and statistically significant at $P \leq 0.1$ (Smetzer et al. 2014). Next, with detection covariates and a year covariate fixed in all models and using the same selection criteria, we identified the variables that best predicted species occupancy within microhabitat, patch, and landscape levels. We then combined these best-performing variables into a final construction of models that included all levels. We used the unmarked package (Fiske and Chandler 2011) to fit models and estimate parameters in the R software environment, version 3.1.1.

We considered occupancy covariates to be supported if they were included in models with a $\Delta QAIC_c \leq 2$ and strongly supported if 95% confidence intervals (CI) of their coefficients did not include 0, following Chandler et al. (2009*a*). We illustrated species-variable relationships by plotting weighted-average model predictions using Akaike weights (Burnham and Anderson 2002) across all models that included the focal variable while holding all other variables at their mean. To examine how the relationship between prairie warbler occurrence and distance to nearest large patch varied by patch size, we plotted this relationship while holding patch area constant at a range of sizes. We avoided model averaging parameter estimates because there are uncertainties associated with the practice (Burnham and Anderson 2002, Cade 2015), parameter estimates are influenced by the number of variables included in a model, and multicollinearity can influence the interpretation of parameters.

Following Shake et al. (2012), we calculated the minimum-area requirement and optimal area value of each species by identifying the area at which the weighted-average probability of occurrence equaled 0.5 and 0.9, respectively. Although birds do occur within patches below their minimum-area requirements as defined using this procedure, because this value indicates the area below which occupancy probability is less than random, it has been adopted as a standard metric for quantifying area sensitivity (Robbins et al. 1989, Vickery et al. 1994, Shake et al. 2012), which facilitates comparison among species, studies, and management application.

RESULTS

We recorded 1,633 detections of 52 bird species in 2014 and 2,046 detections of 48 species in 2015. Detected species included 16 of 41 species identified as core shrubland birds of New England by Schlossberg and King (2007). Seven of these species had sufficient sample sizes for analysis: black-and-white warbler (*Mniotilta varia*), common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler (*Setophaga pensylvanica*), eastern towhee (*Pipilo erythrophthalmus*), gray catbird (*Dumetella carolinensis*), indigo bunting, and prairie warbler (*S. discolor*). We obtained a sufficient sample size for indigo bunting only in 2014.

We found evidence of relationships between occupancy of study species and microhabitat-, patch-, and landscape-level variables (Table 1). Forest opening area was strongly supported in all top models ($\Delta QAIC_c \leq 2$) for all species (Table 1). Black-and-white warbler, common yellowthroat, chestnut-sided warbler, eastern towhee, and gray catbird were capable of occupying smaller openings, with minimum-area requirements of ≤ 0.23 ha and optimal area values of ≤ 0.49 ha (Fig. 2; Table 2). We could not identify a minimum area requirement for chestnut-sided warbler because the predicted probability of occurrence never fell below 0.5 (Fig. 2). Indigo bunting and prairie warbler exhibited greater area-sensitivity, with minimum-area requirements of 0.56 ha and 1.11 ha, respectively. The optimal area value for indigo bunting was 0.7 ha, whereas the probability of occurrence never reached 0.9 for prairie warbler (Fig. 2; Table 2).

Gray catbirds and prairie warblers were the only species that showed strong relationships with the amount of shrubland on the landscape (Table 1). Gray catbirds occurred more frequently in openings with more shrubland within 200 m, whereas prairie warblers occurred less frequently in openings with more shrubland in the surrounding landscape within 500 m (Table 1). Prairie warbler was the only species to show a negative relationship with distance to the nearest large patch (Table 1). Prairie warblers also appeared more likely to occupy smaller openings if they were near larger patches (Fig. 3).

Chestnut-sided warbler showed a strong positive relationship with broadleaf vegetation, whereas eastern towhee displayed a strong negative relationship (Table 1). Gray catbird displayed strong positive relationships with vegetation height, whereas prairie warbler showed a strong negative relationship. Gray catbird was the only species to show a strong relationship with CV of vegetation height, occurring more frequently in openings with less variation in vegetative structure.

DISCUSSION

Previous research reported that certain shrubland birds present in large patches are consistently absent from patches <1 ha (Rodewald and Smith 1998, Robinson and Robinson 1999, Costello et al. 2000, Alterman et al. 2005, Tozer et al. 2010), but little progress has been made identifying the minimum-area requirements below which species are not likely to occur. Shake et al. (2012) determined that there were distinct minimum-area requirements in patch area use for prairie warbler and yellow-breasted chat (*Icteria virens*) in North Carolina, USA. We have supplemented the efforts of Shake et al. (2012) with results for prairie warblers in a different region of the United States and have also included

Table 1. Parameter estimates (SE) of candidate models representing the effect of microhabitat-, patch-, and landscape-level factors on bird occurrence in forest openings in western Massachusetts, USA, 2014 and 2015. Parameter estimates with asterisks have 95% confidence intervals that exclude 0. Parameter estimates for year and detection covariates are not included.

	Microhabitat[b]			Patch[c]		Landscape[d]				
Species[a]	Broad	Ht	CV	Area	Shape	Distance	Pl.200	Pl.500	$\Delta QAIC_c$[e]	w_i[f]
BAWW				32.26 (11.00)*					0.00	0.40
		0.60 (0.38)		41.94 (14.68)*					0.29	0.34
CSWA	0.54 (0.22)*			6.13 (1.86)*					0.00	0.23
	0.52 (0.22)*			5.87 (1.91)*		0.30 (0.23)			0.47	0.18
	0.60 (0.23)*	−0.28 (0.23)		5.39 (1.91)*		0.36 (0.24)			1.19	0.12
	0.60 (0.23)*	−0.22 (0.22)		5.79 (1.87)*					1.28	0.12
COYE				11.86 (3.27)*					0.00	0.43
		−0.34 (0.27)		10.87 (3.14)*					1.30	0.23
				11.57 (3.45)*				−0.43 (0.35)	1.33	0.22
EATO	−0.82 (0.39)*			13.13 (5.16)*					0.00	0.41
	−0.64 (0.32)*			8.41 (4.57)*			0.65 (0.64)		1.32	0.21
	−0.78 (0.37)*			12.10 (5.07)*		0.20 (0.34)			1.84	0.16
GRCA		3.72 (1.02)*		10.53 (2.72)*			1.87 (0.69)*		0.00	0.17
		3.86 (0.96)		11.48 (2.61)*					0.56	0.13
			−0.74 (0.27)*	7.06 (1.80)*			1.59 (0.59)*		1.25	0.09
		3.47 (1.05)*	−0.47 (0.30)	10.09 (2.65)*			1.79 (0.71)*		1.33	0.09
		3.53 (0.93)*	−0.56 (0.30)	10.92 (2.63)*					1.38	0.08
	−0.48 (0.38)	4.00 (1.13)*		12.23 (3.88)*			1.91 (0.69)*		1.51	0.08
INBU				14.93 (5.23)*					0.00	0.20
				21.57 (8.23)*	−1.83 (1.10)				0.25	0.18
				16.55 (6.61)*				−0.99 (0.89)	1.43	0.10
		−1.40 (1.28)		13.65 (5.35)*					1.60	0.09
PRAW	−2.01 (1.01)*			7.70 (2.44)*		−3.74 (1.04)*		−1.30 (0.40)*	0.00	0.56

[a] BAWW = black-and-white warbler; CSWA = chestnut-sided warbler; COYE = common yellowthroat; EATO = eastern towhee; GRCA = gray catbird; INBU = indigo bunting; PRAW = prairie warbler.

[b] Broad = broadleaf vegetation (%); Ht = median vegetation height; CV = coefficient of variation of vegetation height.

[c] Area = forest opening area; Shape = shape index (patch perimeter divided by the minimum possible perimeter of a patch equal in area).

[d] Distance = distance to nearest large patch of shrubland (clearcuts >5 ha or powerlines corridors >50 m wide); PL200 and Pl.500 = amount of shrubland on the landscape at 200-m and 500-m scales. Pl.300 and Pl.400 are not included because no species responded at those scales.

[e] Difference in Akaike's Information Criterion corrected for overdispersion and small sample sizes. We only show models with $\Delta QAIC_c \leq 2$.

[f] $QAIC_c$ weights of models.
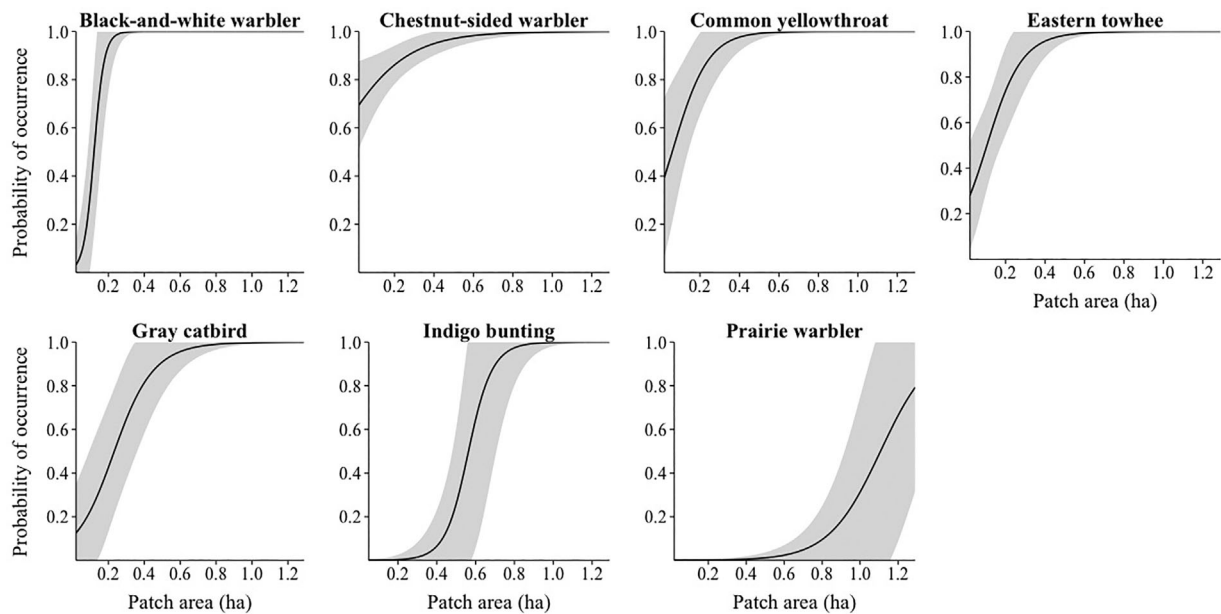
Figure 2. Probability of occurrence of shrubland birds in relation to forest opening size in western Massachusetts, USA, 2014 and 2015. We show weighted-average model predictions for candidate models with differences in Akaike's Information Criterion corrected for overdispersion and small sample size ($\Delta QAIC_c$) ≤ 2. Shaded areas represent 95% confidence intervals.

other species that occur in smaller openings to provide information on the utility of these smaller openings for bird conservation. This information is important for conservation because without knowledge of how individual species respond to management practices we cannot fully understand the effect of management efforts on the avian community.

Our finding that chestnut-sided warbler, common yellow-throat, black-and-white warbler, eastern towhee, gray catbird, indigo bunting, and prairie warbler were positively associated with forest opening area is consistent with the findings of other studies (Annand and Thompson 1997, Rodewald and Smith 1998, Costello et al. 2000, Moorman and Guynn 2001, King and Degraaf 2004). Our finding that indigo buntings were likely to occur only in openings ≥ 0.56 ha contrasts with other studies that frequently reported indigo buntings in openings <0.56 ha (Kerpez 1994, Robinson and Robinson 1999, Moorman and Guynn 2001). This difference might be explained by the minimal forb cover in openings in this study, which has been reported to be positively related to indigo bunting abundance (King

et al. 2009a, Smetzer et al. 2014) and was the dominant vegetation type in ≥ 1 of these studies (Moorman and Guynn 2001). Because forb coverage was low in most openings in our study, indigo buntings may have required larger openings with a greater breadth of resources. Prairie warblers, with an estimated minimum-area requirement of 1.11 ha, were the most area-sensitive species that occurred frequently enough in openings to be modeled. This estimate is nearly identical to that by Shake et al. (2012) in North Carolina and the suggested 1.1-ha opening size in Virginia, USA, by Kerpez (1994). Such consistency of estimated area requirements throughout the prairie warbler range suggests that our results are generalizable beyond our study area.

Group selection opening sizes can influence the composition and structure of regenerating vegetation (Smith et al. 1997), thus a plausible explanation for the apparent area-sensitivity of species that we observed could be that smaller openings simply foster unsuitable vegetative conditions below each species' respective minimum-area requirement. However, if this were the case, vegetation variables would have played a more prominent and consistent role in the models than they did. Another explanation, provided by Askins et al. (2007), suggests that the primary factor determining area-sensitivity is a species' territory size and whether it can fit within a given opening. Lending some general support to this idea, prairie warblers, which were the most area-sensitive species in this study, appear to have larger territories (>1 ha [Nolan 1978]) than the species that we identified as less area-sensitive (e.g., 0.2 ha for common yellowthroat [Brewer 1955]). It is also possible that area-sensitivity may reflect insufficient food resources provided by smaller openings (Schlossberg and King 2007).

Very little attention has been given to how proximity of large shrubland patches influences shrubland birds in smaller

Table 2. Minimum-area requirements (probability of occurrence $= 0.5$) and optimal area values (probability of occurrence $= 0.9$) for shrubland bird species in forest openings in western Massachusetts, USA, 2014 and 2015.

	Opening area (ha)	
Species	**Min.**	**Optimal**
Black-and-white warbler	0.12	0.18
Chestnut-sided warbler		0.27
Common yellowthroat	0.06	0.26
Eastern towhee	0.11	0.31
Gray catbird	0.23	0.49
Indigo bunting	0.56	0.70
Prairie warbler	1.11	
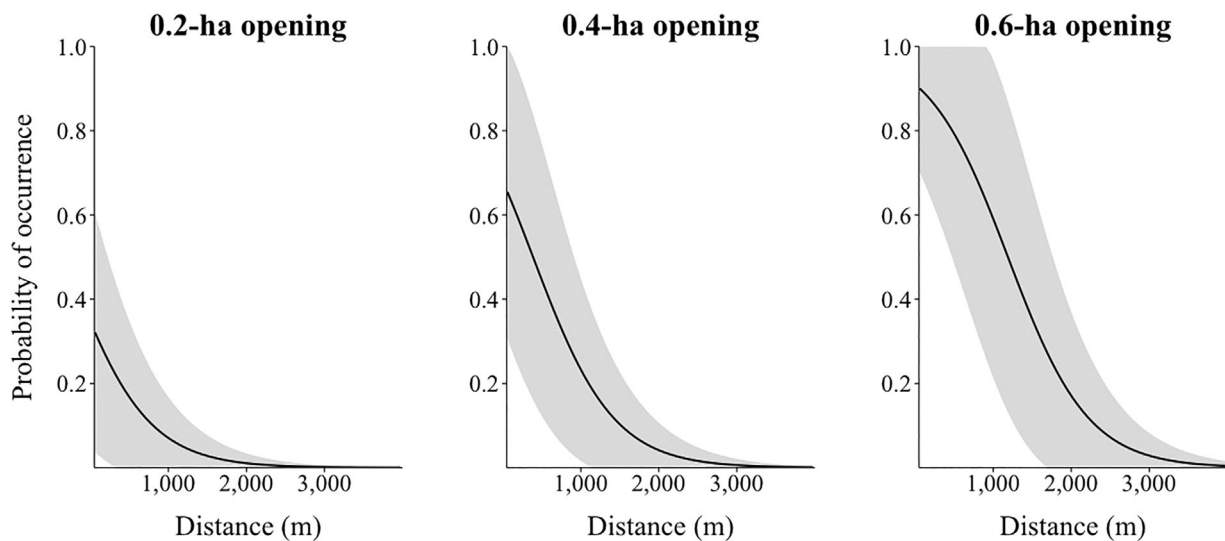
Figure 3. Probability of occurrence of prairie warbler in forest openings of varying size in relation to the distance to the nearest large patch of shrubland (clearcuts >5 ha or powerline corridors >50 m wide). We show weighted-average model predictions for candidate models with differences in Akaike's Information Criterion corrected for small sample size and overdispersion (ΔQAIC$_c$) ≤2. Shaded areas represent 95% confidence intervals. Data come from surveys conducted in western Massachusetts, USA.

adjacent patches. Although Buffum and McKinney (2014) did not specifically examine distance to large patches as an independent variable, they reported that the size of adjacent wetland shrub patches within 50 m increased occupancy of several species in small patches of upland shrubland in Rhode Island, USA. Similarly, we observed that prairie warblers occurred more frequently in openings closer to large patches of shrubland, indicating that shrublands may be enhanced with proximity to large upland shrubland patches, in addition to wetland shrublands. Furthermore, prairie warblers were capable of occupying openings considerably smaller than their standard territory size (typically >1 ha [Nolan 1978]), if the opening was located close to a large patch. Individuals in these patches were able to acquire mates successfully, as indicated by the discovery of the nest of a mated pair occupying a 0.22 ha opening approximately 60 m from a powerline right-of-way. More research is needed to determine whether prairie warblers in small patches confine their activities to shrubland within forest openings (which would suggest they may have flexible territory sizes) or incorporate adjacent mature forest within territories. Regardless, these findings confirm the assumption by conservationists that juxtaposing small shrubland patches near larger openings increases their value as habitat for shrubland birds.

Landscapes that contain a higher proportion of shrubland may be favored by shrubland birds for several reasons including conspecific attraction (Ward and Schlossberg 2004), availability of breeding sites to choose from during settlement (Badyaev et al. 1996), increased possibilities for within-breeding-season dispersal (Schlossberg and King 2007), and perhaps increased potential for extra-pair copulations (Byers et al. 2004). Landscape composition has been reported in other studies to be important for several of the species in this study (Hagan et al. 1997, Hagan and

Meehan 2002, Lichstein et al. 2002); however, we found that only 2 species, gray catbirds and prairie warblers, were strongly associated with the amount of early-successional forest on the landscape. Gray catbirds responded positively to the extent of shrubland on the landscape, which is consistent with findings of Hagan et al. (1997). However, Askins et al. (2007) reported that gray catbirds did not appear to respond to the amount of early-successional forest on the landscape. This discrepancy may be due to residential areas—which Askins et al. (2007) reported increased gray catbird abundance nearby—being largely absent from the study area of Hagan et al. (1997) and our study area.

Our finding that prairie warbler occupancy decreased with more shrubland on the landscape was unexpected in light of prior reports that this species prefers larger openings and our own finding that this species was more likely to occur closer to large patches of shrubland. Although area and the amount of shrubland within 500 m were not correlated enough to exclude from the modeling process, their negative correlation was statistically significant ($r = -0.42$, $P = <0.001$). Therefore, one explanation for this pattern is that the apparent negative relationship with the amount of shrubland on the landscape in the models may be a product of there being less shrubland surrounding larger openings, which are more likely to attract prairie warblers (Shake et al. 2012). Furthermore, the shrubland surrounding most openings occurred in the form of small patches that typically will not host prairie warblers (83% of all openings in our study were smaller than half the size of our estimated minimum-area requirement for prairie warblers). Thus in group selection systems, where openings are generally small, more shrubland on the landscape may not necessarily have the same positive effect for prairie warblers as it might for species that will readily occur in smaller openings.

Forest openings in this study were occupied by birds of high conservation concern. Six of the 7 species analyzed (black-and-white warbler, common yellowthroat, chestnut-sided warbler, eastern towhee, indigo bunting, and prairie warbler) are experiencing significant regional population declines (Sauer et al. 2014). In addition, prairie warbler is listed as a species of continental conservation concern in the Partners in Flight North American Landbird Conservation Plan (Rosenberg et al. 2016). Therefore, although unable to support the full early-successional bird community, openings as small as 0.23 ha can still provide habitat for ≥5 shrubland species, 4 of which are of conservation concern. This is particularly relevant to conservation because a large proportion of forested parcels in southern New England can support openings 0.23 ha in size (Butler et al. 2007) without fully compromising the aesthetic characteristics valued by many land owners and openings of this size are less likely to raise public opposition. Early-successional vegetation has also been reported to be beneficial for birds that breed in mature forest (King et al. 2006, Streby et al. 2011).

The clustered nature of openings restricted the scope of this study to some degree. For example, although there was variation in the amount of shrubland surrounding openings, there were very few openings that were completely isolated. Moreover, most of the more isolated openings were larger, making it difficult to examine occupancy in very small isolated openings. Small and isolated anthropogenic openings are too scarce to study because there is no silvicultural prescription that results in single, small openings. Furthermore, because the limitations of small openings have been communicated to managers (Buffum and McKinney 2014), few small openings have been created for wildlife. Therefore, though we were unable to properly address the lower range of isolation for small openings, it is unlikely that this information would be useful for land managers because small, isolated openings are not practical as a silvicultural prescription or a wildlife management strategy (Chandler et al. 2009a).

Another limitation was our focus on occurrence data, which is not necessarily indicative of habitat quality (Brawn and Robinson 1996). Nevertheless, we did locate nests in many openings, including some of the smallest in the study, although we did not have sufficient resources to monitor them for nesting success. Thus, we are confident birds were at least able to acquire mates in even the smallest openings. Although some studies report increased predation near edges (Suarez et al. 1997, Weldon and Haddad 2005, Shake et al. 2011), certain shrubland birds are able to nest successfully in group selection cuts in extensively forested landscapes regardless of patch size (King and DeGraaf 2004) and appear to nest with similar success in group selection openings and clearcuts (King et al. 2001, Alterman et al. 2005).

MANAGEMENT IMPLICATIONS

The results of this study have important implications for the management of shrubland birds, especially in regions where forest parcel sizes are too small to create large openings. In situations where the goal is to accommodate all species in this study, land managers should consider creating openings >1.1 ha in size. If this is not feasible operationally, as is the case for many private forest owners in southern New England, openings 0.23 ha in size can still provide habitat for several species of high conservation concern, and openings 0.7 ha in size provide optimal habitat for all species but prairie warbler. If managers are not constrained by patch size, openings beyond the size range we sampled (1.29 ha) would further increase the probability of supporting prairie warblers, the most area-sensitive songbird in our study. Because we do not have data on larger patches, we are unable to provide exact guidance on how large the optimum patch size for this species would be. Managers should also consider the importance of landscape context when managing for shrubland birds and prioritize creating openings near existing large shrubland patches. This will increase the probability of occurrence of area-sensitive species such as prairie warblers and thus maximize conservation value of management efforts while also minimizing monetary expenses associated with habitat creation.

LITERATURE CITED

Alterman, L. E., J. C. Bednarz, and R. E. Thill. 2005. Use of group-selection and seed-tree cuts by three early-successional migratory species in Arkansas. Wilson Bulletin 117:353–363.

Annand, E. M., and F. R. Thompson III. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management 61:159–171.

Askins, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. Current Ornithology 11:1–34.

Askins, R. A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin 29:407–412.

Askins, R. A., B. Zuckerberg, and L. Novak. 2007. Do size and landscape context of forest openings influence the abundance and breeding success of shrubland birds in southern New England? Forest Ecology and Management 250:137–147.

Badyaev, A. V., T. E. Martin, and W. J. Etges. 1996. Habitat sampling and habitat selection by female wild turkeys: ecological correlates and reproductive consequences. Auk 113:636–646.

Brawn, J. D., and S. K. Robinson. 1996. Source-sink dynamics may complicate the interpretation of long-term census data. Ecology 77:3–12.

Brawn, J. D., S. K. Robinson, and F. R. Thompson III. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics 32:251–276.

Brewer, R. 1955. Size of home range in eight bird species in a southern Illinois swamp-thicket. Wilson Bulletin 67:140–141.

Buffum, B., and R. A. McKinney. 2014. Does proximity to wetland shrubland increase the habitat value for shrubland birds of small patches of upland shrubland in the northeastern United States? International Journal of Forestry Research 2014:article 329836.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer, London, United Kingdom.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Butler, B. J., C. J. Barnes, S. J. Crocker, G. M. Domke, D. Gormanson, W. N. Hill, C. M. Kurtz, T. Lister, C. Martin, P. D. Miles, R. Morin, W. K. Moser, M. D. Nelson, B. O'Connell, B. Payton, C. H. Perry, R. J. Piva, R. Riemann, and C. W. Woodall. 2007. The forests of southern New England, 2007: a report on the forest resources of Connecticut, Massachusetts, and Rhode Island. U.S. Forest Service, Washington, D.C., USA.

Byers, B. E., H. L. Mays Jr., I. R. K. Stewart, and D. F. Westneat. 2004. Extrapair paternity increases variability in male reproductive success in the chestnut-sided warbler (*Dendroica pensylvanica*), a socially monogamous songbird. Auk 121:788–795.

Cade, B. S. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Chandler, R. B. 2006. Early-successional bird abundance and nest success in managed shrublands on the White Mountain National Forest. Thesis, University of Massachusetts, Amherst, USA.

Chandler, R. B., D. I. King, and C. C. Chandler. 2009a. Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA. Forest Ecology and Management 258:1669–1676.

Chandler, R. B., D. I. King, and S. DeStefano. 2009b. Scrub-shrub bird habitat associations at multiple spatial scales in beaver meadows in Massachuestts. Auk 126:186–197.

Costello, C. A., M. Yamasaki, P. J. Pekins, W. B. Leak, and C. D. Neefus. 2000. Songbird response to group selections harvests and clearcuts in a New Hampshire northern hardwood forest. Forest Ecology and Management 127:41–54.

DeStefano, S., and R. D. Deblinger. 2005. Wildlife as valuable natural resources *vs*. intolerable pests: a suburban wildlife management model. Urban Ecosystems 8:179–190.

Fair, J., E. Paul, and J. Jones. 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., USA.

Fiske, I. J., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Foster, D. R., G. Motzkin, D. Bernardos, and J. Cardoza. 2002. Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29:1337–1357.

Gobster, P. H. 2001. Human dimensions of early successional landscapes in the eastern United States. Wildlife Society Bulletin 29:474–482.

Hagan, J. M., and A. L. Meehan. 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. Forest Science 28:231–242.

Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. Journal of Wildlife Management 61:718–735.

Howell, C. A., S. C. Latta, T. M. Donovan, P. A. Porneluzi, G. R. Parks, and J. Faaborg. 2000. Landscape effects mediate breeding bird abundance in Midwestern forests. Landscape Ecology 15:547–562.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:440–455.

Kerpez, T. A. 1994. Effects of group selection and clearcut openings on wildlife in Appalachian hardwood forests. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, USA.

King, D. I., R. B. Chandler, J. M. Collins, W. R. Petersen, and T. E. Lautzenheiser. 2009b. Effects of width, edge and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. Biological Conservation 142:2672–2680.

King, D. I., R. B. Chandler, S. Schlossberg, and C. C. Chandler. 2009a. Habitat use and nest success of scrub-shrub birds in wildlife and silvicultural openings western Massachusetts, USA. Forest Ecology and Management 257:421–426.

King, D. I., and R. M. DeGraaf. 2000. Bird species diversity and nesting success in mature, clearcut, and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 129:227–235.

King, D. I., and R. M. DeGraaf. 2004. Effects of group-selection opening size on the distribution and reproductive success of an early-successional shrubland bird. Forest Ecology and Management 190:179–185.

King, D. I., R. M. DeGraaf, and C. R. Griffin. 2001. Productivity of early successional shrubland birds in clearcuts and groupcuts in eastern deciduous forest. Journal of Wildlife Management 65:345–350.

King, D. I., R. M. Degraaf, M.-L. Smith, and J. P. Buonaccorsi. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414–421.

King, D. I., and S. Schlossberg 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. Forest Ecology and Management 324:186–195.

Lichstein, J. W., T. R. Simons, and K. E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. Ecological Applications 12:836–857.

Litvaitis, J. A. 1993. Response of early successional vertebrates to historic changes in land use. Conservation Biology 7:866–873.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin 29:425–439.

Lorimer, C. G., and A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185:41–64.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Amsterdam, The Netherlands.

Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

Mazerolle, M. J. 2015. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg. Accessed 06 Mar 2016.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 11 Nov 2014.

Moorman, C. E., and D. C. Guynn Jr. 2001. Effects of group-selection openings size on breeding bird habitat use in a bottomland forest. Ecological Applications 11:1680–1691.

National Oceanic and Atmospheric Administration. 2017. Data tools: 1981–2010 normals. https://www.ncdc.noaa.gov/cdo-web/datatools/normals. Accessed 02 May 2017.

Nolan Jr. V. 1978. The ecology and behavior of the prairie warbler *Dendroica discolor*. American Ornithologists' Union. Allen Press, Lawrence, Kansas, USA.

Oehler, J. D. 2003. State efforts to promote early-successional habitats on public and private lands in the northeastern United States. Forest Ecology and Management 185:169–177.

Oehler, J. D., D. F. Covell, S. Capel, and B. Long. 2006. Managing grasslands, shrublands, and young forest habitats for wildlife: guide for the northeast. The Northeast Upland Habitat Technical Committee and Massachusetts Division of Fisheries & Wildlife. http://www.wildlife.state.nh.us/Wildlife/Northeast_Hab_Mgt_Guide.htm. Accessed 7 Feb 2015.

Perry, R. W., and R. E. Thill. 2013. Long-term responses of disturbance-associated birds after different timber harvests. Forest Ecology and Management 307:274–283.

Ralph, C. J., J. R. Saur, and S. Droege. 1995. Monitoring bird populations by point counts. U.S. Forest Service Pacific Southwest Research Station, Albany, California, USA.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103:3–34.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Robinson, W. D., and S. K. Robinson. 1999. Effects of selective logging on forest bird populations in fragmented landscape. Conservation Biology 13:58–66.

Rodewald, P. G., and K. G. Smith. 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. Journal of Wildlife Management 62:1411–1417.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, A. Couturier, D. W. Demarest, W. E. Easton, J. J. Giocomo, R. H. Keller, A. E. Mini, A. O. Panjabi, D. N. Pashley, T. D. Rich, J. M. Ruth, H. Stabins, J. Stanton, and T. Will. 2016. Partners in flight landbird conservation plan: 2016 revision for Canada and continental United States. Partners in Flight Science Committee, Washington, D.C., USA.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, San Diego, California, USA.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr. W. A. Link. 2014. The North American breeding bird survey, results and analysis 1966–2013. Version 1.30.2015. United States Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schlossberg, S., and D. I. King. 2007. Ecology and management of scrub-shrub birds in New England: a comprehensive review. Natural Resources Conservation Service, Resource Inventory and Assessment Division, Beltsville, Maryland, USA.

Schlossberg, S., and D. I. King. 2015. Measuring the effectiveness of conservation programs for shrubland birds. Global Ecology and Conservation 4:658–665.

Shake, C. S., C. E. Moorman, and M. R. Burchell II. 2011. Cropland edge, forest succession, and landscape affect shrubland bird nest predation. Journal of Wildlife Management 75:825–835.

Shake, C. S., C. E. Moorman, J. D. Riddle, and M. R. Burchell II. 2012. Influence of patch size and shape on occupancy by shrubland birds. Condor 114:268–278.

Smetzer, J. R., D. I. King, and S. Schlossberg. 2014. Management regime influences shrubland birds and habitat conditions in the northern Appalachians, USA. Journal of Wildlife Management 78:314–324.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The practice of silviculture: applied forest ecology. Ninth edition. John Wiley & Sons, New York, New York, USA.

Spetich, M. A., R. W. Perry, C. A. Harper, and S. L. Clark. 2011. Fire in eastern hardwood forests through 14,000 years. Pages 41–58 in C. H. Greenberg, B. S. Collins, F. R. Thompson III, editors. Sustaining young forest communities. Springer, New York, New York, USA.

Streby, H. M., S. M. Peterson, and D. E. Anderson. 2011. Invertebrate availability and vegetation characteristics explain use of nonnesting cover types by mature-forest songbirds during the postfledging period. Journal of Field Ornithology 82:406–414.

Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conservation Biology 11:928–935.

Thompson III F. R., and R. M. Degraaf. 2001. Conservation approaches for woody early successional communities in eastern United States. Wildlife Society Bulletin 29:483–494.

Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119:18–25.

Tozer, D. C., D. M. Burke, E. Nol, and K. A. Elliott. 2010. Short-term effects of group-selection harvesting on breeding birds in a northern hardwood forest. Forest Ecology and Management 259:1522–1529.

Trani, M. K., R. T. Brooks, T. L. Schmidt, V. A. Rudis, and C. M. Gabbard. 2001. Patterns and trends of early-successional forests in the eastern United States. Wildlife Society Bulletin 29:413–424.

Vickery, P. D., M. L. Hunter Jr., and S. M. Melvin. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology 8:1087–1097.

Ward, M. P., and S. Schlossberg. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519–525.

Weldon, A. J., and N. M. Haddad. 2005. The effects of patch shape on indigo buntings: evidence for an ecological trap. Ecology 86:1422–1431.

Associate Editor: Kerri Vierling.