



Effects of width, edge and habitat on the abundance and nesting success of scrub–shrub birds in powerline corridors

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ARTICLE INFO

Article history:

Received 26 March 2009

Received in revised form 8 June 2009

Accepted 17 June 2009

Available online 16 July 2009

Keywords:

Avian

Early-successional

Landscape

Right-of-way

Shrubland

ABSTRACT

Concern about declines in scrub–shrub bird populations has resulted in efforts to create and maintain habitat for these species. Vegetation within powerline corridors is managed to prevent contact of vegetation with transmission lines, and comprises approximately 2% of all of habitat for scrub–shrub birds in southern New England. Although previous studies have documented the use of powerline corridors by scrub–shrub birds, important questions remain about the factors affecting the quality of corridors as habitat for these species. We surveyed birds and monitored nests on 15 corridors in western Massachusetts during 2002 and 2003 to determine whether scrub–shrub birds occupy and successfully reproduce in powerline corridors, and to identify the principal factors affecting scrub–shrub abundance and nesting success. We found that corridors were occupied by scrub–shrub birds of high regional conservation priority, however, four of seven focal scrub–shrub bird species were scarce or absent in narrow corridors, and the abundance of these species was highest in corridors of intermediate width. Overall, nest survival was low (0.14) at these sites relative to other types of early successional habitats in the region, however, if we consider only our sites that were wider than the median width (≥ 49 m), nest survival in corridors was (0.33), similar to survival rates reported in other studies of scrub–shrub birds. We conclude that powerline corridors provide habitat for early successional birds of conservation concern, with wider corridors (≥ 50 m) contributing more to regional conservation of these species.

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1. Introduction

The majority of bird species that breed in scrub–shrub habitats in eastern North America have experienced net population declines in recent decades (Askins, 1993). Declines in scrub–shrub birds are associated with decreased availability of suitable breeding habitat (Askins, 1993; Hagan, 1993). Scrub–shrub habitats are dominated by low, woody vegetation with little or no tree canopy, such as old fields or regenerating clearcuts. Historically, these habitats were created and maintained by fire, blowdowns, American beaver (*Castor canadensis*) activity, clearing by Native Americans and, more recently, by logging and agriculture (DeGraaf and Miller, 1996; Askins, 2000; Chandler et al., 2009). The extent of natural and anthropogenic disturbance has declined as the result of modification or disruption of disturbance processes and changes in land use, and scrub–shrub habitats now comprise a small and decreasing portion of the land area in the northeastern US (DeGraaf and

Miller, 1996; Trani et al., 2001). Because of this, scrub–shrub birds and other disturbance dependent species are becoming more dependent on human activities to maintain the habitat required for their persistence. Deliberate creation of scrub–shrub habitats is a potentially important component of these efforts (King et al., 2009), however, due to the expense of large-scale habitat restoration projects, it is important for managers to take advantage of human activities that inadvertently create or maintain scrub–shrub habitat whenever possible (Thompson and DeGraaf, 2001).

Because powerline corridors are maintained in an early stage of succession, they comprise a potentially important source of habitat for scrub–shrub birds. Powerline corridors vary in many respects that could influence habitat suitability, however, and one potentially critical characteristic is corridor width. Some scrub–shrub birds appear to be “area-sensitive”, and will not occupy otherwise suitable habitat if the patch does not meet their minimum size requirements (Askins et al., 2007; Chandler et al., 2009). Anderson et al. (1977) and Confer and Pascoe (2003) reported that some scrub–shrub birds were more abundant in wider corridors, suggesting that corridor width might affect scrub–shrub birds in a manner analogous to the effect of patch area (Askins, 1994). In addition to its effects on abundance, corridor width might affect

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nest success. Nest success increases with patch size in other habitats, for example, in mature forest (Hoover et al., 1995). Similarly, brood parasitism by brown-headed cowbirds (*Molothrus ater*) is known to be higher in smaller habitat patches (Brittingham and Temple, 1983). If nest success is affected by patch area in scrub-shrub habitats, corridors that are too narrow may not provide sufficient habitat to permit successful reproduction.

Edge avoidance and edge-related nest predation are phenomena associated with area effects that can harm birds (Parker et al., 2005; Weldon and Haddad, 2005). There is evidence that scrub-shrub birds are less abundant near edges (Schlossberg and King, 2008) and predation on scrub-shrub nests is higher near edges (Weldon and Haddad, 2005). Because the proportion of habitat within proximity of an edge decreases with corridor width, edge avoidance and edge-related nest predation could reduce abundance and nesting success of scrub-shrub birds in narrow corridors. This in turn could further compromise the quality of narrow corridors as habitat for scrub-shrub birds. Finally, birds may be influenced by habitat composition of the landscape beyond the bounds of the breeding site either because of potential target or rescue effects (Lomolino, 1990; Gotelli, 1991) or because it is a source for predators or brood parasites (Kurki and Linden, 1995; Rodewald and Yahner, 2001).

We studied scrub-shrub birds in corridors differing in width and other characteristics to help understand the ecology and management of these declining species. Specifically, we were interested in how much scrub-shrub birds use corridors, and whether scrub-shrub bird abundance and nesting success is related to corridor width, edge and habitat at either the site or landscape scale.

2. Methods

We studied birds in powerline corridors over a ≈ 4000 km² study area in western Massachusetts during 2002 and 2003 (Fig. 1). The study area is 86% forested, and in the New England/Acadian Forests ecoregion (Ricketts et al., 1999). All corridor sites within the study area that consisted of shrubby successional upland (as opposed to wetland forest or agricultural field), that traversed mature forest, and were accessible by road were identified. Subsequently, these sites were numbered and 15 chosen randomly for inclusion in the study. In most cases we were able to maintain a minimum distance of 10 km between adjacent sites to maximize statistical independence. These sites averaged 49.3 m (5.69 SE) in width, and represented the full range of available powerline corridor widths in the study area from the narrowest (14.8 m) to the widest (78.4 m). Vegetation within corridors was

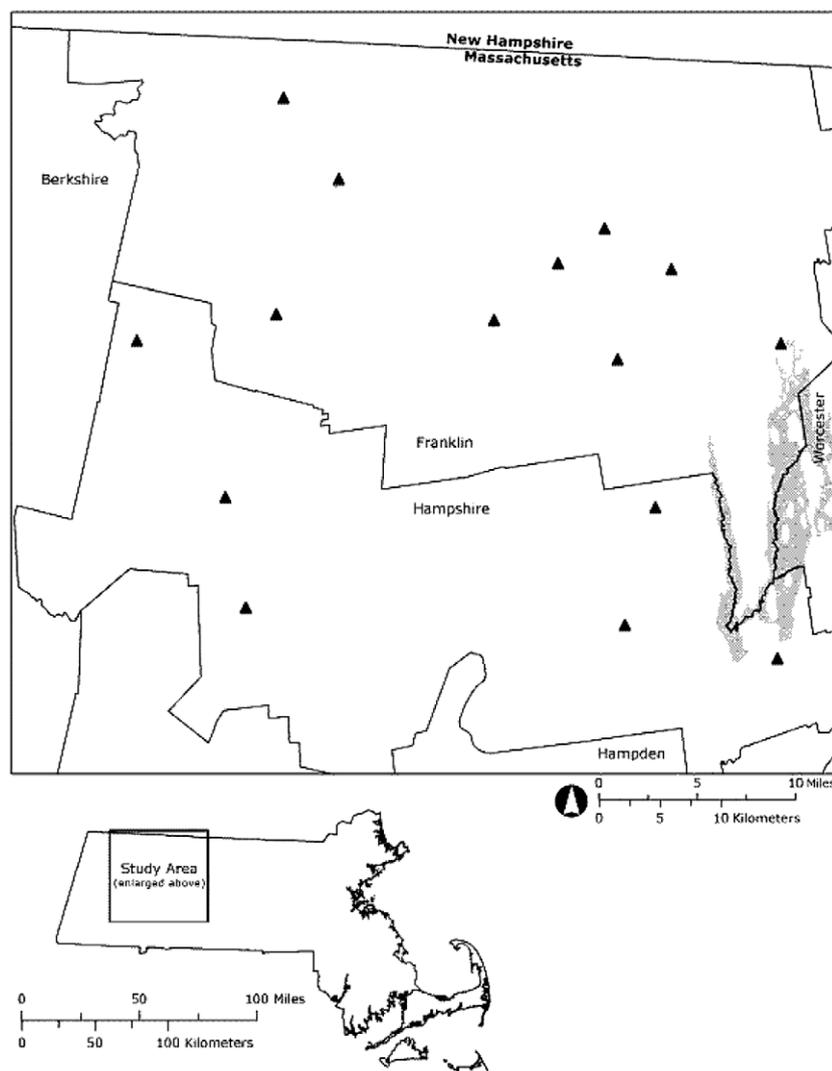


Fig. 1. Map illustrating location of 15 study areas on powerline corridors (\blacktriangle), Franklin and Hampshire counties, Massachusetts, 2002 and 2003. The dark area on the eastern side of the map is the Quabbin Reservoir.

maintained through the selective removal of tree species with cutting and herbicides to create a “stable shrubland” as described by Niering and Goodwin (1974). Ten sites were studied in 2002, and 15 in 2003 (the 2002 sites, plus 5 additional sites).

Bird abundance and species composition were quantified by counting numbers of birds seen or heard during 10-min point count surveys (Ralph et al., 1995) at five point count stations per site, for a total of 50 stations in 2002 and 75 in 2003. Point count stations were located in the center of each corridor by starting at a random point 100–200 m from the end of the plot and then establishing points 250 m apart thereafter. During each survey, all birds detected on a 100 m section of the corridor centered on the observer were recorded. Different individuals were distinguished by counter singing, and the minimum number used in the analyses (Ralph et al., 1995). Point count stations were flagged at 10-m intervals along perpendicular transects extending along the central axis of each point, as well as to the forest edge on either side, to permit estimation of distance of the bird from the observer. Each point count station was surveyed three times between 06:00 and 11:00 h during June and early July, which was the height of the breeding season.

Nest success was used as an index of productivity and was estimated by locating and monitoring nests. Nests were monitored at ≈ 3 day intervals and the contents recorded. When possible, nests were checked from a distance using binoculars and observers avoided leaving dead-end trails leading to nests to minimize observer influences on nest predation. Nests were considered to have been depredated if found empty and it was impossible that the young could have fledged, based on the stage of their development on the previous visit. Nest success was verified in most cases by searching the surrounding area for fledglings or adult birds carrying food.

Although we were primarily interested in the effects of corridor width on birds, we also measured structural and floristic characteristics of the vegetation. This enabled us to control for the potentially confounding effects of width and vegetation, and permitted us to make recommendations for vegetation management at these sites. To characterize the vegetation at each site, we took measurements at 20 randomly located points per point count station. This was done by following the lengthwise axis of each 100 m point count segment down the center of the corridor, and at 10 m intervals, locating two points, one on each side of the centerline, and at a random distance between 0 and half the width of the corridor from the center using a random number table. At each point, we measured vegetation height, as well as vegetation cover, defined as the species of plant on the air–vegetation interface directly below the sampling point. The width of the corridor was measured at each point count station. In addition, we measured distance from each nest to the nearest forest edge.

Landscape-scale data were obtained for each point count station by establishing an area within a 1, 2, and 5-km radius around each point and then merging these areas into a single “buffer” for each site using ArcGIS 9.0. We chose these radii to correspond to the scale at which landscape-scale phenomena in passerines have been reported in our region (e.g. Hagan et al., 1997; Driscoll and Donovan 2004). Next, using ArcView 3.2, we tabulated the areas of MassGIS’s statewide land use data layer within each of the buffer shapefiles, using a 5-m grid size, and calculated the percent area of open habitat, which consisted of other corridors, old fields, etc. to represent additional potential habitat, as well as urban/residential and agricultural land, both of which have been reported to affect bird reproductive success (Robinson et al., 1995a; Rodewald and Yahner, 2001). The amount of urban/residential and agricultural habitat was small (5% and 8%, respectively) and significantly correlated ($r = \geq 0.56$, $P = 0.02$), so we combined them into a single category “anthropogenic habitat”. The resulting values for anthropogenic

habitat at the 1, 2, and 5 km values also were highly correlated ($r = \geq 0.97$, $P \leq 0.001$), thus the 2-km scale was selected as an intermediate value. The percent cover of anthropogenic habitat within 2-km of corridors averaged 14.0%, and ranged from 1.24% to 32.2%.

Vegetation cover data were combined into 12 categories, which included individual plant species or genera that comprised at least 2.5% of point intercept samples (“blueberry” [*Vaccinium* spp.], “juniper” [*Juniperus communis*], “goldenrod” [*Solidago* spp.], “laurel” [*Kalmia latifolia*], “rubus” [*R. allegheniensis*, *R. idaeus*], “spiraea” [*S. latifolia* and *S. tomentosa*], and “white pine” [*Pinus strobus*]) as well as wider groupings such as “fern”, “forb”, “graminoid” [including rushes as sedges], and “woody” [woody plants not listed in the above groups], and “ground” [bare ground, rock, dead wood and moss]. We used factor analysis to reduce the dimensionality of these habitat variables. The resulting factors were rotated using Varimax rotation and factors with eigen values ≥ 1 included as independent variables in the bird-habitat regression models. Component loadings >0.30 were interpreted (Hair et al., 1987). Habitat and landscape data were log- or arcsine-transformed as appropriate to improve normality and homogeneity of variances.

We modeled the relationship between songbird abundance and corridor width and habitat characteristics while correcting abundance estimates for bias due to heterogeneity in detectability using the N -mixture model of Royle (2004), which requires that survey points are temporally replicated and assumes observed count data arise from a binomial distribution with parameters N_i (site-specific abundance) and p the probability of detecting N_i on a single survey. Site-specific abundances are assumed to be distributed according to an exponential family distribution such as the Poisson with mean λ . The abundance and detectability parameters can be modeled in relation to covariates using log and logit link functions, respectively. Because our plots differed in area, we included the natural log of plot area (100 m \times corridor width) as an offset in the abundance component of the model, which is equivalent to standardizing counts by area but maintains the Poisson nature of the data. For this model to yield absolute density estimates, plots must be closed with respect to movement and mortality. Although mortality has been shown to be negligible for adult passerines during the short breeding season in the northern hardwood forests of North America (Sillet and Holmes, 2002; Jones et al., 2004), our plots were not closed with respect to movement. Thus, λ in our case must be interpreted as the mean density of birds available for detection. This includes any bird that could have used the plot over the duration of the study season.

We modeled detectability in relation to time of day, date, and observer because these factors can bias count data (Johnson, 2008). We also modeled detectability in relation to corridor width because birds might be expected to be farther from observers in wider corridors, and thus potentially harder to detect. We modeled abundance in relationship to corridor width, vegetation height and the coefficient of variation of vegetation height, and floristic habitat features (the scores from the PCA of the point intercept data). We also considered both first and second-order (quadratic) terms for width based on observations by Chandler (2006) that abundance of scrub–shrub birds in forest openings increases to the point where the size of a single territory could be accommodated and then declines. We also evaluated the need to account for variation among sites by including site as a predictor in the abundance component of the models. We had originally hypothesized that the abundance of early-successional birds would be affected by the amount of early-successional habitat in the surrounding landscape. There was virtually no suitable habitat in the landscapes surrounding the corridors (2.9%, 3.1% and 3.4%, 1, 2 and 5 km radii, respectively), however, and we had no *a priori* predictions about the

effect of anthropogenic habitat within the landscape on the abundance of these species (beyond its possible effect on reproduction which is considered below), so no landscape-scale habitat variables were included in the bird abundance-habitat investigations.

We estimated daily nest survival and modeled it in relation to distance to edge, corridor width and landscape composition using the logistic exposure model (Schaffer, 2004), a modified form of logistic regression with a link function that incorporates the number of days the nest was observed. This model accounts for positive bias of observed nest success resulting from the fact that nests found later in the nesting period are more likely to succeed than nests found earlier, and it improves upon the Mayfield estimator (Mayfield, 1975) by accommodating continuous and categorical covariates. As recommended by Schaffer (2004), we modeled variation among species and sites as random effects. Edge and area effects on nest predation vary with landscape composition (Robinson et al., 1995a; Rodewald and Yahner, 2001; Driscoll and Donovan, 2004) so we also modeled “distance × landscape” and “width × landscape” interactions. We also analyzed the probability of a nest being parasitized by brown-headed cowbirds (*Molothrus ater*) in relation to the same set of covariates.

For models of abundance and nest survival, we constructed candidate sets of models for each species using only variables which were *a priori* ecologically justified based upon previous research. We did not know which combination of variables would best describe these processes; therefore, we used a manual forward-selection process. Specifically, we included each variable independently and progressively built models of multiple predictors for variables which lowered AIC_c with respect to the null model. We also included a global model in each candidate model set. Models were ranked by their AIC_c values (Akaike’s Information Criterion adjusted for small sample sizes; Burnham and Anderson, 2002). Rather than restrict our discussion to the single best model, all models with AIC_c values within two of the best model were considered to be supported, and models with terms with 95% confidence intervals that did not include zero were considered to be strongly supported. For the most supported model for each species, we used a parametric bootstrap procedure (Davison and Hinkley, 1997) to assess goodness-of-fit and the presence of overdispersion. Specifically, we compared the root mean square error (RMSE) of the model fit to the actual data to the expected RMSE distribution generated by simulating 100 datasets and refitting the model to each.

3. Results

We detected a total of 1639 individuals of 64 species during the study. Seven focal species that were detected on >20% of point counts were included in the analyses; common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler (*Dendroica pensylvanica*), eastern towhee (*Pipilo erythrophthalmus*), field sparrow (*Spizella pusilla*), gray catbird (*Dumetella carolinensis*), indigo bunting (*Passerina cyanea*) and prairie warbler (*Dendroica discolor*). These seven species comprised >95% of all scrub-shrub birds detected and 78% of nests located in corridors.

The most parsimonious habitat models for four species, chestnut-sided warbler, field sparrow, indigo bunting and prairie warbler, included strong support for corridor width (Table 1). In all of these cases, the relationship between abundance and width was quadratic, indicating low abundance in the narrowest corridors, and abundance peaking at intermediate widths (Fig. 2). The relationship of abundance with width varied among species. Chestnut-sided warblers were present in narrow corridors and most abundant in corridors approximately 40 m wide. Prairie warblers and field sparrows were scarce or absent in the narrowest corridors and most abundant in corridors approximately 65 m wide, and abundance only

Table 1
N-mixture models of focal early-successional shrubland bird species detected in powerline corridors, with intercepts (β_0) for abundance (λ) and detectability (p), regression coefficients and selection results (ΔAIC_c , AIC_c weights [w], and R^2) for models with $\Delta AIC_c \leq 2$. Data are from 15 sites in Franklin and Hampshire counties, Massachusetts, 2002–2003. Bold text indicates coefficients with 95% confidence intervals that do not include zero. “Width” and “height” are in meters.

Species ^a	Abundance covariates					Detection covariates _{sc}											
	β_0	Fac1	Fac4	Fac5	Height	Width	Width ²	Year	Year * Fac1	Year * Fac5	$\beta_0 p$	Time	Date	Time * Date	ΔAIC_c	w	R^2
GRCA	0.99	-0.25						-0.69	-0.47		-2.90	0.13	-0.02	0.01	0	0.66	0.22
CSWA	-15.5			-0.16		8.82	-1.18				-0.37		0.04	0	0	0.18	0.11
	-16.9				0.28	8.82	-1.17				-0.39		0.04	0.3	0.3	0.15	0.11
	-18.3				0.36	10.3	-1.38				-0.39		0.04	0.4	0.4	0.14	0.09
PRWA	-0.81					9.30	-1.24				-0.36		0.04	0.8	0.8	0.12	0.07
	-17.4			-0.13	0.20	15.8	-1.88				-0.37		0.04	1	1	0.10	0.12
	-32.2					15.7	-1.86				0.91	-0.15		0	0	0.53	0.13
COYE	-32.3										-0.28			1.4	1.4	0.26	0.10
	1.03			0.20							-0.36			0	0	0.17	0.03
1.05										-0.35				1.2	1.2	0.09	0.00
<i>Birds in powerline corridors</i>																	
EATO	0.89			0.11				-0.42	0.30		-8.22	0.94	0.41	-0.05	0	0.63	0.20
FISP	0.68										-8.61	0.99	0.44	-0.05	1.2	0.35	0.14
INBU	-141.7			0.33		67.4	-8.00				-0.59			0	0	0.57	0.18
	-156.8					75.1	-8.96				-0.58			1	1	0.35	0.15
-223.3					113.8	-14.5				13.8	-1.92	-0.69	0.09	0	0	0.43	0.37

^a GRCA = gray catbird; CSWA = chestnut-sided warbler; PRWA = prairie warbler; COYE = common yellowthroat; EATO = eastern towhee; FISP = field sparrow; INBU = indigo bunting.

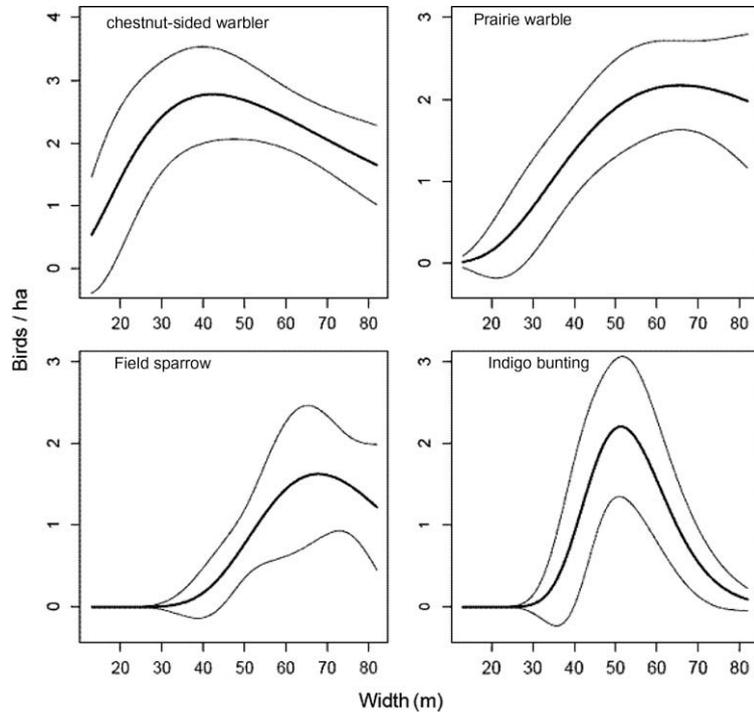


Fig. 2. Density of four species relative to powerline corridor width on 15 powerline corridors, Franklin and Hampshire counties, Massachusetts, 2002 and 2003. Fitted lines and 95% confidence intervals are from most supported model parameters holding all other covariates constant at their mean values. Confidence intervals calculated using the delta method.

Table 2
Factors analysis loadings for habitat variables measured on point intercept surveys within 15 powerline corridors, Franklin and Hampshire counties, Massachusetts, 2002–2003, including eigenvalues and cumulative proportion of variance explained.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
ln(blueberry + 1)	0.10	0.96	-0.11	-0.21	0.04
ln(fern + 1)	-0.15	-0.11	-0.19	-0.12	0.51
ln(forb + 1)	-0.11	-0.26	0.22	-0.04	0.06
ln(goldenrod + 1)	-0.06	-0.17	-0.07	0.49	-0.05
ln(grass + 1)	0.04	0.11	0.02	0.52	0.01
ln(ground + 1)	0.00	-0.04	0.99	-0.10	-0.06
ln(juniper + 1)	0.95	0.07	-0.04	-0.29	-0.05
ln(laurel + 1)	-0.17	-0.02	0.20	-0.34	0.35
ln(rubus + 1)	-0.06	-0.33	-0.13	0.27	0.19
ln(spiraea + 1)	0.44	0.10	-0.03	0.27	-0.05
ln(whitepine + 1)	0.01	0.35	0.01	0.08	-0.02
ln(woody + 1)	-0.44	-0.06	-0.30	-0.38	-0.75
Eigenvalue	1.37	1.30	1.23	1.08	0.99
Cumulative Proportion	0.11	0.22	0.32	0.41	0.50

declined slightly in the widest corridors. Indigo buntings were absent from corridors <25 m in width, most abundant in corridors ≈50 m wide, and scarce or absent in the widest corridors.

Factor analysis yielded five components that explained 50% of the variations in vegetation cover (Table 2). Models indicating that common yellowthroat and field sparrow abundance increased in relation to factor 4, which represented increasing grass and goldenrod cover and decreasing woody plants and laurel, received strong support. Chestnut-sided warblers decreased in abundance with factor 5, which represented decreasing woody cover and increased ferns and laurel. Eastern towhees were also associated with this factor; however, the direction of this relationship differed between years. Gray catbirds abundance was associated with factor 1, which represented increasing cover of juniper and *Spiraea* sp and decreasing woody cover, but the direction of this relationship differed between years. Habitat relationships of these last three species were not strongly supported (95% confidence interval

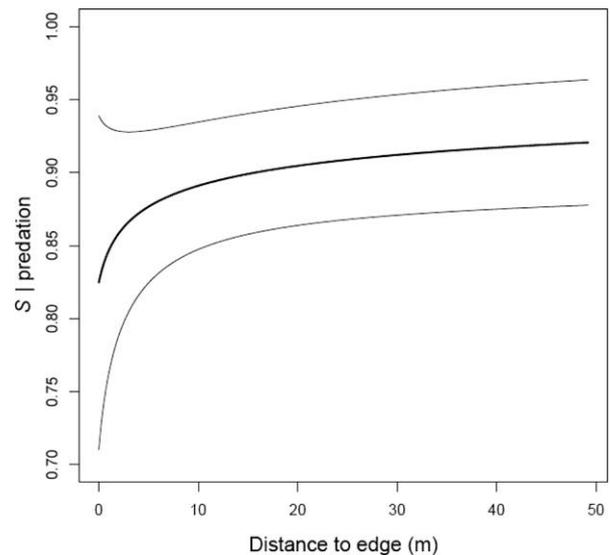


Fig. 3. Daily nest survival rate ($S | \text{predation}$) as a function of distance to edge in 15 powerline corridors, Franklin and Hampshire counties, Massachusetts, 2002 and 2003. Fitted lines and 95% confidence intervals based upon most supported model.

of the coefficient included zero). The abundance of chestnut-sided warblers was the only species associated with vegetation height, and a model indicating abundance of chestnut-sided warblers increased with vegetation height was strongly supported. No species was associated with factors 2 or 3, or CV of vegetation height. Site was not supported as a predictor of abundance for any species indicating that there was little unaccounted for site-level variation. We found no evidence of overdispersion (goodness-of-fit P -value >0.05), justifying our choice of the Poisson distribution as opposed to a more complex distribution such as the negative binomial.

Table 3

Logistic exposure models of the probability of a nest not being depredated or parasitized as a function of powerline corridor characteristics, with intercept (β_0), regression coefficients, and model selection results (ΔAIC_c , AIC_c weights [w_i] and R^2) for models with $\Delta AIC_c \leq 2$. Data are from 15 sites in Franklin and Hampshire counties, Massachusetts, 2002–2003. Estimates for the two random effects, species and site, are standard deviations. Bold text indicates coefficients with 95% confidence intervals that do not include zero. "Distance" and "width" are in meters.

Response	β_0	distance	distance ²	width	width ²	landscape	year	distance * landscape	species	site	ΔAIC_c	w_i	R^2
Predation	1.55	0.23					0.30		0.38	0.13	0	0.20	0.13
	1.60	0.26							0.38	0.13	0.4	0.16	0.12
	14.76	0.24		-7.47	1.04				0.37	0.07	0.6	0.15	0.14
	2.12						0.34		0.36	0.12	1	0.12	0.12
	1.89	-0.14	0.10						0.39	0.12	1.4	0.10	0.13
	14.52			-7.14	1.01				0.36	0.05	1.6	0.09	0.13
Parasitism	20.66	-3.94				-131.5		36.29	2.02		0	0.62	0.35

Detection probability covariates were included in supported models for five species (Table 1). Chestnut-sided warbler detectability increased with date. Prairie warbler detectability declined with time of day. For the other three species we found an interactive effect of time and date on detectability which varied among species. The probability of detecting eastern towhees increased with time of day and date in the early season but declined during late-season surveys. Gray catbird detectability increased with time of day and decreased with date, although it was also high towards the end of the season at later times of day. Indigo bunting detectability decreased with time of day and date during the early portion of the season, but increased slightly at later times of day towards the end of the season. We found no evidence of an effect of observer on the probability of detecting any species.

We monitored 332 nests of 28 species during the study. Nest success (the percentage of nests fledging ≥ 1 young) was 39.5% (37.6% in 2002 and 41.4% in 2003). The probability of a nest surviving to fledging was 0.139 (0.107 in 2002 and 0.182 in 2003), and 94% of failures were due to predation. Brown-headed cowbirds parasitized 4.51% of nests (5.38% in 2002 and 3.43% in 2003). The probability of a nest being parasitized by brown-headed cowbirds was 0.101 (0.127 in 2002 and 0.072 in 2003). Supported models from the logistic exposure analysis indicated that nest survival was positively related to distance from edges (Fig. 3), was greater in 2003, and was highest in narrow and wide corridors and lowest in corridors of intermediate width, although only this last relationship had strong support (Table 3). Nest predation was unrelated to landscape composition. The only supported model for cowbird parasitism indicated that the probability of nest parasitism was related to the interaction of distance to edge and the amount of anthropogenic habitat within the landscape. The parameter estimates in Table 3 indicate that in landscapes with high percentage of anthropogenic cover, parasitism was negatively related to distance from edge. In landscapes with low urban and residential cover, the reverse pattern was evident.

4. Discussion

Our observation that scrub-shrub birds occupied these powerline corridors underscores the potential of these habitats for the conservation of these species. Six of the seven focal species, as well as other early successional bird species that were present in numbers too low for analyses (blue-winged warbler (*Vermivora pinus*), alder flycatcher (*Empidonax alnorum*), brown thrasher (*Toxostoma rufum*) and mourning warbler (*Oporornis formosus*), have declined significantly in southern New England over the past four decades according to the North American Breeding Bird Survey (Sauer et al., 2004). Furthermore, all of these species have higher than average conservation priority in the Partner's of Flight Species Assessment Database (Carter et al., 2000), and the mourning warbler is listed in Massachusetts as a species of special concern. Other studies show these species are only present within corridors

(Anderson et al., 1977; Kroodsmas, 1982; Morneau et al., 1999), and thus, these species would not have been present at these sites if it were not for the presence of the corridors (Anderson, 1979).

Our observation that several species of scrub-shrub birds were scarce or absent from narrow corridors is consistent with the findings of Anderson et al. (1977) and Confer and Pascoe (2003). There are a number of potential explanations for this pattern, including area-sensitivity, edge avoidance, territory elongation or habitat changes. Lower abundance of these species is reported from small silvicultural openings (Annand and Thompson, 1997; Robinson and Robinson, 1999; Costello et al., 2000), as well as beaver meadows (Chandler et al., 2009) and thus, the positive relationship we observed could be a manifestation of area-sensitivity in the form of "width sensitivity" (Askins, 1994; Confer and Pascoe, 2003). This begs the question of why these species are absent from small openings in the first place, however. The territory sizes of some species exceed the size of the habitat patches in some studies, and in these instances, it is not surprising that these species are scarce or absent from these small openings (Askins et al., 2007). In the case of linear habitats like corridors, however, bird territories are contiguous with an essentially unlimited amount of habitat. Thus the scarcity of scrub-shrub birds in narrow corridors is not directly the result of there being insufficient habitat area in which to fit a territory.

An alternative explanation for lower abundance of scrub-shrub birds in narrow corridors is edge avoidance. Schlossberg and King (2008) reported that 8 of 17 scrub-shrub bird species in their meta-analysis were significantly less abundant near edges, and suggested that edge avoidance could exclude scrub-shrub birds from small patches that are effectively all edge. Our observation that the three species that were strongly associated with corridor width (prairie warbler, field sparrow and indigo bunting) were also species reported by Schlossberg and King (2008) to be significantly less abundant near edges is consistent with the notion that the positive relationship between abundance of these species and corridor width is related to edge avoidance. Edge avoidance could result from "passive displacement" (King et al., 1997), or because nest predation depresses bird populations or birds recognize the risk and avoid edges (Parker et al., 2005). We did find that nest predation was elevated near edges, consistent with this latter suggestion.

The potential costs associated with the compression of territories into an elongated shape, as reported in ovenbirds (*Seiurus aurocapillus*) in narrow strips of forest retained near streams to protect water quality during logging operations (Lambert and Hannon, 2000), could be another potential explanation for the positive association between scrub-shrub bird abundance and corridor width. These costs might include increased time and energy expenditure for territory defense (Verner, 1977; Eason, 1992). Patch shape is reported to be a better predictor than patch area for abundance of mature forest (Temple, 1986) and grassland (Davis, 2004) birds, although patch shape does not appear to affect the abundance of most scrub-shrub birds (King and DeGraaf, 2004; Weldon

and Haddad, 2005; Chandler, 2006; Chandler et al., 2009). Nest success of scrub–shrub birds is reported to be lower in more irregularly shaped patches (Weldon and Haddad, 2005; Chandler, 2006), however, and could thus potentially impose an additional cost for occupation of elongated territories in powerline corridors.

Area-related differences in habitat conditions, which have been proposed as a potential mechanism for area-sensitivity in other habitats (Haila, 1986), could also potentially explain the association between scrub–shrub bird abundance and corridor width. This pattern could arise if wider corridors were either managed differently, or if the increased solar radiation created different habitat conditions in wider corridors. The field sparrow was the only species that was strongly related to corridor width and also strongly related to habitat within the corridor. Field sparrow abundance increased with factor 4, which described a gradient of decreasing woody cover and increasing grass cover, however, *post-hoc* analyses indicated that factor 4 was negatively correlated with corridor width ($r_{(14)} = -0.43$, $P = 05$), indicating that habitat conditions for field sparrows were in fact less suitable in wider corridors. Thus we conclude it is unlikely that changes in habitat characteristics caused the association we observed between scrub–shrub bird abundance and corridor width.

Our results were consistent with reports by Anderson et al. (1977) that field sparrows increased with corridor width, and by Confer and Pascoe (2003) that field sparrows and prairie warblers increased with corridor width. In contrast to our findings, Anderson et al. (1977) reported that indigo buntings and prairie warblers were most abundant in the narrowest corridor at their sites in Tennessee. These conflicting results probably reflect different vegetation management practices. The sites studied by Anderson et al. (1977) were intensively mowed and thus had little woody vegetation to support shrubland nesting birds, which were thus probably concentrated at the corridor edges (Schlossberg and King 2008), which would result in the pattern they observed of decreased abundance with width. The observation by Kroodsma (1984) that prairie warbler abundance decreased with width in four corridors ranging in width from 55 to 116 m is consistent with our findings that prairie warbler abundance decreased in corridors >60 m in width.

Although the absence or scarcity of birds in the narrowest corridors is partially responsible for the quadratic relationship of bird abundance with width, it is not clear why bird abundance declined in corridors ≥ 60 m wide. One possibility is decreased detectability in wider corridors due to increased distance of birds from the observers; however, models with width in the detectability term were not supported, probably because the maximum distance of birds from observers was only 34 m in the widest corridors we studied. Chandler (2006) observed that bird abundance increased in steps with patch area, which he suggested represented the addition of bird territories once patch size increased beyond the size of a single territory but not the size sufficient to accommodate a second territory. Kroodsma (1982) offered this explanation for a similar pattern in bird abundance as a function of distance to corridor edges within adjacent mature forest. It seems possible that the same process is occurring in corridors, because territories of the species showing sensitivity to affecting width in this study have territory radii as small as 30 m, but could potentially defend a territory as wide as the widest in our study, effectively resulting in a drop in abundance beyond this minimum value for territory radius.

The proportion of nests fledging in our study was low relative to values reported from other powerline corridor studies (Chasko and Gates, 1982; Bramble et al., 1992; Confer and Pascoe, 2003), in which 55–68% of nests fledged young. Most of these studies took place in wider corridors, however (median width ≈ 55 m), and thus a lower proportion of nests at these sites were near edges compared with our sites, which were as narrow as 15 m. If we consider

only our sites that were wider than the median width (≥ 49 m), the percentage of nests fledging in our study is only slightly lower (50%) than previous studies in powerline corridors.

Nest success calculated as in these other studies as the proportion of nests fledging young can be a biased estimator if nests are found at different stages of development (Mayfield, 1975). The logistic exposure analyses corrects for this bias, however, and indicated that the average probability of a nest surviving to fledging was far lower than 0.38, the average Mayfield survival rate for 14 scrub–shrub bird species summarized by Schlossberg and King (2007). Most of the data summarized by Schlossberg and King (2007) came from regenerating clearcuts and old fields, however, and although distance from edges was not specified in this study, it is likely that it was greater than in the narrow corridor habitats we studied. If we analyze data only from our wider corridors (≥ 49 m) as before, survival rates are more similar between our sites (0.33) and those summarized by Schlossberg and King (2007). Nest survival for chestnut-sided warblers in two corridors studied by King and Byers (2002) was higher on average (0.74) than chestnut-sided warbler nest success in the present study; however, it varied annually over the five years of their study from 1.00 to 0.57, which overlaps with the 95% confidence intervals for chestnut-sided warbler nest success in 2003 of the present study.

Brood parasitism by cowbirds can decrease avian productivity because cowbirds remove host eggs reducing host clutch size and in some cases cowbird chicks outcompete host nestlings (Robinson et al., 1995b). In extreme cases, cowbird parasitism can threaten the viability of native bird populations (Robinson et al., 1995b), however, cowbird parasitism is generally less pronounced in more forested landscapes (Robinson et al., 1995b), which is consistent with the modest rates of cowbird parasitism in our study. The levels of cowbird parasitism we observed were similar to those reported in other studies of birds in corridors in the northeastern US (5.3%; Confer and Pascoe 2003) and Virginia (4.7%; Meehan and Haas, 1997) and are unlikely to present a significant threat to bird populations at our sites (Mayfield, 1977). Our observation that nest parasitism by brown-headed cowbirds was highest near edges in landscapes with urban and agricultural habitat was consistent with our expectations, because both agricultural and urban habitats provide food resources for cowbirds in the form of waste grain, animal feed and bird feeders (Robinson et al., 1995b). Brittingham and Temple (1983) also reported that cowbird parasitism was highest near edges. We are unable to explain why this pattern was reversed in landscapes with less urban and agricultural habitat.

Our finding that nest survival at our sites was greater farther from edges is generally consistent with the few studies there are on the effect of edges on nesting success in scrub–shrub habitats, and like these other studies, the evidence for this relationship is weak. King et al. (2001) reported lower nest survival near edges in regenerating clearcuts in New Hampshire, although this finding was only marginally significant ($0.05 < P < 0.10$). Similarly, Woodward et al. (2001) reported that nest predation was low near edges for some species in Missouri shrublands, but not for others. Finally, Weldon and Haddad (2005) reported that nest survival of indigo buntings was lower in edge-dominated habitats, although the effect of edges on nest success *per se* was weak. Models indicating that nest survival was related to width received more support than models of nest survival as a function of distance to edge. Strangely, these models indicate that nest success declines as corridor width increases from 15 to 30 m, and increases monotonically with width thereafter. The increase in nest survival for corridors >30 m is an expected result, given that nests farther from edges are more likely to fledge, and on average nests in wider corridors are farther from edges, however, we can only speculate on why nest survival is high in the narrowest corridors as well. Perhaps the narrowest corridors

are not perceived as a great enough habitat discontinuity to concentrate predator activity.

The absence of landscape composition from supported models of nest predation is consistent with the assertion that fragmentation effects, such as elevated nest predation associated with reduction of natural habitats in the landscape, only become manifest in landscapes in which forest cover has been reduced beyond a certain threshold (Andren 1994). The landscape conditions of our study sites ($\geq 80\%$ forested) correspond to levels typically considered as extensively forested (Robinson et al., 1995a; Rodewald and Yahner, 2001). To our knowledge, Chandler (2006) is the only other study of landscape-level nest survival in scrub–shrub birds, and he also found that nest survival of scrub–shrub birds was not affected by landscape-level habitat characteristics in a heavily forested landscape.

Our study shows that scrub–shrub birds use powerline corridors, and that wider corridors are good quality habitat, however, the regional importance of this habitat to scrub–shrub birds is relatively minor due to its limited extent. For example, powerline corridors account for $\approx 0.1\%$ of the area of southern New England (Zuckerberg et al., 2004), or ≈ 3556 ha. In comparison, there is $\approx 173,322$ ha of scrub–shrub habitat in this region, largely created by silviculture (Schlossberg and King, 2007). Thus, powerline corridors potentially comprise only 2.1% of scrub–shrub habitat in southern New England. The percentage of some individual northeastern states is higher, for example in Massachusetts corridors comprise 0.61% of the land area (B. Compton, Pers. Com.), which is 11% of the 115,081 ha of scrub–shrub habitat in the state. These are probably overestimates, however, because not all corridors contain suitable scrub–shrub habitat. Some corridors are mowed or sprayed too frequently for suitable habitat conditions to develop, or cross habitats unsuitable for scrub–shrub birds, such as water, agricultural or urban habitats. Other sites are too narrow to support the full suite of scrub–shrub birds and don't support viable populations due to low nesting success. There are not estimates for the area of corridors in different width classes, however, if our random sample of 15 corridors is any indication, it appears that approximately 13% of the powerline corridor habitat in our study area occurred in corridors too narrow for some scrub–shrub species.

Our finding that scrub–shrub birds of high conservation priority occupy corridors applies only to sites that are managed similarly to the sites we studied. Some corridors are treated with broadcast herbicide applications or frequent mowing that prevents sufficient development of habitat conditions required by scrub–shrub birds (Bramble et al., 1992; Yahner et al., 2002). In contrast, selective treatments using mechanical means or herbicides result in a well-developed shrub layer interspersed with grasses and herbaceous vegetation that accommodates the habitat needs of a diversity of scrub–shrub birds (Chasko and Gates, 1982; Bramble et al., 1992; Askins, 1994; Yahner et al., 2002). We recommend that power utilities or other entities engaged in vegetation control activities in powerline corridors adopt habitat management protocols such as those practiced at our sites so the potential of these corridors to provide habitat for scrub–shrub birds will be best realized.

There remain questions unaddressed that would further clarify the value of these habitats. For example, it is important to understand the effect of corridors on the avifauna in adjacent mature forest. Wider corridors are better for early successional birds (this study), but what is the effect of wider corridors on animals in adjacent forest, relative to narrower corridors? It appears that larger silvicultural openings create less fragmentation than many smaller openings of the same total area (King et al., 1998), but it is not clear whether this relationship holds with powerline corridors. Also, corridors may have a positive effect on mature forest avifauna if

they provide habitat for fledgling birds similar to the habitat provided by regenerating clearcuts (Vitz and Rodewald, 2006). All of these topics represent potential avenues for new research that would shed additional light on the conservation value of powerline corridors.

Acknowledgements

We wish to thank the Northeastern Utilities Foundation and the US Fish and Wildlife Service Division of Bird Habitat Conservation for providing funding for this project, and for the following individuals for their help with the field work: H. Bowers M. Conca, M. Kolan, N. Marcy, B. Mazzei, E. Miller, B. Packard, I. Paulman, A. Stein, J. Strules, and M. Williams. J. Confer and S.K. Davis provided valuable comments on an earlier draft of the manuscript.

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