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Effects of management regime on the abundance and nest survival of shrubland birds in wildlife openings in northern New England, USA

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ABSTRACT

Many shrubland bird species are declining in eastern North America and as a result forest managers have used a variety of techniques to provide breeding habitat for these species. The maintenance of permanent "wildlife openings" using prescribed burns or mechanical treatments is a widely used approach for providing habitat for these species, but there have been no studies of the effects of treatment regime on bird abundance and nest survival in managed wildlife openings. We studied shrubland birds in wildlife openings on the White Mountain National Forest (WMNF) in New Hampshire and Maine, USA, during 2003 and 2004. We analyzed bird abundance and nest survival in relation to treatment type (burned versus mowed), treatment frequency, time since treatment, and patch area. We found that wildlife openings provided habitat for shrubland birds that are not present in mature forest. There was relatively modest support for models of focal bird species abundance as a function of treatment regime variables, despite pronounced effects of treatment on habitat conditions. This probably was attributable to the combined effects of complex site histories and bird site fidelity. Overall nest success (52%) was comparable to other types of early-successional habitats in the region, but there were few supported relationships between nest survival and treatment variables. We conclude that wildlife openings provide quality habitat for shrubland birds of high conservation interest as long as managers ensure treatment intervals are long enough to permit the development of woody vegetation characteristic of the later stages of this sere. Also, wildlife openings should be large enough to accommodate the territory sizes of all target species, which was ≥1.2 ha in this study.

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1. Introduction

Many shrubland bird species are declining in eastern North America and as a result have become the focus of substantial conservation concern (Askins, 1993; Brawn et al., 2001; Hunter et al., 2001). These declines are associated with large scale land use changes over the last century as mature forests have replaced old fields (DeGraaf and Miller, 1996; Litvaitis, 1993), and the use of even-aged silviculture has decreased (Trani et al., 2001; Oehler, 2003). In addition, the region's natural disturbance regime has been disrupted by fire suppression, flood control, reduction of beaver (*Castor canadensis*) populations, and establishment of younger forests which are more resistant to wind events (Noss et al., 1995; Boose et al., 2001; Lorimer, 2001; DeGraaf and Yamasaki, 2003; Chandler et al., 2009). Thus, active management will be needed to conserve these species (Hunter et al., 2001; DeGraaf and Yamasaki, 2003).

Silviculture is widely advocated for the creation of early-successional habitat (Thompson and DeGraaf, 2001), but uneven-aged management techniques such as group selection create patches that are too small for some species (Costello et al., 2000). Even-aged management, which is the most effective silvicultural method for creating early-successional habitats (DeGraaf and Yamasaki, 2003), is unpopular with the public (Trani et al., 2001; Oehler, 2003) and impractical on many private lands because most parcels are small (<4 ha) and management activities are often not coordinated among landowners (Brooks, 2003). Wildlife openings, which are maintained in early stages of succession with periodic prescribed fire or mechanical treatments (i.e., mowing, hand clearing, or chipping), are an alternative to silvicultural methods and were originally developed for game species (Tubbs and Verme, 1972; Overcash et al., 1989). These openings vary in a number of potentially important characteristics, including treatment regime and patch size, that might affect their suitability as wildlife habitat; however, despite the fact that wildlife openings have been maintained by state and federal agencies for decades, as well as the widespread and growing interest in the conservation of shrubland birds, few data

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exist on their habitat quality for birds (Tucker and Olson, 1994; King et al., 2009).

The lack of information on the quality of wildlife openings for shrubland birds and the effects of treatment regime and patch area on these species hinder efforts to design and implement effective management practices for these declining species. To address this information need, we studied shrubland birds in wildlife openings to determine whether wildlife openings provided habitat for target species, and whether treatment regime variables were related to shrubland bird abundance and nest survival. Our working hypothesis was that bird abundance and nest survival would be indirectly affected by management practices because these practices directly affect vegetation structure and composition.

2. Methods

2.1. Study area and site selection

We conducted this study during 2003 and 2004 on the White Mountain National Forest (WMNF) located in north-central New Hampshire and southwestern Maine (44°03′N, 71°15′W). The WMNF was 97% forested and 3200 km^2 in extent (U.S. Forest Service, 2005). Mean annual temperature on the WMNF was approximately 5 °C. Mean annual precipitation was 1.1 m with approximately one third of that falling as snow. The primary vegetation covertypes in the study area were beech-birch-maple subtype of northern hardwood (41.7%), spruce-fir softwood (25.6%), and mixed conifer and hardwood (19.3%) stands (U.S. Forest Service, 2005). Less than 3% of the forest within the study area was in early stages of succession younger than 15 years old (Chandler, 2006). Most regenerating forest on the WMNF was created by even-age and uneven-age silvicultural systems, but approximately 218 wildlife openings totaling 250 ha in extent were being maintained.

Managers of the WMNF first created wildlife openings in the late 1970s, primarily for game species. Wildlife openings were created from old log landings, reclaimed apple orchards and agricultural fields, or were originally clearcuts. Prescribed burns and mechanical treatments such as mowing, hand-clearing, and chipping were used to maintain the habitat in an early stage of succession. These treatments were carried out primarily during early spring (1 March–15 May) to avoid interference with nesting birds. Treatment objectives included removing most seedlings and saplings while encouraging shrubs and herbaceous vegetation. Some scattered trees were retained. Flame lengths were kept below 2.5 m and burns were often directed into the wind (backing burn) to increase fire intensity.

We selected 57 wildlife openings as study sites, which represented all the wildlife openings we could locate within 30 km of our research headquarters at the Bartlett Experimental Forest in Bartlett New Hampshire. The median patch size was 1.0 ha and ranged between 0.1 and 15.7 ha. Of these sites, 24 were burned and 33 were treated by mechanical means. The average area of the wildlife openings in our sample did not differ from the average area of all wildlife openings on the forest ($t = 0.12$, df = 56, $P = 0.90$) and neither did the proportion of sites last treated by mechanical means vs. prescribed burns (binomial test $P = 0.12$). Thus, our sample of sites appeared to be representative of all wildlife openings in the WMNF. These sites varied greatly in their treatment histories, ranging from 1 to 18 years since the last treatment (median = 4) and having received between 1 and 11 treatments (median = 4). Treatment frequency (i.e., the number of treatments following site establishment/site age) ranged from 0.0 to 0.69 (median = 0.25). Seven of these sites were treated between the two field seasons in 2003 and 2004.

2.2. Field methods

We surveyed birds at a total of 62 plots within the 57 sites using 5-min 50-m radius point counts (Ralph et al., 1995) during the height of the breeding season, 20 May–10 July. We located survey points in the center of each site with the exception of four sites large enough for more than 1 point location, in which cases we spaced points by 250 m. Two experienced observers conducted surveys between 05.30 and 10.30 h on calm days with no precipitation during which observers recorded the number of individuals of each species detected and the method of detection (i.e., visual, song, or chip). Each observer surveyed each point at least once, and all points were surveyed three times. We only included singing or chipping males in analyses because our aim was to estimate the number of territorial males. For sexually monomorphic species, we only included singing males. Females, juveniles, and visually detected birds likely have different detection probabilities and their inclusion could therefore have obscured underlying relationships.

In a subset of 38 sites, selected to represent the treatment histories and spatial distribution of the full sample, we located nests by following adult birds and by systematic searches. We monitored nests every third or fourth day, and recorded nest contents, approximate age of nestlings, and parental behavior. We made an effort to minimize visit length and impacts upon vegetation by checking nests from a distance through binoculars when possible. We searched for fledgling birds to verify nest success because predators frequently leave no sign of depredation (King and DeGraaf, 2006).

Beginning in mid-July we quantified vegetation structure and composition within each bird survey plot using a point intercept method (King et al., 2009). We measured the substrate and height of vegetation at 20 points within each plot located by selecting random compass bearings and choosing distances from the plot center with a random number sheet. We identified woody plants to species and categorized all other substrates as herbaceous plant, fern, grass, bare ground, or dead woody plant.

2.3. Statistical analyses

For bird species occurring in at least 10% of survey plots in both years, we used the N-mixture model of Royle (2004) to relate abundance to management variables while accounting for variation in detection probability. Accounting for birds present but not detected is important because apparent abundance and detection probability can be confounded. The N-mixture model addresses this problem by assuming that the actual number of birds per plot (N_i) is distributed according to a member of the exponential family, such as the Poisson distribution with mean λ, and that N_i may be detected imperfectly on each survey occasion. The observed count data are modeled as binomial outcomes where p is defined as the probability of detecting N_i on a single survey occasion. The two parameters, λ and p, can be modeled in relation to covariates using the natural log and logit links respectively, but are only identifiable when surveys are temporally replicated. Because our plots were not closed with respect to movement and mortality within each season, λ is defined as the mean number of territorial males that used each plot over the course of the season.

The management regime variables we modeled were treatment method, treatment frequency, and time since last treatment, which correspond to the standard descriptors of disturbance regimes proposed by Pickett and White (1985). We also considered total number of treatments as a descriptor of management regime, but it was closely correlated with treatment frequency ($r = 0.79$) and thus we dropped it from the analyses. We included a quadratic term for time since treatment because these species are known to peak in abundance at intermediate points along successional gradients (Schlossberg and King, 2009). We also modeled interactions between treatment type and time since treatment as well as between each management regime variable and year. We included year in each model to avoid temporal pseudoreplication, and because we were interested in checking the consistency of results among years. Because some study sites were smaller than the size of a 50-m radius plot (0.785 ha), we included the natural logarithm of plot area as an offset in the model, which is equivalent to standardizing counts by plot area but maintains the Poisson nature of the data. We considered the following detection probability covariates: observer, date, time of day, and vegetation height. We included the quadratic effect of date because the song frequency of these species is related to nesting status which changes non-linearly over the breeding season (Byers, 1995). We log-transformed time since last treatment after adding one to improve the normality of its distribution. We estimated parameters via maximum likelihood using the R software package with the "optim" function (R Development Core Team, 2009).

We compared and selected models using AIC$_c$, an information criterion adjusted for small sample size (Burnham and Anderson, 2002). The large number of biologically plausible models representing our working hypothesis and the lack of studies investigating the effects of detection probability covariates led us to construct candidate models in a manual forward-selection process based upon AIC$_c$ values. Specifically, we modeled each covariate independently of all others and then included those variables that lowered AIC$_c$ relative to the null model in more complex models. We also evaluated global models including all parameters in our candidate model sets. We considered variables that were included in models with $\Delta\mathrm{AIC}_c \leq 2$ to be supported, and those with 95% confidence intervals not including zero to be strongly supported. We used Nagelkerke's R^2 index to approximate the amount of variation explained by each model (Nagelkerke, 1991).

We used the logistic exposure model of Schaffer (2004) to analyze daily nest survival in relationship to management regime variables and patch area. We followed the recommendations of Manolis et al. (2000) for determining nest fate and calculating exposure days. Specifically, we considered nests successful if fledglings were seen or heard with parents or if the nest was empty and undisturbed within three days of the expected fledging date. We classified nests as depredated if the nest was empty before three days of the expected fledging date or appeared damaged. We calculated exposure days for nests with known fate using the midpoint between the final two nest checks as the endpoint, whereas we used the final day the nest was observed active as the endpoint for nests with unknown fates. Models were compared and selected using the same methodology we used for models of abundance. We estimated nest success (i.e., the probability of a nest fledging at least one young) by raising daily nest survival rates to the average nesting period length (Mayfield, 1961) determined by either our own data when available or from the literature.

We assessed the effects of treatment method, treatment frequency, and time since treatment upon vegetation composition and structure using general and generalized linear models. We modeled vegetation height using general linear models with the "lm" function in R. For percent cover variables with distributions bounded by zero and one, we modeled effects of treatment variables using generalized linear models with a logit link using the "glm" function in R. We used the same model selection and averaging procedures as described for bird abundance models. We did not directly analyze bird abundance in relation to habitat variables because our objective was to evaluate the effects of factors that can be directly manipulated by managers.

3. Results

3.1. Bird abundance and detection probabilities

We detected 872 individuals of 50 species over the two years of the study. The following shrubland species comprised ≥10% of our sample and were thus included in the analyses as "focal species": chestnut-sided warbler, common yellowthroat, indigo bunting, white-throated sparrow, song sparrow, and alder flycatcher (scientific names in Appendix A). We found evidence of relationships between management regime variables and the abundances of 5 of the 6 focal species; however, R^2 values were low and model selection uncertainty was high (Table 1). Supported models indicated that chestnut-sided warblers were more abundant in mechanically treated openings than openings treated with prescribed fire, common yellowthroat abundance peaked at intermediate times since treatment, white-throated sparrows increased in abundance with treatment frequency, and song-sparrow and alder flycatcher abundance increased with patch area (Fig. 1). The shape of the relationship between common yellowthroat abundance and time since treatment differed between years.

Table 1

Parameter estimates for *N*-mixture models of bird abundance with $\Delta\mathrm{AIC}_c \leq 2$. Abundance covariates include: year (Y), last treatment type (T), treatment frequency (TF), time since last treatment (TS), and patch area (A). Detection probability (p) covariates include: date, vegetation height, and observer. Quadratic terms indicated by squared sign and interactions by multiplication sign. Estimates in bold have confidence intervals that do not include zero. Data from surveys of 57 wildlife openings surveyed in 2003 and 2004 in the White Mountain National Forest, USA.

Species[a]	Abundance										Detectability				ΔAICc	w[b]	R^2
	ß0	Y	T	TF	TS	TS^2	A	Y × TS	Y × TS^2	Y × A	ß0	Date	Veght	Obs			
CSWA	0.84	−0.23	**0.45**								−0.32				0.00	0.36	0.05
	0.89	−0.24	0.40				−0.04				−0.32				1.98	0.13	0.05
COYE	1.90	−0.40			0.64	**−0.59**		−0.17	0.32		−2.07		**0.87**		0.00	0.74	0.20
INBU	0.47	−0.40									−2.15	**0.03**			0.00	0.42	0.04
WTSP	−0.72	−0.61		**3.00**							−2.00	0.03			0.00	0.20	0.08
	−0.73	−0.53		**2.96**							−1.32				0.49	0.16	0.05
	−0.63	−0.55		**2.76**							−0.87		−0.66		1.47	0.10	0.06
SOSP	−1.31	−0.04					**0.94**				−0.82				0.00	0.26	0.25
	−1.64	0.20			1.42	−0.73	**0.88**				−0.88				0.66	0.19	0.27
	−1.31	0.02					**0.91**				−1.15			0.53	0.71	0.18	0.26
	−1.49	−0.02	0.36				**1.02**				−0.86				1.79	0.11	0.25
	−1.44	0.24					**1.03**			−0.18	−0.84				1.92	0.10	0.25
ALFL	−0.98	−0.78					**0.70**				−0.39	**−0.06**	**2.33**	**−1.31**	0.00	0.75	0.27

[a] CSWA = chestnut-sided warbler, COYE = common yellowthroat, INBU = indigo bunting, WTSP = white-throated sparrow, SOSP = song sparrow, ALFL = alder flycatcher

[b] AIC$_c$ weight

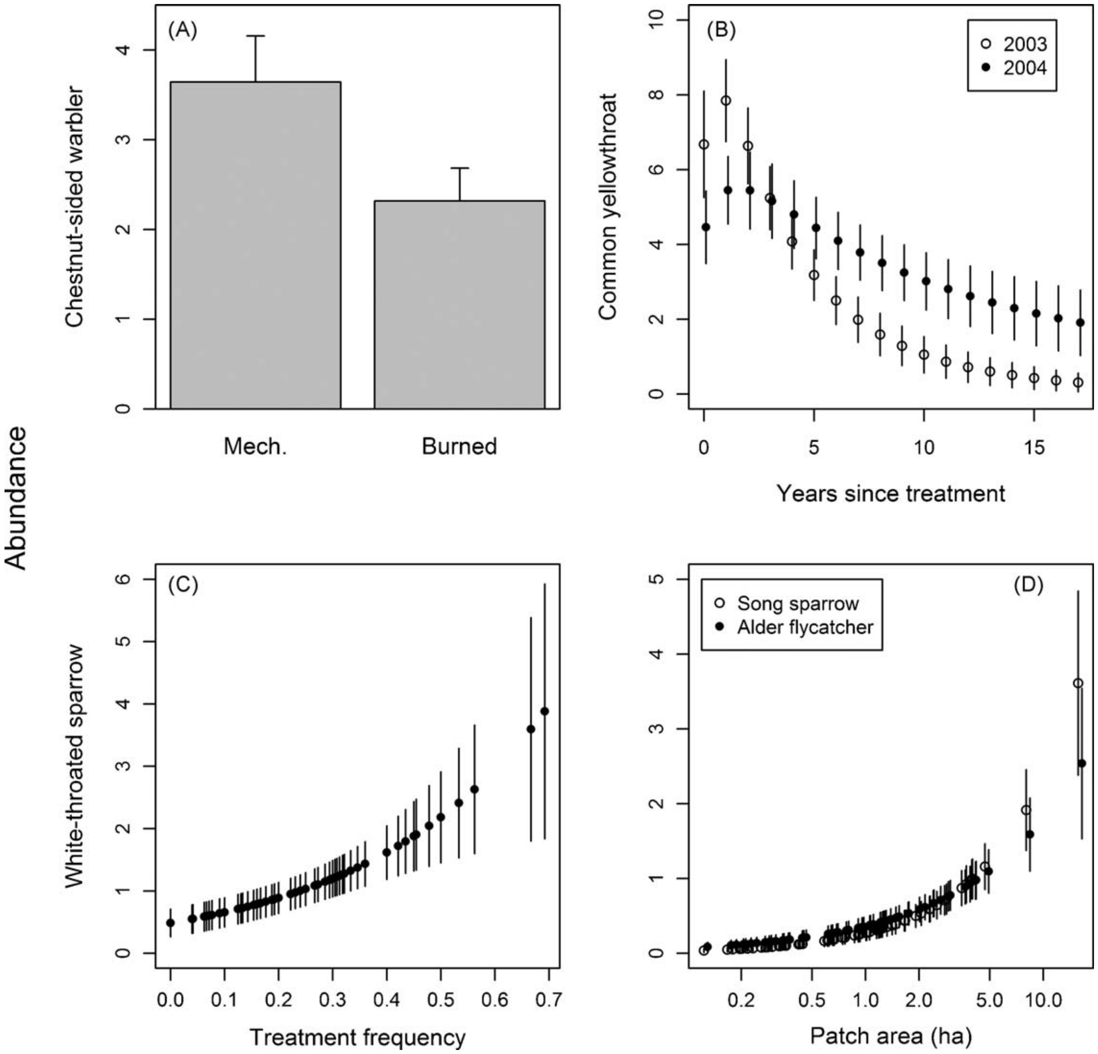

Fig. 1. Supported relationships between abundance and (A) treatment method, (B) years since last treatment, (C) treatment frequency, and (D) patch area. Fitted values calculated from the most supported *N*-mixture model parameter estimates holding all other covariates constant at their means. Error bars are standard errors. Data from surveys of 57 wildlife openings surveyed in 2003 and 2004 in the White Mountain National Forest, USA.

Supported models included detection probability covariates for five out of six bird species; however, these effects were only strongly supported for three species (Table 1). Detectibility of indigo buntings increased with date, and alder flycatcher detectability decreased with date (Table 1). Detectibility of common yellowthroats and alder flycatchers increased with vegetation height (Table 1). Detectibility of alder flycatchers differed among observers. There was no evidence that time of day affected detectibility.

3.2. *Nest survival*

We monitored 165 nests of 19 species in 30 sites over the two years of the study. Overall, daily nest survival was 0.974, equivalent to 52.0% nest success (Table 2). We only monitored enough chestnut-sided warbler and indigo bunting nests to model daily nest survival rates in relation to management variables, but we also modeled all species pooled and estimated the percent of successful nests in each year for an additional 4 species (Table 2).

Table 2
Percent nest success (NS), standard errors, and associated sample sizes (*N*) for focal bird species. Data from surveys of 57 wildlife openings surveyed in 2003 and 2004 in the White Mountain National Forest, USA.

Species[a]	Both years			2003			2004		
	N	NS	SE	N	NS	SE	N	NS	SE
All	160	52.03	5.21	68	37.27	7.79	92	62.65	6.55
Chestnut-sided warbler	78	55.23	7.54	35	37.19	10.72	43	71.84	9.26
Indigo bunting	19	51.20	14.90	6	41.46	28.47	13	55.02	17.26
Alder flycatcher	10	72.99	16.73	1	100.00	0.01	9	69.47	18.49
Common yellowthroat	9	53.28	24.76	4	39.16	40.78	5	52.80	33.80
Song sparrow	7	77.70	19.70	4	100.00	0.01	3	74.20	22.39
White-throated sparrow	7	17.91	19.56	2	49.41	34.76	5	0.31	1.56

[a] Nesting time intervals used for calculating nest success from daily nest survival estimates: 25 days for all species pooled and chestnut-sided warbler, 24 days for common yellowthroat, 27 days for indigo bunting, 27 days for white-throated and song sparrow, and 29 days for alder flycatcher.

Table 3
Parameter estimates for logistic exposure models of nest survival with $\Delta AIC_c \leq 2$. Covariates include time since last treatment (TS) and year 2004 (Y), which was included in all models. Interactions are indicated by a multiplication sign. Estimates in bold have confidence intervals that do not include zero. Data from surveys of 57 wildlife openings surveyed in 2003 and 2004 in the White Mountain National Forest, USA.

Species	ß0	Y	TS	Y × TS	ΔAIC_c	w^a	R^2
All	3.21	**0.76**			0.00	0.27	0.00
Chestnut-sided warbler	1.85	**2.74**	**2.96**	**−3.50**	0.00	0.69	0.14
Indigo bunting	4.26	1.69	−3.62		0.00	0.48	0.32

[a] AIC_c weights.

Logistic exposure models indicated that treatment regime variables did not affect nest survival of all species pooled (Table 3). We found evidence that management regime variables were related to chestnut-sided warbler and indigo bunting nest survival, but explained variation was low and model selection uncertainty high (Table 3). Nest survival of chestnut-sided warblers was positively related to time since treatment in 2003 but negatively related to time since treatment in 2004 (Table 3). Indigo bunting nest survival decreased with time since treatment, but this relationship was not strongly supported (Table 3).

3.3. *Vegetation structure and composition*

Vegetation in wildlife openings was primarily composed of *Rubus* spp. (17.0%), ferns (6.4%), red maple (*Acer rubrum*, 4.8%), quaking aspen (*Populus tremuloides*, 4.4%), *Spirea* spp. (3.7%), and pin cherry (*Prunus pennsylvanica*, 3.1%). All of the habitat characteristic modeled were associated with management regime variables (Table 4). We found strong evidence that the percent cover of woody vegetation, percent cover of ferns, and vegetation height were highest in mechanically treated sites that had been treated frequently and lowest in mechanically treated sites treated infrequency (Table 4). Herbaceous vegetation cover was highest in burned sites that had been treated frequently (Table 4). Cover of herbaceous plants and ferns decreased with time since last treatment. The reverse was true of woody vegetation cover and vegetation height (Table 4).

4. Discussion

Wildlife openings on the WMNF were occupied by bird species of high regional conservation concern, including the shrubland species targeted by these management practices that are not able to inhabit mature forest (Costello et al., 2000). Chestnut-sided and mourning warblers are considered management indicator species for early-successional habitat by the WMNF, and the former is a priority species in the Partners in Flight Landbird Conservation Plan (Rosenberg and Hodgman, 2000; U.S. Forest Service, 2005). Five of the six most common species at our sites, chestnut-sided warbler, common yellowthroat, indigo bunting, white-throated sparrow and song sparrow are experiencing significant population declines in the eastern U.S., according to the North American Breeding Bird Survey (Sauer et al., 2008). Thus, our results demonstrate that wildlife openings can provide habitat for many shrubland bird species of conservation concern in our study area.

Despite their widespread use, ours is the first study of the effects of treatment regime on shrubland bird abundance in managed wildlife openings. Consistent with our expectations, we found that management regime variables were related to the abundance of some focal shrubland birds, and these effects could be explained by the influence of treatment regime on habitat characteristics. For example, chestnut-sided warblers were more abundant in mechanically treated sites, and mechanically treated sites had more woody vegetation, which is favored by chestnut-sided warblers (Schlossberg and King, 2007). Similarly, common yellowthroat abundance peaked at intermediate times following treatment, as has been found in silvicultural openings (Schlossberg and King, 2009). Finally, white-throated sparrow abundance increased with treatment frequency, and treatment frequency was positively related to herbaceous plant cover, which is known to be an important component of white-throated sparrow habitat (Schlossberg and King, 2007). Contrary to our expectations, relationships between other focal bird species and treatment regime variables were less clear. For example, we found no evidence that either indigo bunting or alder flycatcher abundance was affected by treatment variables. Furthermore, few of these relationships had strong support, in the sense that R^2 values were generally low ($\leq$29%) and model uncertainty was generally high (most $w \ll 0.5$).

Our finding that the abundance of only one of six focal bird species differed between mechanically treated and burned wildlife openings contrasts with the observations of Schulte and Niemi (1998), who reported marked contrasts in bird abundance between sites that had been logged and sites that had been burned by wildfire. This contrast, as well as the generally low level of support for our models of bird abundance and treatment variables, is probably due to the complex histories of our study sites that likely obscured the effects of the most recent treatments. The wildlife openings we studied included sites that were formerly regenerating clearcuts, abandoned log landings and agricultural fields, which had variously been subjected to the influences of soil compaction or cultivation. In addition, some of the sites currently being burned appear to have been treated by mowing in the past, and vice versa. The importance of prior land use in influencing current vegetation is well known among plant ecologists (e.g. Motzkin et al., 1996), but has only recently received attention by

Table 4
Parameter estimates for models with $\Delta AIC_c \leq 2$ of relationships between vegetation and management regime variables. Covariates include: mechanical treatment (T), time since treatment (TS), treatment frequency (TF). Effect of year 2004 (Y) was included in each model. Interactions are indicated by a multiplication sign. Estimates in bold have confidence intervals that do not include zero. Data from surveys of 57 wildlife openings surveyed in 2003 and 2004 in the White Mountain National Forest, USA.

Response	ß0	Y	T	TF	TS	T × TF	Y × T	Y × TF	Y × TS	ΔAIC_c	w^a	R^2
GRASS	−2.26	0.44	−0.23	**1.66**				**−1.71**		0.00	0.29	0.09
	−2.40	0.43		**1.71**				−1.61		1.27	0.15	0.06
FORB	−1.65	**0.24**	**0.76**	**1.94**	**−0.48**	**−2.96**				0.00	0.93	0.28
FERN	−1.66	0.20	**−1.38**	**−2.65**	**−0.55**	**4.06**				0.00	0.68	0.19
BARE	−1.92	**−0.35**	**0.77**	**−2.49**		0.62				0.00	0.37	0.44
	−1.97	**−0.35**	**0.92**	**−2.14**	−0.06					0.25	0.33	0.44
	−2.12	−0.05	**1.08**	**−2.57**	0.11		−0.35	0.84	−0.33	1.64	0.17	0.46
WOODY	−0.03	−0.15	**−0.67**	**−1.03**	**0.53**	**2.38**				0.00	0.99	0.25
HEIGHT	0.90	0.00	**−0.77**	−0.84	**0.56**	**1.98**				0.00	0.99	0.31

[a] AIC_c weights

avian ecologists. For example, King et al. (2009) reported that bird communities differed between mechanically treated wildlife openings and regenerating clearcuts, which they attributed in part to differences in vegetation characteristics resulting from different site histories.

Another potential explanation for the contrasts between our results and those of Schulte and Niemi (1998) is related to the fact that their sites had been disturbed only once, whereas the wildlife openings we studied had been treated repeatedly. These frequent treatments, combined with high site fidelity exhibited by adult birds, may have resulted in a de-coupling of bird abundance and habitat characteristics similar to that reported by Wiens et al. (1986) from highly variable shrub-steppe environments. Consistent with this hypothesis, we observed chestnut-sided warblers occupying sites in which reproductive success was high the previous year but a subsequent treatment left no suitable nesting habitat (Chandler, unpublished data).

Our finding that song sparrow and alder flycatcher abundance was positively related to patch area is consistent with the results of Costello et al. (2000), who reported that alder flycatchers were present in large clearcuts, but not in small group selection cuts at their sites in northern New Hampshire. Species such as indigo bunting that did not respond to patch area are known to be capable of occupying very small openings (Greenberg and Lanham, 2001). Various mechanisms have been proposed to explain the phenomenon of area-sensitivity, including: increased habitat heterogeneity in larger patches, lower food abundance in small fragments, higher nest predation and the limited opportunity of extra-pair copulations in small patches (see review in Faaborg et al., 1995; Rodewald and Vitz, 2005; Lehnen and Rodewald, 2009). In our study there is no need to invoke these more complicated explanations because the smallest patches are probably smaller than the species' minimum territory sizes (Wilcove et al., 1986). With respect to the discussion of area sensitivity this finding is trivial; however, it has great significance for the management practices for wildlife openings as practiced on the WMNF and other areas because many of these openings are smaller than the territory sizes of some shrubland bird species. In fact, 55% of all WMNF wildlife openings were smaller than 1.2 ha, the average territory size of alder flycatchers (Stein, 1958). These smaller sites are using up management resources and not effectively promoting populations of target species.

Despite the relatively unpronounced effects of treatment regime variables on bird abundance, we did find strong relationships between treatment regime variables and vegetation characteristics. Specifically, we found evidence that managers can promote woody plant cover via mechanical treatments and herbaceous plant cover using prescribed fire, and can encourage woody plant cover and vegetation height by increasing the time intervals between treatments. These results are consistent with other studies of the effects of disturbance on vegetation structure (Luken et al., 1992; Heisler et al., 2003).

Detection probability covariates were included in supported models for all but one species, which is consistent with concerns expressed by others about the influence of these factors on detection probabilities (Thompson, 2002). The finding of a positive correlation between detectibility and vegetation height for common yellowthroats and alder flycatcher was inconsistent with our expectations and the findings of other studies (e.g. Bibby et al., 1985). However, McShea and Rappole (1997) reported that birds sing more often when they are in their preferred habitat, which might explain the positive relationship between detectibility and vegetation height for these species since both nest in woody vegetation.

The nest success rates we report from wildlife openings are substantially lower than those reported from New Hampshire clearcuts (King and DeGraaf, 2000; King et al., 2001), but were higher than the average value for nest success of 0.43 reported by Schlossberg and King (2007) from a review of 38 studies of 22 shrubland bird species. This suggests that both local- and landscape-level factors may affect nest success of these species. Within the heavily forested WMNF, the fact that nest success was higher in clearcuts could be explained by the ephemeral nature of clearcuts that do not support high numbers of nest predators (King et al., 1998). The lower nest success rates in the other regions might be due to a less diverse predator community in New Hampshire and Maine relative to the Midwest and southern New England, including a lower diversity of snakes (King and DeGraaf, 2006), which are known to be important predators in the Midwest (Thompson et al., 1999). Furthermore, we did not encounter any brown-headed cowbirds (*Molothrus ater*) in our study sites, in contrast to the other studies reporting lower nest success. The relatively weak relationships we found between nest survival and management variables indicate that managers have limited ability to affect productivity in wildlife openings in this landscape.

The habitat quality of wildlife openings relative to more intensively studied managed habitats such as silvicultural openings has only recently been investigated (King et al., 2009), and is an important issue because the maintenance of habitat expressly for wildlife through repeated treatments is expensive, whereas timber sales can generate revenue (Thompson and DeGraaf, 2001). It appears that overall, our wildlife opening sites are similar to nearby clearcuts. For instance, four of the six focal species in our study were also among the most abundant six species in regenerating clearcuts in New Hampshire (Costello et al., 2000; King and DeGraaf, 2000). However, species such as indigo bunting and song sparrow, which are associated with grasses and herbaceous plant cover, were more abundant in wildlife openings than in clearcuts suggesting that this management strategy can complement even-aged management. Conversely, several species of shrubland birds including mourning warbler, Nashville warbler, and gray catbird were rarely encountered in wildlife openings and may be better accommodated by even-aged management. Furthermore, pronounced differences have been reported between regenerating clearcuts and other early-successional shrub habitats in southern New England (King et al., 2009) and the southern Appalachians (Bulluck and Buehler, 2006), suggesting this question deserves further study.

5. Conclusions

We conclude that wildlife openings are an effective method for providing habitat for several shrubland birds of conservation concern in the northeastern United States. However, the overall benefit of wildlife openings for shrubland birds may be limited by the small amount of habitat provided by this management system and the high costs of maintaining wildlife openings in relation to silvicultural openings. Although the response of birds to treatment regime variables was not pronounced, it is known that many species of shrubland birds require the taller woody vegetation characteristic of the later stages of the seedling, sapling sere (Schlossberg and King, 2009), and thus we recommend that managers maintain time intervals between treatments sufficient to permit the development of woody vegetation characteristics. This optimum post-treatment time is 10–15 years in regenerating clearcuts (Schlossberg and King, 2009). Finally, we recommend that wildlife openings should be large enough to accommodate the territory sizes of all target species, in this case approximately 1.2 ha.

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Appendix A. Number of detections, mean number of individuals per plot over 3 sampling occasions standardized by plot area in all plots (Total), mechanically treated plots (Mech), and plots treated with prescribed burns (Burn). Data from 57 wildlife openings surveyed in 2003 and 2004 on the White Mountain National Forest, New Hampshire and Maine.

Common name	*Scientific name*	Detections	Total	Mech	Burn
Chestnut-sided warbler	*Dendroica pensylvanica*	219	1.22	1.56	0.81
Common yellowthroat	*Geothlypis trichas*	199	0.91	0.79	1.05
Cedar waxwing	*Bombycilla cedrorum*	54	0.27	0.26	0.29
Indigo bunting	*Passerina cyanea*	54	0.25	0.26	0.23
Song sparrow	*Melospiza melodia*	42	0.16	0.08	0.26
White-throated sparrow	*Zonotrichia leucophrys*	37	0.17	0.11	0.25
Alder flycatcher	*Empidonax alnorum*	35	0.14	0.09	0.2
Ruby-throated hummingbird	*Archilochus colubris*	22	0.11	0.16	0.06
American redstart	*Setophaga ruticilla*	19	0.09	0.09	0.09
American robin	*Turdus migratorius*	15	0.08	0.09	0.05
Black-capped chickadee	*Poecile atricapilla*	14	0.09	0.08	0.1
Chipping sparrow	*Spizella passerine*	14	0.06	0.02	0.11
Tree swallow	*Tachycineta bicolor*	12	0.05	0.03	0.08
Blue jay	*Cyanocitta cristata*	11	0.07	0.08	0.05
American goldfinch	*Carduelis tristis*	10	0.05	0.04	0.05
Red-eyed vireo	*Vireo olivaceus*	10	0.04	0.03	0.04
Mourning warbler	*Oporornis philadelphia*	9	0.06	0.09	0.02
Nashville warbler	*Vermivora ruficapilla*	9	0.09	0.11	0.06
Black-and-white warbler	*Mniotilla varia*	8	0.05	0.02	0.08
Least flycatcher	*Empidonax minimus*	8	0.07	0.1	0.02
Rose-breasted grosbeak	*Pheucticus ludovicianus*	7	0.05	0.03	0.06
Veery	*Catharus fuscescens*	7	0.03	0.02	0.05
Dark-eyed junco	*Junco hyemalis*	6	0.03	0.05	0.02
American crow	*Corvus brachyrhynchos*	4	0.02	0.00	0.03
Black-throated green warbler	*Dendroica virens*	4	0.02	0.04	0.01
Chimney swift	*Chaetura pelagica*	4	0.02	0.02	0.02
Magnolia warbler	*Dendroica magnolia*	4	0.02	0.00	0.04
Broad-winged hawk	*Buteo platypterus*	3	0.03	0.04	0.01
Blackburnian warbler	*Dendroica fusca*	2	0.01	0.00	0.02
Black-throated blue warbler	*Dendroica caerulescens*	2	0.01	0.02	0.00
Evening grosbeak	*Coccothraustes vespertinus*	2	0.01	0.02	0.01
Hairy woodpecker	*Picoides villosus*	2	0.01	0.01	0.01
Ovenbird	*Seiurus aurocapillus*	2	0.01	0.01	0.01
Pileated woodpecker	*Dryocopus pileatus*	2	0.02	0.03	0.01
Swainson's thrush	*Catharus ustulatus*	2	0.01	0.01	0.00
Wild turkey	*Meleagris gallopavo*	2	0.01	0.02	0.00
Yellow-rumped warbler	*Dendroica coronata*	2	0.01	0.00	0.02
Gray catbird	*Dumetella carolinensis*	2	0.01	0.00	0.02
Blue-headed vireo	*Vireo solitarius*	1	0.01	0.00	0.01
Common raven	*Corvus corax*	1	0.00	0.00	0.01
Northern flicker	*Colaptes auratus*	1	0.00	0.01	0.00
Purple finch	*Carpodacus purpureus*	1	0.00	0.01	0.00
Ruffed grouse	*Bonasa umbellus*	1	0.00	0.01	0.00
Red-winged blackbird	*Agelaius phoeniceus*	1	0.00	0.00	0.01
Wood thrush	*Hylocichla mustelina*	1	0.01	0.00	0.01
Yellow-bellied sapsucker	*Sphyrapicus varius*	1	0.00	0.00	0.01
Eastern phoebe	*Sayornis phoebe*	1	0.00	0.00	0.01
Eastern towhee	*Pipilo erythrophthalmus*	1	0.01	0.00	0.01
Field sparrow	*Spizella pusilla*	1	0.00	0.00	0.01
Red-tailed hawk	*Buteo jamaicensis*	1	0.01	0.01	0.00

References

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

Bibby, C.J., Phillips, B.N., Seddon, A.J.E., 1985. Birds of restocked conifer plantations in Wales. Journal of Applied Ecology 22, 619–633.

Boose, E.R., Chamberlin, K.E., Foster, D.R., 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 71, 27–48.

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

Brooks, R.T., 2003. Abundance, distribution, trends, and ownership patterns of early-successional forests in the northeastern United States. Forest Ecology and Management 185, 65–74.

Bulluck, L.P., Buehler, D.A., 2006. Avian use of early successional habitats: are regenerating forests, utility rights-of-ways, and reclaimed surface mines the same? Forest Ecology and Management 236, 76–84.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference, second ed. Springer-Verlag Inc., New York, NY, USA.

Byers, B.E., 1995. Song types, repertoires, and song variability in a population of chestnut-sided warblers. Condor 97, 390–401.

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

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

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

DeGraaf, R.M., Miller, R.I., 1996. The importance of disturbance and land-use history in New England: implications for forested landscapes and wildlife conservation. In: DeGraaf, R.M., Miller, R.I. (Eds.), Conservation of Faunal Diversity in Forested Landscapes. Chapman and Hall, London, UK, pp. 3–35.

DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. Forest Ecology and Management 185, 179–191.

Faaborg, J., Brittingham, M., Donovan, T., Blake, J., 1995. Habitat fragmentation in the temperate zone. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, USA, pp. 357–380.

Greenberg, C.H., Lanham, J.D., 2001. Breeding bird assemblages in hurricane-created gaps and adjacent closed canopy forest in the southern Appalachains. Forest Ecology and Management 154, 251–260.

Heisler, J.L., Briggs, J.M., Knapp, A.K., 2003. Long-term patterns of shrub expansion in a C_4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. American Journal of Botany 90, 423–428.

Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29, 407–494.

King, D.I., DeGraaf, R.M., 2000. Bird species diversity and nesting-success in mature, clearcut, and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 121, 227–235.

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

King, D.I., DeGraaf, R.M., 2006. Predators at bird nests in a northern hardwood forest in New Hampshire. Journal of Field Ornithology 77, 239–243.

King, D.I., Griffin, C.R., DeGraaf, R.M., 1998. Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape. Forest Ecology and Management 104, 151–156.

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

Lehnen, S.E., Rodewald, A.D., 2009. Investigating area-sensitivity in shrubland birds: responses to patch size in a forested landscape. Forest Ecology and Management 257, 2308–2316.

Litvaitis, J.A., 1993. Response of early succession 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.

Luken, J.O., Hinton, A.C., Baker, D.G., 1992. Response of woody plant communities in power-line corridors to frequent anthropogenic disturbance. Ecological Applications 2, 336–362.

Manolis, J.C., Anderson, D.E., Cuthbert, F.J., 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117, 615–626.

Mayfield, H., 1961. Nesting success calculated from exposure. The Wilson Bulletin 73, 255–261.

McShea, W.J., Rappole, J.H., 1997. Variable song rates in three species of passerines and implications for estimating bird populations. Journal of Field Ornithology 68, 367–375.

Motzkin, G., Foster, D., Allen, A., Harrod, J., Boone, R., 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs 66, 345–365.

Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.

Noss, R.F., LaRoe, III, E.T., Scott, J.M. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. National Biological Service, Washington, DC, 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.

Overcash, J.L., Roseberry, J.L., Klimstra, W.D., 1989. Wildlife openings in the Shawnee National Forest and their contribution to habitat change. Transactions of the Illinois Academy of Science 82, 137–142.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, Inc., Orlando, FL, USA.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org.

Ralph, C.J., Sauer, J.R., Droege, S. 1995. Monitoring bird populations by point counts. U.S. Department of Agriculture. Forest Service General Technical Report PSW-149, Albany, NY, USA.

Rodewald, A., Vitz, A., 2005. Edge- and area-sensitivity of shrubland birds. Journal of Wildlife Management 69, 681–688.

Rosenberg, K.V., Hodgman, T.P., 2000. Partners in Flight Landbird Conservation Plan: Physiographic Area 28: Eastern Spruce-Hardwood Forest. American Bird Conservancy, The Plains, VA, USA.

Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60, 108–115.

Sauer, J.R., Hines, J.E., Fallon, J., 2008. The North American Breeding Bird Survey Results and Analysis 1966–2007. USGS Patuxent Wildlife Research Center, Laurel, MD, Version 5.15.2008.

Schaffer, T.L., 2004. A unified approach to analyzing nest success. Auk 121, 526–540.

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

Schlossberg, S., King, D.I., 2009. Postlogging succession and habitat usage of shrubland birds. Journal of Wildlife Management 73, 226–321.

Schulte, L.A., Niemi, G.J., 1998. Bird communities of early-successional burned and logged forest. Journal of Wildlife Management 62, 1418–1429.

Stein, R.C., 1958. The behavioral, ecological and morphological characteristics of two populations of the Alder Flycatcher, *Empidonax traillii* (Audubon). New York State Museum and Science Service Bulletin 371, 1–63.

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

Thompson III, F.R., Dijak, W., Burnhans, D., 1999. Video identification of predators at songbird nests in old fields. Auk 116, 259–264.

Thompson, W.L., 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 199, 18–25.

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

Tubbs, C.H., Verme, L.J., 1972. How to create wildlife openings in northern hardwoods. In: Unnumbered Pamphlet, USDA Forest Service, NC Forest Experimental Station, St. Paul, MN, USA.

Tucker Jr., J.W., Olson, D.P., 1994. Birds at log landings in the White Mountain National Forest, New Hampshire. Maine Naturalist 2, 91–104.

U.S. Forest Service, 2005. White Mountain National Forest: Land and Resource Management Plan. Laconia, New Hampshire. http://www.fs.fed.us/r9/forests/white_mountain/. Accessed 21 June 2007.

Wiens, J.A., Rotenberry, J.T., Van Horne, B., 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67, 365–376.

Wilcove, D.S., Mclellan, C.M., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soule, M. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, pp. 237–256.