Management and Conservation

Management Regime Influences Shrubland Birds and Habitat Conditions in the Northern Appalachians, USA

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ABSTRACT Population declines of birds that breed in early-successional shrubland habitat are of great concern to conservationists throughout the northeastern United States. To help increase the efficiency and effectiveness of efforts to conserve these species and their habitats, we studied birds in temporary forest openings created through even-aged timber harvest, and permanent wildlife openings maintained through mechanical treatment and prescribed burning in the Northern Appalachians, USA in 2010 and 2011. We assessed the effects of treatment method, time since last treatment, and retained tree cover on shrubland bird abundance and habitat conditions. Burned and mechanically treated wildlife openings differed only in grass and fern cover. Both types of wildlife openings had more grasses and forbs, and less bare ground than silvicultural openings. Six out of 8 focal bird species were less abundant in silvicultural openings than in wildlife openings. In contrast, abundance of only 1 species differed between burned and mechanically treated wildlife openings. Silvicultural openings supported the same species as wildlife openings, indicating that this management option could be used in place of more costly wildlife opening management. However, because birds were more abundant in wildlife openings, maintaining the current population size of shrubland birds under a management strategy based entirely on silviculture would require a 50–300% increase in the area of silvicultural openings, depending on the species. Individual species peaked in abundance at different times post treatment, indicating that managers must maintain a range of early-successional conditions across the landscape to provide habitat for the entire suite of shrubland birds. Six species exhibited a negative relationship with the basal area of retained conifer cover, and 7 species with deciduous tree cover, indicating that the retention of overstory trees in openings reduced their utility to early-successional birds. © 2014 The Wildlife Society.

KEY WORDS clearcut, early-successional habitat, management history, N-mixture models, silviculture, wildlife opening.

In response to recent declines in shrubland bird populations, numerous state and federal agencies are actively working to create and maintain shrubland habitats (Oehler et al. 2006). Silviculture has been widely advocated as an effective method of creating shrubland habitat (DeGraaf and Yamasaki 2003). However, a very small proportion of the forested public land in the middle Atlantic region or New England has been subject to recent timber harvest (Oehler 2003). Moreover, harvest activities on these lands increasingly emphasize uneven-aged management (Trani et al. 2001), which is ineffective for most species of shrubland birds (Costello et al. 2000, King and DeGraaf 2004). Consequently, maintaining permanent wildlife openings through mechani-

cal treatment or prescribed burning has become a widespread approach for conserving early-successional shrublands in the northeastern United States (Oehler 2003).

Although permanent wildlife openings are widely used in shrubland bird management, the relative conservation value of wildlife openings and silvicultural openings is still poorly understood (Chandler et al. 2009a, King et al. 2009). Understanding the relative effectiveness of silvicultural openings and permanent openings is important, as wildlife openings are costly to create and maintain (Oehler 2003). Moreover, few studies have investigated the manner in which shrubland bird abundance changes as a function of how much time has passed since a site's last treatment. The timing of management regimes is important, however, because shrubland birds breed in ephemeral habitats that are undergoing succession, and have only a short time period (roughly 5–20 yr depending on the species) in which their

habitat needs will be met in a given patch (DeGraaf and Yamasaki 2003, Schlossberg and King 2009). Information on shrubland bird habitat associations in different early-successional habitat types and along successional stages is important to the effective conservation of shrubland birds because it informs the choice of management techniques as well as treatment schedules, which affects the allocation of scarce resources (Chandler et al. 2009*a*). The objective of this study was to examine the effects of management regime on bird abundance and habitat conditions by sampling birds systematically over a successional gradient in silvicultural openings and in wildlife openings maintained by burning and mechanical treatment.

STUDY AREA

We conducted this study during 2010 and 2011 on the Green Mountain National Forest (GMNF), located in the southwestern and central portion of Vermont (VT), in the northern Appalachian Mountains, USA (43.95°N, 73.07°W). The GMNF, approximately 162,000 ha in area, consisted primarily of northern hardwoods in the lower elevation zones in which this study occurred (U.S. Department of Agriculture [USDA] Forest Service 2006). Approximately 4% of the GMNF consisted of habitat in the early stages of plant succession, including 1,533 ha of managed upland openings, 703 ha of regenerating forest, and 2,932 ha of shrubby wetlands (USDA Forest Service 2006). Managed early-successional habitat in this forest included regenerating silvicultural openings and permanent wildlife openings that were originally old log landings, silvicultural openings, pastures, agricultural fields, or orchards. Permanent openings were maintained through prescribed burning and mechanical treatment with handsaws, chippers, or heavy machinery.

The dominant plant species in wildlife openings and silvicultural openings were seedlings and saplings of trees in the surrounding forests, including American beech (*Fagus gradifolia*), red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), and pin cherry (*Prunus pensylvanica*), as well as raspberry (*Rubus* spp.), goldenrod (*Solidago* spp.), bracken fern (*Pteridium aquilinum*), and several grass (*Poaceae* spp.), and spiraea (*Spiraea* spp.) species. The openings across the forest varied in the amount of retained pole and saw-timber, typically consisting of American beech, red maple, sugar maple (*Acer saccharum*), pin cherry, yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*). Apple trees (*Malus domestica*) were also present on many openings.

METHODS

From an initial list of all openings on the National Forest, we established sampling points in 90 early-successional shrubland openings. We eliminated openings <1 ha in area, because this size is below the threshold for which area sensitivity has been observed in shrubland birds (Costello et al. 2000, Chandler 2006). We surveyed all silvicultural openings we found on the GMNF between 1 and 15 years post treatment that met this size requirement. We also surveyed 5 silvicultural openings on private or town-forest land, because a temporary ban on timber harvest in the GMNF limited the availability of openings in the 4–8-year time since treatment range. We surveyed in most of the available wildlife openings that met the size and age requirements, excluding only sites that had been treated repeatedly with both prescribed burning and mechanical treatment, as complex treatment histories may obscure the effects of management (Chandler et al. 2009*a*). Within each management type (silviculture, burning, and mechanical treatment), openings ranged from 1 to 15 years since last treatment.

We established 42 survey points in silvicultural openings, 31 in permanent wildlife openings maintained with prescribed fire, and 31 in permanent wildlife openings maintained by mechanical means. Survey points were located randomly within patches with the constraints that they were at least 350 m apart (Ralph et al. 1995), and located such that 1 point on the circumference of the flagged 50-m radius fixed plot was within 5 m of an edge. This latter condition was adopted to avoid confounding patch area and edge distance because a number of shrubland species avoid edges (Rodewald and Vitz 2005, Schlossberg and King 2008) and more habitat is near edges in smaller openings. A few openings were irregularly shaped, and though greater than 1 ha in area, they were not wide enough to fully encompass a 50-m radius count circle. For these sites, we used aerial orthophotos and ArcGIS (ESRI, Redlands, CA) to establish a survey plot with the equivalent area of a 50-m radius plot (0.785 ha), and we counted birds only within that area (Chandler et al. 2009*b*). Seventy-four openings contained a single sample point, and 16 openings were large enough to encompass 2 points spaced at least 350 m apart. We surveyed a small proportion of points ($n = 19$) in only 1 year because of changes in habitat conditions or access.

Vegetation and Bird Surveys

We measured vegetation structure and composition at 20 randomly selected points within each 50-m point-count plot following King et al. (2009). At each point, we recorded the maximum height of the understory substrate, with woody plants classified to genus or species, and all other cover types categorized as forb, fern, grass, or bare ground. We classified all vegetation cover ≤3 m in height as understory. We recorded the species and diameter at breast height (dbh) of all trees with dbh > 10 cm at 5 15-m radius sub-plots. We did not repeat tree species and dbh measurements at sites that we re-surveyed in the second year of the study, because tree growth did not markedly change the vegetative condition.

We surveyed each site for birds 3 times each year with 10-minute, 50-m radius point counts (Ralph et al. 1995). We conducted surveys between 0530 and 1045 hours from late May to early-July on calm days with no precipitation. During each count, we recorded the species, sex, and detection method for all birds seen and heard. We also recorded the wind speed and cloud cover during the survey. To reduce observer bias, we rotated technicians through survey points, and varied the time at which we visited points in each replicate survey (Ralph et al. 1995). We did not include

females, birds of unknown sex (except for cedar waxwings (*Bombycilla cedrorum*) for which sex could not be determined), fly overs, or birds heard outside the 50-m radius point-count circle in the analysis.

Statistical Analysis

We modeled the habitat data from the 2 years of the study separately to avoid pseudoreplication, to investigate the consistency of the results between the 2 years, and because a number of the sites were not surveyed in both years of the study.

We assessed the impact of management on habitat using both univariate and multivariate methods. We used a multi response permutation procedure (MRPP) to test for multivariate differences in habitat characteristics among the 3 treatments (McGarigal et al. 2000). Habitat variables included counts of woody vegetation, bare ground, ferns, grasses, and forbs; mean understory vegetation height; and basal area of retained coniferous and deciduous trees. We conducted analyses using the vegan package in R 2.14 (Oksanen et al. 2006), and considered statistical comparisons with $P \leq 0.05$ as significant.

We related counts of ferns, forbs, grasses, bare ground, and total woody vegetation to management variables (treatment type, time since treatment, and a quadratic term for time since treatment) using generalized linear models (Quinn and Keough 2003). For each vegetation variable, we chose the most appropriate exponential distribution by comparing the Akaike's Information Criterion corrected for small sample size (AIC$_c$) and goodness of fit of the global model under the Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial distributions. We related understory vegetation height to management variables with general linear models (Quinn and Keough 2003). For each habitat variable, we fit all subsets of the management variables (Bolker 2008).

We selected among candidate models using AIC$_c$, and approximated the amount of variability explained by the models using Nagelkerke's (1991) R^2 index. We considered top models to be those within 2 AIC$_c$ of the most parsimonious model (Burnham and Anderson 2002, Kery et al. 2005, Bolker 2008). We considered covariates moderately supported if they were in top models, and strongly supported if they were present in top models and had 95% confidence intervals that did not include 0 (Chandler et al. 2009a). We compared parameter estimates for the silvicultural and mechanical treatments using Z tests. We fit models and parameter estimates using the R software package, version 2.10.0 (R Version 2.10, http://www.r-project.org/, accessed 1 Sep 2010).

We modeled the effects of management on abundance of shrubland birds with N-mixture models using a log link (Royle 2004). This modeling approach uses repeated counts to account for detectability (Thompson 2002). N-mixture models assume that no permanent immigration, emigration, or death occurs during the sampling period (Kery et al. 2005). We deemed that this assumption was met, given territoriality and that repeated sampling events were typically separated by no more than 10 days (Kery et al. 2005, Chandler 2006). We

analyzed data only for shrubland-breeding species with ≥ 40 observations per year and found in $\geq 10\%$ of the plots, following Schlossberg and King (2007). As above, we modeled the abundance data from the 2 years of the study separately.

We modeled abundance in relation to predictors using a log link. Predictor variables included treatment method, time since last treatment, and a quadratic term for time since last treatment, because some shrubland species peak in abundance at intermediate times within the successional gradient (Schlossberg and King 2009). We also included the basal area of all retained deciduous and coniferous trees larger than saplings as management covariates, because these factors can affect the abundance of shrubland birds (Witmer et al. 1997, Schulte and Niemi 1998, DeGraaf and Yamasaki 2001, Hagan and Meehan 2002, Jobes et al. 2004), were highly variable across the sites, and can be directly controlled by managers. We modeled deciduous and coniferous basal area separately because we expected that species could respond differentially to coniferous and deciduous cover. We considered interaction terms for time since treatment and treatment type; however, interactions were not in top models for any species, so we dropped them from the analysis. We modeled probability of detection in relation to observer, time of day, date, a quadratic term for date, understory vegetation height, and wind intensity (Aldredge et al. 2007, Johnson 2008) using a logit link (Kery et al. 2005). We did not include habitat variables in N-mixture models because they were correlated with management variables, and our primary goal was modeling the factors that can be directly controlled by managers.

For each species, we first determined a set of best detection covariates to include in subsequent candidate models. We accomplished this by fitting all subsets of the detection covariates with the global suite of abundance variables, and identifying the detection covariates that were in models with a $\Delta AIC_c \leq 2$, and statistically significant at $P = 0.1$. For each species, we then fit all subsets of the management variables with this set of best detection covariates fixed. We used AIC$_c$ values and goodness of fit of global models to determine whether the Poisson or negative binomial error distributions provided the best fit. We standardized all continuous variables to $\bar{x} = 0$ and $SD = 1$ to facilitate model convergence. We fit models and estimated parameters using the unmarked package (Fiske and Chandler 2011) in the R software environment, version 2.10.0.

We used the same model selection procedures, and the same criteria for assessing the strength of evidence of covariates for bird abundance models as we did for the habitat models. To display results we averaged model predictions over all candidate models using Akaike weights (w_i; Burnham and Anderson 2002). We did not use model averaging for parameter estimates because values of parameter estimates depend on what other variables are in a model, and correlations between predictors change the interpretation of parameters. For each species, we derived estimates of mean bird abundance (per 50-m radius plot) in each treatment type by back-transforming the treatment

parameter estimates in all candidate models, while holding all other variables at their mean, then model-averaging the back-transformed parameter estimates over all candidate models. We used the delta method to estimate standard errors (Bolker 2008).

Though our primary goal was to determine how the management factors under the direct control of managers influenced bird abundance and habitat composition, to better understand these relationships, we also assessed the manner in which the bird community was related to habitat characteristics. To accomplish this, we described multivariate associations between bird communities and habitat using canonical correspondence analysis (CCA). We standardized all habitat variables by their maximum value to relativize differences in scale of measurement. We used detection-corrected estimates of bird abundance as derived from the N-mixture models in the multivariate analyses. We standardized all bird abundance values by site maxima to relativize differences among species and reduce any potential bias from sites with a high total abundance. We analyzed data from the 2 years separately as before. We conducted analyses using the vegan package (Oksanen et al. 2006) in R 2.14.

RESULTS

Habitat Characteristics

The MRPP indicated the 3 treatment types differed in habitat characteristics ($P < 0.001$). Post-hoc comparisons indicated habitat differences between silvicultural openings and both wildlife-opening treatments ($P < 0.04$), but no overall difference between burned and mechanically treated wildlife openings ($P < 0.11$).

Management covariates were in supported univariate models for nearly all habitat response variables (Table 1). Silvicultural openings had more bare ground and less fern cover than burned openings, fewer grasses than mechanically treated sites, and less forb cover than both wildlife-opening types. Mechanically treated openings had more grass and less fern cover than burned wildlife openings.

We found strong evidence that understory vegetation height and woody vegetation were positively related to time since treatment, and that grass cover decreased with time since treatment (Table 1). Bare ground was positively related to time since treatment in 1 year, and negatively in another year. Bare ground, woody vegetation, and understory vegetation height all had a quadratic term for time since treatment in top models.

Bird Abundance and Detection Probabilities

We recorded 2,031 observations of 66 species in 2010 and 2,199 observations of 69 species in 2011. These data included 21 species of shrubland birds. Of these shrubland birds, we had sufficient sample sizes to estimate abundance for 8 species: alder flycatcher (*Empidonax alnorum*), cedar waxwing, common yellowthroat (*Geothlypis trichas*), mourning warbler (*G. Philadelphia*), chestnut-sided warbler (*Setophaga*

Table 1. Candidate general and generalized linear models representing the effect of management on habitat characteristics in silvicultural openings and burned and mechanically treated wildlife openings on the Green Mountain National Forest, Vermont, 2010 and 2011. We show coefficients for burn, silvicultural (Silv), and mechanical (Mech) treatments, and for linear (Tst) and quadratic (Tst²) time since treatment effects. Treatment effects with different letters are different ($P \leq 0.05$). We compared mechanical and silvicultural treatments with Z tests. Linear and quadratic Tst parameter estimates with an asterisk have 95% confidence intervals that exclude 0.

Variable	Yr	Burn	Silv	Mech	Tst	Tst²	ΔAIC$_c$[a]	w_i[b]	R^{2}[c]
Bare ground	2010	−1.32A	0.95B	0.23	−0.16	0.02	0.00	0.40	0.24
		−0.74			−0.20	0.02	0.86	0.26	0.19
		−2.27A	1.09B	0.35	0.15*		0.96	0.25	0.21
	2011	−1.09A	2.03B	0.73	−0.38	0.03*	0.00	0.86	0.27
Woody vegetation	2010	2.36			0.02*		0.00	0.40	0.06
		2.24			0.10	0.26	1.01	0.24	0.06
	2011	2.52					0.00	0.45	0.00
		2.34			0.06	−0.004	1.69	0.19	0.03
Forbs	2010	0.93	−0.61A	0.41B			0.00	0.58	0.11
		1.02	−0.56A	0.43B	−0.02		0.91	0.22	0.10
	2011	0.38					0.00	0.35	0.00
		0.55	−0.44	−0.14			0.84	0.23	0.04
		0.47			−0.01		1.83	0.14	0.00
Grasses	2010	0.76A	−0.01	0.76B	−0.13*		0.00	0.45	0.16
		1.13			−0.14*		1.01	0.27	0.11
	2011	1.03	−0.06A	0.85B	−0.09*		0.00	0.67	0.22
		1.26A	−0.08A	0.87B	−0.18	0.01	1.63	0.30	0.22
Ferns	2010	1.10A	−0.38	−0.79B			0.00	0.37	0.05
		0.75					0.90	0.24	0.00
		1.25A	−0.36	−0.77B	−0.02		1.65	0.16	0.06
	2011	1.13A	−0.55B	−0.21			0.00	0.36	0.05
		−1.71					0.36	0.30	0.00
Understory vegetation height	2010	96.96			5.35*		0.00	0.52	0.20
		83.48			10.48*	−0.34	0.65	0.38	0.21
	2011	42.20			17.99*	−0.78*	0.00	0.82	0.28

[a] Difference in Akaike's Information Criterion for small sample sizes. We only show models with ΔAIC$_c \leq 2$.
[b] AIC$_c$ weights, calculated from all fitted models.
[c] Index from Nagelkerke (1991).

pensylvanica), indigo bunting (*Passerina cyanea*), song sparrow (*Melospiza melodia*), and white-throated sparrow (*Zonotrichia albicollis*).

Management variables were in top N-mixture models for all 8 focal species (see Table S1, available online at www.onlinelibrary.wiley.com). We found strong evidence that all species except song sparrow and mourning warbler were more abundant in burned openings than in silvicultural openings in both years of the study (Table 2). We also found strong evidence that chestnut-sided warblers, common yellowthroats, indigo buntings, and white-throated sparrows were more abundant in mechanically treated openings than in silvicultural openings. The 2 wildlife-opening treatments had less distinct differences in bird abundance, though 1 species, the white-throated sparrow, was more abundant in mechanically treated sites than in burned openings. Mourning warblers were the only species most abundant in silvicultural openings; however, this difference was weakly supported (95% CI for parameter estimates overlapped 0) and only apparent in 2011.

Time since treatment was a strong predictor of bird abundance. Linear and quadratic terms for this covariate were both present in top models for all species in both years, though for mourning warbler and song sparrow we found strong support for these covariates in only 1 year (see Table S1, available online at www.onlinelibrary.wiley.com). White-throated sparrows reached maximum abundance immediately following treatment in both years (Fig. 1). All other species reached maximum abundance between 4 and 8 years post treatment (Fig. 1).

Basal area was highly variable across the plots for both deciduous (0–17.4 m²/ha) and coniferous trees (0–18.7 m²/ha), and had a strong effect on bird abundance (Fig. 2). We found moderate evidence that cedar waxwings, alder flycatchers, indigo buntings, and song sparrows were negatively associated with deciduous basal area and strong support for this relationship for white-throated sparrows,

chestnut-sided warblers, and common yellowthroats (see Table S1, available online at www.onlinelibrary.wiley.com). We found moderate evidence that common yellowthroats and mourning warblers were negatively associated with the basal area of conifers, and strong support for this relationship for alder flycatchers, indigo buntings, song sparrows, and chestnut-sided warblers. We found moderate evidence that white-throated sparrow abundance was positively associated with coniferous basal area. All the detection covariates that were considered in the modeling process were in top models for at least 1 species. Detection covariates present in top models varied among species.

Multivariate Habitat Associations

The canonical correspondence analysis differentiated between silviculture treatments, characterized by bare ground and a high basal area of retained conifers and deciduous trees, and wildlife openings, characterized by ferns, forbs, and grasses (Fig. 3). Chestnut-sided warblers were associated with tall woody understory vegetation; mourning warblers with deciduous basal area; alder flycatchers, indigo buntings and song sparrows with forbs; and white-throated sparrows with grasses and coniferous basal area. Cedar waxwings exhibited an association with grasses and ferns in 2010 and with conifers and bare ground in 2011.

DISCUSSION

This is the first study to sample systematically over a gradient of stand ages in early successional habitats created through silviculture, prescribed burning, and mechanical treatment. As such, it offers insight into management outcomes across a wider range of treatment types and stand ages than has been previously available. By providing estimates of abundance in each treatment type, and data on how bird abundance changed with time since treatment and basal area retention, our work gives managers the information needed to more accurately weigh the tradeoffs between treatment options,

Table 2. Mean abundance (per 50-m radius plot) of focal shrubland birds in silvicultural, burned, and mechanically treated openings on the Green Mountain National Forest, Vermont in 2010 and 2011.[*]

Species	Yr	Burn	(SE)	Silvicultural	(SE)	Mechanical	(SE)
Alder flycatcher	2010	2.55	0.97	1.74	0.67	0.74	0.37
	2011	1.40	0.44	0.98	0.37	1.20	0.38
Cedar waxwing	2010	6.34	2.33	2.18	1.16	7.38	2.61
	2011	8.11	2.28	3.98	1.29	5.30	1.70
Mourning warbler	2010	1.31	0.56	1.28	0.59	1.25	0.58
	2011	0.98	0.48	2.41	0.95	1.13	0.46
Common yellowthroat	2010	5.11	0.95	2.09	0.50	4.52	0.87
	2011	5.83	1.43	3.49	0.97	6.01	1.47
Chestnut-sided warbler	2010	4.93	0.82	3.14	0.61	4.20	0.72
	2011	5.72	0.93	3.56	0.65	6.64	1.08
Song sparrow	2010	0.47	0.26	0.12	0.17	0.54	0.32
	2011	0.43	0.39	0.43	0.40	0.64	0.55
White-throated sparrow	2010	2.17	0.73	0.96	0.35	1.66	0.57
	2011	2.24	0.67	1.19	0.39	1.26	0.45
Indigo bunting	2010	2.09	0.77	0.50	0.33	3.73	1.46
	2011	1.88	0.45	0.67	0.25	1.81	0.49

[*] For each species, we derived estimates of mean bird abundance (per 50-m radius plot) in each treatment type by back-transforming the treatment parameter estimates in all candidate models, while holding all other variables at their mean, then model-averaging the back-transformed parameter estimates over all candidate models. We used the delta method to estimate standard errors.
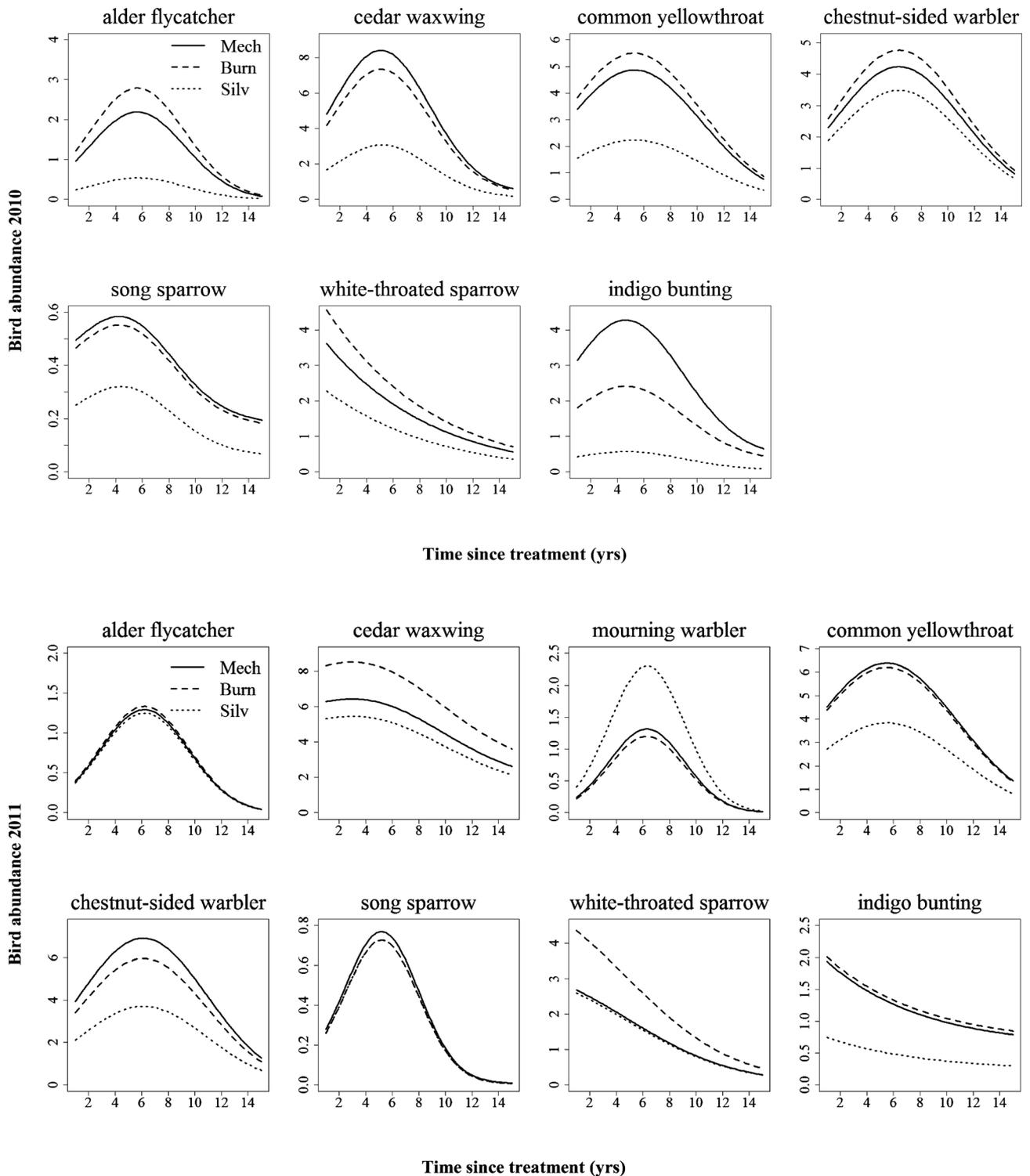
Figure 1. Effect of treatment and time since treatment on bird abundance (mean number of birds per 50-m radius plot) in silvicultural (Silv) burned (Burn), and mechanically treated (Mech) openings on the Green Mountain National Forest, Vermont, 2010 and 2011. We show model-averaged predictions for effects present in models with differences in corrected Akaike's Information Criterion ($\Delta AIC_c) \leq 2$.

and to predict the likely population consequences of management choices.

Bird Abundance

Our results highlight that the timing and mechanism of treatments, and the amount of tree cover maintained during

treatment are all important factors to consider when designing management programs to conserve shrubland birds and their habitats. In the GMNF, the abundance of shrubland birds was strongly related to time since last treatment, and the timing of peak abundance varied across species, reinforcing that a variety of stand ages must be
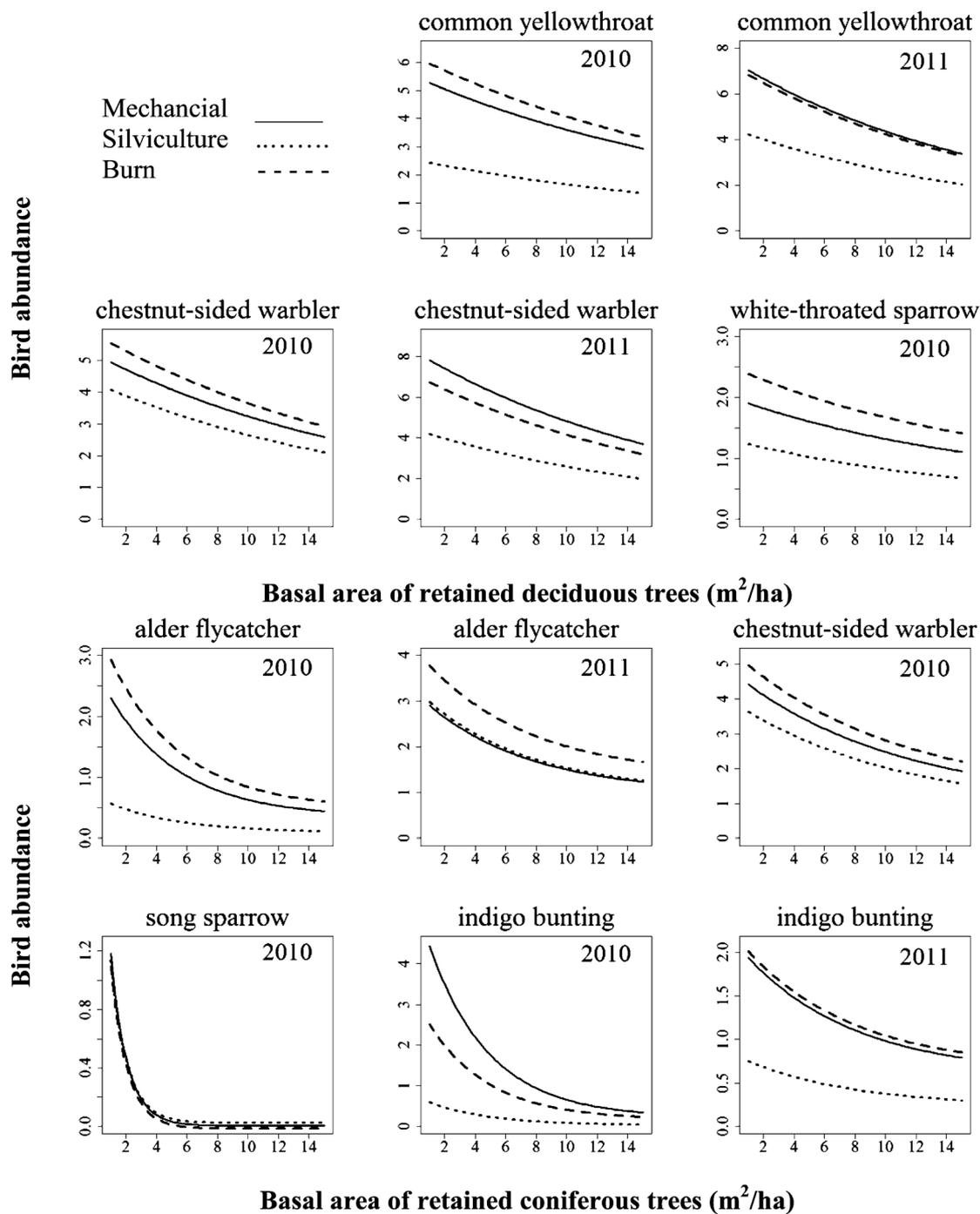
Figure 2. Effect of deciduous and coniferous basal area on shrubland bird abundance (mean number of birds per 50-m radius plot) in silvicultural, burned, and mechanically treated openings on the Green Mountain National Forest, Vermont, 2010 and 2011. We show model-averaged predictions for effects present in models with differences in corrected Akaike's Information Criterion (ΔAIC_c) $\leq$ 2 and with 95% confidence intervals that do not contain 0.

maintained to fully support the shrubland community. The focal species were present in all treatment types; however, most species were more abundant in wildlife openings than in silvicultural openings. This indicates that a management strategy based solely on silviculture could support shrubland birds, but would require significantly more habitat area than ones that incorporate wildlife openings. For instance, on the GMNF, maintaining the current population size of shrubland birds with only silviculture would require an

increase of 50–300% in the area of silvicultural openings across the landscape. In contrast, burned and mechanically treated openings in the GMNF had similar abundance of shrubland species, indicating that managers can select either method to manage vegetation in wildlife openings. Finally, retention of even a moderate basal area of 4 m²/ha resulted in a 50–80% reduction in indigo bunting abundance and an approximately 90% reduction in song sparrow abundance, indicating that even modest concessions to accommodating
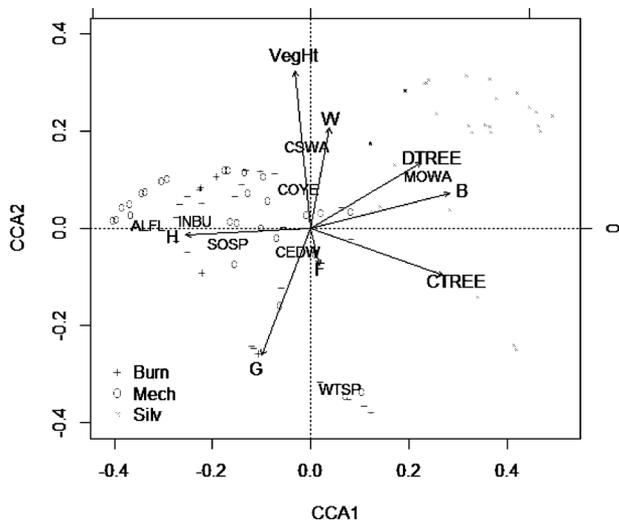
Figure 3. Canonical correlation analysis of focal birds and habitat characteristics in silvicultural (Silv), burned (Burn), and mechanically treated (Mech) openings on the Green Mountain National Forest, Vermont. We show only analyses for 2010 because results were consistent between years. Environmental variables are represented by arrows, the length of which is directly proportional to their importance in influencing bird community structure. Species close together occur in similar environmental conditions. The projected location of each species point along each arrow indicates how important the environmental variable is to the abundance and distribution of that species. Sites are also represented similarly in habitat space, and coded by their treatment. ALFL, alder flycatcher; CEDW, cedar waxwing; MOWA, mourning warbler; COYE, common yellowthroat; CSWA, chestnut-sided warbler; SOSP, song sparrow; WTSP, white-throated sparrow; INBU, indigo bunting; B, bare ground; F, ferns; G, grasses; H, forbs; W, woody vegetation; VegHt, understory vegetation height; DTREE, basal area of deciduous trees; CTREE, basal area conifers.

mature forest birds in openings can have substantial implications for some shrubland birds.

Most of the relationships that we observed between bird abundance and treatment mechanism can be explained by habitat characteristics within the different opening types. For instance, silvicultural openings had the greatest cover of bare ground, and the lowest abundance of shrubland birds, and bare ground has been shown to negatively influence abundance of shrubland species (Schlossberg et al. 2010). Mourning warblers were most abundant in silvicultural openings in our study; in the CCA, this species was associated with deciduous basal area, which was greatest in silvicultural openings. Indigo buntings, alder flycatchers, and white-throated sparrows were more abundant in both wildlife-opening types than silvicultural openings. Our analyses indicated that indigo buntings and alder flycatchers were associated with forbs, and white-throated sparrows with grasses, and these habitat characteristics were more abundant in wildlife openings.

Our observation that bird abundance did not differ markedly between mechanically treated and burned wildlife openings could be due to the lack of pronounced differences in habitat between wildlife-opening treatments as indicated by the results of the MRPP. In support of this, relatively few bird species were associated with the habitat characteristics that differed between burned and mechanically treated

openings (grass and fern cover). Indeed, the only species that was strongly associated with grasses in the CCA, the white-throated sparrow, was also the only species that differed in abundance between burned and mechanically treated sites.

We observed little variability in woody cover between treatment types in the GMNF; however, many of the species typically associated with dense woody cover, such as chestnut-sided warblers, alder flycatchers, and common yellowthroats (Thompson and Capen 1988, Holmes and Pitt 2007, Chandler et al. 2009b) were more abundant in wildlife openings than in silvicultural openings. This suggests that secondary habitat associations with specific plant groups may also be driving observed abundance patterns in the GMNF. For instance, both common yellowthroats and alder flycatchers are associated with alders and willows (Schlossberg et al. 2010, Baril et al. 2011), and 41 out of the 51 observations of alders and willows were in wildlife openings. Common yellowthroats require a combination of dense herbaceous and shrub cover (Guzy and Ritchison 1999, Confer and Pascoe 2003, Schlossberg and King 2007), and both types of wildlife openings had a more even distribution of herbaceous and woody plant cover than the silvicultural openings, in which 75% of the understory substrate was either bare ground or woody vegetation. Chestnut-sided warblers are known to prefer deciduous cover (Schulte and Niemi 1998), and avoid conifers (Keller et al. 2003, Schlossberg and King 2007, King et al. 2009), and silvicultural openings had the greatest basal area of conifers in the GMNF. These secondary habitat associations may be responsible for the inconsistencies between our finding that chestnut-sided warblers were most abundant in wildlife openings and those of King et al. (2009) and Schulte and Niemi (1998), who observed greater numbers of them in silvicultural openings, compared to mechanically treated wildlife openings and burned sites, respectively.

The species-specific relationships between abundance and stand age that we observed were also largely consistent with previously documented habitat associations. For instance, white-throated sparrows were most abundant immediately post-treatment. This species is associated with grasses and herbaceous cover (Schlossberg and King 2007), which were most abundant immediately or shortly after treatment. White-throated sparrows avoid the dense tall woody stems (Hagan and Meehan 2002) that were characteristic of older stands, but require the low vegetation cover that was characteristic of the younger openings in this study, because they nest and forage on or near the ground. The species most abundant at an intermediate time since treatment, such as chestnut-sided warblers, common yellowthroats, and alder flycatchers either nest or forage in dense, woody understory vegetation (Richardson and Brauning 1995, Guzy and Ritchison 1999, Lowther 1999), which was most abundant approximately 6 to 10 years post-treatment, when both short and tall woody vegetation were present. Song sparrows and indigo buntings peaked in abundance earlier than these species, but later than white-throated sparrows, perhaps reflecting that both require forbs and grasses for seed foraging (Arcese et al. 2002, Payne 2006), as well as low-

stature vegetation in which to place and hide nests (Confer and Pascoe 2003, Chandler 2006, Payne 2006).

The relationships we observed between bird abundance and management variables were generally consistent with those from previous studies. For instance, in accordance with our finding that most species were less abundant in silvicultural openings than wildlife openings, King et al. (2009) reported that white-throated sparrows and indigo buntings were more abundant in mechanically treated wildlife openings relative to regenerating forest, Schulte and Niemi (1998) found that indigo buntings were more abundant in burned areas than in silvicultural openings, and Bulluck and Buehler (2006) reported that chestnut-sided warblers, indigo buntings, and common yellowthroats were less abundant in silvicultural openings than in other early-successional habitats. We found that mourning warblers were more abundant in silvicultural openings than wildlife openings, which is consistent with other studies comparing silvicultural openings with mechanically treated wildlife openings (King et al. 2009) and burned openings (Schulte and Niemi 1998).

The relationships we observed between time since treatment and bird abundance were also generally consistent with those from previous investigations. White-throated sparrows were most abundant immediately following treatment in the GMNF. This pattern was also observed by Keller et al. (2003), Chandler (2006), and Schlossberg and King (2009). Our finding that a number of species peaked in abundance at intermediate time since treatment was previously demonstrated for common yellowthroats (Keller et al. 2003), alder flycatchers, song sparrows (Chandler 2006), and chestnut-sided warblers (Keller et al. 2003, Holmes and Pitt 2007, Schlossberg and King 2009). Schlossberg and King (2009) found that song sparrows and indigo buntings were most abundant immediately following treatment, whereas they peaked in abundance around year 4 or 5 on the GMNF.

Our observation that many shrubland birds were less abundant in sites with a greater basal area of trees is consistent with previous research. A negative relationship between the basal area of deciduous trees and abundance of shrubland birds was previously documented for white-throated sparrows (King and DeGraaf 2000), common yellowthroats (King and DeGraaf 2000, Hagan and Meehan 2002), chestnut-sided warblers, and mourning warblers (Jobes et al. 2004). Similarly, both alder flycatchers, (Schulte and Niemi 1998, DeGraaf and Yamasaki 2001, Schlossberg and King 2007) and cedar waxwings (Witmer et al. 1997, Schlossberg and King 2007) are more common in areas with little retained tree cover. In contrast, our finding that indigo bunting, alder flycatcher, and song sparrow abundance was inversely related to conifer cover is inconsistent with the results of King and DeGraaf (2000), who compared bird abundance in mature forest, clearcuts, and shelterwood cuts in New Hampshire. However, the range of variation in basal area of conifers was significantly greater in the GMNF than it was in the King and DeGraaf (2000) study.

Habitat Characteristics

Our observation that overall woody vegetation cover did not differ significantly among treatments was inconsistent with quite a few previous studies. At least 6 previous investigations found evidence that treatment type affects woody vegetation (Christensen 1985, Bulluck and Buehler 2006, Fink et al. 2006, Zuckerberg and Vickery 2006, Chandler et al. 2009a, King et al. 2009). This inconsistency is likely related to differences among study areas in the intensity or timing of treatments, as well as land-use history and initial stand composition, all of which can influence how plant communities respond to disturbance (Pickett and White 1985). Many of the burned wildlife openings on the GMNF are managed for fire-tolerant wild blueberry (*Vaccinium* spp.), which regenerate more quickly following burning than other shrub species. In addition, many of the mechanically treated wildlife openings on the GMNF are previously forested areas that after repeated mechanical treatment are dominated by woody stump-sprouted vegetation. Regeneration in these mechanically treated sites that are dominated by fire-adapted species or stump-sprouts may tend towards woody cover more than the old-field sites investigated in other studies. In support of this, Luken et al. (1992) found very little difference in habitat characteristics between regenerating forest and mechanically treated power line rights-of-way that were originally forest.

Many of our observations about how management influenced non-woody vegetation were consistent with those from previous investigations. For example, our finding that mechanically treated wildlife openings had a greater cover of grasses and forbs than silvicultural openings is consistent with results from previous studies (Bulluck and Buehler 2006, King et al. 2009). We also observed more forbs in burned openings than in silvicultural openings, which is consistent with the findings of Fink et al. (2006). Finally, our finding that silvicultural openings had more bare ground than wildlife openings was consistent with the findings of King et al. (2009).

MANAGEMENT IMPLICATIONS

Our results have direct implications for creating and maintaining habitat for shrubland birds. First, wildlife openings and silvicultural openings supported similar bird species, indicating that either method can be implemented. However, because silvicultural openings supported fewer birds than wildlife openings, more area (50–300%) must be treated if this approach is selected. Furthermore, since shrubland bird abundance and community composition were similar in burned and mechanically treated wildlife openings, managers have some leeway regarding their choice of treatment methods depending on operational constraints. The presence of as little as 4 m^2/ha of overstory-tree basal area in openings reduced abundance of some species by 50–90% in the GMNF. Although managers need to balance the needs of interior and shrubland birds, the value of these openings to shrubland birds may be more of a critical priority in extensively forested landscapes, since shrubland species are facing more severe declines than forest species in much of the

study region (Askins 2000). Finally, the abundance of some species did not peak until 8 years post-treatment, suggesting that a return interval of at least this duration should be maintained to ensure that species characteristic of all stages of early-succession are represented.

ACKNOWLEDGMENTS

LITERATURE CITED

Aldredge, M. W., T. R. Simmons, and K. H. Pollock. 2007. Factors affecting aural detections of songbirds. Ecological Applications 17:948–955.

Arcese, P. M., M. K. Sogge, A. B. Marr, and M. A. Patten. 2002. Song sparrow (*Melospiza melodia*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/704/introduction>. Accessed 15 Nov 2010.

Askins, R. A. 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, New Haven, Connecticut, USA.

Baril, L. M., A. J. Hansen, R. Renkin, and R. Lawrence. 2011. Songbird response to increased willow (*Salix* spp.) growth in Yellowstone's northern range. Ecological Applications 21:2283–2296.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA.

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

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer-Verlag, New York, New York, USA.

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

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

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

Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 85–100 in S. T. A. Pickett, and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando, Florida, USA.

Confer, J. L., and S. M. Pascoe. 2003. Avian communities on utility rights-of-ways and other managed shrublands in the northeastern United States. Forest Ecology and Management 185:193–205.

Costello, C. A., M. Yamasaki, P. J. Perkins, W. B. Leak, and C. D. Neefus. 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., and M. Yamasaki. 2001. New England wildlife. University Press of New England, Hanover, New Hampshire, USA.

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

Fink, A. D., F. R. Thompson, III, and A. A. Tudor. 2006. Songbird use of regenerating forest, glade, and edge habitat types. Journal of Wildlife Management 70:180–188.

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

Guzy, M. J., and G. Ritchison. 1999. Common yellowthroat (*Geothlypis trichas*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/448/articles/introduction>. Accessed 15 Nov 2010.

Hagan, J. M., and A. L. Meehan. 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. Forest Science 48:231–242.

Holmes, S. B., and D. G. Pitt. 2007. Response of bird communities to selection harvesting in a northern tolerant hardwood forest. Forest Ecology and Management 238:280–292.

Jobes, A. P., E. Nol, and D. R. Voigt. 2004. Effects of selection cutting on bird communities in contiguous eastern hardwood forests. Journal of Wildlife Management 68:51–60.

Johnson, D. H. 2008. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.

Keller, J. K., M. E. Richmond, and C. R. Smith. 2003. An explanation of patterns of breeding bird species richness and density following clearcutting in northeastern USA forests. Forest Ecology and Management 174:541–564.

Kery, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications 15:1450–1461.

King, D. I., R. B. Chandler, and S. Schlossberg. 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.

King, D. I., and R. M. DeGraaf. 2000. Bird species diversity and nesting-success in mature, clearcut, and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 12:227–235.

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

Lowther, P. E. 1999. Alder flycatcher (*Empidonax alnorum*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/446/articles/introduction>. Accessed 15 Nov 2011.

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

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York, New York, USA.

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

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

Oehler, J. D., D. F. Covell, S. Capel, and B. Long. 2006. Managing grasslands, shrublands, and young forest habitats for wildlife: a guide for the northeast. The Northeast Upland Habitat Technical Committee and Massachusetts Division of Fisheries & Wildlife. <http://www.wildlife.state.nh.us/Wildlife/Northeast_Hab_Mgt_Guide.htm>. Accessed 24 Sep 2009.

Oksanen, J., R. Kindt, P. Legendre, and R. B. O'Hara. 2006. Vegan: community ecology package version 1.7-5. <http://cran.r-project.org/>. Accessed 15 Nov 2010.

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

Payne, R. B. 2006. Indigo bunting (*Passerina cyanea*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/004/articles/introduction>. Accessed 15 Nov 2010.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbances and patch dynamics. Academic Press, Inc., Orlando, Florida, USA.

Quinn, G. P., and M. J. Keough. 2003. Experimental design and data analysis for biologists. University Press, Cambridge, United Kingdom.

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

Richardson, M., and D. W. Brauning. 1995. Chestnut-sided warbler (*Setophaga pensylvanica*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/190/articles/introduction>. Accessed 12 Mar 2012.

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

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

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

Schlossberg, S., and D. I. King. 2008. Are shrubland birds edge specialists? Ecological Applications 18:1325–1330.

Schlossberg, S., and D. I. King. 2009. Postlogging succession and habitat usage of shrubland birds. Journal of Wildlife Management 73:226–231.

Schlossberg, S., D. I. King, R. B. Chandler, and B. Mazzei. 2010. Regional synthesis of habitat relationships in shrubland birds. Journal of Wildlife Management 74:1513–1522.

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

Thompson, F. R. III, and D. E. Capen. 1988. Avian assemblages in seral stages of a Vermont forest. Journal of Wildlife Management 52:771–777.

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

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

U.S. Department of Agriculture [USDA] Forest Service. 2006. Green Mountain National Forest land and resource management plan. USDA Eastern Region, Milwaukee, Wisconsin, USA.

Witmer, M. C., D. J. Mountjoy, and L. Elliot. 1997. Cedar waxwing (*Bombycilla cedrorum*). The birds of North America online. Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/309/articles/introduction>. Accessed 15 Nov 2010.

Zuckerberg, B., and P. D. Vickery. 2006. Effects of mowing and burning on shrubland and grassland birds on Nantucket Island, Massachusetts. Wilson Journal of Ornithology 118:353–363.

Associate Editor: Daniel Twedt.

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