



SCRUB–SHRUB BIRD HABITAT ASSOCIATIONS AT MULTIPLE SPATIAL SCALES IN BEAVER MEADOWS IN MASSACHUSETTS

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ABSTRACT.—Most scrub–shrub bird species are declining in the northeastern United States, and these declines are largely attributed to regional declines in habitat availability. American Beaver (*Castor canadensis*; hereafter “beaver”) populations have been increasing in the Northeast in recent decades, and beavers create scrub–shrub habitat through their dam-building and foraging activities. Few systematic studies have been conducted on the value of beaver-modified habitats for scrub–shrub birds, and these data are important for understanding habitat selection of scrub–shrub birds as well as for assessing regional habitat availability for these species. We conducted surveys in 37 beaver meadows in a 2,800-km² study area in western Massachusetts during 2005 and 2006 to determine the extent to which these beaver-modified habitats are used by scrub–shrub birds, as well as the characteristics of beaver meadows most closely related to bird use. We modeled bird abundance in relation to microhabitat-, patch-, and landscape-context variables while adjusting for survey-specific covariates affecting detectability using *N*-mixture models. We found that scrub–shrub birds of regional conservation concern occupied these sites and that birds responded differently to microhabitat, patch, and landscape characteristics of beaver meadows. Generally, scrub–shrub birds increased in abundance along a gradient of increasing vegetation complexity, and three species were positively related to patch size. We conclude that these habitats can potentially play an important role in regional conservation of scrub–shrub birds and recommend that conservation priority be given to larger beaver meadows with diverse vegetation structure and composition. Received 8 May 2008, accepted 1 October 2008.

Key words: American Beaver, *Castor canadensis*, detectability, early-successional habitat, *N*-mixture model, shrubland.

Asociaciones entre Ambientes para Aves de Matorral-Arbustal a Múltiples Escalas Espaciales en Prados Húmedos Habitados por Castores en Massachusetts

RESUMEN.—La mayoría de las especies de aves de matorrales-arbustales está disminuyendo en el noreste de Estados Unidos, y estas disminuciones son atribuidas principalmente a una reducción en la disponibilidad de hábitat a escala regional. Las poblaciones de castor americano (*Castor canadensis*) han ido incrementando en el noreste en las décadas recientes, y los castores crean ambientes de matorral-arbustal por medio de la construcción de represas y sus actividades de forrajeo. Pocos estudios sistemáticos han sido llevados a cabo sobre el valor de los ambientes modificados por los castores para las aves de matorral-arbustal. Estos datos son importantes tanto para comprender la selección de hábitat de las aves de matorral-arbustal, como para evaluar la disponibilidad de hábitat para estas especies a nivel regional. Realizamos censos en 37 prados húmedos creados por los castores sobre un área de estudio de 2,800 km² en el oeste de Massachusetts durante 2005 y 2006. Determinamos el grado en el que estos ambientes modificados por los castores son usados por las aves de matorral-arbustal, así como también las características de los prados más vinculadas con el uso por parte de las aves. Modelamos la abundancia de las aves con relación a variables a escala de micro hábitat, de parche y de paisaje ajustando por las covariables específicas de los censos que afectan la detectabilidad usando modelos mixtos. Encontramos que las aves de matorral-arbustal con estatus de conservación vulnerable a nivel regional ocuparon estos sitios y que las aves respondieron de modo diferente a las características de micro hábitat, parche y paisaje de los prados húmedos habitados por castores. Generalmente, las aves de matorral-arbustal incrementaron su abundancia a lo largo de un gradiente de incremento de la complejidad de la vegetación y tres especies se relacionaron positivamente con el tamaño de parche. Concluimos que estos ambientes pueden potencialmente jugar un rol importante en la conservación regional de las aves de matorral-arbustal. Recomendamos que se dé prioridad de conservación a los prados de castores más grandes con estructura y composición vegetal diversa.

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MOST BIRD SPECIES that breed in early-successional or shrub-land habitats (hereafter “scrub–shrub birds”) have declined in the northeastern United States over the past 50 years (Askins 1993). These declines are largely attributed to changes in forest management (Trani et al. 2001), as well as to reduction in natural disturbances resulting from fire suppression, increased resistance of younger forests to windthrow, and flood control (Askins 1993, Litvaitis 1993, Bellemare et al. 2002, Schlossberg and King 2007). Potential conservation strategies include creation and maintenance of scrub–shrub habitat using silviculture, repeated prescribed fires, or mechanical treatments (Annand and Thompson 1997, King et al. 2009). Although the loss of naturally occurring scrub–shrub habitats justifies active management, the quality of natural habitats and their potential role in conserving these species is poorly understood (Brawn et al. 2001).

Historically, American Beavers (*Castor canadensis*; hereafter “beavers”) created large areas of scrub–shrub habitats in the Northeast by felling trees and impounding streams (Naiman et al. 1988, Askins 2000). For instance, beavers impounded ~4,000 km² (3% of the total land area) in New York state alone before European settlement (Gotie and Jenks 1984). Beavers were extirpated from most of the region during the 18th and 19th centuries through trapping and human development, but beaver populations are now increasing over much of their range as trapping declines (Deblinger et al. 1999, DeStefano and Deblinger 2005). Although the amount of land susceptible to beaver influences is unlikely to ever reach historical levels, beavers may be a substantial factor in providing habitat for declining bird species (Gotie and Jenks 1984, DeGraaf and Yamasaki 2003). However, the actual potential of beavers to influence habitat availability depends on the degree to which scrub–shrub birds use beaver impoundments.

Beaver-modified habitats vary greatly with respect to microhabitat characteristics as a result of complex multisuccessional pathways. Research concerning bird conservation in beaver-modified habitats has focused primarily on waterfowl, rails, and herons, all of which thrive in sites characterized by open water and emergent vegetation (Rosell et al. 2005). However, shrub and sapling cover can be high in sites referred to as “beaver meadows,” depending on the level of beaver activity and other site-specific factors (McMaster and McMaster 2001, Wright et al. 2003). Scrub–shrub birds in upland habitats such as regenerating clearcuts respond to vegetation height and structural complexity (DeGraaf et al. 1998, Schlossberg and King 2007) and, thus, should also vary across the diverse microhabitat conditions found in beaver meadows.

Scrub–shrub bird density can also be related to environmental variables at patch and landscape scales. For instance, the abundance of some species is positively related to patch area (Annand and Thompson 1997, Costello et al. 2000; but see Kremetz and Christie 2000). Some scrub–shrub bird species avoid forest edges (Schlossberg and King 2008), and, thus, the shape of a patch can affect abundance (Rodewald and Vitz 2005). Although a few studies have found relationships between surrounding land-cover types and the abundance of scrub–shrub birds, these landscape-context variables typically do not affect abundance as strongly as microhabitat or patch variables (Hagan and Meehan 2002, MacFaden and Capen 2002).

Because the extent to which scrub–shrub birds use beaver meadows is poorly understood, and the consequences of beaver re-establishment for regional populations is thus unknown, we undertook the following objectives: (1) determine the extent to which beavers can provide habitat for scrub–shrub bird species of conservation concern; (2) investigate relationships between the abundances of these species and environmental variables at microhabitat, patch, and landscape scales while accounting for heterogeneous detection probabilities; and (3) provide recommendations for the conservation of beaver meadows for scrub–shrub birds.

METHODS

Study area.—We conducted the study in a 2,800-km² area in western Massachusetts in 2005 and 2006 (Fig. 1). We selected this area because it was representative of rural landscapes in the Northeast occupied by beavers. Most (79.6%) of the 30-km-radius study area was covered by northern hardwoods mixed with Eastern Hemlock (*Tsuga canadensis*) and Eastern White Pine (*Pinus strobus*) in lower elevations or Red Spruce (*Picea rubens*) and Balsam Fir (*Abies balsamea*) at higher elevations. Small farms (8.9%) and residential

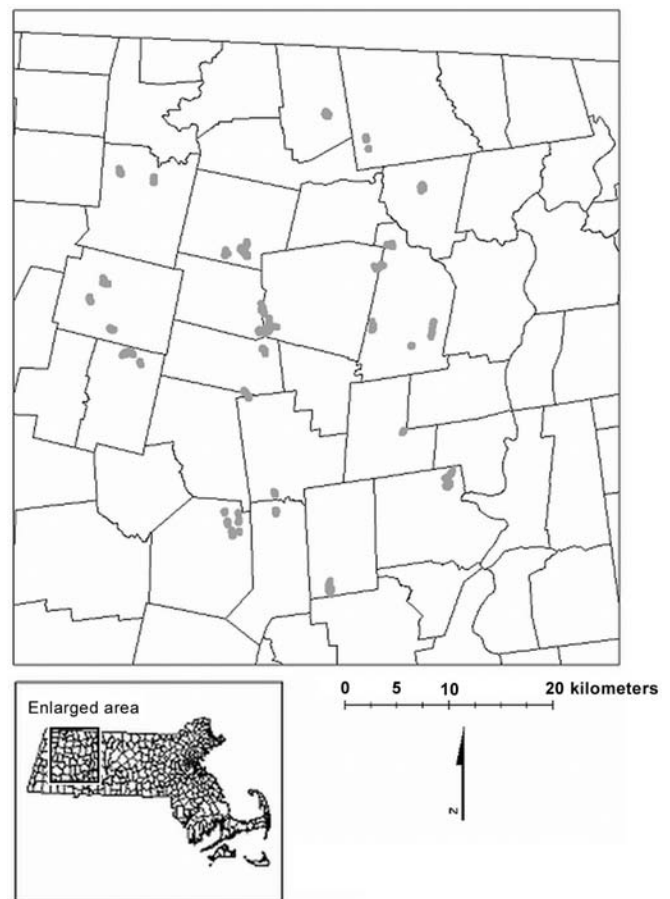


FIG. 1. Map of study area and study sites in western Massachusetts. Town lines are shown in black and beaver meadows in gray.

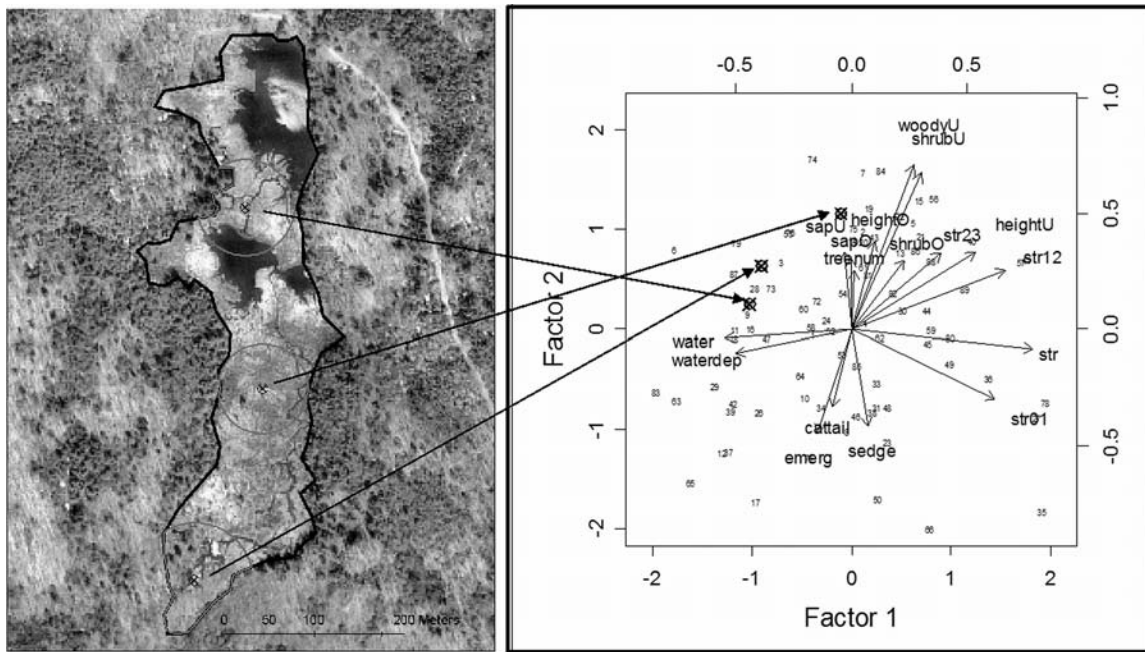


FIG. 2. Variation in microhabitat characteristics within and among beaver meadows shown by an aerial photograph of a study site with three sample plots (left) and a factor analysis biplot (right). The within-patch variation in microhabitat conditions can be seen on the photograph, with water represented by black, woody cover by gray, and herbaceous cover by white. The locations of these plots (circles with crosshairs) in biplot space are illustrated by arrows. Note that the upper plot is aligned along the first factor in a position characterized by open water, the lower plot is located along the second factor in a position characterized by high woody cover, and the middle plot lies in an intermediate location. The other study plots' site scores are shown as numbers, and the strength and direction of the microhabitat variables with loadings >0.3 are shown as arrows. Variable abbreviations are defined in Table 1.

areas (5.5%) were the other common land-cover types in the study area. The hilly terrain ranged in elevation from 30 m to 780 m.

Site and survey point selection.—We selected study sites by identifying all visible beaver meadows on 2003 MassGIS digital infrared orthophotographs (see Acknowledgments). Both beaver dams and lodges were clearly visible on these images. We eliminated sites <0.785 ha, the size of a 50-m-radius point-count plot, and sites with $>75\%$ open water, given that open water is not suitable habitat for scrub–shrub species. To locate survey points within sites, we overlaid a randomly placed 50-m grid over a map of each site and chose as many points as possible at grid intersections that were ≥ 200 m apart. This selection process resulted in a sample of 89 survey plots in 37 beaver meadows. Many of the sites were narrow and irregularly shaped; therefore, we could not use standard 50-m-radius plots that would have overlapped forest habitats, which are not typically used by scrub–shrub birds. Instead, we established a survey area of 0.785 ha centered on the survey point but totally within the meadow.

Bird surveys.—We surveyed each plot three times each season (23 May–15 July) using 10-min point counts. Surveys were conducted by two experienced observers between dawn and 1100 hours. Surveys were not conducted in persistent rain or wind. We recorded bird locations, movements, and method of detection (i.e., song, call, flyover, or visual) on scaled orthophotographs with plot boundaries (Fig. 2).

Microhabitat measurements.—In each plot, we quantified vegetation cover and structure at 20 points on a 15-m grid using a point-intercept method. At each of the 20 points, we recorded the

cover type <3 m and >3 m by classifying woody plants to species or genus and classifying all other cover types as bare ground, cattail (*Typha* spp.), herbaceous plants, grass, rush, sedge, or water. We quantified vertical structure by recording the number of vegetation contacts on 0–1 m, greater than 1–2 m, and greater than 2–3 m segments of a 1-cm-diameter metal pole held vertically on the ground or at the water surface at each of the 20 points. We also recorded water depth at each point.

Patch- and landscape-context variables.—We quantified beaver meadow size and shape using ARCGIS, version 9.0 (ESRI, Redlands, California) and FRAGSTATS, version 3.3 (McGarigal et al. 2002), because these metrics are known to affect bird abundance in beaver meadows (Grover and Baldassarre 1995, Edwards and Otis 1999, Riffell et al. 2001). We digitized the boundaries of beaver meadows and directly calculated patch area using these shapefiles. We used the FRAGSTATS shape index, the perimeter divided by the minimum possible perimeter for a given area, to quantify site shape because this metric removes the bias that results from varying patch areas in the commonly used edge-to-area ratio. FRAGSTATS 3.3 accepts only raster images; therefore, we rasterized the original shapefiles using a grid size of 5 m.

We used a MassGIS statewide land-cover layer (see Acknowledgments) to quantify the percent cover of forest, agriculture, residential developments, and open lands within 1 km of each beaver meadow. Previous work on scrub–shrub birds in forested landscapes in the Northeast has indicated that birds respond to habitat at a 1-km scale (Hagan and Meehan 2002), and little extra information is gained by including habitat at larger scales (Chandler

2006). This layer was created by interpreting 1999 1:250000 orthophotographs. We grouped all residential categories into a single category and did the same for agricultural land uses.

Data analysis.—We used N -mixture models (Royle 2004) to relate the abundances of bird species occurring in >30% of plots to environmental variables while adjusting for variables affecting detection probability. We chose this model because failure to account for individuals present but not detected can bias abundance models (Thompson 2002), and this is one of the few models that can incorporate covariates affecting both detectability and abundance. These models require that plots are surveyed during multiple periods and utilize the repeated count data to estimate detection probability (p) assuming a binomial distribution while simultaneously modeling abundance (λ) as a random variable from the exponential family of distributions. The model is particularly well suited for point-count data because it assumes there exists a fixed number of birds per plot, which may be detected imperfectly on each survey occasion. We used a Poisson distribution to model λ , rather than the negative binomial distribution, which accounts for overdispersion, because it was generally more parsimonious (lower Akaike's information criterion, corrected for small sample size [AIC_c]) or had a higher convergence rate. Because our plots were not closed with respect to movement, λ was defined as the mean number of singing males that could have used a plot (detected and undetected), and p as the mean probability of detecting the actual number of birds per plot on a single survey. We restricted our analysis to singing males because the number of males per plot is a clearly defined parameter and precludes the inclusion of individuals such as juveniles and floaters, which likely have different detection probabilities and cannot always be visually distinguished from territorial males. Furthermore, singing males accounted for most of the detections (Appendix).

We modeled λ in relation to microhabitat, patch, and landscape variables using a natural log link. We modeled p in relation to time of day, date, observer, and an interaction between time of day and date because previous studies have demonstrated that each of these covariates can affect detectability (Kéry et al. 2005, Alldredge et al. 2007, Johnson 2008). We were not able to account for all the factors that could potentially affect p (reviewed in Johnson 2008); however, by including only singing males and by using small survey plots, our design controlled two of the other widely acknowledged sources of variation: detection cue and distance (Alldredge et al. 2007). We related p to detectability covariates with a logit link. We assessed collinearity in predictor variables and eliminated the poorer predictor of variables that were closely correlated (i.e., $r > 0.6$). This led us to remove two of the landscape-context variables, the percent cover of agriculture and the percent cover of open areas. We fit these models via maximum likelihood using the "nlm" function in R, version 2.5.1 (R Development Core Team 2007).

We ranked and compared models using AIC_c values. We encountered substantial model-selection uncertainty and used model averaging to incorporate this uncertainty into parameter estimates (Burnham and Anderson 2002). We considered predictor variables to be strongly supported if they were included in models with $\Delta AIC_c \leq 2$ and had unconditional confidence intervals that did not include zero.

We used factor analysis (FA) to extract the dominant gradients in the vegetation data set. We used FA rather than principal component analysis because the gradients were easier to interpret ecologically. We used varimax rotation to shift more of the variation onto the first five factors. We ran this analysis with the "factanal" function in R.

RESULTS

We detected 3,849 individuals of 84 species during surveys of 89 points within 37 beaver meadows in 2005 and 2006. Most of these species breed in scrub–shrub habitats, though we also detected numerous marsh birds, waterfowl, aerial insectivores, and woodpeckers (Appendix). Red-winged Blackbird, Common Yellowthroat, Swamp Sparrow, Song Sparrow, Alder Flycatcher, Gray Catbird, Chestnut-sided Warbler, and Eastern Kingbird were detected in >30% of survey plots (scientific names are provided in the Appendix).

Although there was evidence of recent beaver activity at all the beaver meadows we surveyed, microhabitat characteristics varied greatly within and among survey plots in a pattern typically attributed to vegetation succession following beaver abandonment (Table 1 and Fig. 2). This variation was characterized by two dominant gradients that explained 34.7% of the variation of 23 microhabitat variables. The first factor-analysis gradient described plots that varied from simple to complex in vertical structure (Fig. 2). The second gradient described variation in composition from plots dominated by emergent vegetation to plots dominated by woody plants (Fig. 2).

Scrub–shrub bird abundances were related to microhabitat-, patch-, and landscape-context variables, with the best detection-probability corrected models explaining 8–70% of the total variation (Table 2). Microhabitat variables were included in supported models more often than patch and landscape variables. Common Yellowthroat, Swamp Sparrow, Alder Flycatcher, and Chestnut-sided Warbler increased in abundance with increasing structural complexity (Table 3 and Fig. 3A). Common Yellowthroat, Alder Flycatcher, Yellow Warbler, Gray Catbird, and Chestnut-sided Warbler abundances were positively related to the gradient in vegetation composition ranging from plots dominated by emergent plants to plots with extensive coverage of woody plants (Table 3 and Fig. 3B). Common Yellowthroat and Yellow Warbler peaked in abundance at intermediate points along this gradient (Fig. 3B). Red-winged Blackbird was the only species that declined in abundance along this gradient (Fig. 3B).

Patch and landscape variables were also supported as important predictors of scrub–shrub bird abundance (Table 2). Red-winged Blackbird, Yellow Warbler, and Eastern Kingbird abundances increased with beaver-meadow area (Table 3 and Fig. 3C). Eastern Kingbird abundance decreased with increasing patch-shape complexity (Fig. 3D). Red-winged Blackbird abundance declined with increasing surrounding forest cover (Fig. 3E).

Detection probabilities for several species were affected by survey-specific covariates (Table 2). Red-winged Blackbird, Yellow Warbler, and Chestnut-sided Warbler detection probabilities decreased over the course of the breeding season, though Swamp Sparrow detection probability increased (Table 3 and Fig. 4A). Detection probabilities differed between observers for Red-winged

TABLE 1. Summary statistics for microhabitat, patch, and landscape variables of 89 plots in 37 beaver meadows in western Massachusetts surveyed in 2005 and 2006.

Variable	Abbreviation	Mean \pm SD	Minimum	Maximum
Percent cattail	cattail	6.6 \pm 12.9	0.0	85.0
Percent emergent	emerg	29.2 \pm 24.4	0.0	100.0
Percent herbaceous	herb	6.3 \pm 10.1	0.0	55.0
Percent grass	grass	14.6 \pm 12.1	0.0	50.0
Percent <i>Phragmites</i> sp. < 3 m	phragU	2.8 \pm 12.6	0.0	95.0
Percent rush	rush	3.9 \pm 7.0	0.0	40.0
Percent sedge	sedge	18.7 \pm 21.8	0.0	85.0
Percent sapling < 3 m	sapU	3.6 \pm 6.9	0.0	50.0
Percent shrub > 3 m	shrubO	5.4 \pm 11.3	0.0	70.0
Percent shrub < 3 m	shrubU	29.5 \pm 20.4	0.0	80.0
Percent open water	water	12.6 \pm 15.0	0.0	70.0
Percent sapling > 3 m	sapO	7.0 \pm 10.2	0.0	60.0
Percent woody < 3 m	woodyU	33.1 \pm 21.9	0.0	85.0
Height > 300 cm	heightO	93.4 \pm 140.3	0.0	890.0
Height < 300 cm	heightU	124.2 \pm 46.1	37.0	261.5
Water depth (cm)	waterdepth	14.6 \pm 16.9	0.0	98.0
Structure 0–3 m	str	8.3 \pm 3.2	2.1	20.1
Structure 0–1 m	str01	6.0 \pm 2.4	1.5	14.4
Structure 1–2 m	str12	1.8 \pm 1.2	0.1	7.3
Structure 2–3 m	str23	0.5 \pm 0.6	0.0	4.0
Tree height (m)	treeht	6.3 \pm 4.3	0.0	16.6
Tree diameter at breast height (cm)	treedbh	15.2 \pm 10.7	0.0	61.0
Trees > 2.5 cm	treenum	14.6 \pm 19.8	0.0	137.0
Patch area	A	8.3 \pm 4.6	1.1	22.4
Patch shape	S	2.4 \pm 0.7	1.4	3.9
Percent forest within 1 km	F	85.3 \pm 9.7	59.6	97.3
Percent residential within 1 km	R	2.5 \pm 2.2	0.0	9.5

Blackbird, Swamp Sparrow, and Song Sparrow (Fig. 4B). Red-winged Blackbird and Alder Flycatcher detection probabilities decreased with time of day (Fig. 4C). We observed an interactive effect of time and date on Alder Flycatcher detectability, which was lowest at late dates and times of day and highest early in the season at late times of day (Table 3 and Fig. 4D).

DISCUSSION

The present study is the first to describe scrub–shrub bird habitat associations at multiple spatial scales in a natural habitat while accounting for heterogeneous detection probabilities. These results demonstrate that numerous scrub–shrub bird species of conservation concern use beaver meadows in western Massachusetts and that the abundance of several species is related to microhabitat, patch, and landscape-level variables. Two of the eight species that were detected at >30% of the survey plots (Chestnut-sided Warbler and Gray Catbird), as well as 11 additional species (Appendix) are considered priority species in the Northern New England Partners in Flight Landbird Conservation Plan (Hodgman and Rosenberg 2000). Sharp-shinned Hawk is listed as a species of “special concern” by the Massachusetts Division of Fisheries and Wildlife’s Natural Heritage and Endangered Species Program. Finally, Red-winged Blackbird, Common Yellowthroat, Song Sparrow, Chestnut-sided Warbler, and Eastern Kingbird have declined in Massachusetts according to the North American Breeding Bird Survey Data (Sauer et al. 2008).

Many of the scrub–shrub bird species we encountered in beaver meadows were species that are also commonly encountered in other types of scrub–shrub habitats. For example, Common Yellowthroat, Alder Flycatcher, Gray Catbird, Chestnut-sided Warbler, and White-throated Sparrow were among the 10 most abundant scrub–shrub species in both beaver meadows (Appendix) and regenerating clearcuts in New Hampshire (King and DeGraaf 2000) and powerline rights-of-way in Massachusetts (King and Byers 2002, King et al. 2006). There were also notable differences in species composition between beaver meadows and upland sites. Wetland species such as Red-winged Blackbird and Swamp Sparrow are obvious examples of species that were present in beaver meadows but absent from upland habitats. There were also several bird species that were present in upland habitats but absent from beaver meadows, including Prairie Warbler (*Dendroica discolor*) and the state-listed Mourning Warbler (*Oporornis philadelphia*).

The microhabitat relationships we found are consistent with other studies of birds in beaver meadows. First, we found strong, highly variable gradients in vegetation cover and structure in beaver meadows, similar to conditions reported by McMaster and McMaster (2001) and Grover and Baldassarre (1995), which those authors attributed to vegetation succession following beaver abandonment. In our case, these gradients were not attributable to beaver abandonment, given that almost all sites were occupied. Rather, the high degree of variability appeared to be a result of variation in water depth, as determined by dam

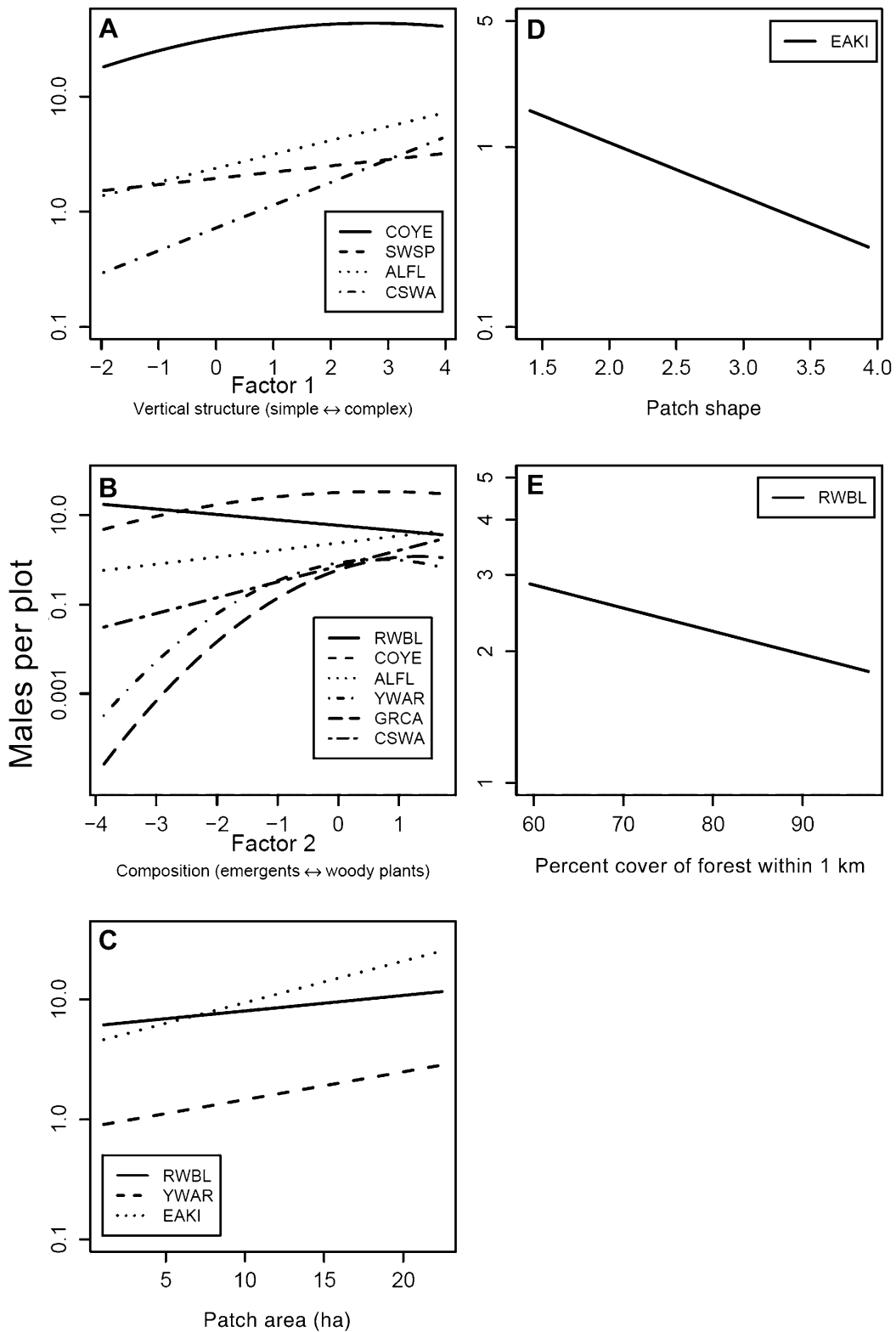


FIG. 3. *N*-mixture model results showing detection-probability corrected relationships between abundance and (A) a gradient of simple to complex vertical structure, (B) a gradient in vegetation composition ranging from plots dominated by emergent vegetation to plots dominated by woody plants, (C) patch area, (D) patch shape, and (E) percent cover of forest within 1 km. Only strongly supported relationships are shown. Abundance is shown on a log scale. Confidence intervals are excluded for clarity, but measures of precision are reported in Table 3. See Table 2 for species abbreviations.

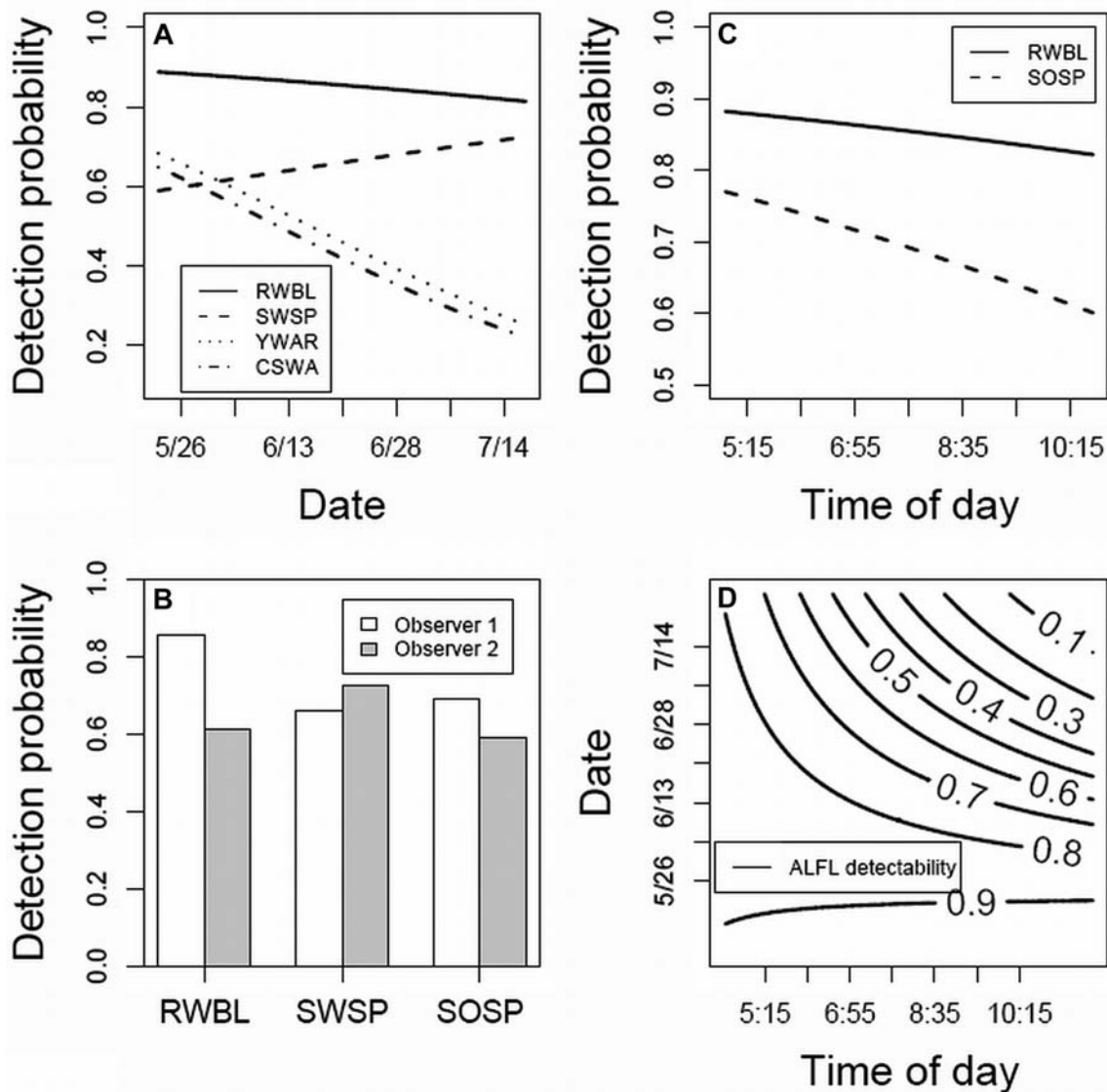


FIG. 4. *N*-mixture model results showing relationships between detection probability and (A) date, (B) observer, (C) time of day, and (D) the interaction between time of day and date. Only strongly supported relationships are shown. Confidence intervals are excluded for clarity, but measures of precision are reported in Table 3. See Table 2 for species abbreviations.

habitats to regional bird conservation will best be realized if beaver meadows with natural flow regimes and, thus, complex microhabitat conditions are present in the landscape (Grover and Baldassarre 1995).

Our finding that some species, such as Red-winged Blackbird, Yellow Warbler, and Eastern Kingbird, were positively associated with meadow size is consistent with previous studies. Grover and Baldassarre (1995) reported that numerous species were absent in the smaller beaver meadows they surveyed, yet present in larger meadows, and that the frequency of occurrence of Eastern Kingbird was twice as high in the largest meadows compared with the smallest ones. Similarly, Riffell et al. (2001) reported that patch area was the best predictor of abundance and occupancy of nine species in scrub-shrub wetlands, though these wetlands were not

modified by beavers. Most species, however, were not strongly correlated with patch area, which probably reflects the fact that most of our sites were considerably larger than 1 ha, the lower limit of patch area used by many scrub-shrub bird species in the Northeast (Askins et al. 2007, Schlossberg and King 2007). Our observation that Eastern Kingbird abundance decreased with increasing shape complexity is consistent with the findings of Edwards and Otis (1999) and Riffell et al. (2001), who also found relationships between bird abundance and patch shape in similar habitats.

Although evidence exists that landscape context can affect scrub-shrub bird abundance (Hagan and Meehan 2002), the only supported relationship we found was a decrease in Red-winged Blackbird abundance with increasing forest cover. This suggests that these species are capable of occupying beaver meadows

irrespective of surrounding land-cover types and that they appear to be most strongly affected by microhabitat and patch variables. The lack of relationships between scrub–shrub bird abundance and percent cover of surrounding forest may indicate that these species are able to colonize isolated patches, a possible adaptation to the ephemeral nature of early-successional habitats (Lent and Capen 1995). Alternatively, the lack of significant relationships between landscape variables and bird abundance could be attributable to differences in landscape conditions between study areas. Hagan and Meehan (2002) worked in an industrial forest, with large areas of clearcut and regenerating forest. By contrast, studies in landscapes with extensive mature forest typically report few or no landscape effects (MacFaden and Capen 2002, Chandler 2006, Askins et al. 2007). Birds in the industrial forest may have had more habitat available and more opportunity to select habitats in a preferred landscape setting. In the other two study areas, birds may have been constrained by the lack of early-successional habitat and forced to settle in whatever patches were available, irrespective of isolation from similar habitat. Grover and Baldassarre (1995) also did not report any evidence that isolation affected birds in beaver meadows.

Detection probability varied for five species in relationship to survey-specific variables, which indicates the need to correct for these influences when modeling habitat associations. Decreases in detectability with time of day and date are consistent with previous research (Kéry et al. 2005, Chandler 2006). We detected differences in observers' abilities to detect two species even though we attempted to standardize observer skill before the surveys began. Similar results have been found even when other sources of variation were experimentally controlled (Allredge et al. 2007). Although our study design and modeling approach removed important sources of bias in abundance attributable to heterogeneity in detectability, the possibility always exists that some bias may still have been present because of other factors not included in our models.

Beaver meadows were historically a common component of landscapes throughout the Northeast, and our results indicate that the re-establishment of beavers in this region could have profound positive effects on scrub–shrub bird populations. However, it is not clear how much habitat beavers supply for scrub–shrub birds in the Northeast. Approximately 4.3% of southern New England is in young forest (U.S. Forest Service 2006), and historical records suggest that beavers could have created a comparable percentage (~3%) of habitat in New York (Gotie and Jenks 1984). Beaver populations are believed to be a small fraction of their pre-colonial numbers, and it is unlikely they will ever recover to their earlier numbers (Naiman et al. 1988). Nevertheless, even 10% of their historical numbers could create a substantial amount of habitat, on the order of hundreds of thousands of hectares.

Our detection-probability corrected abundance models have further elucidated the habitat-selection patterns of these declining birds and will allow conservationists to predict and monitor the consequences of beaver re-establishment for scrub–shrub bird populations. In spite of the predicted positive benefits to scrub–shrub birds, beavers are often considered pests in rural and suburban areas, and many management agencies have been forced to remove beavers or regulate water levels in beaver meadows to prevent their encroachment onto private lands (DeStefano and

DeGraaf 2003). As long as beavers are considered pests, conservation organizations will need to prioritize beaver meadows according to their habitat quality. For scrub–shrub birds, we recommend that efforts be focused on conserving large beaver meadows with natural water-flow regimes. This will allow for the maintenance of spatial and temporal variation in microhabitat conditions required by this specialized bird community while accommodating area-sensitive species.

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APPENDIX. Surveys detected (S), individuals detected (I), mean detections per survey (\bar{x} and SD), and detection cues (s = song, c = call, f = flyover, and v = visual).

Common name	Scientific name	S	I	\bar{x}	SD	Detection cue			
						s	c	f	v
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	119	698	4.95	4.45	679	5	7	7
Common Yellowthroat	<i>Geothlypis trichas</i>	133	562	3.99	1.99	527	20	0	15
Swamp Sparrow	<i>Melospiza georgiana</i>	129	541	3.84	2.48	522	12	0	7
Song Sparrow	<i>Melospiza melodia</i>	100	270	1.92	1.82	260	10	0	0
Alder Flycatcher	<i>Empidonax alnorum</i>	98	251	1.78	1.70	192	53	0	6
Yellow Warbler	<i>Dendroica petechia</i>	64	190	1.35	1.96	184	4	0	2
Tree Swallow	<i>Tachycineta bicolor</i>	74	126	0.89	1.03	12	1	111	2
Gray Catbird	<i>Dumetella carolinensis</i>	58	110	0.78	1.19	87	14	2	7
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	49	100	0.71	1.25	100	0	0	0
American Goldfinch	<i>Carduelis tristis</i>	63	91	0.65	0.85	43	1	44	3
Cedar Waxwing	<i>Bombycilla cedrorum</i>	68	87	0.62	0.77	48	0	36	3
Common Grackle	<i>Quiscalus quiscula</i>	47	72	0.51	0.84	37	4	26	5
Black-capped Chickadee	<i>Poecile atricapillus</i>	45	68	0.48	0.84	63	0	0	5
Eastern Kingbird	<i>Tyrannus tyrannus</i>	50	65	0.46	0.70	56	0	5	4
Veery	<i>Catharus fuscescens</i>	23	44	0.31	0.85	34	9	0	1
Baltimore Oriole	<i>Icterus galbula</i>	25	36	0.26	0.61	31	0	1	4
American Robin	<i>Turdus migratorius</i>	28	35	0.25	0.54	19	9	5	2
Red-eyed Vireo	<i>Vireo olivaceus</i>	20	28	0.20	0.55	16	1	8	3
Blue Jay	<i>Cyanocitta cristata</i>	21	28	0.20	0.56	24	2	0	2
Least Flycatcher	<i>Empidonax minimus</i>	18	26	0.18	0.56	26	0	0	0
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	20	22	0.16	0.40	4	14	4	0
Wood Duck	<i>Aix sponsa</i>	17	20	0.14	0.42	0	3	11	6
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	18	19	0.14	0.36	18	0	0	1
Mallard	<i>Anas platyrhynchos</i>	18	19	0.14	0.36	0	3	15	1
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	15	19	0.14	0.42	16	1	0	2
Magnolia Warbler	<i>Dendroica magnaolia</i>	13	17	0.12	0.42	1	0	16	0
Canada Warbler	<i>Wilsonia canadensis</i>	11	17	0.12	0.50	17	0	0	0
Barn Swallow	<i>Hirundo rustica</i>	12	17	0.12	0.44	17	0	0	0
Black-and-white Warbler	<i>Mniotilta varia</i>	14	16	0.11	0.36	16	0	0	0
White-throated Sparrow	<i>Zonotrichia albicollis</i>	12	15	0.11	0.39	15	0	0	0
Willow Flycatcher	<i>Empidonax traillii</i>	13	15	0.11	0.35	13	0	0	2
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	12	14	0.10	0.34	0	2	5	7
American Redstart	<i>Setophaga ruticilla</i>	10	13	0.09	0.38	12	0	0	1
Eastern Wood-Pewee	<i>Contopus virens</i>	12	12	0.09	0.28	1	6	5	0
Eastern Phoebe	<i>Sayornis phoebe</i>	11	12	0.09	0.30	9	0	0	3
Belted Kingfisher	<i>Megaceryle alcyon</i>	11	12	0.09	0.30	11	0	0	1
Hairy Woodpecker	<i>Picoides villosus</i>	9	10	0.07	0.28	0	9	1	0
Chimney Swift	<i>Chaetura pelagica</i>	8	8	0.06	0.23	1	0	7	0
Virginia Rail	<i>Rallus limicola</i>	7	7	0.05	0.22	0	6	1	0
Purple Finch	<i>Carpodacus purpureus</i>	6	7	0.05	0.25	6	1	0	0
Yellow-rumped Warbler	<i>Dendroica coronata</i>	7	7	0.05	0.22	5	0	1	1
Mourning Dove	<i>Zenaida macroura</i>	6	7	0.05	0.25	2	5	0	0
White-breasted Nuthatch	<i>Sitta carolinensis</i>	5	6	0.04	0.24	6	0	0	0
Northern Waterthrush	<i>Seiurus noveboracensis</i>	5	6	0.04	0.24	0	4	1	1
Northern Flicker	<i>Colaptes auratus</i>	5	6	0.04	0.24	6	0	0	0
Great Blue Heron	<i>Ardea herodias</i>	5	6	0.04	0.24	0	1	4	1
Dark-eyed Junco	<i>Junco hyemalis</i>	5	6	0.04	0.24	0	3	1	2
Canada Goose	<i>Branta canadensis</i>	6	6	0.04	0.20	0	6	0	0
Brown Creeper	<i>Certhia americana</i>	6	6	0.04	0.20	5	0	1	0
Warbling Vireo	<i>Vireo gilvus</i>	5	5	0.04	0.19	5	0	0	0
Northern Cardinal	<i>Cardinalis cardinalis</i>	5	5	0.04	0.19	5	0	0	0
Tufted Titmouse	<i>Baeolophus bicolor</i>	4	4	0.03	0.17	0	0	2	2
Scarlet Tanager	<i>Piranga olivacea</i>	3	4	0.03	0.21	1	1	1	1
Indigo Bunting	<i>Passerina cyanea</i>	4	4	0.03	0.17	4	0	0	0
Green Heron	<i>Butorides virescens</i>	4	4	0.03	0.17	0	3	1	0
Downy Woodpecker	<i>Picoides pubescens</i>	4	4	0.03	0.17	0	4	0	0

(continued)

APPENDIX. Continued.

Common name	Scientific name	<i>S</i>	<i>I</i>	\bar{x}	SD	Detection cue			
						<i>s</i>	<i>c</i>	<i>f</i>	<i>v</i>
Yellow-throated Vireo	<i>Vireo flavifrons</i>	3	3	0.02	0.15	1	0	2	0
Red-shouldered Hawk	<i>Buteo lineatus</i>	3	3	0.02	0.15	0	0	3	0
Pileated Woodpecker	<i>Dryocopus pileatus</i>	3	3	0.02	0.15	0	3	0	0
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	3	3	0.02	0.15	0	0	3	0
American Crow	<i>Corvus brachyrhynchos</i>	2	3	0.02	0.19	3	0	0	0
House Wren	<i>Troglodytes aedon</i>	2	2	0.01	0.12	1	0	0	1
Golden-crowned Kinglet	<i>Regulus satrapa</i>	2	2	0.01	0.12	2	0	0	0
Chipping Sparrow	<i>Spizella passerina</i>	2	2	0.01	0.12	2	0	0	0
Black-throated Green Warbler	<i>Dendroica virens</i>	2	2	0.01	0.12	2	0	0	0
Blue-headed Vireo	<i>Vireo solitarius</i>	2	2	0.01	0.12	2	0	0	0
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	1	2	0.01	0.17	2	0	0	0
Wood Thrush	<i>Hylocichla mustelina</i>	1	1	0.01	0.08	1	0	0	0
Sharp-shinned Hawk	<i>Accipiter striatus</i>	1	1	0.01	0.08	0	0	1	0
Spotted Sandpiper	<i>Actitis macularius</i>	1	1	0.01	0.08	0	1	0	0
Sora	<i>Porzana carolina</i>	1	1	0.01	0.08	0	1	0	0
Ruffed Grouse	<i>Bonasa umbellus</i>	1	1	0.01	0.08	0	1	0	0
Red-breasted Nuthatch	<i>Sitta canadensis</i>	1	1	0.01	0.08	1	0	0	0
Ovenbird	<i>Seiurus aurocapilla</i>	1	1	0.01	0.08	0	0	1	0
Nashville Warbler	<i>Vermivora ruficapilla</i>	1	1	0.01	0.08	0	1	0	0
Louisiana Waterthrush	<i>Seiurus motacilla</i>	1	1	0.01	0.08	0	1	0	0
European Starling	<i>Sturnus vulgaris</i>	1	1	0.01	0.08	1	0	0	0
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	1	1	0.01	0.08	1	0	0	0
Common Merganser	<i>Mergus merganser</i>	1	1	0.01	0.08	0	1	0	0
Blue-winged Warbler	<i>Vermivora pinus</i>	1	1	0.01	0.08	0	1	0	0
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	1	1	0.01	0.08	0	1	0	0
Blackburnian Warbler	<i>Dendroica fusca</i>	1	1	0.01	0.08	0	0	1	0
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	1	1	0.01	0.08	0	0	0	1