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RESEARCH ARTICLE

Habitat occupancy of Rusty Blackbirds (*Euphagus carolinus*) breeding in northern New England, USA

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ABSTRACT

The Rusty Blackbird (*Euphagus carolinus*), an uncommon songbird often associated with northern coniferous wetlands, has experienced a precipitous population decline since at least the early 20th century. Here, we provide the first analysis of breeding-habitat occupancy at the wetland scale and make recommendations for streamlined monitoring. We modeled occupancy and detectability as a function of site (i.e. habitat-based) and sampling (i.e. visit-specific) variables collected at 546 wetlands in northern New England, USA. Wetland occupancy (mean \pm SE = 0.07 ± 0.02 in randomly selected wetlands, and 0.12 ± 0.02 in all wetlands surveyed) was best explained by variables describing Rusty Blackbird foraging habitat (PUDDLES: a proxy for shallow water), nesting habitat (coniferous adjacent uplands), and evidence of beavers. In contrast to Rusty Blackbirds' selection of pole-stage conifers at the nest-site scale, stand age did not affect occupancy at the wetland scale. It appears that most wetlands in northern coniferous forest landscapes, regardless of stand age, offer dense conifer patches nearby and provide suitable breeding habitat if quality foraging sites (e.g., areas of shallow water) also are available. Detectability (0.29 ± 0.04) decreased with increasing wind speed, and decreased about fourfold over the course of the breeding season. Rusty Blackbirds responded to broadcast of conspecific vocalizations by flying toward the observer and perching more often than prior to broadcast, demonstrating that broadcasts can be a useful tool to enhance visual detectability. Given our results, observers can now focus site selection on wetlands and sampling conditions most likely to maximize detections of Rusty Blackbirds.

Keywords: boreal wetlands, broadcast experiment, detectability, *Euphagus carolinus*, monitoring, occupancy, Rusty Blackbird

Occupation de l'habitat par *Euphagus carolinus* nichant dans le nord de la Nouvelle-Angleterre, aux États-Unis

RÉSUMÉ

Euphagus carolinus, un oiseau chanteur peu commun souvent associé aux milieux humides conifériens nordiques, a connu un déclin précipité de ses populations depuis au moins le début du 20^e siècle. Nous fournissons ici la première analyse de l'occupation de l'habitat de reproduction à l'échelle du milieu humide et faisons des recommandations pour un suivi simplifié. Nous avons modélisé l'occupation de l'habitat et la détectabilité comme une fonction du site (i.e. basé sur l'habitat) et des variables d'échantillonnage (i.e. spécifique à la visite) recueillies dans 546 milieux humides du nord de la Nouvelle-Angleterre, aux États-Unis. L'occupation des milieux humides (moyenne \pm SE = 0.07 ± 0.02 dans les milieux humides sélectionnés aléatoirement et 0.12 ± 0.02 dans tous les milieux humides inventoriés) était davantage expliquée par les variables décrivant l'habitat d'alimentation d'*E. carolinus* (PUDDLES: un terme représentant l'eau peu profonde), l'habitat de nidification (milieux secs conifériens adjacents) et la présence de castors. Contrairement à la sélection par *E. carolinus* de conifères au stade de perchis à l'échelle du site de nidification, l'âge du peuplement n'affectait pas l'occupation à l'échelle du milieu humide. Il semble que la plupart des milieux humides dans les forêts conifériennes nordiques, sans égard à l'âge du peuplement, offrent des parcelles de conifères denses à proximité et fournissent un habitat de reproduction propice si des sites d'alimentation de qualité (e.g., zones d'eau peu profonde) sont aussi disponibles. La détectabilité (0.29 ± 0.04) diminuait avec l'augmentation de la vitesse du vent et diminuait d'environ quatre fois au cours de la saison de reproduction. *E. carolinus* répondait à la repasse de chants de ses congénères en volant vers l'observateur et en se perchait plus souvent qu'avant cette émission, ce qui démontre que la repasse de chants peut être un outil utile pour augmenter la détectabilité visuelle. Compte tenu de nos résultats, les observateurs peuvent maintenant concentrer la sélection des sites sur les milieux humides et les conditions d'échantillonnage les plus susceptibles de maximiser les détections d'*E. carolinus*.

Mots-clés: milieux humides boréaux, expérience de repasse de chants, détectabilité, *Euphagus carolinus*, suivi, occupation.

INTRODUCTION

Declining population trends of migratory birds, especially in eastern North America (Sauer and Droege 1992), provided much of the impetus for bird conservation since the mid-1990s. Through the actions of Partners in Flight (Rich et al. 2004), the North American Bird Conservation Initiative (U.S. NABCI Committee 2000), and key conservation organizations (e.g., American Bird Conservancy, Cornell Laboratory of Ornithology, and Rocky Mountain Bird Observatory), species were first prioritized to identify those needing attention (Carter et al. 2000). More recently, with the help of State Wildlife Grants, agencies and organizations have begun the arduous tasks of understanding what drives populations of many of these formerly poorly studied species and developing programs to assist in recovery. During this process, a number of species quickly rose to the top of the list for conservation action. In the northeastern USA, species like Bicknell's Thrush (*Catharus bicknelli*) and Saltmarsh Sparrow (*Ammodramus caudacutus*) became the focus of research and conservation (Atwood et al. 1996, Greenberg et al. 2006, Townsend et al. 2009), often owing to the large percentage of the global population in that region. The Cerulean Warbler (*Setophaga cerulea*) became emblematic of Neotropical migrants needing conservation efforts both in North America and on its wintering grounds in the Andes (Robbins et al. 1992, Rosenberg et al. 2008). The Rusty Blackbird (*Euphagus carolinus*), though widely distributed continentally, has suffered a precipitous long-term decline (Greenberg and Droege 1999, Niven et al. 2004), but of late has been the focus of much research on

both breeding and wintering grounds (e.g., Greenberg and Matsuoka 2010).

The Rusty Blackbird is a migratory songbird that breeds in northern conifer-dominated forests often associated with a variety of wetland types typical of boreal and Acadian forests (Figures 1 and 2). Although population declines are well documented in this now uncommon species (Greenberg and Droege 1999, Niven et al. 2004, Sauer et al. 2005), few studies have quantified breeding habitat at small spatial scales (Buckley 2013) and most information is based on anecdotal accounts, breeding bird atlas records, and government reports. From the information available, it is clear that Rusty Blackbirds use swampy woodlands (Laughlin and Kibbe 1985), fens (Avery 1995), bogs (Peterson 1988, Erskine 1992), damp alder swales (Erskine 1992), and beaver-influenced wetlands (Ellison 1990, Foss 1995). Rusty Blackbirds in the northeastern USA nest primarily in young spruce and fir trees (Kennard 1920, Ellison 1990, Powell et al. 2010b, Buckley 2013), often in stands regenerating from timber harvest, seemingly well away from large wetlands. Although Rusty Blackbirds forage in wetlands and consume aquatic prey (Beecher 1951, Ellison 1990, Avery 1995), it remains unclear what habitat characteristics influence occupancy.

There are so few encounters of Rusty Blackbirds on the Breeding Bird Survey and during state atlas projects that population trend estimates are not reliable for the northeastern USA and the Maritime Provinces of Canada (Erskine 1977, Sauer et al. 2005). At the continental scale,



FIGURE 1. Typical Rusty Blackbird breeding habitat in New England as seen in mid-May prior to leaf-out. Foraging habitat (i.e. shallow water and puddles) is visible in the foreground, while nesting habitat (i.e. thick, short spruce and fir) can be seen in the background.



FIGURE 2. Research technician James Osenton points to a Rusty Blackbird nest located about 1.5 m high in the thick fir to the right of the double-snag. Here a beaver impoundment had created foraging habitat for the species (i.e. shallow water; foreground) within a stand of mostly mature spruce and fir (background). Water level had dropped since the initial impoundment of the creek, creating a drier patch of perhaps 25 thick young conifers in which the Rusty Blackbirds nested (midground).

Rusty Blackbird populations have declined by 85% (Sauer et al. 2004) to >95% (Sauer et al. 2005) since 1966, and there is strong qualitative evidence for population declines dating back at least 100 years (Greenberg and Droege 1999). The species' range has contracted by 160 km in Maine since 1983 (Powell 2008), but the lack of contemporary data makes it difficult to determine whether declines are ongoing. Causes of the decline are unknown, although the loss of wooded wetlands on nonbreeding grounds in the southeastern USA is a likely contributor (Greenberg and Droege 1999). On the breeding grounds, timber management (Powell et al. 2010b), road construction, changes in wetland hydrology (Klein et al. 2005), competition with other icterids (Ellison 1990, Erskine 1992), and mercury accumulation (Edmonds et al. 2010) have all been hypothesized as contributing to the species' decline.

Here, we use an occupancy framework to quantify Rusty Blackbirds' habitat use at the wetland scale and, using our findings, we make recommendations to streamline future efforts to locate meaningful numbers of the species. Given the species' nesting and foraging habits, we hypothesize that wetland occupancy is linked to (1) coniferous growth in and adjacent to wetlands and (2) indicators of shallow water (e.g., puddles, mud). Our primary objectives were to provide the first analysis of breeding-habitat occupancy at the wetland scale and to use the results of our detectability and occupancy analyses to provide recommendations to improve efficiency of monitoring efforts for this uncommon yet widely distributed species. Secondarily, we examined behavior of Rusty Blackbirds following broadcast of conspecific vocalization to determine whether detectability could be improved by this simple technique.

METHODS

Study Area

We conducted our study in northern and western Maine and northeastern Vermont, USA (Figure 3). Our northern Maine sites occurred in a largely uninhabited and relatively flat industrial forest landscape, within which we surveyed mostly low-elevation wetlands adjacent to coniferous forests of varying ages. Few wetlands in northern Maine were protected from timber harvest by riparian buffers during the 1970s and 1980s, when many wetlands were subjected to clear-cut or partial harvests to their edges or within their boundaries. Forest type and management in western Maine and northeastern Vermont were similar but, unlike in northern Maine, characterized by small-scale timber operations. In Vermont, rural communities perforate a landscape with considerably more topographic relief than in northern Maine. From the ground, we estimated that most wetlands we surveyed were in the 0.5 to 2 ha range, although size varied from about 0.1 ha to about 10

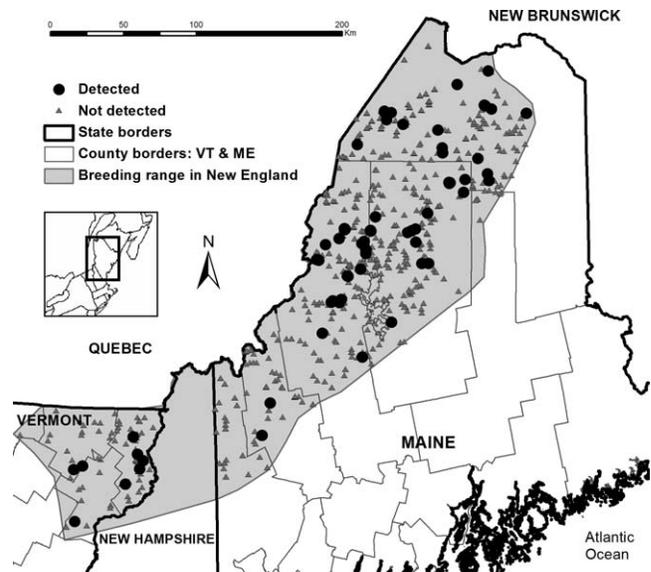


FIGURE 3. Map of Rusty Blackbird surveys in 546 wetlands in Maine and Vermont, USA, 2006–2007.

ha. We surveyed a variety of wetland types, including bogs, wooded fens, alder (*Alnus incana*) swamps, cattail (*Typha latifolia*) marshes, and flowages created by American beaver (*Castor canadensis*). Black spruce (*Picea mariana*), red spruce (*P. rubens*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), speckled alder, and *Sphagnum* spp. were the dominant species in surrounding forests.

Sampling Design

We performed point counts for breeding Rusty Blackbirds at 546 wetlands from 29 April to 27 June in 2006 and 2007. All 546 wetlands were within the Rusty Blackbird's current breeding range (Figure 3; Greenberg et al. 2011) as defined by Powell (2008). Because of time constraints, we only surveyed wetlands in which wetland vegetation (typically alder or standing dead cedars) was visible from roads. Our sampling units, which we define as wetland-scale, were restricted to what we could see and hear (and what the birds could hear, i.e. broadcast) from a single point-count location from a road at the edge of a wetland.

We used results of these surveys to model occupancy and detectability. We selected wetlands for survey on the basis of four approaches, as denoted by the variable CHOICE (Table 1). For CHOICE_{Literature}, we drove accessible forest roads and selected 352 wetlands in the field on the basis of descriptions of suitable habitat (Ellison 1990, Avery 1995, Hodgman and Hermann 2003) and our previous field experience with Rusty Blackbirds in Maine. CHOICE_{Literature} wetlands had at least some short coniferous vegetation (nesting habitat) and some visible

TABLE 1. Variables used to model detectability and habitat occupancy of Rusty Blackbirds in Maine and Vermont, USA, 2006–2007.

| Variable | Description ^a |
|----------------------|---|
| Site variable | |
| BEAVER | Current evidence of beaver activity, including freshly chewed wood, scat, or an actively maintained dam |
| CHOICE | Categorical variable; denotes whether wetland was selected on the basis of literature (CHOICE _{Literature}), by stratified random design (CHOICE _{Random}), because it was previously occupied by Rusty Blackbirds (CHOICE _{Old+}), or because of an opportunistic encounter of Rusty Blackbirds while driving between sites (CHOICE _{Driveby}) |
| HARVEST5TO15 | Upland was harvested between 5 and 15 years prior |
| MUD | Presence of any mud in or adjacent to the wetland |
| PUDDLES | Presence of shallow water not contiguous with open or flowing water |
| ROAD | Four ordinal categories: unimproved dirt road, little-used improved dirt road, well-used improved dirt road, paved road |
| SOFTWD_UP | Adjacent upland >70% softwood; binary |
| WETAREA ^b | Four wetland area categories (ha) as estimated by the observer from the survey location: <0.1, 0.1–0.5, 0.6–2.0, >2.0 |
| YNGSF | Presence of spruce or fir <3 m tall within wetland |
| Sampling variable | |
| DATE | Julian day/100 |
| MIN | Minute of day at which survey began |
| BROADCAST | Categorical variable allowing detectability to vary among survey intervals before (3 min), during (38 s), and after (5 min) broadcast of Rusty Blackbird vocalization |
| PRECIIP | Binary measure of precipitation during survey |
| SHRUB | Percentage of the wetland vegetation composed of shrubs (<2 m) |
| SKY | Three categories: <10% clear, 11–90% clear, >90% clear |
| WIND | Mean wind index during survey (continuous): 0 = no wind (<1 km h ⁻¹), 1 = leaves rustle gently (1–5 km h ⁻¹), 2 = feel wind on face (6–11 km h ⁻¹), 3 = wind clogs one ear (12–19 km h ⁻¹), 4 = wind clogs both ears (20–29 km h ⁻¹) |
| YEAR | Binary variable: whether the survey was performed in 2006 (i.e. not 2007) |

^a All variables estimated by the observer from the survey point.

^b Run as both a site and a sampling variable.

shallow water (i.e. foraging habitat). However, to better represent the variability of wetlands across the landscape, in 2007 we added 143 wetlands in northwestern Maine and northeastern Vermont that we selected using a geographically stratified random design (CHOICE_{Random}); we identified those wetlands using a digital copy of the National Wetlands Inventory layer (Cowardin et al. 1979). If a randomly selected site was obviously unsuitable upon first visitation (e.g., no coniferous nesting habitat, no open water), we surveyed the next nearest wetland that appeared suitable. To increase our detections and, thus, our predictive power, we also surveyed 46 wetlands that, according to the best available information (anecdotal reports from birders; Hodgman and Hermann 2003, Sauer et al. 2005), were previously occupied by Rusty Blackbirds (CHOICE_{Old+}). Finally, we included six sites on the basis of opportunistic detections of Rusty Blackbirds when driving between sites (CHOICE_{Driveby}).

During the 2006 season, we conducted one survey per wetland. After this first field season, it became clear that occupancy modeling was rapidly becoming the preferred technique to model presence–absence of animals in discrete habitat patches (MacKenzie et al. 2006); accordingly, in the 2007 season, we performed multiple surveys at

a random subset of wetlands to estimate detectability (Table 2). Each survey included 3 min of passive observation followed by a prerecorded 38-s broadcast of a male Rusty Blackbird vocalization and then 5 min of passive observation. The broadcast, recorded in New York State, consisted of ~90% male songs and call (*chek*) notes and ~10% garbled chatter (Avery 1995). We broadcasted the recorded vocalization using a Predation MP3 Game Caller (Western Rivers, Lexington, Tennessee) with the volume set to 20, resulting in a broadcast ~30% louder than vocalizations of live birds. During each survey interval (i.e. before, during, and after broadcast), we recorded detections and behavior of Rusty Blackbirds.

Following each point count, we recorded site (i.e. habitat) and sampling (i.e. visit-specific) variables (Table

TABLE 2. Number of visits by year to each of 546 wetlands in Maine and Vermont, USA, 2006 and 2007.

| Year | Number of visits | | |
|------|------------------|----|----|
| | 1 | 2 | 3 |
| 2006 | 251 | 0 | 0 |
| 2007 | 223 | 22 | 50 |

1). We selected site variables that we thought would affect habitat selection on the basis of descriptions in the literature (Kennard 1920, Ellison 1990, Avery 1995, Hodgman and Hermann 2003) and our previous field experience with the species. Specifically, we recorded site variables indicative of shallow-water foraging habitat (MUD, PUDDLES, and BEAVER) and area of foraging habitat (WETAREA), indicators of nesting habitat (HARVEST5to15, SOFTWOOD_UP, YNGSF), and the class of road (e.g., primary or secondary) we were surveying from (ROAD). We used 5 to 15 years old as the age class for HARVEST5to15 because this seemed the appropriate age for nesting habitat according to the literature and our experience finding nests in 2006. We arbitrarily used >70% softwoods in the adjacent uplands as the cutoff for SOFTWOOD_UP. We documented sampling variables that we believed would decrease detectability (PRECIP, SHRUB, SKY, WIND, DATE, MIN). We also added BROADCAST, a variable that allowed detectability to vary among survey periods. This variable included the combined effects of conspecific broadcast and survey period length. We surveyed during all daylight hours in 2006 but detected few individuals during midday (Powell 2008); accordingly, we did not survey from 1100 to 1600 hours in 2007. We did not survey in heavy rain or strong wind ($> \approx 25 \text{ km h}^{-1}$).

Modeling Occupancy and Detectability

We modeled Rusty Blackbird occupancy (ψ_i) as a function of site characteristics affecting presence–absence, contingent on site and sampling covariates affecting detectability (MacKenzie et al. 2002), using the package UNMARKED (Fiske and Chandler 2010) in Program R (R Development Core Team 2009). Our general strategy was to formulate a candidate set of models describing detectability (p), select a best-fit model, then use that best-fit detectability model as the base model in the candidate set of occupancy models.

We used several statistical adjustments to account for our unique sampling design using UNMARKED. We used a “single-season” occupancy models (MacKenzie et al. 2006), with 2 years worth of data collapsed into 1 year. To account for potential year effects, we included YEAR in the occupancy candidate set as a site variable. To conform to the data structure required for “single season” models, in the handful of cases in which we surveyed the same wetland in both years, we used only the data from 2007. Rather than discard our single-visit data set from 2006 (Table 2), we pooled it with our multiple-visit dataset from 2007, treated the second and third visits in 2006 as missing data, and developed models under the assumption that detectability did not vary between 2006 and 2007. Sites that we selected because of opportunistic sightings of Rusty Blackbirds (CHOICE_{Driveby}) were obviously occupied; hence, to avoid biasing our overall estimates of occupancy, we fixed occupancy of those six sites to 1.0. To

avoid potential errors associated with values much greater than zero, we transformed sampling variables with large values by dividing by 100. We treated each sampling interval (BROADCAST_{before}, BROADCAST_{during}, BROADCAST_{after}) as a separate visit, simultaneously accounting for the difference in use of a prerecorded broadcast and length of survey intervals by modeling each survey interval separately as a unique categorical variable (A. Royle, Patuxent Wildlife Research Center, personal communication). We were able to treat those consecutive sampling intervals as separate visits because in occupancy modeling, all detections at a site are modeled conditionally on the latent occupancy state of the site. Thus, correlation among detection methods (treated as separate visits in the model) is implicit in the hierarchical occupancy model because all visits depend on the same ψ_i .

To model Rusty Blackbird detectability, we formulated 18 a priori models that included combinations of the eight variables that we hypothesized were affecting detection probability (Table 1). Because one of our goals was to make recommendations for monitoring that maximize species detections, we were particularly interested in testing hypotheses that detectability decreased over the course of the season (DATE) as males became less territorial, or decreased over the course of the day (MIN), so we included additive combinations of those variables that we believed were biologically plausible. We included two quadratic models to test the alternative hypotheses that (1) detectability was highest near dawn and dusk (MIN²) and (2) birds were most detectable early in the season (when males were strongly territorial) and again late in the season (when fledglings were vocal and volant; DAY²). Other variables that we suspected would decrease detectability (WIND, SKY, PRECIP, SHRUB, WETAREA) were included in univariate models and as part of nested models with BROADCAST, DATE, and MIN. Finally, we suspected negative interactions between WETAREA and BROADCAST as well as WETAREA and WIND, so we included two bivariate interactive models.

To model wetland occupancy, we first used the literature on breeding Rusty Blackbirds (Kennard 1920, Laughlin and Kibbe 1985, Ellison 1990, Erskine 1992, Avery 1995) and our own field observations to compile a candidate set of 15 a priori models. We used the detectability model with the lowest Akaike's Information Criterion (AIC) value (the “best-fit” model) as the base detection model for all occupancy models. We believe that the Rusty Blackbird is inherently a wetland bird and that, at the wetland scale, Rusty Blackbird occupancy is driven primarily by selection for foraging habitat (i.e. shallow water high in invertebrates; Avery 1995) and nesting habitat (i.e. coniferous growth; Ellison 1990), so all occupancy models were what we believed to be biologically plausible combinations of foraging and nesting habitat. Beavers can create both

nesting habitat (by selectively eating hardwoods; Johnston and Naiman 1990) and foraging habitat (through flooding; McDowell and Naiman 1986), so $\psi(\text{BEAVER})$ was our only univariate occupancy model. To test for year effects, we created nested models by repeating combinations of habitat in two models, adding only YEAR. Finally, we wondered whether the disturbance caused by larger, more heavily used roads decreased Rusty Blackbird occupancy, so again we added ROAD to otherwise identical habitat models.

We ranked the fit of models using AIC and considered models with ΔAIC values <2 as those with substantial support (Burnham and Anderson 2002). We assumed, a priori, that occupancy varied among wetlands selected (1) for apparent suitability, (2) with a stratified random design, and (3) on the basis of opportunistic sightings, so we included the categorical variable CHOICE as the base model for all models in the study. We checked for correlations among explanatory variables with Spearman's rank correlation test and avoided using correlated variables ($P < 0.05$) in the same model. We used AIC to select models that best described occupancy and detectability. In the few cases in which we had missing data (e.g., one category was omitted on the data sheet), we replaced missing values for continuous and binary variables with the mean and categorical variables with the mode. When model-averaging, we used all models in the candidate set for occupancy. We evaluated model fit of the global models for occupancy and detectability using a goodness-of-fit test with 100 parametric bootstraps (Burnham and Anderson 2002, MacKenzie et al. 2006).

Broadcast Experiment

Because survey interval length was tightly linked to use of the broadcast in our experimental design (see above), we were not able to disentangle the effects of broadcast and interval length in an occupancy modeling framework—UNMARKED does not have such flexibility (R. Chandler personal communication). Therefore, to gain insight into how behavioral response to broadcast vocalizations may affect detectability, we used counts of five behaviors (i.e. flew toward observer, song, calls, perched, flew away from observer) recorded during each survey interval to run generalized linear models in Program R with the deviance distributed as chi-square and an offset that accounts for the difference in survey interval length. We tested the null hypotheses that behavioral counts in the prebroadcast interval were no different from those in the during-broadcast and postbroadcast intervals. To avoid potential pseudoreplication of individuals, we included only the first survey per wetland in which we detected the species. Results are presented as means \pm SE.

RESULTS

Detectability

The best-fit model for detectability ($-2 \log\text{-likelihood} = 495.6$, number of parameters $K = 8$, $\text{AIC} = 511.6$) included the variables WIND ($\beta = -0.36 \pm 0.20$), DATE ($\beta = -5.3 \pm 1.2$), BROADCAST ($\beta_{\text{before}} = [\text{no estimate; reference category}]$, $\beta_{\text{during}} = -0.61 \pm 0.39$, $\beta_{\text{after}} = 0.75 \pm 0.35$), and an intercept ($\beta = 7.8 \pm 1.9$). The best-fit model performed far better than any other model ($w_i = 0.99$), and no other models received substantial support ($\Delta\text{AIC} > 9$). In the best-fit model, absolute levels of detection before, during, and after broadcast (not corrected for interval length) were 0.28 ± 0.06 , 0.18 ± 0.05 , and 0.45 ± 0.07 , respectively. Detectability decreased steeply throughout the season, with surveys in early May nearly $4\times$ more likely to detect a Rusty Blackbird than those in late June (Figure 4A). Predictably, detectability decreased steadily with wind speed (Figure 4B). Post hoc models including interaction terms did not outperform the additive best-fit detectability model. Although we suspected that detectability was lowest during midseason, we found no evidence to support those suspicions, in that the quadratic model (DATE^2) received considerably less support than the univariate model with DATE. Contrary to earlier results using naive detections (Powell 2008), our approach found no evidence that time of day affected detectability ($\Delta\text{AIC} > 32$). We estimated a mean detectability of 0.29 ± 0.04 (95% confidence interval [CI]: $0.22\text{--}0.37$); in other words, given that a site was occupied, we detected one or more Rusty Blackbirds in ~ 3 out of 10 surveys. A goodness-of-fit test indicated that our global model fit the data ($P = 0.14$), and post hoc models that included an interaction term did not outperform the best-fit model ($\Delta\text{AIC} > 4$).

Occupancy

We detected Rusty Blackbirds in 46 of the 546 wetlands surveyed during 2006 and 2007 (naive occupancy = 0.084). The best-fit model for occupancy included the variables SOFTWOOD_UP , BEAVER, and PUDDLES (Tables 3 and 4). SOFTWOOD_UP was included in only the top five models (Table 3), and sites with $>70\%$ softwoods in the upland were about twice as likely to be occupied by Rusty Blackbirds (Figure 5). Age of softwoods was considerably less important: the 11 models that included YNGSF or HARVEST5to15 received little support (Table 3). PUDDLES was included in the top six models because Rusty Blackbirds were more than $4\times$ more likely to be found at sites with independent shallow water than those without (Figure 5). MUD, however, was a poor predictor of foraging habitat; models that included this variable received little support (Table 3). Wetlands with evidence of beaver activity were positively correlated with Rusty

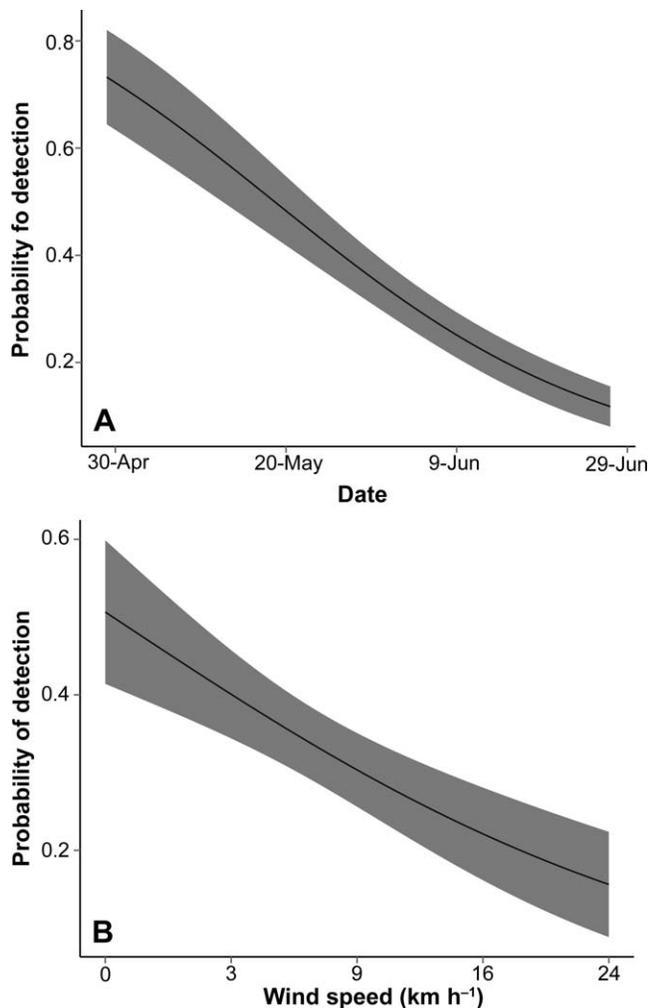


FIGURE 4. Estimated probability of detection (\pm SE) of Rusty Blackbirds in Maine and Vermont, USA, 2006–2007, over the course of the season (A) and with increasing wind speed (B), as generated from the best-fit model for detectability. Scale on x-axis in (B) is not linear, because it is based on nonlinear ordinal categories of wind speed (see Table 1).

Blackbird occupancy; BEAVER appeared in three of the five best-fit models. Further, removing BEAVER from the best-fit model decreased model fit (Δ AIC = 2.6; Table 3), and wetlands with BEAVER were twice as likely to be occupied by Rusty Blackbirds as those without (Figure 5). The univariate model with BEAVER was only marginally better than the null model, suggesting that Rusty Blackbird occupancy cannot be explained by the presence of beavers alone. To confirm, post hoc, that CHOICE was an appropriate variable to include in the base model, we ran the best-fit model without CHOICE—predictably, model fit suffered (Δ AIC = 1.6) despite the steep penalty (+6) imposed by AIC for including this three-category variable. Wetlands occupied in previous seasons were more than twice as likely to be occupied, compared with sites selected

from the literature or using stratified random design (Figure 5). Further, CHOICE_{old+} wetlands (those that were occupied in previous years) were more than twice as likely to be occupied, compared with wetlands chosen by other means (Figure 5). Adding YEAR to the best-fit model decreased model fit (Δ AIC = 1.2), the parameter estimate for YEAR ($\beta = 0.41 \pm 0.46$) was imprecise, and estimates showed practically no difference in occupancy between years (Figure 5), providing no substantial evidence that YEAR affected occupancy; thus, we made the simplifying assumption that the population was closed to changes in occupancy between 2006 and 2007. Although we detected one or more Rusty Blackbirds in only 1 of 78 wetlands smaller than 0.1 ha, the categorical variable WETAREA as a whole did not receive strong support ($\sum w_i = 0.08$); however, predicted probabilities suggest that wetlands smaller than 0.5 ha were less likely to be occupied than larger wetlands (Figure 5). Adding ROAD to the best-fit model decreased model fit (Δ AIC = 6.3), providing essentially no evidence that relatively large roads had a negative impact on Rusty Blackbird occupancy. Contingent on our detectability analysis, mean wetland occupancy was 0.12 ± 0.02 (95% CI: 0.08–0.18), which applies only to the wetlands we surveyed in the present study. In other words, when we considered birds that were present but not detected, ~12% of surveyed wetlands were occupied. Sites selected using stratified random design were marginally less likely to be occupied (CHOICE_{Random}: 0.07 ± 0.02 , 95% CI: 0.03–0.11) than those selected in the field on the basis of literature and our experience (CHOICE_{Literature}: 0.10 ± 0.01 , 95% CI: 0.07–0.13; Figure 5).

Broadcast Experiment

After correcting for survey length, we found that during wetland surveys, Rusty Blackbirds flew toward the observer and perched significantly more during the broadcast than before the broadcast ($P < 0.001$; Figure 6). Rusty Blackbirds also flew toward the observer marginally more in the postbroadcast interval than in the prebroadcast interval ($P < 0.06$); no other comparisons were significantly different.

DISCUSSION

Habitat Occupancy

The availability of Rusty Blackbird nesting habitat positively influenced occupancy—specifically when trees in the adjacent uplands were $\geq 70\%$ softwoods. In New England, most (62 of 65) documented Rusty Blackbird nests were placed in conifers (Kennard 1920, Ellison 1990, Powell et al. 2010b), and many nests in our study were in dense balsam fir 1–3 m high (Powell et al. 2010b). Comparatively, in coastal Alaska and Canada, most nests were placed in small spruce (*Picea* sp.) trees, but in interior

TABLE 3. Akaike's Information Criterion (AIC)^a model selection results for models predicting wetland occupancy (ψ) of Rusty Blackbirds in Maine and Vermont, USA, 2006–2007.

| Model | -2 Log-likelihood | K^a | AIC | Δ AIC | w_i |
|--|-------------------|-------|-------|--------------|-------|
| ψ (SOFTWD_UP + BEAVER + PUDDLES) ^b | 471.7 | 11 | 493.7 | 0.0 | 0.47 |
| ψ (SOFTWD_UP + BEAVER + PUDDLES + YEAR) | 470.9 | 12 | 494.9 | 1.2 | 0.26 |
| ψ (SOFTWD_UP + PUDDLES) | 476.2 | 10 | 496.2 | 2.6 | 0.13 |
| ψ (SOFTWD_UP + PUDDLES + WETAREA) | 471.4 | 13 | 497.4 | 3.7 | 0.07 |
| ψ (SOFTWD_UP + BEAVER + PUDDLES + ROAD) | 469.9 | 15 | 499.9 | 6.3 | 0.02 |
| ψ (PUDDLES + YNGSF) | 480.8 | 10 | 500.8 | 7.1 | 0.01 |
| ψ (MUD + HARVEST5TO15) | 481.0 | 10 | 501.0 | 7.3 | 0.01 |
| ψ (PUDDLES + YNGSF + YEAR) | 479.2 | 11 | 501.2 | 7.5 | 0.01 |
| ψ (WETAREA + MUD + BEAVER) | 476.3 | 13 | 502.3 | 8.7 | 0.01 |
| ψ (YNGSF + MUD) | 483.0 | 10 | 503.0 | 9.4 | 0.00 |
| ψ (WETAREA + HARVEST5TO15) | 480.3 | 12 | 504.3 | 10.7 | 0.00 |
| ψ (YNGSF + MUD + YEAR) | 482.8 | 11 | 504.8 | 11.1 | 0.00 |
| ψ (BEAVER + YNGSF) | 487.3 | 10 | 507.3 | 13.7 | 0.00 |
| ψ (MUD + HARVEST5TO15 + YEAR) | 489.1 | 10 | 509.1 | 15.5 | 0.00 |
| ψ (BEAVER) | 491.8 | 9 | 509.8 | 16.1 | 0.00 |
| ψ (-) | 495.6 | 8 | 511.6 | 18.0 | 0.00 |

^a K is number of parameters; Δ AIC is difference in AIC in relation to the most parsimonious value; w_i is Akaike weight.

^b Base model for all models shown: ψ (CHOICE), p (WIND + DATE + BROADCAST), where p denotes detectability.

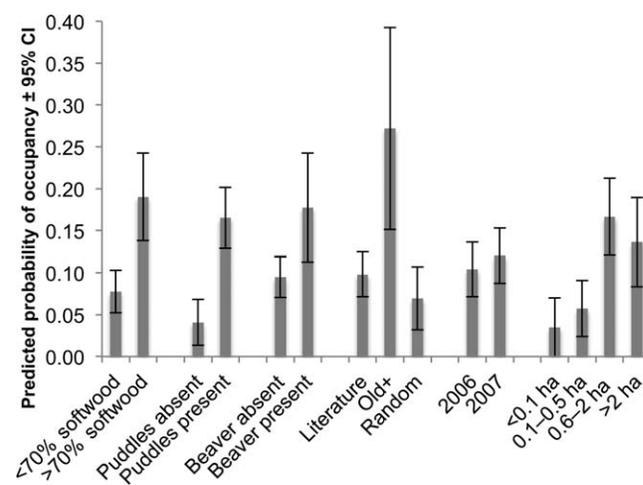
Alaska, most nests were in willows (*Salix* sp.), which suggests some flexibility with respect to nest-site selection (Matsuoka et al. 2010b). We detected Rusty Blackbirds in wooded fens, in wetlands adjacent to mature coniferous forest, and in wetlands adjacent to 10- to 15-year-old clearcuts, which suggests that the species is also somewhat flexible with respect to selection at the wetland scale. Although most nests found in our study area were in thick

young conifers regenerating from timber harvests (Powell et al. 2010b), and Rusty Blackbirds in New Hampshire may select for young coniferous regrowth at the landscape scale (P. Newell and C. Foss personal communication), occupancy at the wetland scale was apparently not influenced by age of coniferous growth. In contrast to the results of a previous analysis (Powell 2008), YNGSF and HARVEST5-to15 were poor predictors of occupancy at the wetland scale, providing no evidence that Rusty Blackbirds in our study area select wetlands solely on the basis of young coniferous growth either within or adjacent to the wetlands; rather, they appeared to select wetlands sur-

TABLE 4. Model-averaged parameter estimates, standard errors, and 95% confidence intervals (CI) for models describing occupancy of Rusty Blackbirds in Maine and Vermont, USA, 2006–2007.

| Covariate | Estimate | 95% CI |
|--|----------|----------------|
| Habitat occupancy | | |
| CHOICE _{Old+} ^a | 1.20 | 0.23 to 2.17 |
| CHOICE _{Random} | -0.35 | -1.30 to 0.59 |
| PUDDLES | 1.97 | 0.73 to 3.21 |
| BEAVER | 0.88 | 0.10 to 1.67 |
| SOFTWD_UP | 1.06 | 0.32 to 1.80 |
| WETAREA _{0.1–0.5ha} | 0.18 | -1.52 to 1.88 |
| WETAREA _{0.6–2ha} | 1.17 | -0.38 to 2.72 |
| WETAREA _{>2ha} | 0.86 | -0.76 to 2.49 |
| YEAR | 0.35 | -0.53 to 1.23 |
| Detection probability | | |
| DATE | -5.13 | -7.43 to -2.84 |
| BROADCAST _{during} ^a | -0.54 | -1.26 to 0.18 |
| BROADCAST _{after} | 0.72 | 0.06 to 1.37 |
| WIND | -0.33 | -0.71 to 0.06 |

^a Categories CHOICE_{Literature} and BROADCAST_{before} do not have parameter estimates because they are reference categories. CHOICE_{Driveby} is not shown because occupancy was fixed at 1.0 for those six observations. Absolute levels of occupancy or detectability for those categories are presented in Results.

**FIGURE 5.** Mean predicted probabilities of occupancy for Rusty Blackbirds in Maine and Vermont, USA, as described by six explanatory variables, from left to right: SOFTWOOD_UP, PUDDLES, BEAVER, CHOICE, YEAR, and WETAREA.

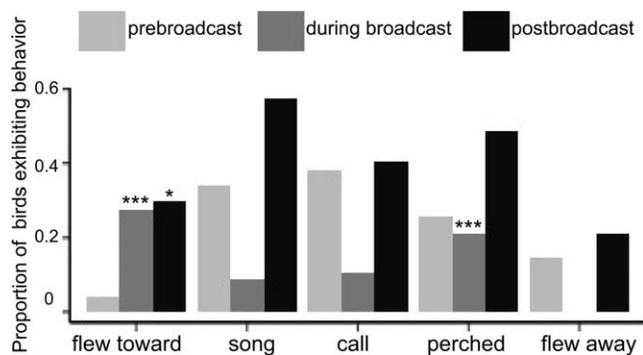


FIGURE 6. Behavioral responses of Rusty Blackbirds ($n = 47$) prior to (3 min), during (38 s), and after (5 min) broadcast of Rusty Blackbird vocalizations in Maine and Vermont, USA, 2006–2007. Symbols indicate significant difference from prebroadcast period, correcting for difference in period length, at $P < 0.1$ (*) and $P < 0.001$ (***). Proportions shown are not corrected for period length.

rounded by conifers, regardless of age. In the absence of timber harvests, Rusty Blackbirds may be content to nest in naturally stunted conifers such as those found in bogs and fens or in small patches of regenerating coniferous growth created by beavers or resulting from windthrow (Kennard 1920, Ellison 1990).

Although the species frequently nests in short coniferous growth, regenerating clear-cuts adjacent to wetlands may attract Rusty Blackbirds into uplands where their nests are subject to higher predation risk (Powell et al. 2010b) and, possibly, ecological traps (Robertson and Hutto 2006). That Rusty Blackbirds do not appear to target regenerating conifer stands at the wetland scale is thus significant. We suspect that in the early spring, individuals returning to breeding grounds select habitat at multiple scales, targeting landscapes with wetlands surrounded by at least some short coniferous growth that contain cues indicating good foraging habitat, such as shallow water with high invertebrate biomass. After pairing, females probably select nest sites in the thickest coniferous growth that are often (but not always) near wetlands (Ellison 1990, Matsuoka et al. 2010b, Powell et al. 2010b, Buckley 2013).

Rusty Blackbirds forage in shallow water, where they probe for aquatic prey in leaf litter (Bent 1958, Ellison 1990, Avery 1995). We strongly suspect that the area of shallow water (<6 cm deep) is an important driver of habitat selection, but due to logistical constraints we were unable to quantify the availability of shallow water at each wetland, and instead used MUD and PUDDLES as proxies. PUDDLES was a strong predictor of occupancy and was generally indicative of shallow water, which we believe is ideal foraging habitat for Rusty Blackbirds. Shallow water unconnected to flowing tributaries often teems with prey items (e.g., tadpoles and Odonates; L. Powell personal observation), presumably because of a lack of predatory

fish and evaporation by seasonal drying. We believe that amphibian eggs and larvae, as well as invertebrate larvae, likely provide an easily accessed, calorie-rich food source in sites with shallow water; this warrants further investigation. Unlike PUDDLES, MUD was a poor predictor of occupancy. Although we observed Rusty Blackbirds foraging on mud, the presence of mud likely indicates a recent lowering of the water table (e.g., failed beaver dam, rapid seasonal drying) but appears to be less indicative than shallow water of quality foraging conditions. The amount of shallow water varies both within and among years, but it remains unclear how seasonal variations in rainfall affect occupancy, colonization, or extinction of suitable habitat on the breeding grounds. To better understand the dynamic nature of rainfall and hydrology on Rusty Blackbird occupancy, future efforts could design studies similar to that of DeLeon (2012), who used repeated site visits to model the effect of shallow water on occupancy of wintering Rusty Blackbirds both within and among years. Furthermore, future research could aid management efforts by understanding the scale of selection for shallow water. For example, do Rusty Blackbirds select breeding habitat on the basis of general abundance of surface water on the landscape (Matsuoka et al. 2010a) or the prevalence of shallow water at small spatial scales?

American beavers probably create both foraging and nesting habitat for Rusty Blackbirds, and our data correspondingly suggest that beaver presence increases the probability of occupancy when nesting and foraging habitat are already present. Beavers selectively remove hardwoods, which increases light gaps and encourages growth of nonpreferred trees such as spruces (Johnston and Naiman 1990). McDowell and Naiman (1986) found that beavers increase the density of coarse particulate organic matter and the biomass of invertebrates by 2–5 times, and beavers specifically increased the abundance of four of the Rusty Blackbird's prey items: dragonflies (Odonata), damselflies (Odonata), caddisflies (Trichoptera), and snails (Gastropoda; Avery 1995, Harthun 1999). Beavers may facilitate Rusty Blackbird habitat use by augmenting nesting and foraging habitat, so a logical next step would be to test the hypothesis that active beaver control (e.g., beaver exclusion devices, trapping, lethal control; all common practices in New England) has a negative impact on Rusty Blackbirds. Further, it remains unclear which stage(s) of beaver colonization or abandonment offer the most Rusty Blackbird foraging and nesting habitat.

Detectability

Accounting for heterogeneous detectability is essential to generating unbiased estimates of habitat occupancy (MacKenzie et al. 2003). Detectability decreased with

increasing wind speed and decreased steeply over the course of the season (Figure 4). Mean detectability of Rusty Blackbirds was 0.29, so about two thirds of surveys at occupied wetlands produced nondetections. Our estimates of detectability were considerably lower than estimates from Alaska using line transects (Machtans et al. 2007) or area searches (Matsuoka et al. 2010a), presumably because of the relative scarcity of the species in our study areas. Given that Rusty Blackbirds in New England often used multiple noncontiguous wetlands ($= 2.8 \pm 0.4$ wetlands) within relatively large home ranges (Powell et al. 2010a), perhaps it is not surprising that detectability from single survey points at one wetland was low. Two scenarios could have produced false absences during surveys: either individual(s) were nearby and heard the broadcast but remained inconspicuous, or they responded and we failed to see or hear their response. Wind decreased our ability to detect Rusty Blackbirds, probably by (1) limiting our ability to hear singing birds; (2) discouraging birds from flying, thus decreasing our probability of detecting them visually; and (3) limiting the birds' ability to hear the broadcast. Male Rusty Blackbirds often responded aggressively to our broadcast by performing song spread displays (Orians and Christman 1968) interspersed with short flights to perches that encircled the source of the broadcast (L. Powell and T. Hodgman personal observation). The species is about 4× easier to detect early in the season, which probably corresponds to the egg-laying period (about early to mid-May; Matsuoka et al. 2010b), when males aggressively defend females and territories. On the basis of adults' aggressive defense of fledglings and older chicks (Powell 2008), we suspected that detectability would increase again toward the end of the season, but we found no evidence to support this hypothesis. Buckley (2013) noted behavioral differences between years and suggested that these differences resulted from changes in the abundance of a predator, the red squirrel (*Tamiasciurus hudsonicus*); perhaps these behavioral differences also affect detectability. Because we had relatively few midday detections in 2006 (Powell 2008), we concentrated our surveys in the early morning and late afternoon in 2007; however, the fact that few wetlands were repeatedly surveyed during midday almost certainly contributed to the lack of support for detectability models that included time of day. Future surveys should take a more systematic approach in analyzing the importance of time of day on detectability, because we cannot rule out the hypothesis that early mornings have the highest detectability.

Broadcast Experiment

Including BROADCAST clearly improved the fit of detectability models, indicating that the combined effects of a broadcast and survey length affected detectability. Even without correcting for interval length, the effect of

the broadcast was obvious: during 38-s broadcast intervals, Rusty Blackbirds flew toward observers 6× more often than during 3-min prebroadcast intervals (Figure 6). Qualitatively, Rusty Blackbirds appeared to be aggressive to the broadcast, singing and performing song-spread displays (Orians and Christman 1968, Avery 1995) as they circled the observer, particularly early in the season. Given the combined low abundance and low detectability, a simple and time-efficient technique such as a brief broadcast can improve efforts to monitor this species.

Recommendations for Monitoring

The substantial challenges of studying this species' breeding biology include remote and often inaccessible breeding habitat, low abundance and detectability, and a population that may continue to decline. Quantitative information on occupancy or detectability would greatly improve selection of sites for monitoring and would be consistent across broad geographic areas, thus increasing power to detect population (e.g., occupancy) trends. Our study provides robust estimates of occupancy and detectability using several different site-selection techniques, along with parameter estimates quantifying the effects of site and sampling variables on occupancy and detectability of the species. Researchers can use these findings collectively to help design an efficient monitoring plan for the species (e.g., Powell 2009). For example, with mean estimates of occupancy and detectability, researchers can determine the number of wetlands and number of repeat surveys that maximize statistical precision (e.g., MacKenzie and Royle 2005). Specifically, researchers can increase detectability of Rusty Blackbirds by (1) broadcasting a conspecific vocalization, (2) avoiding windy days (especially $>25 \text{ km h}^{-1}$), and (3) concentrating surveys early in the season (i.e. early May in our study areas, depending on road conditions). Given the inability of UNMARKED to adjust to unequal interval lengths within surveys, we recommend that future technicians independently record blackbird detections within 1-min intervals for the duration of the survey (e.g., Powell 2009). This would effectively increase sample size for estimating detectability and allow researchers to disentangle the effects of survey interval length and use of a broadcast. Further, researchers should also adjust the broadcast interval length to 1 min while making special note of new detections from 39 to 60 s so that future surveys can be compared to the 1,000+ surveys performed to date using the 3-min/38-s/5-min protocol (L. Powell personal observation).

Given our results, biologists can now systematically focus their site selection on wetlands most likely to be occupied by Rusty Blackbirds: wetlands of various types containing areas of shallow water (e.g., beaver-created flowages, seeps, peatlands) with dense softwoods nearby,

including those previously occupied by the species. Wetlands larger than 0.5 ha (as estimated on the ground) appear more likely to be occupied than smaller wetlands (Figure 5); future surveys should consider this during design and planning, and consider estimating wetland size remotely (e.g., satellite imagery, aerial photographs) if possible. Given recent advances in occupancy modeling (especially in UNMARKED), we believe that a well-designed, multiseason occupancy model can provide rich insights into how habitat change and colonization–extinction dynamics interact to affect trends in Rusty Blackbird occupancy over time. Further, with the insights into habitat occupancy and detectability we provide here, monitoring efforts can be streamlined—a critical first step toward ensuring that Rusty Blackbirds continue to breed in northern New England.

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