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Abstract. Animals are subject to ecological traps when anthropogenic changes create habitat that appears suitable but when selected results in decreased fitness. The Rusty Blackbird (*Euphagus carolinus*) breeds in boreal wetlands and has declined by 85–95% over the last half century. We studied nest-site selection and daily nest-survival rate (DSR) of 43 Rusty Blackbird nests in northern New England and evaluated whether regenerating logged areas adjacent to wetlands created ecological traps. Although nesting adults avoided high-canopied forests and selected areas with dense balsam fir (*Abies balsmea*) 1 to 3 m high, those characteristics were not associated with DSR. Conversely, the frequency of speckled alder (*Alnus incana*) and sedges (Cyperaceae) in the nest plot varied with DSR, suggesting that the risk of predation of nests within wetlands was lower. DSR also varied with past logging; nests in plots not harvested recently were 2.3× more likely to fledge young than nests in plots harvested within 20 years. When logging extends to the edges of or into wetlands, the subsequent dense regenerating conifers appear to attract Rusty Blackbirds to nest closer to or within these human-altered uplands, exposing their nests to increased predation not typical of unaltered wetlands. Three surrogates for habitat preference did not differ by timber-management history, suggesting that the birds do not prefer habitats that increase their fitness. Rusty Blackbirds nesting in harvested wetlands may be subject to "equal preference" ecological traps, and we suggest that buffers 75 m wide around the perimeter of suitable wetlands should increase DSR.

Key words: *boreal wetlands*, *ecological trap*, Euphagus carolinus, *forest fragmentation*, *nest-site selection*, *nest survival*, *Rusty Blackbird*.

Selección de Sitios de Nidificación y Supervivencia de Nidos de *Euphagus carolinus*: ¿El Manejo Forestal Adyacente a los Humedales Crea una Trampa Ecológica?

Resumen. Los animales son sujeto de trampas ecológicas cuando cambios antropogénicos crean un hábitat que parece apropiado pero, al ser seleccionado, resulta en una disminución de la aptitud biológica. *Euphagus carolinus* se reproduce en humedales boreales y sus poblaciones han disminuido en un 85-95% durante los últimos cincuenta años. Estudiamos la selección de sitios de nidificación y la tasa diaria de supervivencia (TDS) de 43 nidos de *E. carolinus* en el norte de Nueva Inglaterra y evaluamos si las áreas aprovechadas en recuperación adyacentes a los humedales generaron trampas ecológicas. Aunque los adultos que anidaban evitaron bosques de dosel alto y seleccionaron áreas densamente pobladas de *Abies balsmea* de 1 a 3 m de altura, estas características no estuvieron asociadas con la TDS. Por el contrario, la frecuencia de *Alnus incana* y de ciperáceas en la parcela del nido varió con la TDS, sugiriendo que el riesgo de depredación de los nidos dentro de los humedales era menor. La TDS varió también con los aprovechamientos antiguos; los nidos de las parcelas no cosechadas recientemente tuvieron una probabilidad 2,3 veces mayor de criar pichones que los nidos en parcelas aprovechadas hace 20 años. Cuando el aprovechamiento maderero se extiende a los bordes de los humedales o dentro de los mismos, la regeneración posterior de coníferas parece atraer a individuos de *E. carolinus* a nidificar más cerca o dentro de estas tierras altas alteradas por los humanos, exponiendo sus nidos a una depredación mayor, atípica en humedales inalterados. Tres indicadores de preferencia de hábitat demostraron no ser diferentes entre historias de manejo forestal, sugiriendo que las aves no prefieren habitats que incrementen su aptitud biológica. Los individuos de *E. carolinus* que nidifican en humedales aprovechados pueden ser sujeto de trampas ecológicas de "igual preferencia", y sugerimos que las zonas de amortiguamiento de 75 m de ancho alrededor del perímetro de los humedales adecuados deberían incrementar la TDS.

INTRODUCTION

Animal behaviors that increase reproductive success are strongly favored by natural selection. Thus, nesting birds should respond to environmental cues that indicate the presence of habitat that maximizes nest survival (Martin 1998). Recently, ecologists have documented situations where an animal is attracted to habitat cues that ultimately result in reduced fitness compared to fitness in other available habitat, a phenomenon referred to as an "ecological trap" (Remes 2003, Lloyd and Martin 2005, Weldon and Haddad 2005). Ecological traps are of particular interest to wildlife managers because they can lead to population declines—even if the less suitable but preferred habitat represents a small proportion of the available landscape (Robinson et al. 1995, Delibes et al. 2001, Kokko and Sutherland 2001).

For unknown reasons, the Rusty Blackbird (*Euphagus carolinus*), a once abundant North American songbird, is declining dramatically: by 85–95% over the last half-century, with a particularly precipitous drop in the 1970s (Greenberg and Droege 1999, Niven 2004, Sauer et al. 2005). Rusty Blackbirds breed in remote wetlands within boreal landscapes (Avery 1995), and their decline has been documented repeatedly in portions of the breeding range where seemingly appropriate habitat remains. The best available evidence suggests that the southern boreal forest, a region of intensive timber harvest and management, is the region of greatest decline (Greenberg et al. 2011). Therefore, the possibility that timber management has reduced the quality of nesting habitat and perhaps created an ecological trap needs further investigation. After all, the term "ecological trap" was introduced to describe how an increase in edge habitat as a result of logging led songbirds to selectively nest in habitats that appeared suitable on the basis of evolved behavioral cues but resulted in increased rates of nest predation (Gates and Gysel 1978). We focus this study on populations of Rusty Blackbird in Maine and Vermont, at the southeast edge of the species' range, which has contracted to the northwest by 160 km since 1983 (Powell 2008).

Three conditions must be met to provide strong evidence of an ecological trap (Robertson and Hutto 2006): (1) individuals' fitness in two habitats must be unequal, (2) individuals must prefer one habitat over another (in a severe trap) or prefer both habitats equally (in an equal-preference trap), and (3) individuals' fitness in the preferred (or equally preferred) habitat must be lower. To address these three conditions and to fill a knowledge gap resulting from the lack of published quantitative studies of the species' requirements for breeding habitat (but see Matsuoka et al. 2010), we (1) identified habitat features associated with the Rusty Blackbird's nest-site selection at two spatial scales, (2) estimated daily nest-survival rate (DSR) and determined the habitat features associated with nest fate, and (3) used the data from (1) and (2) to evaluate the hypothesis that regenerating clear-cuts adjacent to wetlands are an ecological trap for nesting Rusty Blackbirds.
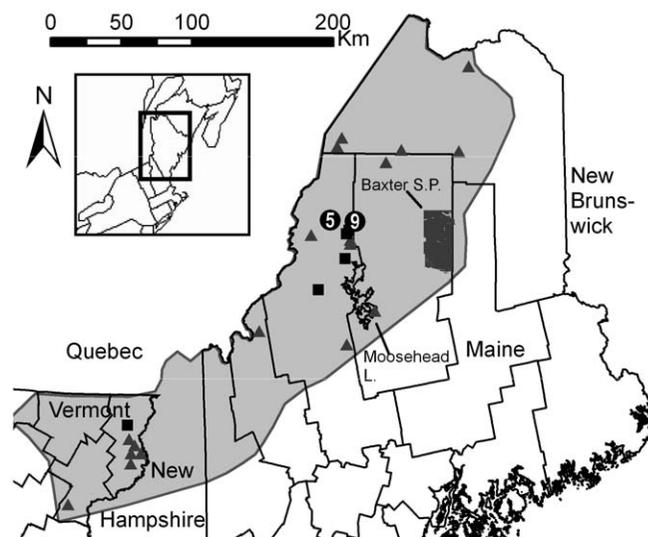

FIGURE 1.   Rusty Blackbird nests found in Maine and Vermont, 2006–2008. Triangles represent sites with one nest, squares represent sites with two nests, and numbered circles represent sites with three or more nests. Light gray fill represents the extent of the Rusty Blackbird's known current breeding range in the continental United States (Powell 2008).

METHODS

STUDY AREAS

We conducted our study in northwestern Maine in May and June of 2006, 2007, and 2008 and in northeastern Vermont in May and June 2007 (Fig. 1). The landscape of northern Maine is relatively flat, uninhabited, and dominated by large-scale industrial timber management. Clear-cutting was widespread in this area during the 1970s and early 1980s in an effort to salvage timber killed during a spruce budworm (*Choristoneura fumiferana*) outbreak (Griffith and Alerich 1996). Although partial harvests became the primary method of logging after the Maine Forest Practices Act was implemented in 1991 (Maine Forest Service 1999, McWilliams 2005), regenerating clear-cuts covering dozens of hectares currently occupy a substantial portion of the landscape in our study area. Forested lands in western Maine and northeastern Vermont are similar; small-scale logging and rural communities perforate a landscape with considerably more topographic relief than northern Maine.

Rusty Blackbirds nest in or adjacent to swampy woodlands (Laughlin and Kibbe 1985), wooded fens (Avery 1995), bogs (Peterson 1988, Erskine 1992), damp swales with speckled alder (*Alnus incana*; Erskine 1992), and wetlands modified by beaver (*Castor canadensis*; Ellison 1990, Richards 1995). In New England, nest sites selected by Rusty Blackbirds are variable; the birds use conifers of short stature because of poor growing conditions (e.g., nutrient-poor peatlands), natural regrowth (e.g., wetlands modified then abandoned by

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beavers), or artificial regrowth (e.g., regenerating clear-cuts; Kennard 1920, Ellison 1990, Powell 2008). Common trees and understory plants include black spruce (*Picea mariana*), red spruce (*P. rubens*), balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), speckled alder, *Viburnum* sp., heath shrubs (family Ericaceae), and *Sphagnum spp.* Potential nest predators we observed in the study areas included the Gray Jay (*Perisoreus canadensis*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), and red squirrel (*Tamiasciurus hudsonicus*).

SELECTION OF STUDY SITES

As part of a concurrent study (Powell 2008), we surveyed for breeding Rusty Blackbirds at 561 wetlands throughout the species' breeding range in Maine and northeastern Vermont (Fig. 1) during May and June 2006, 2007, and 2008. We selected 353 wetlands on the basis of personal field experience or historical descriptions that suggested the presence of suitable habitat (Ellison 1990, Avery 1995), 196 wetlands with a geographically stratified random design, and 12 wetlands as the result of opportunistic roadside encounters of Rusty Blackbirds. In total, 544 wetlands (97%) were within 50 m of roads and the remaining 17 (3%) were between 100 m and 1 km of roads. Each survey included 3 min of passive observation followed by a 38-sec broadcast of a male Rusty Blackbird's vocalization (recorded in New York State by Peter Kellogg, stored at Cornell Laboratory of Ornithology) and 5 min of post-broadcast observation.

NEST MONITORING AND INDEX OF SITE FIDELITY

After detecting one or more pairs of Rusty Blackbirds at a given wetland, we searched for nests and monitored nest success (Martin and Geupel 1993). For each nest found, we calculated fecundity by counting the number of eggs or nestlings, estimated the clutch or brood's age to within 2–3 days, calculated fledging dates and number of exposure days, and scheduled subsequent visits. We accessed most nests from the ground or a stepladder, but two (5.2 m and 8.8 m high) required climbing the nest tree itself. We determined a clutch's age by candling eggs (Lokemoen 1996) as described for the Red-winged Blackbird (*Agelaius phoeniceus*) and a brood's age by assessing nestlings' development (Balph 1975), as described for Brewer's Blackbird (*Euphagus cyanocephalus*). As active nests were often separated by large distances (Fig. 1), we checked nests approximately every 7 days to determine nest fate. We were careful to minimize disturbance (Martin and Geupel 1993), and we defined successful nests as those that fledged at least one nestling. In most instances, we confirmed success with observations of parents feeding fledglings. In a few instances, we considered the nest successful if there were no signs of predation and an abundance of white feather sheaths within the nest lining (T. Hodgman, pers. obs.).

VEGETATION SAMPLING

After the completion of each nest attempt, we used protocols modified from James and Shugart (1970) and Ellison (1990) to quantify the habitat in plots (5-m radius) around the nest and control points. To evaluate nest-site selection at two scales, between wetlands and within wetlands, we selected two control plots for each nest plot: one randomly placed plot at the nearest wetland (>1 km away) where we detected no Rusty Blackbirds (hereafter "outside control") and one randomly placed plot within the wetland containing the nest (hereafter "inside control"). To position inside control plots in wetlands with little or no open water (e.g., wooded bogs with wet pockets of *Sphagnum* spp.), we started at the nest tree (or for outside control plots, what we considered the center of the wetland), randomly selected a direction of travel, then walked 50 m in that direction. To position control plots in wetlands with ample open water, we used a different protocol because the above procedure often would have placed the control plot in open water. Therefore, we began at what we considered the center of the wetland, randomly selected a direction of travel and continued in that direction until the vegetation indicated that we had reached the wetland/upland interface. From there, we used a random-number table including integers −5 through 15 to select a point corresponding to a distance from 5 m outside to 15 m inside the wetland and perpendicular to the upland/wetland interface. From our randomly selected location, we centered all control plots on the nearest spruce or fir of size suitable for a nest (2–5 m tall; Avery 1995).

Within each 5-m-radius circular plot, we took measurements at 40 points, ten in each cardinal direction ("plot scale"; Table 1). We spaced points every 0.5 m along four 5-m transects, each radiating from the plot's center in the four cardinal directions. At each point, we recorded the number of stems and the height (in 1-m interval classes below 5 m and in 5-m height classes above 5 m) of all vegetation, plus the presence or absence of mud and water in contact with a 7.6-cm-diameter pole. We used an ocular tube (James and Shugart 1970) to estimate the vegetation that the pole would have contacted if it was longer than 5 m and used a range finder to determine the height class of tall vegetation. Because we suspected the effects of canopy height extended beyond 5 m from nests, we used a range finder to measure maximum canopy height within 11 m of the plot's center (James and Shugart 1970). Within several sites, timber-harvest history was heterogeneous, so we described the history of logging at the plot scale as either (1) no evidence for >20 years (hereafter "no recent harvests") or (2) within 20 years (hereafter "recently harvested"). We estimated the number of years since the last harvest by counting the number of branch whorls on conifers of the youngest size class. We took additional measurements at the site scale and the microsite scale (Table 1).

TABLE 1.   Descriptions of variables used to (1) describe plots in which Rusty Blackbirds nested, (2) model nests' daily survival rate (DSR), (3) and compare plots by history of logging in northern New England, 2006–2008.

Variable	Description	Analyses performed		
		Nest-plot selection	DSR	Logging
YEAR	Year nest was active: 2006, 2007, or 2008		×	
Site scale				
DIST_ROAD	Distance (m) to the nearest road		×	
DIST_UPLAND	For nests in uplands, distance (m) to the wetland/upland interface.		×	×
Plot scale[a]				
ALDERS	Frequency[b] of alder cover; wetland indicator	×	×	×
CANOPY_HT[a]	Height (m) of tallest tree within 11 m of nest	×	×	×
DIST_WATER	Distance (m) from nest to standing water			×
FIRS1–3M	Frequency[b] of fir cover 1–3 m high	×	×	×
MUD	Frequency[b] of mud; wetland indicator			×
SPHAGNUM	Frequency[b] of *Sphagnum* cover; indicator of acidic wetlands	×		
SPRUCES1–3M	Frequency[b] of spruce 1–3 m high	×		
WATER	Frequency[b] of standing water; wetland indicator	×		×
SEDGES	Frequency[b] of sedge cover; wetland indicator		×	×
TIMBER_MGMT	Binary variable describing whether the nest plot was located in a stand logged within 20 years or within a plot that had not been cut for >20 years		×	
Microsite scale				
NEST_TREE_AGE	Age (year) of the tree that the nest was placed on, calculated from a count of the number of branch whorls		×	×
NEST_TREE_DBH	Diameter at breast height (cm) of the tree the nest was placed on			×
NEST_TO_GROUND	Distance (cm) from the nest to the ground			×
NEST_TREE_GENUS	Genus of the tree the nest was placed on (spruce or fir)		×	
NEST_TREE_HT	Height (m) of the tree the nest was placed on			×
CONCEAL	Minimum % concealment of the nest among six measurements taken 1 m away from the nest in the four cardinal directions, from above, and from below		×	×

[a] Within 5 m of the plot's center, except for CANOPY_HT, which was measured to within 11 m.
[b] Frequency refers to the total number of times a given cover type was detected within each plot. At each point, presence/absence of each variable was recorded, except woody plants, for which the number of stems at each point was recorded.

STATISTICAL ANALYSES

Nest-plot selection. We modeled nest-plot selection by comparing nest and control plots at two different spatial scales, between and within wetlands. Using matched-pairs logistic regression, we compared each nest plot with both its between-wetland and its within-wetland control plot. Prior to the analysis, we reviewed the literature and used our field experience to compile 22 variables that we considered plausible contributors to the Rusty Blackbird's nest-site selection. These variables fell into four general categories: spruce and fir density near the height of nests (Ellison 1990), alder density, canopy height/density, and indicators of the wetland's condition. To reduce the number of variables, we combined correlated variables where appropriate (e.g., frequency of firs 1 to 2 m high plus frequency of firs 2 to 3 m high; Spearman's rank correlation test, $r > 0.5$) or retained the correlated variable most relevant to our hypotheses. Using the remaining six variables (Table 1), we ran 15 a priori models: six univariate models, one null model, and eight additive models in combinations

that we considered biologically meaningful descriptors of Rusty Blackbird nesting habitat. For analyses both between and within wetlands, we assessed the relative fit of the same set of 15 candidate models with Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We checked for interaction terms in two best-fit models and assessed goodness of fit with the variance-inflation factor from the global model.

Nest survival. We analyzed 40 nests to determine DSR; we excluded from our analyses one nest that may have never contained eggs and two nests that may have been abandoned because of disturbance during our attempts to capture the birds as part of our concurrent studies (Powell 2008). To test the hypothesis that Rusty Blackbirds select nest sites that are positively associated with DSR, we started our candidate set with the two most influential variables from the nest-site analysis, CANOPY_HT and FIRS1–3M. We then added eight variables that we considered ecologically plausible influences on DSR (Table 1). We formed 28 models total: 11 univariate

models, a null model, 15 bivariate models, and one trivariate model based on combinations of nest, canopy, and vegetation variables that we considered ecologically plausible influences on DSR. We formed 24 of the 28 models a priori, then later added four a posteriori models that included an 11th variable, SEDGES, after we found that ALDERS, another wetland indicator, influenced DSR. We used AIC_c to rank each model's performance in program MARK (White and Burnham 1999).

When the nests in a given category have DSR = 1.0 (i.e., no nests in the category failed), the usual methods for variance estimation are not appropriate (Aebischer 1999), and DSR = 1.0 for YEAR = 2006 and TIMBER_MGMT = no recent harvest. To account for this, we added an additional, fictitious, nest to the dataset (with YEAR = 2006, TIMBER_ MGMT = no recent harvest) and "depredated" this nest after 23 days of exposure. For the other covariates of this fictitious nest, we used the mean values for nests with no recent harvest. We believe this represents a conservative approach, as we artificially raised the rate of nest predation above what we observed in the field.

We assessed the relative importance of each variable by summing the Akaike weights of each model that included that variable (Burnham and Anderson 2002); to reduce bias in this procedure, we included each variable in four models. As we recorded an average clutch size of 4.5 ± 1.1 SE and parents tend to begin incubation with the penultimate egg (Matsuoka et al. 2010), we used 4 days for the period of egg laying, 13 days for incubation, and 12 days for the nestling period for a total of 29 exposure days. We thus calculated nest success with the model-averaged DSRs (Burnham and Anderson 2002) as DSR^{29} (Klett et al. 1986).

Comparing timber-management histories. To examine differences between nests in plots with no recent harvests and in those recently harvested, we tested relevant variables from the plot scale and microsite scale (Table 1) for normality (Shapiro–Wilk W, $P < 0.05$) and equality of variances

(Levene's tests, $P < 0.05$), then transformed nonparametric variables as needed and ran Student's t-tests on the normally distributed variables. When transformed variables failed to meet the normality assumption of t-tests, we ran nonparametric unpaired Mann–Whitney U-tests.

Other than the nest-survival analysis in MARK, we performed all statistical analyses in Program R (R Development Core Team 2008). We present means and parameter estimates ± 1 SE, considered probability tests significant at $\alpha < 0.1$, and considered models with $\Delta AIC_c < 2.0$ as those with substantial support (Burnham and Anderson 2002). When more than one model containing a given variable received substantial support, we present model-averaged parameter estimates and DSRs (Burnham and Anderson 2002).

RESULTS

NESTING ECOLOGY

We found 43 Rusty Blackbird nests, 7 in 2006, 28 in 2007, and 8 in 2008 (Fig. 1). Rusty Blackbirds placed their nests in black or red spruce ($n = 23$), balsam fir ($n = 16$), white spruce ($n = 2$), northern white cedar, ($n = 1$) and a *Viburnum* shrub ($n = 1$). Median age of the primary nest tree was 14 years ($\overline{x} = 17.87 \pm 1.46$ yrs, range 8–50). All nests were within 75 m of standing water ($\overline{x} = 12.07 \pm 3.04$ m, range 0–71); 29 nests were within wetlands, and the 14 nests found in uplands averaged 7.25 ± 3.01 m (range 0.3–95) from the wetland/upland interface.

NEST-PLOT SELECTION

Both between and within wetlands, the best-fit model describing Rusty Blackbird nest-site selection included CANOPY_HT (between wetlands: $\beta = -0.349 \pm 0.078$; within wetlands: $\beta = -0.183 \pm 0.072$) and FIRS1–3M (between wetlands: $\beta = 0.104 \pm 0.034$; within wetlands: $\beta = 0.039 \pm 0.072$; Table 2), indicating that Rusty Blackbirds selected for short canopies with dense cover of pole-stage firs. CANOPY_HT was included in the three best-fit models at both scales, and no other models received

TABLE 2. Three best-fit models, by Akaike's information criterion (AIC_c)[a], predicting differences between 5-m-radius plots centered on a Rusty Blackbird nest ($n = 43$) and randomly placed control plots at two spatial scales in northern New England, 2006–2008.

	Between wetlands				Within wetlands			
Model[b]	−2 log (likelihood)	K	ΔAIC_c[c]	w_i	−2 log (likelihood)	K	ΔAIC_c[c]	w_i
CANOPY_HT + FIRS1–3M	41.0	4	0.00	0.69	53.9	4	0.00	0.57
CANOPY_HT + FIRS1–3M + SPRUCES1–3M	40.8	5	1.59	0.31	53.9	5	2.32	0.18
CANOPY_HT	49.6	3	14.75	0.00	56.9	3	3.74	0.09
Null	59.6	2	32.43	0.00	59.6	2	6.96	0.02

[a]K, number of parameters; AIC_c, AIC adjusted for small sample size; ΔAIC_c, difference in AIC_c relative to the most parsimonious value; w_i, Akaike weight.

[b]This table excludes 11 models that received little support ($\Delta AIC_c > 5.9$, $w_i < 0.05$).

[c]AIC_c value of the best-fit between-wetlands model: 91.0, within-wetlands: 116.4; variance-inflation factor ($\hat{c}$) for global model between wetlands: 1.02, within wetlands: 1.33.

substantial support (ΔAIC$_c$ > 5.9). Adding SPRUCES1–3M (between wetlands: β = 0.024 ± 0.038; within wetlands: β = 0.001 ± 0.018) to the best-fit model decreased the fit at both scales (Table 2). Our analyses provided no substantial evidence that variables representing wetland conditions (WATER, ALDERS, *SPHAGNUM*) influenced nest-site selection; no other models including those variables received substantial support at either scale (ΔAIC$_c$ > 5.9).

NEST SURVIVAL

All 14 nests that failed were located in plots harvested within the previous 20 years. We concluded that 11 nests were depredated, as all eggs or chicks were destroyed or disappeared prior to the estimated date of fledging, while three nests were abandoned. We did not observe evidence of brood parasitism, nor did we detect Brown-headed Cowbirds (*Molothrus ater*) in our study areas; we documented only two addled eggs. In our original nest-survival analysis preceding the addition of the fictitious nest, the three best-fit models predicting DSR were TIMBER_MGMT + YEAR (AIC$_c$ = 60.1), TIMBER_MGMT + ALDERS (ΔAIC$_c$ = 0.2) and TIMBER_MGMT (ΔAIC$_c$ = 1.9), respectively. No other model received substantial support (ΔAIC$_c$ > 3.8), and the null model received essentially no support (ΔAIC$_c$ = 8.7).

Predictably, the addition of the fictitious depredated nest (no recent harvest, YEAR = 2006) shifted the relative importance of the models (Table 3). The five models receiving substantial support included combinations of ALDERS, TIMBER_MGMT, SEDGES, and TREE_AGE, with ALDER included in each of the four best-fit models. When we averaged the Akaike weights (w_i) of each variable across all the candidate models, the most influential variables, ordered in decreasing order of importance, were ALDERS (Σw_i = 0.53), TIMBER_MGMT (Σw_i = 0.23), SEDGES (Σw_i = 0.22), and NEST_TREE_AGE (Σw_i = 0.16); no other variable received more than Σw_i = 0.07—including YEAR (Σw_i < 0.02). Two variables indicating wet conditions, ALDERS (β = 0.113 ± 0.089) and SEDGES (β = 0.082 ± 0.076), were positively correlated with DSR. Consistent with our original analysis, DSR was higher for nests in plots with no recent harvests (DSR = 0.990 ± 0.010, 114 exposure days, estimated nest success = 76%, n = 10) than in recently harvested plots (DSR = 0.963 ± 0.012, 309 exposure days, estimated nest success = 33%, n = 30); accordingly, DSR was positively correlated with NEST_TREE_AGE (β = 0.052 ± 0.049). Again as in our original analysis, we found no substantial support for models that included CANOPY_HT or FIRS1–3M—the best predictors of nest-plot placement (ΔAIC$_c$ > 4.2; Σw_i < 0.02). Averaged among the five models with substantial support, DSR for all 40 nests was 0.983 ± 0.008, (estimated nest success = 61%, 423 exposure days).

COMPARING TIMBER-MANAGEMENT HISTORIES

In plots with no recent harvests, only two of 10 nests (20%) were placed in uplands (mean distance 4.0 ± 3.0 m), while 12 of 33 nests (36%) at recently harvested sites were placed in uplands (mean distance 21.7 ± 7.9 m). Furthermore, nests in plots with no recent harvests were closer to standing water (2.04 ± 0.87 m) than were nests at recently harvested sites (15.05 ± 1.13 m; t_{28} = 3.48, P = 0.002). When we examined indicators of wetland conditions, we found that nest plots with no recent harvests contained more WATER (no recent harvest, 8.7 ± 2.9; recently harvested, 3.3 ± 1.1; U = 93, P = 0.03), MUD (no recent harvest, 4.5 ± 1.6; recently harvested, 0.8 ± 1.1; U = 94, P = 0.014), and SEDGES (no recent harvest, 5.0 ± 1.3, recently harvested, 2.6 ± 0.7; U = 72.5, P = 0.005), although ALDERS did not differ by logging history (no recent harvest, 6.4 ± 2.3; recently harvested, 6.9 ± 2.7; U = 119.5, P = 0.16).

Variables associated with nest-plot placement did not vary with logging history (FIRS1–3M: no recent harvest = 17.9 ± 3.1, recently harvested = 19.4 ± 3.4, t_{41} = 0.06, P = 0.56; CANOPY_HT: no recent harvest = 7.8 m ± 0.4, recently harvested = 7.6 m ± 0.4, t_{41} = −0.85, P = 0.40). Although NEST_TREE_AGE was predictably less in plots that had been recently harvested (no recent harvest, 28.0 ± 4.6; recently harvested, 14.9 ± 0.7, t_9 = −2.82, P = 0.02), no other microsite variables differed by logging history (CONCEAL: no recent harvest = 34.4 ± 3.8, recently harvested = 38.7 ± 4.3, U = 220.5, P = 0.091; NEST_TO_GROUND: no recent harvest = 2.3 ± 0.8, recently harvested = 1.5 ± 1.1, t_{41} = −1.50, P = 0.14; NEST_TREE_HT: no recent harvest = 3.6 ± 0.8, recently harvested = 3.5 ± 1.2, t_{41} = 0.17, P = 0.86; NEST_TREE_DBH: no recent harvest = 5.2 ± 2.0, recently harvested = 4.6 ± 1.2, t_{10} = 0.53, P = 0.61).

TABLE 3. Result of model selection by Akaike's information criterion (AIC$_c$)[a] for survival of Rusty Blackbird nests (n = 40) in northern New England, 2006–2008.[b]

Model	−2 log (likelihood)	K	ΔAIC$_c$[c]	w_i
SEDGES + ALDERS	68.6	3	0.00	0.15
TIMBER_MGMT + ALDERS	68.7	3	0.08	0.14
ALDERS	70.8	2	0.20	0.13
ALDERS + NEST_TREE_AGE	69.3	3	0.72	0.10
TIMBER_MGMT	72.0	2	1.34	0.08
SEDGES[d]	73.0	2	2.35	0.05
NEST_TREE_AGE	73.3	2	2.65	0.04
Null	75.3	1	2.70	0.04

[a]K, number of parameters; AIC$_c$, AIC adjusted for small sample size; ΔAIC$_c$, difference in AIC$_c$ relative to the most parsimonious value; w_i, Akaike weight.
[b]This table excludes 20 models that received less support than the null model. The table describes the results after the addition of a fictitious, depredated nest to the uncut treatment as described in methods.
[c]AIC$_c$ value of the best-fit model = 74.6; of global model = 1.57.
[d]SEDGES was added a posteriori.

DISCUSSION

Animals are subject to ecological traps when anthropogenic changes create habitat that appears suitable, yet when preferred and subsequently selected, results in decreased fitness. Here we discuss the Rusty Blackbird's nest-site selection in a historical and current perspective. We argue that the availability of nesting habitat has increased with large-scale logging, which has created an incongruence between nest-site selection and nest survival. Finally, we frame our findings in terms of Robertson and Hutto's (2006) three conditions necessary to demonstrate an ecological trap and discuss additional data that address habitat preference rather than selection.

NEST-PLOT SELECTION: PRESENT AND PAST

Both within and between wetlands, we found that nesting Rusty Blackbirds avoid tall canopies, select plots with dense growth of firs from 1 to 3 m high, and place nests in short conifers that average less than 18 years old. Similarly, Ellison (1990) found that in Vermont, nests were associated with coniferous regeneration and thick cover from 2 to 4 m high. Across the boreal forest, Matsuoka et al. (2010) found that Rusty Blackbirds are most likely to nest in conifers (nest height $\bar{x}$ = 1.6) in all regions but interior Alaska, where they nest in what is available—deciduous shrubs. Thick coniferous growth provides relatively dense foliage at nest height ($\bar{x}$ = 1.7 m in our study), presumably to conceal nests from predators. Rusty Blackbirds clearly select for nest sites in areas of dense coniferous growth and undoubtedly did so before the appearance of humans in the boreal forest. Historical nesting sites likely included bogs and fens with naturally stunted coniferous growth, as well as coniferous regeneration resulting from irregular forest fires and blow-downs adjacent to wetlands. Beavers may benefit the Rusty Blackbird by providing disturbed yet relatively unfragmented nesting habitat, as they selectively remove hardwoods, increasing light gaps and encouraging coniferous regeneration on a local scale (Johnson and Naiman 1990).

Although Rusty Blackbirds are attracted to disturbed sites that support dense young coniferous growth, it seems unlikely that historical disturbances approached the current spatial scale of anthropogenic disturbance from timber harvesting. During the 20th century, landscape-scale anthropogenic changes (e.g., clear-cutting, fire suppression) led to increasingly destructive outbreaks of the spruce budworm in the coniferous forests of northeastern North America, with those of 1910–1920, 1945–1955, and 1968–1985 defoliating 10, 25, and 55 million ha, respectively (Blais et al. 1981, Blais 1983, 1985, Hardy et al. 1983). In Maine (Griffith and Alerich 1996) and elsewhere, extensive post-budworm salvage cutting followed these outbreaks, creating a superabundance of even-aged coniferous regrowth, attractive nesting habitat for Rusty Blackbirds. Already vulnerable to the spruce budworm, dense stands of riparian conifers were hit particularly hard by the budworm and post-budworm salvaging because buffers preventing spraying were imposed to protect water bodies from the effects of pesticides (Irland 1988).

NEST SURVIVAL

Contrary to what one might expect if nest-site selection is adaptive, the variables associated with DSR differed substantially from those that nesting Rusty Blackbirds selected. Canopy height and fir density at nest height were poor predictors of nest fate, while timber-management history and alder and sedge density were the best predictors of DSR. We attributed 11 of the 14 nest failures to predation (the other three failed nests were abandoned); all of these were in sites cut <20 years earlier. Even after we added a fictitious depredated nest to the category of no recent harvest, nests in that category were still 2.3× more likely to fledge young than those in plots logged <20 years earlier. This difference between habitats in nest success (a component of fitness) meets the first of three conditions necessary to demonstrate an ecological trap (Robertson and Hutto 2006).

Predictably, nest-tree age also was positively correlated with DSR, suggesting that nests in older trees were more likely to fledge young. DSR varied with the frequency of alder and sedges, suggesting that nests within wetlands are less likely to suffer depredation. Nest plots in recently harvested sites had less water, less mud, and fewer sedges; nests in recently harvested sites were also farther into uplands than nests at sites not recently logged. When logging extends to the edges of or into wetlands, the resulting regeneration of conifers probably attracts Rusty Blackbirds to nest closer to or farther into uplands, exposing nests to increased predation pressure. Therefore, the cues that Rusty Blackbirds use to select nest sites may be maladaptive when habitat within or adjacent to wetlands is logged. Nests in recently harvested plots were placed in trees younger than in those with no recent harvest, but other than nest-tree age and the nest's position relative to wetlands, characteristics (CANOPY_HT, FIRS1–3M, CONCEAL, NEST_TO_GROUND, NEST_TREE_HT, and NEST_TREE_DBH of nests) in the two categories of timber-management history were indistinguishable. This suggests that Rusty Blackbirds have not evolved to perceive cues that logged uplands are relatively risky places in which to nest.

The Gray Jay, Blue Jay, and American Crow were among the avian nest predators in our study areas, and the latter two tend to be more abundant in fragmented habitats (Robinson et al. 1995). Using 954 artificial nests in southeast Alaska, DeSanto and Willson (2001) never detected jays or red squirrels in open wetlands and found that nest-predation rates in regenerating clear-cuts 15–20 years old (58% of nests depredated), wetland edges (40%), and wetland openings (20%) differed. Robertson and Hutto (2007) found that Olive-sided Flycatchers

(*Contopus cooperi*) prefer selectively harvested over naturally burned forest, despite higher rates of nest predation in the human-altered landscape. In regenerating clear-cuts in eastern Maine, Rudnicky and Hunter (1993) documented that depredated nests differed from undisturbed nests only in the increased cover of pole-stage conifers (0–3 m tall). They suggested that to avoid predation themselves, small nest predators (i.e., the red squirrel) may remain close to dense cover, where they are more likely to find nests in young stands with thick cover that are less voluminous and less structurally complex than mature stands.

EVIDENCE FOR AN ECOLOGICAL TRAP

Rusty Blackbird nests in stands with no recent harvests were more than twice as likely to fledge young than nests at sites logged within the past 20 years, so the first of three conditions necessary to demonstrate an ecological trap (Robertson and Hutto 2006) is met. To satisfy the other two conditions, the data must show equal preference for both habitats (an equal-preference trap) or preference for the less favorable habitat over the other (a severe trap) and higher fitness in the nonpreferred habitat. We found strong evidence that Rusty Blackbirds select for nest sites with a high density of pole-stage firs—the typical condition in regenerating logged boreal forest. However, nonrandom habitat use (e.g., nest-site selection) is not necessarily a suitable surrogate for preference (Van Horne 1983). For example, subordinate individuals can be found in nonpreferred habitat if they are excluded by dominant individuals (Sherry and Holmes 1988).

Therefore, in a post hoc effort to determine if Rusty Blackbirds not only select for but prefer the habitat in which their fitness suffers, we examined three surrogates for habitat preference (Robertson and Hutto 2006): year-to-year site fidelity, clutch size, and variation in year-to-year occupancy. Robertson and Hutto (2006) argued that year-to-year site fidelity is a useful surrogate for preference because individuals claiming territories in preferred habitat have the greatest site fidelity and lowest emigration rates (e.g., Sergio and Newton 2003). To estimate the Rusty Blackbird's year-to-year site fidelity, we searched for breeding pairs for at least 2 hr during mid-May at all sites with nesting pairs in previous years. We had only four sites with banded birds, so we calculated species-level fidelity rather than individual fidelity. We argue that if individual preference is repeated across the landscape, species-level site fidelity should be higher in preferred nesting habitats. We found that year-to-year nest-site fidelity was no different at sites that had been recently harvested (8 of 14 returned) than at sites with no recent harvest (3 of 6 returned; $\chi^2_1 = 0.04$, $P = 0.85$). Moreover, we documented five cases in which timber management adjacent to wetlands was heterogeneous (i.e., the site included both clear-cut and unlogged patches), yet Rusty Blackbirds nested in the regenerating clear-cuts in all five cases—presumably because they preferred regenerating conifers (L. L. Powell, pers. obs.).

The distribution of dominant individuals among habitat types can also imply preference (e.g., Davies 1992, Robertson and Hutto 2006), so, assuming that dominant individuals have larger clutches, we used clutch size to explore possible differences in habitat preference. Clutches in plots with no recent harvest were no larger (4.4 ± 0.3) than in recently harvested plots (4.5 ± 1.1; Mann–Whitney $U = 98.5$, $P = 0.91$, $n = 32$ nests), providing no evidence for the unequal distribution of dominant individuals or a particular habitat preference. Finally, temporal variation in population size can serve as a surrogate for preference (Robertson and Hutto 2006), as poor-quality habitats can fluctuate in population size and "buffer" population fluctuations in relatively stable high-quality habitats (Kluyver and Tinbergen 1953, Brown 1969, O'Connor 1981, Gill et al. 2001). After surveying more than 700 wetlands in Maine and Vermont in 2001, 2002, 2006 and 2007, we found no evidence that variance in wetland occupancy varies with timber-management history (L. Powell, unpubl. data), again providing no evidence for a particular habitat preference. None of these surrogates for preference suggests that Rusty Blackbirds prefer habitats that maximize their fitness, suggesting an "equal preference" ecological trap (Robertson and Hutto 2006).

Because Rusty Blackbirds are sparsely distributed even in the core of their breeding range (Flood 1978, Avery 1995), large-scale timber harvesting across northeastern North America may have been especially damaging. Ecological traps may trigger the Allee effect at low population densities (i.e., reduced reproduction or survival), because with little intraspecific competition, individuals are relatively free to act on their (now maladaptive) preferences (Kokko and Sutherland 2001). Given the synchrony of the species' range contraction in Maine (Powell 2008), its sharp rangewide population decline (Greenberg and Droege 1999), and the most recent spruce budworm outbreak, we believe that large-scale reduction of DSR in logged forest may have contributed to the population decline and range contraction of the Rusty Blackbird in northeastern North America.

FUTURE RESEARCH NEEDS

Although we suspect that red squirrels and jays are the primary predators of Rusty Blackbird nests, this hypothesis should be tested with motion-detecting cameras. Furthermore, the overall nest success we recorded (61%) is similar to levels found in Alaska (56%; Matsuoka et al. 2010), but we have little data on fitness at other life-history stages with which to understand the stage(s) driving population declines. Studies of nest survival provide valuable information, yet they evaluate only one component of fitness. For example, although nesting White-throated Robins (*Turdus assimilis*) prefer forest fragments to coffee plantations despite higher nest predation in the fragments (Sekercioglu 2007), fledglings' survival was relatively high in the forest fragments, which mitigated the effects of low DSR and thus nullified the potential ecological trap (C. H.

Sekercioglu, unpubl. data). To understand the interaction between logging and Rusty Blackbird fitness on the breeding grounds, DSR and survival of fledglings and juveniles must be studied at multiple spatial scales and under a variety of timber-management schemes, ideally in manipulative studies.

MANAGEMENT IMPLICATIONS

Regardless of whether Rusty Blackbirds are suffering from ecological traps on a large scale, we demonstrated relatively low DSR at recently logged sites (33% vs. 76% in plots with no recent harvest), and showed that DSR increased with alder and sedge density, indicators of wetlands. We thus expect that the establishment of buffer zones of no logging around the perimeter of wetlands would increase the DSR of Rusty Blackbird nests. However, upland buffers will not reduce disturbance to the species entirely unless they are wide enough to (1) reduce predation via edge effects and (2) prevent Rusty Blackbirds from nesting in regenerating conifers in the uplands and simply flying across thin strips of mature forest to forage in wetlands.

Rusty Blackbird nests are almost always placed near water (Kennard 1920, Avery 1995, Matsuoka et al. 2010), which could work to their advantage, as even small forest fragments in Maine are less subject to nest predation if they are adjacent to water (Small and Hunter 1988). The 14 nests we found in uplands averaged 19.2 ± 7.0 m away from wetlands, with the three farthest located 32, 48, and 95 m away. In two cases, Rusty Blackbirds nested in regenerating clear-cuts in the upland yet regularly flew over modest unlogged buffers (<30 m), presumably to feed in nearby wetlands (L. L. Powell, pers. obs.). For birds in general, predation rates are highest within 50 m of edges (Paton 1994), and in Maine, Vander Haegen and Degraaf (1996) found the effects of predation on artificial nests to extend 75 m into riparian buffers. Therefore, we suggest an unlogged buffer of 75 m around the perimeter of wetland occupied by or suitable for the Rusty Blackbird. Given the extensive literature on nest predation near edges and an improved understanding of breeding Rusty Blackbirds' use of space, 75-m buffers will likely increase nest survival in managed landscapes, although they may have limited utility for protecting habitat for foraging (Powell et al. 2010). Wetlands suitable for nesting are generally larger than 0.5 ha, are surrounded by softwoods, and feature pools of shallow water available as foraging substrate (Powell 2008). Thorough protection of such sites from disturbance will be difficult without a detailed understanding of the species' use of space (Powell et al. 2010), its social organization (Powell et al., in press), and the value of different types of foraging substrates. Management designed to improve young Rusty Blackbirds' survival rates could help prevent further population decline and range contraction. However, effective strategies to protect breeding Rusty Blackbirds in actively managed forests such as those in the Northeast will require close working relationships between land managers and conservation agencies, and the best possible data to guide them.

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