

**RUSTY BLACKBIRD (*EUPHAGUS CAROLINUS*) BREEDING ECOLOGY IN
NEW ENGLAND: HABITAT SELECTION, NEST SUCCESS
AND HOME RANGE**

By

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**RUSTY BLACKBIRD (*EUPHAGUS CAROLINUS*) BREEDING ECOLOGY
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Thesis Advisor: Dr. William E. Glanz

An Abstract of the Thesis Presented
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The Rusty Blackbird (*Euphagus carolinus*) is a poorly understood wetland-breeding songbird that has experienced an 85–95% population decline since the mid 20th century. Although anecdotal evidence suggests that Rusty Blackbirds are “loosely colonial” and breed in bogs, fens, beaver-modified wetlands, and wooded swamps of the boreal forest, ornithologists have few or no data with which to comprehend the species’ habitat use, nesting success, social organization or spatial use of the landscape. To quantify habitat selection, I modeled Rusty Blackbird habitat occupancy and detectability (the probability of detecting a Rusty Blackbird) as functions of wetland site variables and sampling variables, respectively (Chapter 2). Furthermore, I studied nest site selection and nest survival for 35 Rusty Blackbird nests in northern Maine and northeastern

Vermont (Chapter 3). Finally, I calculated 95% kernel density estimates of home range size for 13 radio-tagged individuals, eight of which were part of the first “loose colony” reported in New England (Chapter 4).

Four variables predicted wetlands occupied by Rusty Blackbirds best: puddles (shallow, unconnected to flowing water and often ephemeral), wetland area > 0.5 ha, a coniferous upland, and the area of forest less than 5 m tall within 1 km buffers. This analytical description of Rusty Blackbird breeding habitat, along with my estimates of mean wetland occupancy (0.37 ± 0.12 SE) and detectability (0.19 ± 0.05 SE), can improve the efficiency of efforts to monitor the species. Nest success was 61.6% (n=32) overall, 32.7% (n=20) in regenerating clear-cuts and 100% (n=12) in nests not in regenerating clear-cuts. Compared to non-colonial individuals, birds at the colony had lower nesting success (22.4% vs. 66.2%), and larger home ranges (71.1 ha vs. 15.2 ha). The best *a priori* predictor of nest mortality (the abundance of firs < 3” diameter at breast height) and the best predictor of nest site selection (the abundance of firs 2-3 m tall) were highly correlated, suggesting that Rusty Blackbirds used maladaptive cues to select nest sites. Furthermore, both the aforementioned measures of pole-stage fir abundance were excellent predictors of regenerating clear-cuts less than 20 years old, which was ultimately the best predictor of nest mortality. All failed nests were located in regenerating clear-cuts, and 73% of failed nests were predated.

When anthropogenic changes create habitat that appears suitable, yet when chosen, ultimately results in decreased fitness, animals become caught in an “ecological trap”. I hypothesize that regenerating clear-cuts are an ecological trap for Rusty Blackbirds, because although they mimic natural nesting habitat (e.g. stunted conifers in

bogs), the inevitable fragmentation increases nest predation risk. To reduce nest predation, I recommend that forest practitioners maintain at least a 100 m buffer around wetlands suitable for (or occupied by) Rusty Blackbirds, and that they delineate wetlands during May and June when ephemeral wetlands are present. Given the steep decline of this species and the need for effective management actions, it is critical to understand how social organization, spatial use and reproductive success vary under different timber management schemes

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Chapter 1

INTRODUCTION AND OVERVIEW

The challenge in studying a poorly known species is focusing one's ideas on the most important questions. Any new piece of information gathered is potentially valuable, and this value increases exponentially when working with species of conservation concern. Although it is tempting to begin research by testing hypotheses for why a particular species may be declining, a far more prudent approach is to start by establishing the basic ecology of the species in question. Only by gathering basic ecological information can ecologists begin to generate meaningful hypotheses on why the species is troubled. This was my general approach in studying the little-known Rusty Blackbird (*Euphagus carolinus*) in New England.

1.1 Natural History

Although the Rusty Blackbird's breeding biology has been the focus of only one peer-reviewed study (Kennard 1920), the best available data place the species among North America's fastest-declining birds (Niven 2004). From mostly anecdotal accounts, it is known that Rusty Blackbirds nest in swampy woodlands (Laughlin and Kibbe 1985), fens (Avery 1995), bogs (Peterson 1988, Erskine 1992), damp alder swales (Erskine 1992), and beaver-modified wetlands (Ellison 1990, Richards 1995) across the boreal forest. Rusty Blackbirds in New England also nest in regenerating coniferous forest near wetland foraging habitat (pers. obs., Ellison 1990). The species winters in the southeast U.S., primarily in the Mississippi Valley and Southeast coastal plain (Figure 1.1, Avery 1995), where it can be found roosting with other blackbirds (*Icteridae*) or foraging in

small, single-species flocks (Beal 1900, Neff et al. 1957). Rusty Blackbirds in the Northeast nest primarily in small spruce and fir trees (Kennard 1920, Ellison 1990). The species is more reliant on aquatic invertebrates than other blackbirds (Beal 1900, Martin et al. 1951, Neff et al. 1957) and forages more like a Northern Waterthrush (*Seiurus noveboracensis*, Greenberg and Droege 1999). Adults forage by probing and leaf flipping while walking in shallow water, plunging their bills, and occasionally their whole heads, into the water after insect larvae and crustaceans (Forbush 1927, Bent 1958, Ellison 1990, Avery 1995, L. Powell, unpublished data, S. Matsuoka, USFWS, Anchorage, AK). Bill morphology and jaw musculature support the observations of Rusty Blackbirds targeting aquatic prey (Beecher 1951, Ellison 1990, Avery 1995).

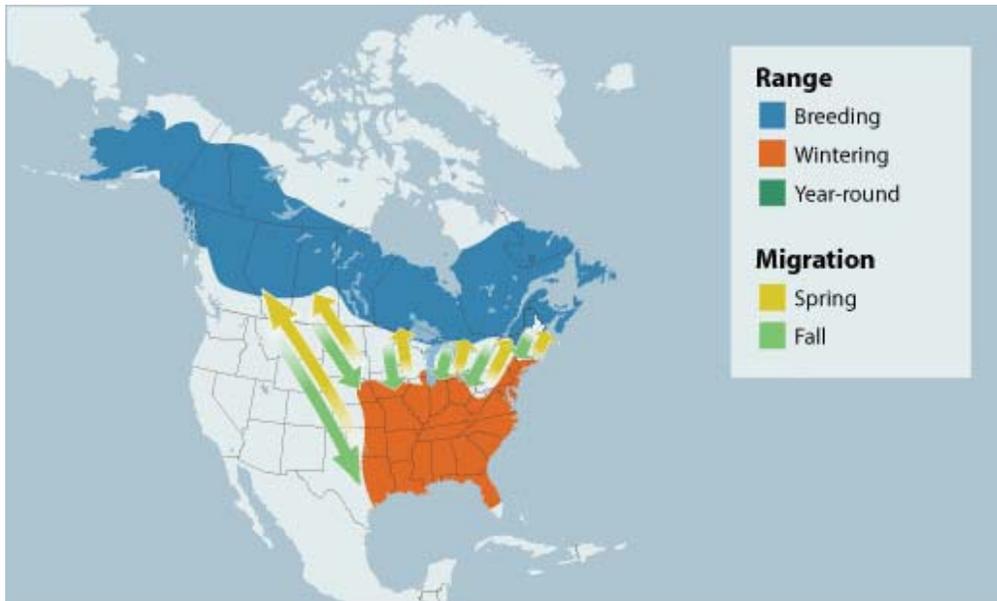


Figure 1.1. Breeding and wintering range of the Rusty Blackbird modified from Wells (2008). The latest evidence (Adrienne Leppold, University of Maine, unpublished banding data) suggests that Rusty Blackbirds breeding in the Western boreal forest funnel through the Great Lakes region, rather than crossing the Midwest as depicted above. However, more research is needed to confirm this pattern.

1.2 Where are the remaining Rusty Blackbirds? The Need for Habitat Analysis and Monitoring

Although population declines are well-established in this rare species (Greenberg and Droege 1999, Niven 2004), efforts to locate breeding habitat in the Northeast are still based only on anecdotal accounts, breeding bird atlas records, and descriptions in “gray” literature (Kennard 1920, Laughlin and Kibbe 1985, Ellison 1990, Erskine 1992, Avery 1995, Hodgman and Hermann 2003, Hodgman and Yates 2007). Unfortunately, there are now so few encounters of Rusty Blackbirds in breeding bird surveys and state atlas programs that population trend estimates are not possible in the Northeast (e.g. Sauer et al. 2005). Efforts to locate this diffusely-distributed species are currently labor intensive, with many surveys performed at unoccupied wetlands. Therefore, there remains a critical need to establish an efficient monitoring plan that can provide trend estimates.

Given these logistical challenges, it is essential that this study obtain estimates of wetland occupancy and detectability (the probability of detecting a species, given that it is present) so that biologists designing a monitoring plan can use those estimates to create an efficient sampling design (e.g. MacKenzie and Royle 2005). Sampling designs can be further streamlined if they focus surveys and repeated surveys (for an estimate of detectability, MacKenzie et al. 2006) on wetlands that are likely to be occupied, while statistically accounting for the biased sampling effort. As there are no peer-reviewed habitat analyses for the species, and no known estimates of occupancy or detectability, there is a critical need for this information so that monitoring can be made feasible.

1.3 Range-wide, Long-term Population Declines

Until Russell Greenberg and Sam Droege (1999) addressed the decline of the Rusty Blackbird, the issue was unknown to most ornithologists. Although a declining trend was apparent based on even a cursory inspection of existing datasets, it was thought that, due to the unpredictable nature of wintering Rusty Blackbird flocks and the scattered and remote nature of the species on the breeding grounds, survey data would not be a reliable indicator of population trend. To strengthen their claims of a steep population decline and convert skeptics, Greenberg and Droege (1999) took a comprehensive approach, looking at nearly 130 years of population survey data, state and regional accounts, and checklists compiled during migration. Despite the differences in survey methods and ecology across the range, population survey data were remarkably consistent. Greenberg and Droege (1999) found that the Christmas Bird Count (Sauer et al. 1996), North American Breeding Bird Survey (Sauer et al. 1997), and Quebec Checklists Program (Cyr and Larivee. 1995) all reported statistically significant population declines at approximately 91% (+/- < 2%) during the second half of the 20th century.

Niven et al.'s (2004) analysis of the Christmas Bird Count data (Figure 1.2) showed that Rusty Blackbirds have declined continent-wide at an average of 5.1% per year since 1968 for a conservative estimate of 85% overall. Furthermore, Niven et al. (2004) reported statistically significant declines from Christmas Bird Count data throughout every region of their wintering range, and estimated that the 13.3 million Rusty Blackbirds in 1965 had been reduced to only 2 million by 1999. The most recent analysis (International Rusty Blackbird Technical Group, unpublished analysis, 2007) of

Christmas Bird Count data is even less encouraging, indicating survey-wide population declines averaging $12.5 \cdot \%/yr^{-1}_{95\%}$ ($CI \pm 6.3 \cdot yr^{-1}\%$, $P < 0.01$) for the period 1966–2005 (Sauer et al. 2005). This trend corresponds to a loss of more than 95% of the population since 1966, and represents one of the largest population declines ever documented by the Breeding Bird Survey (Link and Sauer 1996, Sauer et al. 2005).

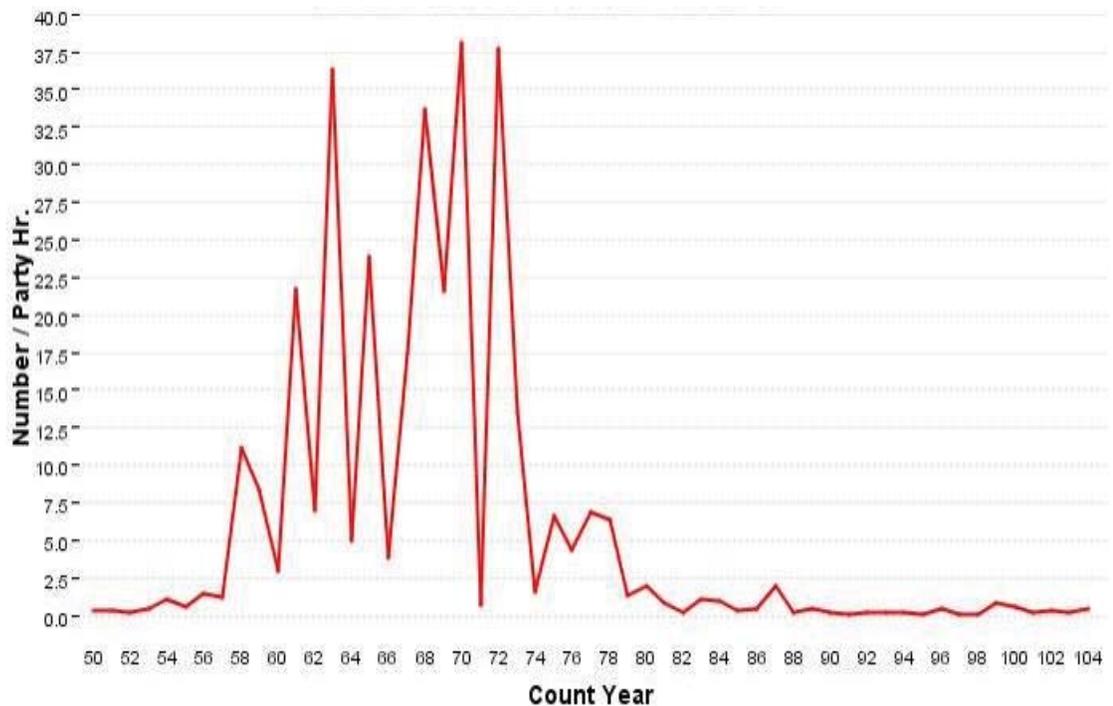


Figure 1.2. Trend in Rusty Blackbird abundance from the Christmas Bird Count (Sauer et al. 2004). Year 50 corresponds to 1950, etc.

To determine population trends prior to the existence of standardized bird surveys of the mid-20th century, Greenberg and Droege (1999) also sifted through qualitative descriptions of the species' abundance in the historical literature. Their results suggest that range-wide declines have been occurring over at least the entire 20th century (Figure

1.3). Regionally, Rusty Blackbird accounts decreased in 14 of 15 states during the late 20th century.

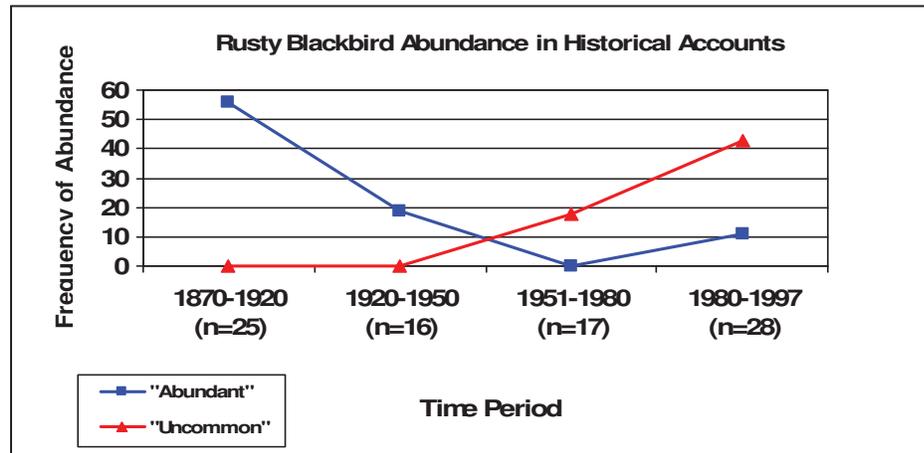


Figure 1.3. Frequency of two adjectives used to describe Rusty Blackbirds in the literature from 1870 to 1997. Adapted from Greenberg and Droege, 1999.

1.4 Range Contraction in Maine

The best available records from Maine suggest that the Rusty Blackbird's breeding range has been contracting for the last century (Figure 1.4). The earliest known record comes from an account of the birds of Maine in which Knight (1908) reported Rusty Blackbirds as summer residents throughout most of northern Maine including Washington County and parts of Hancock, Waldo and Kennebec counties. Forty years later, Palmer's (1949) account excluded Waldo, Kennebec, and southwestern Penobscot counties. In Maine's Breeding Bird Atlas (conducted from 1978 to 1983), Adamus (1987) confirmed that Rusty Blackbirds were breeding across much of northern Maine, with higher concentrations in the western part of the state. Although population declines may have taken place during the period between 1949 and 1983, a substantial range contraction is not evident from known records of this period

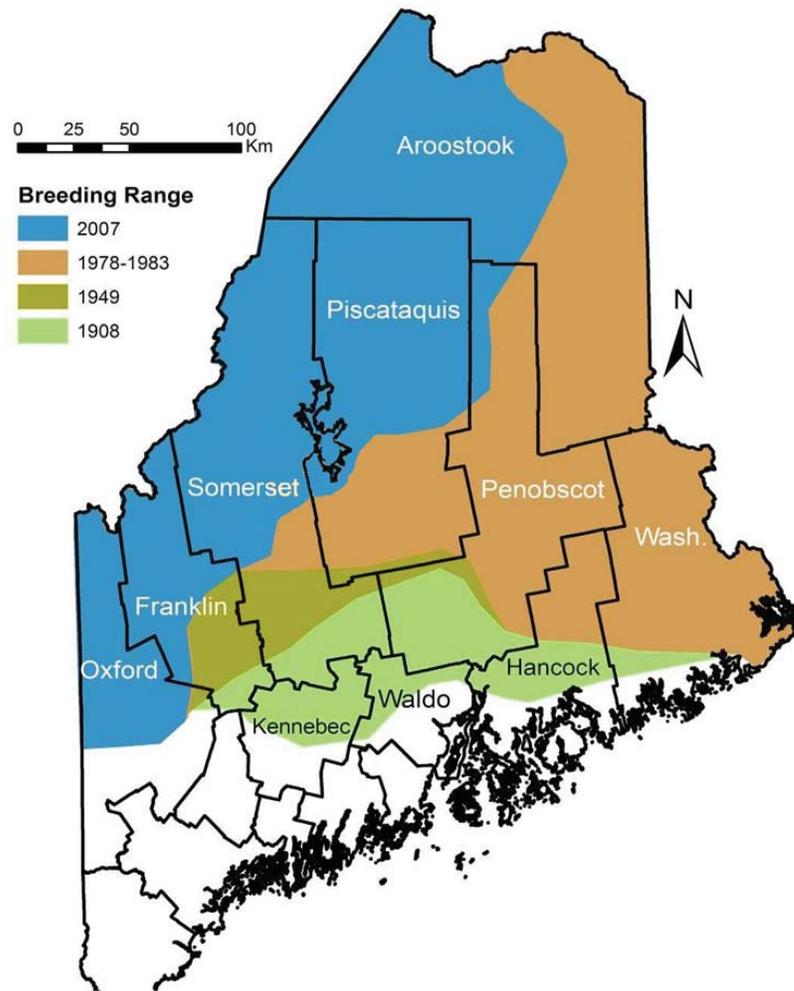


Figure 1.4. Range contraction of the Rusty Blackbird in Maine. 1908 range from Knight (1908), 1949 range from Palmer (1949), 1978-83 range from Adamus (1987), and 2007 range from Maine Ecoregional Surveys (Hodgman and Hermann 2003, Hodgman and Yates 2007) and survey work by Powell, 2008 (Chapter 2).

Two decades later, Hodgman and Hermann (2003), Hodgman and Yates (2007) and Powell (Chapter 2) targeted Rusty Blackbirds with call-response surveys at nearly 1000 wetlands in Maine (Figure 1.1). In eastern and northeastern Maine, more than 350 wetlands were surveyed within the former range of the species without a single confirmed sighting of a Rusty Blackbird. Follow-up surveys in 2007 found that the species is extant but rare in Maine’s western mountains (T. Hodgman, unpublished data),

but effectively extirpated from breeding in Washington County (W. Glanz, unpublished data). From southeast to northwest, the Rusty Blackbird's breeding range in Maine contracted approximately 160 km since 1983. This represents a range loss 26,414 km², 46% of the species' range in 1983. These data suggest that the greatest range contraction took place during the 1980s and 1990s. In comparison, the steepest known range-wide population declines probably occurred during the 1970s (Sauer et al. 2004).

1.5 Hypotheses for Population Decline/Contraction

As there is little known about the species' breeding biology, are few insights the reasons for population declines. Loss of wooded wetlands used for wintering habitat in the southeastern United States is certainly a plausible contributor (Greenberg and Droege 1999) as at least 80% of the country's flooded bottomland hardwood habitats have been converted to agriculture since European colonization (Hefner and Brown 1984). However, only 25% of those wetlands were lost between the mid-1950s and the mid-1980s, which does not explain the approximately 91% population decline during the same period (Greenberg and Droege 1999). Furthermore, agricultural blackbird control programs have killed some wintering Rusty Blackbirds as parts of mixed-species roosts (Dolbeer et al. 1997). However, it appears unlikely that these efforts are having a major impact on the species (M. Avery, U.S. Dept. of Agriculture, Gainesville, FL, pers. comm.), as Rusty Blackbirds typically represent < 1% of these roosts (Avery 1995), and relatively few Rusty Blackbird kills are historically documented. In the boreal forest, logging practices (Erskine 1992), changes in wetland hydrology due to climate change (Klein et al. 2005), competition with other icterids (Ellison 1990, Erskine 1992), and

mercury accumulation (D. Evers, Biodiversity Research Institute, unpublished data) are all potential contributors to the species' decline.

1.6 Understanding Social Structure and Effects of Human-modified Landscapes

Although the species is thought to be “loosely colonial” (Orians 1985), a colony has never been documented in New England (Avery 1995). Therefore, there is little information with which to generate hypotheses for how social structure may have played a part in population declines in the northeast. Obtaining an understanding of how animals use the landscape is a critical step in formulating conservation strategies (Storch 1995, Caro 1999, Powell and Bjork 2004). In particular, knowledge of home range, defined as the area used by an individual during a specific period of its life (Burt 1943), can be essential for understanding social structure, identifying habitat requirements, and evaluating the effects of habitat alterations (Bingham and Noon 1997). There is a critical need to understand the interaction between Rusty Blackbird spacing behavior, social organization, habitat quality and reproductive success.

Habitat features selected by nesting birds (e.g. tree species, cover) are generally associated with increased nest survival (Martin 1998) because behaviors that increase reproductive success should be under strong selection. Although foraging habitat and guild are influential components of habitat selection (Robinson et al. 1995), vegetation structure is particularly influential on nest site selection and structure of bird communities (James 1971, Martin 1992). Predation and brood parasitism, the most common causes of nest failure in songbirds (Ricklefs 1969), likely drive the evolution of nest site selection, and both have caused declines of several species and populations (Martin 1992, Robinson

et al. 1995). Knowledge of habitat features associated with nest success can then guide appropriate management practices on the breeding (Martin 1992).

Recently, ecologists have focused their attention on cases in which habitat preference actually results in *reduced* survival. The term “ecological trap” was first used to describe how an anthropogenic change (i.e., increase in edge habitat) in Michigan led songbirds to select nesting habitats that appeared suitable based on evolved behavioral cues, but resulted in increased predation rates (Gates and Gysel 1978). In this example, a novel anthropogenic habitat mimicked a traditional cue for habitat selection, and when triggered, resulted in reduced nest success. In New England, Rusty Blackbirds often nest in regenerating clear-cuts adjacent to wetlands (pers. obs., Ellison 1990) where it is believed that the landscape mimics the naturally stunted coniferous growth in bogs and fens, creating an attractive alternative nesting habitat for Rusty Blackbirds. Although nest predation tends to be relatively high in fragmented landscapes (Robinson et al. 1995), the effects on Rusty Blackbird nesting success in clear-cuts and other anthropogenically-modified habitats are unknown. Ecological traps can cause population declines even if the less suitable yet preferred habitat represents a small proportion of the landscape (Robinson et al. 1995, Delibes et al. 2001, Kokko and Sutherland 2001). Furthermore, ecological traps can be particularly destructive at low population densities (i.e., trigger the Allee effect) because with little interspecific competition, individuals are relatively free to act on their (maladaptive) preferences (Kokko and Sutherland 2001). Rusty Blackbirds are diffusely distributed across remote wetlands of the boreal forest (Avery 1995), so their populations may be particularly vulnerable to the population declines often associated with ecological traps. Given the potential susceptibility of the

species to negative effects of human-modified landscapes, there is a need to understand how nesting success varies under different timber management regimes.

1.7 Thesis Objectives

None of my three main objectives (habitat selection, nest survival, landscape use) has ever been addressed in a peer-reviewed study of Rusty Blackbirds. First, I sought to analyze breeding habitat occupancy as a function of wetland characteristics and species detectability as a function of sampling variables (Chapter 2). In Chapter 3, my goals were to determine the habitat features associated with nest site selection and nest survival, evaluate evidence supporting the hypothesis that regenerating clear-cuts are an ecological trap for nesting Rusty Blackbirds, and use my findings to provide management recommendations for forest landowners. Finally, I sought to capture and radio-track Rusty Blackbirds in order to map each individual's home range and compare differences in spatial use between colonial vs. non-colonial individuals (Chapter 4).

Chapter 2

MULTI-SCALE HABITAT OCCUPANCY IN NORTHERN NEW ENGLAND

2.1 Chapter Abstract

Rusty Blackbirds (*Euphagus carolinus*) are poorly known boreal wetland-breeding songbirds that have experienced a precipitous population decline since at least the mid 20th century. To quantify Rusty Blackbird habitat selection, I used Akaike's information criterion (AIC) to model species occupancy as a function of wetland variables at both the site scale and the landscape scale. In the best-fit model, puddles (shallow pools not connected to flowing water), wetland area, a coniferous upland and the area of short-canopy forest (< 5 m tall) within 1 km described occupied habitat. Wind speed during surveys had a small negative effect on detectability. My analytical description of Rusty Blackbird breeding habitat along with my mean estimates of habitat occupancy (0.37 ± 0.12 SE) and mean species detectability (0.19 ± 0.05 SE) can be used to improve the efficiency of future efforts to locate and monitor the population.

2.2 Chapter Introduction

The Rusty Blackbird (*Euphagus carolinus*) is a wetland-breeding songbird of the boreal forest (Avery 1995). Although population declines are well documented in this now rare species (Greenberg and Droege 1999, Niven 2004), efforts to locate breeding habitat in northeastern North America are still based only on anecdotal accounts, breeding bird atlas records and government reports (Kennard 1920, Laughlin and Kibbe 1985, Peterson 1988, Ellison 1990, Erskine 1992, Hodgman and Hermann 2003,

Hodgman and Yates 2007). In fact, Rusty Blackbird breeding habitats are described in only one peer-reviewed study (Kennard 1920), and the descriptions are entirely qualitative. 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 Northeast nest primarily in young spruce and fir trees (Kennard 1920, Ellison 1990, Chapter 3). The species forages by probing and leaf flipping while walking in shallow water, plunging their bill, and occasionally their whole head, into the water after insect larvae and crustaceans (Forbush 1927, Bent 1958, Ellison 1990, Avery 1995). Bill morphology and jaw musculature suggest that Rusty Blackbirds target aquatic prey (Beecher 1951, Ellison 1990, Avery 1995).

There are now so few encounters of Rusty Blackbirds in breeding bird surveys and state atlas programs that population trend estimates are not possible in the Northeast where the species was perhaps most common (Erskine 1977, Sauer et al. 2005). Rusty Blackbird populations have declined 85% (Sauer et al. 2004) to > 95% (Sauer et al. 2005) since 1966, with qualitative evidence of a decline throughout the last century (Greenberg and Droege 1999). Causes of this decline are unknown, although loss of wooded wetlands used for wintering in the southeastern United States is a likely contributor (Greenberg and Droege 1999). In the boreal forest, timber management, road construction, changes in wetland hydrology (Klein et al. 2005), competition with other icterids (Ellison 1990, Erskine 1992), and mercury accumulation (D. Evers, Biodiversity Research Institute, unpublished data) are all potential contributors to the species' decline.

I quantitatively described breeding habitat with Quasi-Akaike Information Criterion (QAIC, Burnham and Anderson 2002), and selected the family of models that best described detectability and habitat occupancy of Rusty Blackbirds. My objective was to facilitate the efficient design of future monitoring efforts by quantitatively describing breeding habitat at multiple scales and providing robust estimates of detectability and occupancy of the species.

2.3 Study Area

I conducted my study in northern and western Maine and northeastern Vermont, USA (Figure 2.1). Northern Maine is a vast uninhabited and industrial forest landscape, where I surveyed low elevation wetlands adjacent to clear-cuts, partial cuts, seed-tree cuts and “mature forest” (un-harvested for 40 years). Because of salvage efforts associated with the spruce budworm (*Choristoneura fumiferana*) outbreak in Maine, clear-cutting was widespread in the 1970s and 1980s (Irland 1988), but gave way to primarily partial cutting soon after the Maine Forest Practices Act was implemented in 1991 (Maine Forest Service 1999, McWilliams et al. 2005). In western Maine, the terrain is more mountainous, with scattered human settlements at low elevations. Similarly, northeastern Vermont is a mosaic of lands with small-scale timber management and rural development. The wetlands I surveyed were highly variable, including bogs, wooded fens, alder (*Alnus incana*) swamps, cattail (*Typha latifolia*) marshes and flowages modified by beaver (*Castor canadensis*). Black spruce (*Picea mariana*), red spruce (*Picea rubens*), Balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*) quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), red maple (*Acer*

rubrum), speckled alder, cattails, and *Sphagnum sp.*, were the dominant forms of vegetation.

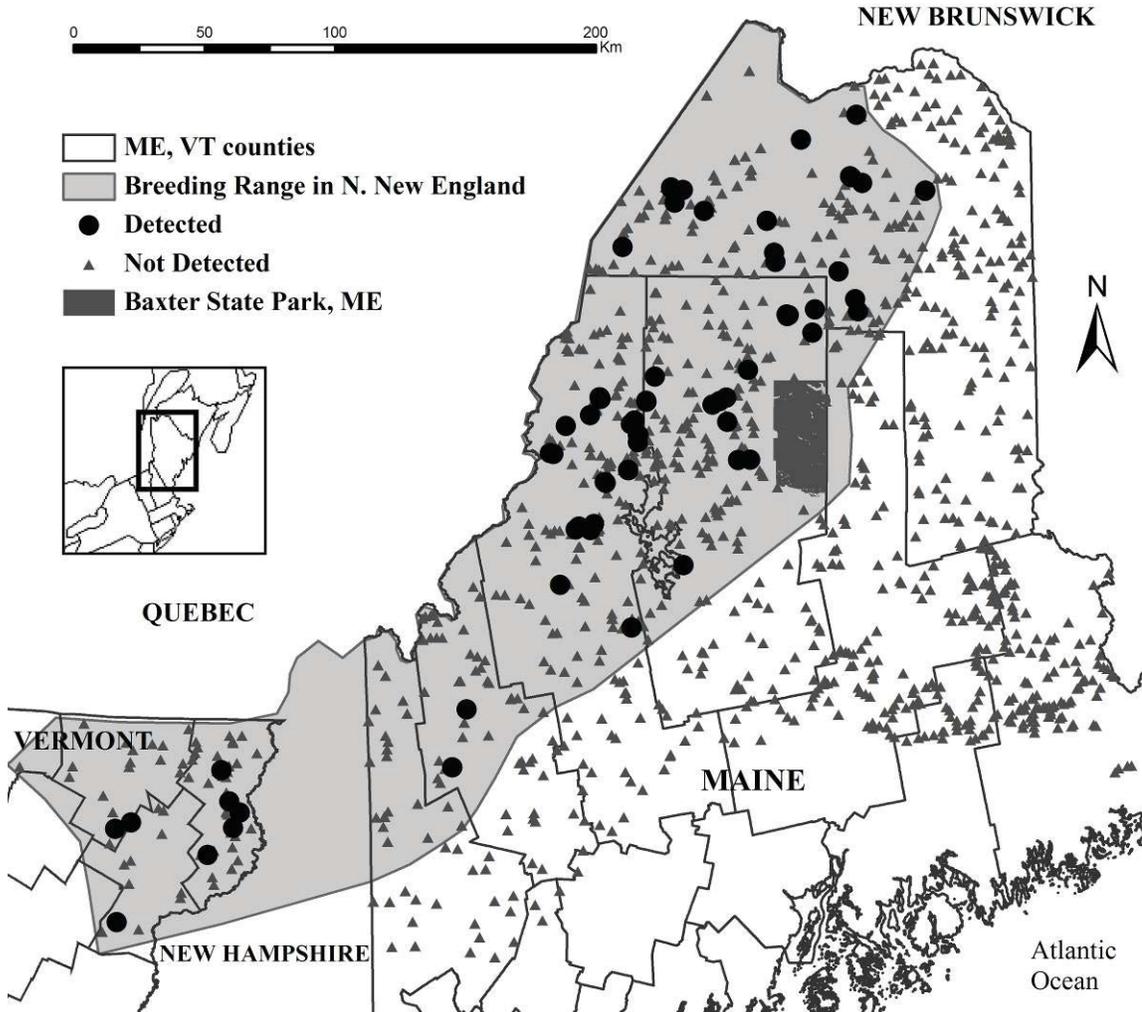


Figure 2.1. Map of callback surveys performed for Rusty Blackbirds in Maine and Vermont, USA, 2001-2007. All 550 wetlands used in my analysis of habitat occupancy were located within the highlighted breeding range.

2.4 Methods

2.4.1 Rusty Blackbird Survey Protocols

I performed point counts for breeding Rusty Blackbirds at 550 wetland sites during May-June 2006 and 2007. Of these 550, 144 were roadside wetlands in northern

Maine that were previously surveyed for Rusty Blackbirds in 2001 and 2002 (Hodgman and Hermann 2003). These and additional wetlands surveyed in 2006 were selected based on historical descriptions of suitable habitat (Ellison 1990, Avery 1995) and accessibility. I surveyed during all daylight hours in 2006, but detected few individuals during mid-day (Figure 1.2). Accordingly, I did not survey from 1100 h to 1600 h in 2007.

To represent the variability of wetlands across the landscape in 2007, I selected wetlands to survey in northwestern Maine and northeastern Vermont using a geographically stratified random design. To estimate Rusty Blackbird detectability in 2007, I repeatedly visited randomly selected wetlands and wetlands where I detected Rusty Blackbirds. I visited 22 wetlands on two occasions and 50 wetlands three times (MacKenzie et al. 2006). Based on map characteristics and opportunistic encounters, I also surveyed other wetlands that appeared suitable. Each survey included three minutes of passive observation followed by a pre-recorded 38-second broadcast of a male Rusty Blackbird vocalization (recorded in New York State by Peter Kellogg, stored at Cornell Lab of Ornithology) and five minutes of passive observation. Following each point-count, I recorded site and sampling variables (Table 2.1). I recorded Rusty Blackbird presence and also the presence of Common Grackles (*Quiscalus quiscula*) (Erskine 1992) and Red-winged Blackbirds (*Agelaius phoeniceus*) (Ellison 1990) at each site.

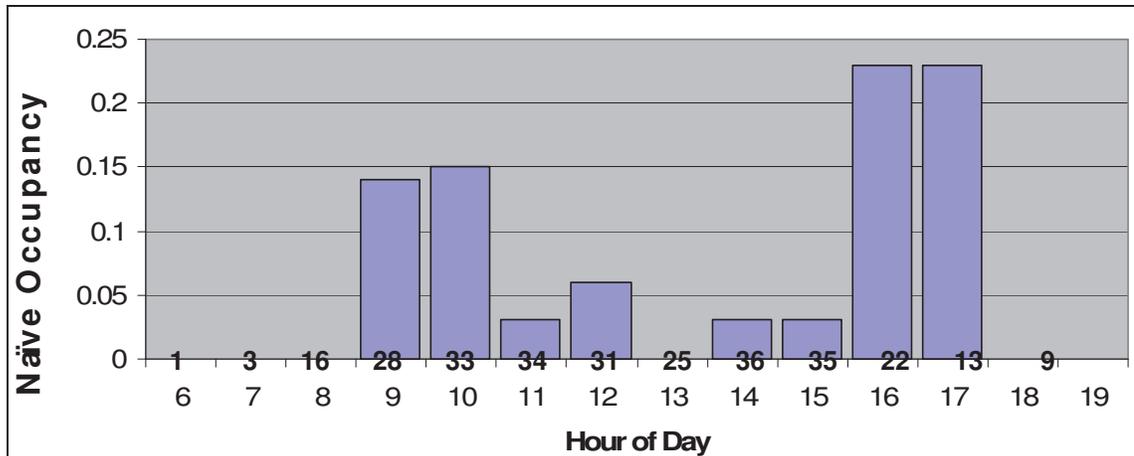


Figure 2.2. Naïve occupancy of Rusty Blackbirds in wetlands surveyed during 2006. Numbers in graph area represent the number of wetlands surveyed during that time period. Hour of day = 6 is from 0600 h to 0659 h.

Table 2.1. Field-collected variables used in modeling the detectability and habitat occupancy of Rusty Blackbirds in Maine and Vermont, USA, 2006 and 2007.

Occupancy Variable ^a	Description
PUDDLES	Presence of puddles that were discontinuous from open water; often temporary
WETAREA	4 wetland area categories, in Ha as estimated by the observer: <0.1, 0.1 - 0.5, 0.5 - 2.0, >2.0
SOFTWD_UP	Upland > 70 % softwood
MUD	Presence of mud
CUR_BEAV	Presence of active beaver at the wetland
YNGSF	Young (< 3m tall) spruce or fir within wetland
HARVEST5TO15	Upland was harvested between 5 and 15 years prior
COGR	Common grackle(s) detected during that season
RWBL	Red-winged blackbird(s) detected during that season
ROADCLASS	3 road classes: unimproved dirt road, improved dirt road, paved road
Detectability Variable	
WIND	4 categories: 0=no wind, 1= leaves move 2= feel wind on face 3= cloggs one ear, not both 4=cloggs both ears
PRECIP	Precipitation during survey
MIN_TR	Minute of day transformed with((MinuteOfDay – 780)2)/100
DAY	Julian day / 100
%SHRUB	% of wetland vegetation composed of shrubs (<2m)
SKY	3 categories: <10% clear, 0-90% clear, >90% clear
%TREE	% of wetland vegetation composed of trees (>2m)

2.4.2 Wetland-scale habitat analysis

I modeled occupancy of Rusty Blackbirds as a function of site characteristics and sampling covariates (PRESENCE, MacKenzie et al.(2002). In modeling occupancy, I first selected the best-fit model for detectability with QAIC and incorporated it into the occupancy models. I excluded all surveys performed outside the Rusty Blackbird's current breeding range (Fig. 2.1). I used "single-season" occupancy models (MacKenzie et al. 2006), with two seasons' worth of data, because I was primarily concerned with modeling habitat occupancy rather than a trend in Rusty Blackbird wetland occupancy.

To estimate Rusty Blackbird detectability, I held occupancy constant and formulated 12 *a priori* detectability models that included combinations of the sampling variables I hypothesized were affecting detection probability (Table 2.1). To avoid errors in PRESENCE associated with values much greater than zero, I transformed sampling variables with large values by dividing by 100. I evaluated model fit with a goodness-of-fit test and calculated c_{hat} in the global detectability model with 100 parametric bootstraps (Burnham and Anderson 2002, MacKenzie et al. 2006). I selected the detectability model with the lowest QAIC value (the "best-fit" model) for use as a base model when building models of habitat occupancy by Rusty Blackbirds. Rather than discard my single-visit dataset from 2006, I pooled it with my 2007 dataset (with resurveys) and developed models under the assumption that detectability was constant from 2006 to 2007. With a colonial or densely breeding wetland species in decline, this would not have been a safe assumption, as detectability would likely decrease with decreasing density within a given wetland. However, in New England, the Rusty Blackbird's distribution is sparse, with mostly single pairs *per* wetland (Chapter 3). Detectability is an estimate of the

probability of detection, given that that wetland is occupied (MacKenzie et al. 2002), so it seems unlikely that detectability would change significantly with a primarily non-colonial species, even if occupancy is decreasing.

Using the literature on Rusty Blackbirds (Kennard 1920, Laughlin and Kibbe 1985, Ellison 1990, Erskine 1992, Avery 1995) and my own field observations, I first compiled an *a priori* list of site variables I hypothesized to be affecting habitat use (Table 2.1). To reduce the number of site variables included in the candidate models, I performed univariate logistic regressions and retained only the variables that were significant at $P < 0.3$ (modified from Hosmer and Lemshow 2000). Using the remaining site variables, I compiled a set of *a priori* candidate models that described Rusty Blackbird breeding habitat (Table 2.2). I checked for correlation among explanatory variables with Spearman's rank correlation test and avoided using correlated variables in the same model. I incorporated the best-fit detectability model into each candidate occupancy model. I assessed goodness-of-fit and obtained estimates of c_{hat} for the global occupancy model using 100 parametric bootstraps. I selected the best-fit occupancy model using QAIC (Burnham and Anderson 2002).

2.4.3 Landscape habitat analysis

To determine if Rusty Blackbird occupancy could be predicted remotely on a landscape scale, I used the National Land Cover Dataset (NLCD), a publicly-available land cover map derived from 2001 satellite imagery (<http://www.csc.noaa.gov/crs/lca/ccap.html>), to quantitatively describe the landscape within a 1-km buffer around each survey point. The 2006 NLCD was not publicly available during analyses, so I used the 2001 NLCD, which did not conflict with my field

observations of land cover types. I chose the 1-km buffer based on the mean home ranges of 37.9 Ha for 13 Rusty Blackbirds (Chapter 4), which if circular, would have a mean radius of 347 m. I assumed that most survey locations were not in the center of an individual's home range (Chapter 4), so I took a conservative approach and used 1-km radius buffer. I quantified the landscape around each buffered survey point using Hawth's Analysis Tools for ArcGIS (Beyer 2004). In addition to NLCD data, models at the 1-km scale also included variables associated with the nearest wetland to the survey point, as indicated by the National Wetlands Inventory (NWI) layer (U.S. Fish and Wildlife Service 2008).

I also summarized the landscape within a 10-km radius of each survey point as well. Several bird studies have shown landscape-level effects of fragmentation using a 10-km radius (Robinson et al. 1995, Hartley and Hunter 1998) and I suspected that this scale might help explain the "patchiness" of Rusty Blackbirds observed on the landscape (Figure 2.1).

In addition to the dataset I used in the site-scale analysis, this landscape analysis also included 144 wetlands surveyed in 2001 and 2002 (Hodgman and Hermann 2003). I excluded the 2001-2002 dataset from the site-scale analysis because technicians at the time collected a different suite of site variables. Consequently, the 2001-2002 data were only valid for a habitat analysis using remotely sensed site variables.

I reduced the number of variables by excluding those with means differing between occupied and unoccupied points by $< 5\%$. At each scale, I then compiled the remaining variables (Table 2.3) into a set of candidate models using combinations of wetland and upland characteristics. I ranked the models in my candidate set using QAIC

as described in the previous section. To compare the performance of the landscape analysis and the site-scale analysis, I compared the best model from each analysis using QAIC.

2.5 Results

2.5.1 Site-scale habitat analysis

I detected Rusty Blackbirds in 48 of the 550 wetlands surveyed during 2006-2007 (Naïve occupancy = 0.087). The best-fit model for detectability included only the variable WIND (-) (Table 2.4). The null model and univariate models including PRECIP and MIN_TR had Δ QAIC values < 2 , indicating that they also received substantial support (Burnham and Anderson 2002). Seven of the remaining 10 candidate models had Δ QAIC values < 4 , meaning that they had some support, although substantially less support than the best-fit model (Table 2.4) (Burnham and Anderson 2002).

Table 2.2. Summary of Quasi-Akaike’s Information Criterion (QAIC)^a model selection results for habitat occupancy by Rusty Blackbirds in Maine and Vermont, USA, 2006-2007.

Model	-2 Log-likelihood	<i>K</i>	QAIC	Δ QAIC	w_i
ψ (PUDDLES, WETAREA, SOFTWD_UP), p(WIND)	343.2	6	156.3	0.00	0.69
ψ (.), p(WIND)	363.8	3	159.0	2.66	0.18
ψ (CUR_BEAV), p(WIND)	360.7	4	159.6	3.33	0.13
ψ (COGR ^b), p(WIND)	361.9	4	160.2	3.86	0.00
ψ (.), p(.) ^c	371.9	2	160.4	4.06	0.00
Gobal model	408.7	9	189.8	33.52	0.00

^a *K*, no. of parameters; QAIC, QAIC adjusted for overdispersion; Δ QAIC, difference in AIC relative to the most parsimonious value; w_i , Akaike wt.

^b Estimate is positive, opposite the hypothesized effect.

^c 22 other models were tested but not listed here due to lack of support (Δ QAIC > 25 . $w_i = 0.00$).

Table 2.3. Landscape variables used in modeling the habitat occupancy of Rusty Blackbirds in Maine and Vermont, USA, 2006 and 2007.

Occupancy Variable	Description	Data Source
ADJAREANWINONFO	Area of non-forested wetland within buffer	NWI
ADJPERIMNWINONFO	Perimeter of non-forested wetland within buffer	NWI
ADJCNTNWINONFO	Area of non-forested wetland within buffer	NWI
NEARESTNWINONFOAREA ^a	Area of nearest non-forested wetland complex	NWI
NEARESTNWINONFOPERIM ^a	Perimeter of nearest non-forested wetland complex	NWI
AREANWIFOBYSUB	Area of forested wetland within buffer	NWI
CCAPPCTPALNONFO	% of non-forested wetland within buffer	NLCD
CCAPPCTPFO	% of forested wetland within buffer	NLCD
CCAPPCTPSSWETLAND	% of scrub-shrub wetland within buffer	NLCD
%SHRUBFOREST	% of upland scrub-shrub forest (< 5m) within buffer	NLCD
%DEVELOPMENT ^b	% of development ^c within buffer	NLCD

^a These variables were only used at the 1Km scale

^b "Development" summarized "developed", "cultivated crops", "pasture/hay" raster classes.

Table 2.4. Quasi-Akaike's Information Criterion (QAIC)^a model selection results including the 90% confidence interval set of models predicting the detectability of Rusty Blackbirds in Maine and Vermont, USA, 2006-2007.

Model	-2 Log-likelihood	K	QAIC	ΔQAIC	w _i
ψ(.), p(WIND)	363.8	3	150.4	0.00	0.24
ψ(.), p(.)	371.9	2	151.6	1.21	0.13
ψ(.), p(PRECIP)	368.5	3	152.2	1.86	0.10
ψ(.), p(MIN_TR)	368.9	3	152.4	1.99	0.09
ψ(.), p(PRECIP, MIN_TR)	364.2	4	152.5	2.13	0.08
ψ(.), p(PRECIP, MIN_TR, WIND)	359.3	5	152.6	2.21	0.08
ψ(.), p(DAY)	370.8	3	153.2	2.78	0.06
ψ(.), p(%SHRUB)	371.7	3	153.5	3.11	0.05
ψ(.), p(%TREE)	371.9	3	153.6	3.20	0.05
ψ(.), p(MIN_TR, DAY)	367.6	4	153.9	3.50	0.04

^a K, no. of parameters; QAIC, AIC adjusted for overdispersion; ΔQAIC, difference in QAIC relative to the most parsimonious value; wⁱ, Akaike wt.

I used the best-fit model for detectability as the base model for site-scale habitat occupancy models. The best-fit model for Rusty Blackbird occupancy, which included the site variables PUDDLES, WETLAND AREA and SOFTWOOD (Table 2.1), was the only model that received substantial support (Table 2.2, Table 2.5). I estimated a mean occupancy of 0.37 ± 0.12 SE, and a mean detectability of 0.19 ± 0.05 SE at the 550 sites. The model including CUR_BEAV received at least some support (Δ QAIC = 3.33, Table

2.2), although it did not perform as well as the base model ($\Delta\text{QAIC} = 2.66$, Table 2.2) and had a low Akaike weight (0.13).

Table 2.5. Untransformed parameter estimates, standard errors, and 95% confidence intervals for the best habitat occupancy model for Rusty Blackbirds at 550 wetlands in Maine and Vermont, USA, 2006-2007.

Covariate	Estimate	SE	95% CI	
Habitat occupancy				
Intercept (Ψ)	-3.090	0.809	-4.676 ,	-1.504
PUDDLES	1.110	0.524	0.083 ,	2.137
WETAREA ^a	0.513	0.273	-0.022 ,	1.048
SOFTWD_UP	1.511	0.650	0.237 ,	2.785
Detection probability				
Intercept(p)	-1.421	0.327	-2.062 ,	-0.780
WIND	-0.002	0.001	-0.004 ,	0.000

^aWETAREA was a categorical variable. Wetlands <0.5 Ha had negative parameter estimates while wetlands > 0.5 Ha had positive parameter estimates.

2.5.2 Landscape habitat analysis

The best-fit 1-km-scale habitat model included % SHRUBFOREST (Table 2.6). Of the 28 candidate models, the top seven included %SHRUBFOREST(+)(95% confidence interval in best-fit model: 0.09 - 9.03). Models ranked two through eight, which included variables quantifying the area and perimeter of the nearest wetland and the percent development, also received substantial support. Although the null model received some support as well, ($\Delta\text{QAIC} = 1.93$), it ranked ninth, with an Akaike weight of only 0.04. Several models that included %DEVELOPMENT as a negative predictor also received some support (Table 2.6), although the confidence interval for the variable included zero (-52.52 - 12.28).

Table 2.6. Quasi-Akaike’s Information Criterion (QAIC)^a model selection results including the 90% confidence interval set of models predicting the occupancy of Rusty Blackbirds at the 1 km landscape scale in Maine and Vermont, USA, 2001, 2002, 2006 and 2007. The top 9 models plus the global model are displayed.

Model	-2 Log-likelihood	K	QAIC	ΔQAIC	w _i
psi(%SHRUBFOREST),p(.)	469.2	3	190.5	0.00	0.11
psi(%DEVEL+%SHRUBFOREST),p(.)	466.2	4	191.3	0.85	0.07
psi(CCAP%SSWET+%SHRUBFOREST),p(.)	466.6	4	191.5	1.01	0.07
psi(NEARNWINONFOAREA+%SHRUBFOREST),p(.)	467.9	4	192.0	1.52	0.05
psi(NEARNWINONFOPERIM+%SHRUBFOREST),p(.)	468.1	4	192.0	1.57	0.05
psi(AREANWINONFO+%SHRUBFOREST),p(.)	468.7	4	192.3	1.81	0.04
psi(PERIMNWINONFO+%SSHURUBFOREST),p(.)	468.7	4	192.3	1.83	0.04
psi(%DEVELOPMENT),p(.)	473.9	3	192.3	1.84	0.04
psi(.),p(.)	479.3	2	192.4	1.93	0.04
Global Model	479.4	13	214.4	23.97	0.00

^a K, no. of parameters; QAIC, QAIC adjusted for overdispersion; ΔQAIC, difference in AIC relative to the most parsimonious value; w_i, Akaike wt.

At the 10-km scale, the null model was the best-fit model, while nine other models had ΔQAIC values < 2 indicating “substantial support” (Burnham and Anderson 2002). The Akaike weight of the null model was 0.17, while no other models had Akaike weights > 0.083.

2.5.3 Scale Comparison

The best-fit model was the global model, $\psi(\text{PUDDLES, WETLAND AREA, SOFTWOOD UPLAND, \%SHRUBFOREST1km})$ (Table 2.7). This model, with an Akaike weight of 0.65, included all variables from the best-fit model at each scale. The site-scale model received some support ($\Delta\text{QAIC} = 2.13$), but the 1 km landscape model received little support ($\Delta\text{QAIC} = 5.01$).

Table 2.7. Summary of Quasi-Akaike’s Information Criterion (QAIC)^a model selection results for comparison of best-fit site-scale model and best-fit landscape scale model predicting habitat occupancy by rusty blackbirds in Maine and Vermont, USA, 2006-2007.

Model	-2 Log-likelihood	K	QAIC	ΔQAIC	w _i
psi(PUDDLES+SOFTWOOD+WETAREA+%SHRUBFOREST1km),p(.)	343.8	6	165.2	0.00	0.65
psi(PUDDLES+SOFTWOOD+WETAREA),p(.)	353.1	5	167.3	2.13	0.22
Null model	371.9	2	169.6	4.39	0.07
psi(%SHRUBFOREST1km),p(.)	368.8	3	170.2	5.01	0.05

^a K, no. of parameters; QAIC, QAIC adjusted for overdispersion; ΔQAIC, difference in AIC relative to the most parsimonious value; w_i, Akaike wt.

2.6 Discussion

2.6.1 Habitat Occupancy

Four site variables best explained wetland occupancy of Rusty Blackbirds (estimated at 0.371 ± 0.12 SE): the presence of puddles (+), the area of the wetland (+), a softwood upland (+), and the percentage of shrubby forest within 1 km (+). Rusty Blackbirds forage in shallow water where they probe for aquatic prey among the leaf litter (Bent 1958, Ellison 1990, Avery 1995). Puddles were generally shallow and unconnected to flowing water, with abundant invertebrates and presumably lacking predatory fish. The best-fit site-scale model indicates that wetland occupancy increases with increasing wetland size. Wetlands greater than 0.5 ha may not provide enough foraging habitat for Rusty Blackbird (unless they are entirely shallow), while wetlands greater than 0.5 ha probably provide ample perimeter foraging habitat. The edges of beaver flowages may provide small patches of relatively unfragmented nesting habitat, as beavers selectively remove hardwoods which increases light gaps and encourages non-preferred trees such as spruces (Johnson and Naiman 1990). Furthermore, McDowell and Naiman (1986) found that beaver increased the density and biomass of wetlands by 2-5

times, and Harthun (1999) found that beaver specifically increased the abundance of four known Rusty Blackbird prey items: dragonflies (*Odenata*), damselflies (*Odenata*), caddisflies (*Trichoptera*) and snails (*Gastropoda*) (Avery 1995). Consequently, the presence of beavers may serve as important factors facilitating Rusty Blackbird habitat selection.

In addition to foraging habitat, the availability of nesting habitat influenced occupancy as well. The presence of softwoods in the adjacent upland increased the probability of occupancy, as did the area of shrubby forest (< 5 m tall) within 1 km of survey points. Of the 35 nests that I found both in and adjacent to wetlands, 34 were located in conifers, and mean nest tree height was only 3.5 m \pm 1.6 SD (Chapter 3). In the 1-km area around the surveyed wetlands, shrubby forest predicted occupancy better than any of the wetland characteristics I evaluated. The sensitivity of Rusty Blackbirds to human disturbance may make them vulnerable to activities associated with development and forest harvest (Chapter 3). Although several supported models included %DEVELOPMENT at the 1-km scale (Table 2.6), the confidence interval for this parameter included zero (-52.52, 12.28), indicating that this variable has little predictive power.

2.6.2 Detectability

Detectability of Rusty Blackbirds in a given wetland was 0.19 (\pm 0.05 SE), so an estimated 81% of surveys at occupied wetlands produced “false absences”. Although nine detectability models received some support, the best-fit model indicated only a small effect of wind (-) on detectability (Table 2.5). Although I provide evidence suggesting that Rusty Blackbirds are relatively difficult to detect between 1100 h and 1600 h (Figure

2.2), I purposely did not repeatedly visit wetlands during this period, which is likely the reason that models did not reflect this heterogeneous temporal detectability. In the modeling exercise, no sampling variable strongly influenced detectability, which may be the result of low predictive power due to few repeated surveys.

2.7 Management Implications

Although Rusty Blackbirds are sensitive to human presence (S. Matusoka, U.S. Fish and Wildlife Service, Anchorage, AK, P. Meyers, U.S. Forest Service, AK, pers. comm.) and neophobic (have a fear of novel objects, C. Mettke-Hofmann, Smithsonian Migratory Bird Center, manuscript in review), the effects of human disturbance on Rusty Blackbird habitat occupancy and reproductive success are unknown (but see Chapter 3). Rusty Blackbirds clearly forage in ephemeral puddles, but it is critical to understand precisely how of the arrangement of foraging habitat (i.e. shallow water) affects habitat selection, social structure (Chapter 4) and reproductive success.

There is no monitoring plan providing data to estimate a regional population trend for Rusty Blackbirds in the Northeast. The inaccessibility of habitat and the species' rarity and low detectability offer substantial challenges to monitoring efforts. Wetlands greater than 0.5 ha and adjacent to shrubby softwoods are more likely to be occupied by Rusty Blackbirds than other wetlands in northern New England, and those wetlands can be remotely targeted. Furthermore, given the considerable logistical challenges in monitoring this species, biologists can increase detections of this rare but widely distributed species by 1) surveying before 1100 h and after 1600 h, 2) using my estimates of occupancy and detectability to determine optimal survey design (MacKenzie and

Royle 2005) and 3) initially targeting and repeatedly surveying wetlands with characteristics identified to be suitable in this study (i.e. puddles, shrubby softwoods, wetlands > 0.5 ha).

Chapter 3

NEST SITE SELECTION AND NESTING SUCCESS: ARE REGENERATING CLEAR-CUTS ADJACENT TO WETLANDS ECOLOGICAL TRAPS FOR RUSTY BLACKBIRDS?

3.1 Chapter Abstract

Ecological theory predicts that animals will prefer habitat features that increase their fitness. When anthropogenic changes create habitat that appears suitable, yet when chosen, results in decreased fitness, animals become caught in an ecological trap (Robertson and Hutto 2006). I studied nest site selection (a comparison of nest sites to randomly-selected sites) and nest survival (a measure of fitness) for 35 Rusty Blackbird nests in northern Maine and northeastern Vermont to evaluate the weight of evidence supporting the hypothesis that Rusty Blackbirds were experiencing ecological traps. The abundance of firs 2-3 m tall, the best positive predictor of nest site selection, and the abundance of firs < 3" DBH, the best *a priori* positive predictor of nest mortality, were highly correlated, suggesting that Rusty Blackbirds used maladaptive cues to select nest sites. Both the aforementioned measures of pole-stage fir abundance were excellent predictors of regenerating clear-cuts less than 20 years old, which was ultimately the best predictor of nest mortality. Nest success was 32.7% in regenerating clear-cuts, 100% in nests not in regenerating clear-cuts, 61.6% overall, and 73% of nests that failed were presumed predated. To test the hypothesis that regenerating clear-cuts are ecological traps for nesting Rusty Blackbirds, ecologists must demonstrate that preference for (not

just selection for) nest sites in regenerating clear-cuts is greater than or equal to preference for non-clear-cut sites. To reduce the probability of nest predation on Rusty Blackbird nests, I recommend that foresters maintain at least a 100 m buffer around wetlands suitable for or occupied by Rusty Blackbirds, and that they delineate the boundaries of wetlands during May and June when ephemeral wetlands are present.

3.2 Chapter Introduction

Habitat features selected for by nesting birds (e.g. stem density, foliage height etc.) are generally associated with increased nest survival (Martin 1998), because behaviors that increase reproductive success should be strongly selected for. Although foraging habitat and guild are influential components of habitat selection (Chapter 2, Robinson et al. 1995), vegetation structure is particularly influential on nest site selection and the structure of bird communities (James 1971, Martin 1992). Predation and brood parasitism, the most common causes of nest failure in songbirds (Ricklefs 1969), likely drive the evolution of nest site selection, and both are known to have caused declines of several species and populations (Martin 1992, Robinson et al. 1995). Thus, knowledge of habitat features associated with nest success can guide appropriate management practices (Martin 1992).

Recently, ecologists have focused their attention on cases in which habitat preference actually results in *reduced* survival. The term “ecological trap” was first used to describe how an anthropogenic change (i.e., increase in edge habitat) in Michigan led songbirds to select nesting habitats that appeared suitable based on evolved behavioral cues, but resulted in increased predation rates (Gates and Gysel 1978). In perhaps the

most extreme example of an ecological trap, Kriska et al. (1998) demonstrated that Mayflies (*Ephemeroptera*), which select nesting habitat based on the cue of horizontally polarized light, preferred to oviposit on asphalt rather than on water. In this example, a novel anthropogenic habitat mimicked a traditional cue for habitat selection, and when triggered in mayflies, resulted in clutch mortality. Ecological traps can cause population declines, even if the less suitable, but preferred habitat represents a small proportion of the landscape (Robinson et al. 1995, Delibes et al. 2001, Kokko and Sutherland 2001). Furthermore, ecological traps can be particularly destructive at low population densities (i.e., trigger the Allee effect), because with little interspecific competition, individuals are relatively free to act on their (maladaptive) preferences (Kokko and Sutherland 2001).

On their breeding grounds in the boreal forest, Rusty Blackbirds are diffusely distributed across remote wetlands (Avery 1995). The species has suffered steep, range-wide population declines over at least the last half-century (Greenberg and Droege 1999, Niven 2004, Sauer et al. 2004, Sauer et al. 2005), and has contracted its range northward by 160 km in Maine (Chapter 1). In the first known effort to quantify Rusty Blackbird nesting success, my objectives were to: (1) determine the features Rusty Blackbirds used to select nest sites at two scales (5 m and 11 m radii), (2) estimate daily nest survival and determine the habitat features associated with nest fate, (3) evaluate evidence supporting the hypothesis that regenerating clear-cuts are an ecological trap for nesting Rusty Blackbirds and (4) use my findings to provide management recommendations for foresters.

3.3 Methods

3.3.1 Study Area

I conducted my study in northern Maine and northeastern Vermont, USA (Figure 2.1). The northernmost area in Maine is primarily uninhabited industrial timberland. Due to salvage efforts following a spruce budworm (*Choristoneura fumiferana*) epidemic in Maine, clear-cutting was widespread in the 1970s and 1980s (Griffith and Alerich 1996). This gave way to primarily partial cutting soon after the Maine Forest Practices Act was implemented in 1991 (Maine Forest Service 1999, McWilliams et al. 2005). Forestland in northeastern Vermont is considerably less industrial, consisting of a mosaic of small-scale timber operations and rural development.

Rusty Blackbirds nested in a variety of different habitats, including wooded bogs, wooded fens, vernal pools, beaver (*Castor canadensis*) flowages, alder swamps, and regenerating clear-cuts adjacent to wetlands. Vegetation near nest sites included black spruce (*Picea mariana*), red spruce (*Picea rubens*), Balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), speckled alder (*Alnus incana*), and *Sphagnum* sp. Likely nest predators included Gray Jays (*Perisoreus Canadensis*), Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchus*), and Red Squirrels (*Tamiasciurus hudsonicus*).

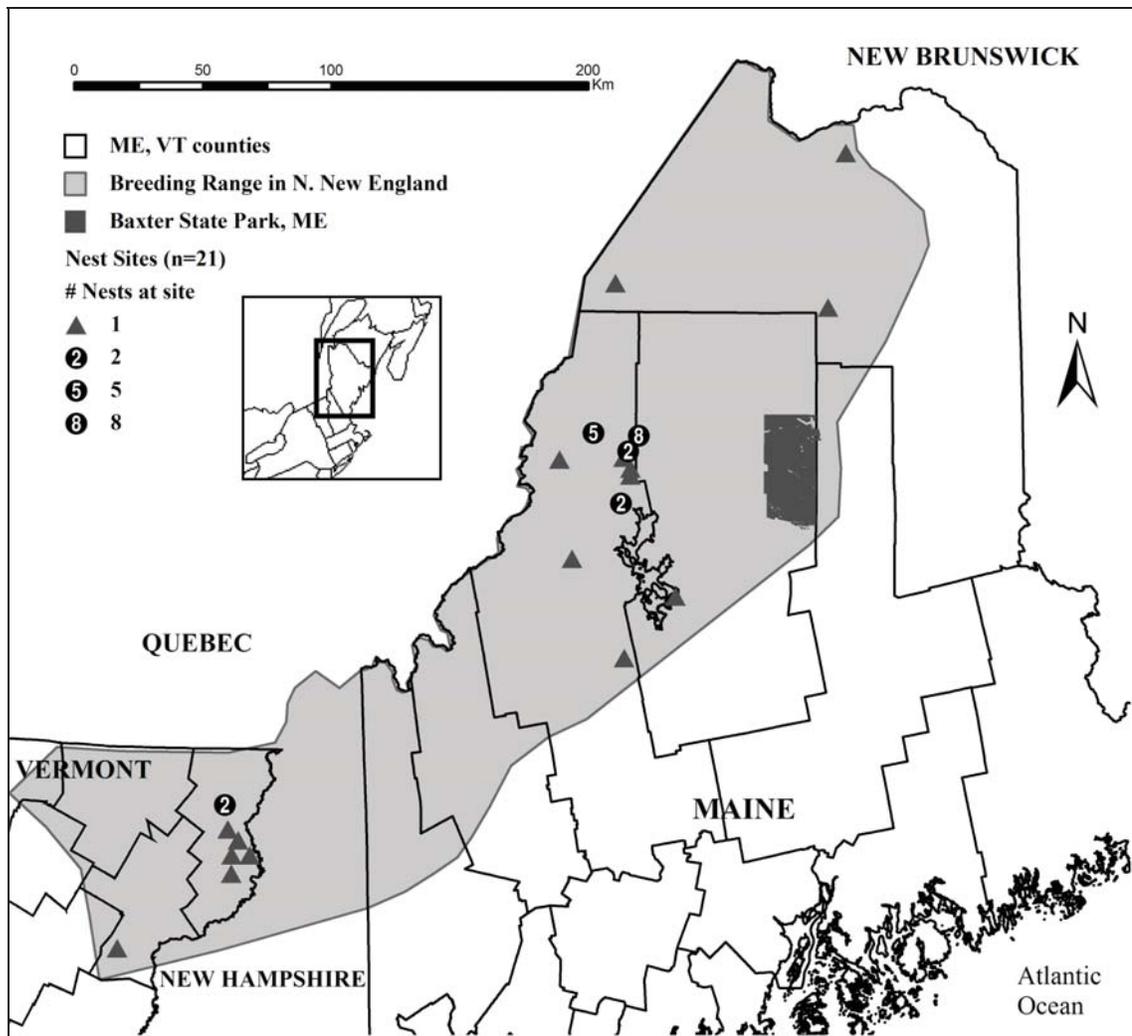


Figure 3.1. Locations of Rusty Blackbird nests found in Maine and Vermont, 2006-2007.

3.3.2 Field Protocols

After the completion of each Rusty Blackbird nesting attempt, I quantified the characteristics of nest and control sites using protocols modified from James and Shugart (1970) and Ellison (1990). I sought to evaluate nest site selection both within wetlands and between wetlands; therefore, I assigned two control plots to each nest plot: one randomly placed within the nesting wetland (inside wetland control), and one randomly placed plot in the nearest wetland (outside wetland control) where I had never detected a

Rusty Blackbird (Chapter 2). As Rusty Blackbirds almost always nest near water (Kennard 1920, Avery 1995), I restricted control plots to the area from 5 m outside to 15 m inside the upland/wetland interface. I centered control plots on a randomly selected spruce or fir of suitable nesting size (i.e. 2-5 m tall, Avery 1995). If a designated control plot overlapped a nest plot, I randomly selected a new location for the control plot. Every 0.5 m from the plot center, for 11.3 m in each of the four cardinal compass directions, I recorded ground cover and the height and DBH (diameter at breast height) of vegetation in contact with (or for tall vegetation, potentially in contact with) a 7.6 cm diameter pole. Every 2 m, I recorded canopy cover (vegetation or sky) with an “ocular tube”, and calculated the average of those binary values to estimate percent canopy cover in nest plots (James and Shugart 1970). For each nest, I recorded a suite of nest measurements (Table 3.1) including estimates of percent concealment at 1 m above, below, and in each of the four cardinal directions around the nest.

In 2006 and 2007, I searched for nests and monitored nest success based on the recommendations of Martin and Geupel (1993). Males often fed incubating females at a conspicuous perch near the nest (pers. obs., Hoffman and Hoffman 1982), so I paid close attention to females being fed. After eggs had hatched, nests were easier to locate, as both parents regularly returned to the nest carrying food. Observations of parents vocalizing with their mouths shut (to keep food items from dropping) were especially informative. I aged eggs with “candlers”, as was originally described for Red-winged Blackbird (*Agelaius phoeniceus*) eggs (Lokemoen 1996). This technique is also accurate to within 2-3 days for Rusty Blackbird eggs (Steve Matsuoka, U.S. Fish and Wildlife Service, Anchorage AK, pers. comm., pers. obs.). I estimated the age of chicks to within

2-3 days based on descriptions of Brewer's Blackbird (*Euphagus cyanocephalus*) nestling development (Balph 1975). I checked nests approximately every five days to determine nest fate, and defined successful nests as those that fledged at least one nestling. In most instances, I confirmed success with observations of parents feeding fledglings. In several instances, I checked nests with well-developed chicks (i.e. > 8 days old), but was not able to check again until well after the expected fledging date. If I was unable to locate parents or young, I considered the nest successful only if there was an abundance of white feather sheaths under the nest lining, and no signs of predation.

3.3.3 Statistical Methods

I modeled nest plot selection by comparing nest and control plots using matched-pairs logistic regression (MPLR) in Program R (R Development Core Team 2008). In two separate analyses, I paired each nest plot with a within-wetland control plot and an outside-wetland control plot. To select variables for the MPLR, I entered each of the initial 22 nest-site variables into univariate MPLRs and retained the variable if a likelihood ratio test was significant at $P < 0.25$ (Hosmer and Lemshow 2000). Using the remaining nine variables, I compiled combinations of ground, mid-height, and canopy-height variables into *a priori* models that I considered biologically meaningful descriptors of Rusty Blackbird nesting habitat. I did not include highly correlated variables (Spearman's rank correlation test, $P < 0.001$) in the same multivariate models (Chase 2002). I continued to filter out inconsequential variables by starting with a full model and eliminating variables when they did not significantly contribute to the model (Likelihood Ratio Tests $P < 0.15$, modified from Werner et al. 2007).

I ranked the final candidate models using Akaike's information criterion corrected for small sample sizes (AIC_c , Burnham and Anderson 2002). I checked for interaction terms in the reduced models and assessed goodness-of-fit on the global model. I assessed the relative importance of influential variables by summing the Akaike weights of each model including the variable in question (Burnham and Anderson 2002). As there is a considerable time commitment involved in vegetation measurements, yet no universally used method for measuring nest vegetation, I compared the best-fit models describing 11-m-radius plots (e.g. James and Shugart 1970) to those describing 5-m-radius plots (e.g. Martin et al. 1997) to determine which more closely matched the scale at which Rusty Blackbirds selected nest sites.

Prior to modeling daily nest survival, I excluded one nest found after young fledged, and two nests that may have been abandoned due to disturbance during capture attempts (Chapter 4), leaving 32 nests. I estimated fledging dates and number of exposure days for successful nests. As most pairs lay five eggs (pers. obs., Avery 1995), and parents tend to begin incubation with the penultimate egg (Steve Matsuoka, U.S. Fish and Wildlife Service, Anchorage, AK, pers. comm.), I used 4 days for the laying period, 13 days for incubation, and 12 days for the nestling period (Steve Matsuoka, pers. comm.), for a total of 29 exposure days. I compiled nest variables that could have influenced nest success; to test the hypothesis that selected nest plot features were also associated with survival, I added the most influential variables from the nest vegetation analysis. I reduced the number of variables in the candidate models by excluding those with $P > 0.25$ in univariate MPLRs (with nest fate as the response variable, Hosmer and Lemsho 2000). I initially formed 11 *a priori* models based on combinations of nest,

canopy and vegetation variables that I hypothesized were affecting fate. I ran this initial set in Program MARK (White and Burnham 1999) and again performed backwards elimination, excluding variables if they did not significantly contribute to the model (Likelihood Ratio Test, $P < 0.15$). I used AIC_c to rank the performance of the final candidate set of four univariate models. After discovering that the variables important for nest site selection were associated with nest failure, I added a *post hoc* model that included a binary covariate for nest plot within a regenerating clear-cut less than 20 years old. Because I used 29 exposure days from the day the first egg was laid to fledging date, I calculated adjusted nest success with the best-fit model using: (daily nest survival)²⁹. Finally, to determine the relationship between regenerating clear-cuts < 20 years old (a binary variable) and the abundance of pole-stage spruce and fir (several continuous variables), I ran simple logistic regressions in Program R (R Development Core Team 2008).

3.4 Results

3.4.1 Nesting Ecology

I found a total of 35 Rusty Blackbird nests, seven in 2006 and 28 in 2007. Eight nests were located in northeastern Vermont (all in 2007) and 27 in northern Maine (Figure 3.1). Nests were large relative to nests of similar sized birds (Table 3.1), and were constructed of dried mud, sticks, lichens, and a grass lining. Nests generally matched the descriptions in Avery (1995), although several of the nests that I found were lined with white pine (*Pinus Strobus*) needles rather than grass. All but one nest was placed in a conifer (Figure 3.2), with median age of the primary nest tree being 14 years.

If eggs needed to be “candled”, most were easily accessible from the ground or with a stepladder, but two nests (5.2 m and 8.8 m high) required climbing the nest tree itself. Only two nests were further than 13.1 m from the wetland/upland interface (32 m, 95 m). I found eight nests in a colony in 2007 (Chapter 4), whereas the remaining nests were non-colonial. Of the non-colonial sites or wetland complex, three had two active nests at a time, whereas the remainder had had only one nesting pair at a time (Figure 3.1).

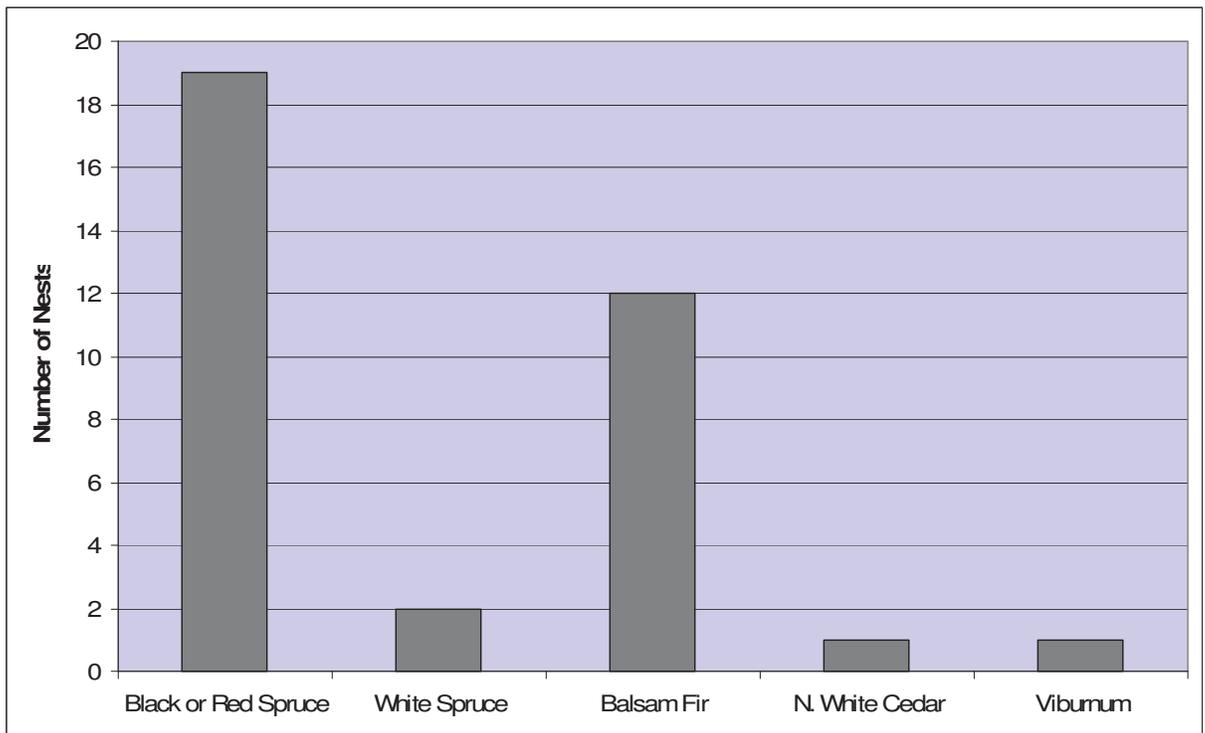


Figure 3.2. Tree species selected by Rusty Blackbirds for nesting in Maine and Vermont 2006-2007. Black and red spruce were not differentiated as the species readily hybridize.

Table 3.1. Summary characteristics of Rusty Blackbird nests (n = 35) found in Maine and Vermont, USA, 2006-2007.

Variable	Mean	SD
Age of primary nest tree (yrs)	18.1	10.4
Height of primary nest tree (m)	3.46	1.63
DBH ^a of primary nest tree (cm)	4.79	3.73
Diameter of primary branch (cm)	1.11	0.65
Distance from nest to primary trunk (cm)	1.12	1.99
Nest height off ground (m)	1.75	1.49
Number of trees supporting nest	1.51	0.70
Nest bowl inside diameter (cm)	10.04	0.88
Nest bowl outside diameter (cm)	13.84	1.36
Nest bowl height (cm)	9.54	2.81
Concealment ^b	63.66	14.16
Distance to wetland (m)	7.41	18.77
Distance to standing water (m)	13.74	20.61
Distance to nearest road (m)	203.8	267.4

^aDBH = diameter at breast height

^bMean % nest concealment estimated from 1m below, above, north, east, south and west of nest.

3.4.2 Nest Vegetation Analysis

I first compared vegetation between 11-m-radius nest plots and the inside wetland control plots (James and Shugart 1970). The only explanatory nest site variables retained after the filtering process described either the abundance of woody vegetation (+), or the abundance or height of vegetation in the canopy (-) (Table 3.2).

Table 3.2. Influential variables used in modeling procedures.

Variable	Description
Trees >10m tall	Abundance of all trees >10 m tall
Canopy Height	Maximum height of canopy in plot
Firs 1-2m tall	Abundance of firs 1-2 m tall
Firs 2-3m tall	Abundance of firs 2-3 m tall
Firs < 3" DBH	Abundance of 3-6" (7.6-15.2 cm) DBH ^a firs
Firs 3-6" DBH	Abundance of 6-9" (15.2-22.9 cm) DBH firs
Spruces 4-5m tall	Abundance of spruce from 4-5 m tall
Spruces 4-5m tall	Abundance of spruce from 4-5 m tall
All stems within 5m	Abundance of commercially valuable trees (i.e. alder) > 1.3 cm in DBH and within 5m of nest
Social structure (colonial/not)	Binary: nest located in a colony of rusty blackbirds.
Regen Clear-Cut	Binary: nest plot located in a regenerating clear-cut or seed tree clear-cut < 20 yrs. old.

^aDBH = diameter at breast height

The best-fit model included the abundance of 2-3 m tall fir (parameter estimate: 0.045 ± 0.025 SE) and the abundance of vegetation above 10 m (parameter estimate: -0.021 ± 0.010 SE, Table 3.3), and three other models produced ΔAIC_c values < 2 indicating “substantial” support (Burnham and Anderson 2002). The two variables in the best-fit model were the two most influential (Table 3.4).

Table 3.3. Confidence set (95%) of Akaike's Information Criterion (AIC_c)^a models predicting differences between 11 m radius nest plots (n=35) and randomly placed control plots within the same wetland for nesting rusty blackbirds in Maine and Vermont, 2006-2007.

Model	-2 Log Likelihood	K	AIC _c	ΔAIC _c	w _i
Firs 2-3m tall + Trees >10m tall	42.5	4	93.5	0.00	0.21
Firs 2-3m tall + Canopy Height	42.5	4	93.6	0.11	0.20
Trees >10m tall + Spruces 4-5m tall	42.6	4	93.9	0.36	0.18
Firs <3" DBH + Trees >10m tall	43.1	4	94.8	1.31	0.11
Firs 2-3m tall + Firs 3-6" DBH	43.5	4	95.6	2.06	0.08
Trees >10m tall	45.2	3	96.8	3.25	0.04
Canopy Height + Spruces 4-5m tall	44.4	4	97.4	3.90	0.03
Firs 3-6" DBH + Spruces 4-5m tall	43.3	5	97.6	4.08	0.03
Firs 2-3m tall	45.7	3	97.7	4.16	0.03
Firs <3" DBH + Canopy Height	44.8	4	98.2	4.73	0.02
Canopy Height	46.0	3	98.4	4.91	0.02
Null	48.5	2	101.2	7.66	0.00
Global ^c	38.5	11	103.5	10.01	0.00

^a K, no. 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 wt.

^b DBH, Diameter at breast height.

^c Model included all variables; Variance inflation factor, C_{hat} = 1.30.

Table 3.4. Relative importance of variables in the best model comparing 11m radius rusty blackbird nest plots to random control plots within the same wetland.

Variable	β ^a	No. Models Variable is in	Σw _i ^b
Trees >10m tall	negative	4	0.54
Firs 2-3m tall	positive	4	0.52
Canopy Height	negative	4	0.27
Spruces 4-5m tall	positive	4	0.25
Firs <3" DBH	positive	3	0.13

^a β, direction of sign of parameter estimate for the variable.

^b Σw_i, sum of Akaike weights of all models the variable is included in.

When I modeled the difference between 11-m-radius nest plots and outside wetland control plots, two models received substantial support (Table 3.5). The top three models included canopy height(-), and the sum of their Akaike weights was 0.95,

indicating a high probability that canopy height (-) was the best predictor of nest plots. The top five models all included an explanatory variable quantifying the abundance of pole-stage firs (+).

Table 3.5. Confidence set (99%) of Akaike’s Information Criterion (AIC_c)^a models predicting differences between 11 m radius nest plots (n=35) and randomly placed control plots at the nearest non-occupied wetland for rusty blackbirds nesting in Maine and Vermont 2006-2007.

Model	-2 Log Likelihood	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>
Canopy Height + Firs 2-3m tall	74.4	4	75.0	0.0	0.45
Canopy Height + Firs 1-2m tall	74.9	4	75.6	0.5	0.35
Canopy Height + Firs <3" DBH	76.5	4	77.2	2.1	0.16
Trees >10m tall + Firs <3" DBH	79.8	4	80.4	5.4	0.03
Trees >10m tall + Firs 2-3m tall	82.1	4	82.8	7.7	0.01
Global ^c	81.6	10	85.3	10.2	0.00
Null	101.0	2	101.2	25.6	0.00

^a *K*, no. 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 wt.

^b DBH, Diameter at breast height.

^c Variance inflation factor, *C_{hat}* = 1.03.

I compared the best-fit models quantifying Rusty Blackbird nest plot selection for 11-m-radius plots and 5-m-radius plots. Unfortunately, for this analysis of nest plots vs. outside control plots, I did not measure canopy height on the 5 m scale, which turned out to be the strongest predictor variable for the 11 m plots. Therefore, for each plot size, I compared the best-fit model that did not include canopy height. In each case, the remaining best-fit model included abundance of > 10 m tall trees (-) and abundance of < 7.6 cm DBH firs (+), and the 11-m-radius model performed only marginally better than the 5 m radius model (ΔAIC_c = 1.6). Furthermore, the best-fit models comparing nest plots to inside control plots at each scale included the same two variables, the abundance of 2-3 m tall fir and the abundance of vegetation above 10 m. Again, the best-fit model

using data collected at the 11-m-radius scale performed only marginally better ($\Delta AIC_c = 1.4$) than the best-fit model using data collected at the 5-m-radius scale.

3.4.3 Nest Survival Analysis

All eleven failed nests were located in regenerating clear-cuts. Of these, eight were presumed predated as all eggs or chicks were destroyed or disappeared prior to the estimated fledging date. I did not observe any evidence of brood parasitism, nor did I detect any brown-headed cowbirds (*Molothrus ater*) in my study areas. After applying coarse filters to reduce the number of variables in the set of *a priori* candidate models describing nest success, only four correlated variables remained (Table 3.6).

Table 3.6. Summary of Akaike’s Information Criterion (AIC_c)^a model selection results for nest survival (n=32 nests) of rusty blackbirds in Maine and Vermont, USA, 2006-2007.

Univariate Model	-2 Log Likelihood	K	AIC_c	ΔAIC_c	w_i
Regen clear-cut ^c	49.1	2	53.1	0.00	0.60
Firs < 3" DBH within 11m	50.8	2	54.9	1.76	0.25
All stems within 5m	53.9	2	57.9	4.84	0.05
Firs 2-3m tall within 11m	54.6	2	58.6	5.53	0.04
Social structure (colonial/not)	54.7	2	58.8	5.65	0.04
Null	57.8	1	59.8	6.72	0.02

^a K, no. 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 wt.

^b DBH, Diameter at breast height.

^c Model run post hoc.

Contrary to my hypotheses, the *a priori* four variables, which were all strong positive predictors of nest plot selection, were *negative* predictors of nest success (i.e. associated with nest mortality). None of the variables that I measured were positively associated with nest survival. The best-fit *a priori* model, including the abundance firs less than 3”

DBH, was well supported (Akaike weight = 0.63, no other model with $\Delta AIC_c < 2$). Based on the best-fit *a priori* model for nest survival, overall daily nest survival was 0.984 ± 0.007 SE (n = 32, Figure 3.3), and thus overall nest success was 61.6%. Based on the colonial model, daily nest survival for colonial pairs was 0.950 ± 0.025 SE (22.4% success, n = 7) and daily non-colonial nest survival was 0.986 ± 0.007 SE (66.2% success, n = 25, Figure 3.3).

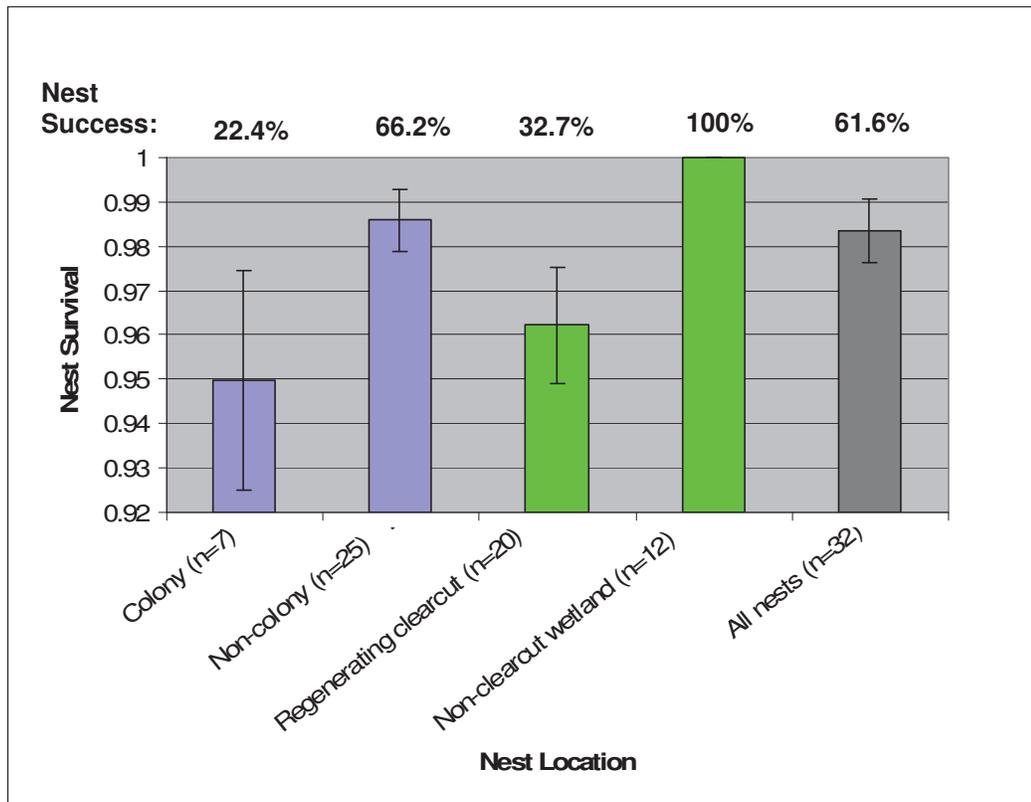


Figure 3.3. Daily nest survival of Rusty Blackbird nests in different timber harvest regimes (green bars) and social situations (blue bars). Error bars represent mean daily nest survival ± 1 standard error. Percentages above bars are adjusted nest success, calculated using 29 exposure days.

The univariate *post hoc* model, which included the variable “Regen clear-cut”, was marginally better than my best-fit model in the *a priori* candidate set ($\Delta AIC_c = 1.8$). Based on the *post hoc* model, daily nest survival in regenerating clear-cuts was $0.962 \pm$

0.013 SE (32.7% success, $n = 20$) and daily survival for nests not in regenerating clear-cuts was 1.00 (100% success, $n = 12$, Figure 3.3). Simple logistic regressions confirmed that the probability that a nest plot was located in a regenerating clear-cut less than 20 years old increased with increasing abundance of firs 2-3 m tall (the positive predictor of nest sites) and abundance of firs < 3" DBH (the best predictor of nest mortality) ($P < 0.001$). Abundance of firs 2-3 m tall and abundance of firs < 3" DBH were also highly correlated with each other (Spearman's $RHO = 0.926$, $P < 0.001$).

3.5 Discussion

Rusty Blackbirds were less likely to nest under numerous trees greater than 10-m-tall and more likely to nest where pole-stage firs were abundant. Nest plots with 11-m-radii were only marginally better predictors of nest site selection than 5-m-radius plots, and they ultimately produced the same conclusions with respect to nest site selection. Therefore, the larger nest plots added little additional insight into nest site selection. Researchers studying Rusty Blackbirds will save time yet sacrifice little precision by using 5 m plots rather than 11 m plots.

Unexpectedly, the abundance of pole-stage firs was associated with nest mortality, opposite what one might expect if nest site selection is adaptive. Initially, I suspected that relatively poor nest survival at the colony site (Figure 3.3), which was located in a regenerating clear-cut, was perhaps confounding this observation. However, at all sites, the abundance of firs < 3" DBH was a better predictor of nest mortality than parental social structure (Table 3.6), suggesting that habitat rather than social structure was responsible for the low nest survival in the colony. Furthermore, the fact that

regenerating clear-cuts were ultimately a better predictor of nest mortality than the abundance of pole-stage fir suggests that the factors that drive nest mortality operate on a scale larger than my 11 m plots. Many nests that I found outside regenerating clear-cuts (e.g. wooded fens, bogs, edges of beaver ponds) were placed in dense stands of short conifers, but in every case, Rusty Blackbirds fledged young in relative isolation from the effects of clear-cutting practices.

The abundance of firs 2-3 m tall, the best positive predictor of nest site selection, and the abundance of firs < 3" DBH, the best *a priori* positive predictor of nest mortality, were highly correlated, suggesting that Rusty Blackbirds used maladaptive cues to select nest sites. Furthermore, regenerating clear-cuts had relatively high abundance of both the aforementioned measures of pole-stage firs, and nest placement in regenerating clear-cuts was ultimately the best predictor of nest mortality. Rusty Blackbirds appear to be selecting for vegetation typical of regenerating clear-cuts, yet producing relatively few young there. Robertson and Hutto (2006) explain that when an animal prefers and consequently selects a habitat in which it is relatively unsuccessful, it is caught in an ecological trap. They specify three conditions that together provide strong evidence for the existence of an ecological trap: 1) individual preference for one habitat over another (in a severe trap) or an equal preference for both habitats (in an equal-preference trap), 2) unequal individual fitness between the two habitats, and 3) individual fitness cannot be higher in preferred habitats. Rusty Blackbirds selected for nest sites with vegetation typical of regenerating clear-cuts (i.e. many pole-stage firs), yet had lower fitness (i.e. nesting success) in regenerating stands, so this study satisfies conditions two and three. However, non-random habitat use (e.g. nest site selection) is not a suitable surrogate for

preference (Van Horne 1983) because, for example, subordinate individuals can be found in non-preferred habitat if they are excluded by dominant individuals (Sherry and Holmes 1988). Robinson and Hutto (2006) use Johnson’s (1980) definition of preference, “the likelihood of a resource being chosen if offered as an option with other available options”. Therefore, though Rusty Blackbirds selected for sites with many pole-stage firs, this finding provides no evidence that the species preferred to nest in regenerating clear-cuts.

Table 3.7. Feasibility of assessing rusty blackbird habitat preference in northeast North America. Lines of evidence adapted from Robinson and Hutto (2006).

Line of Evidence	Currently Feasible?	Reasoning
Settlement patterns	No	Breeding habitats too dispersed to determine migratory arrival times.
Distribution of dominant individuals	No	No consensus on how to age breeding adults. Individual site fidelity is not known, thus it is not
Site fidelity	Yes	Determining nesting fidelity is straightforward.
Temporal variance in population size	Yes	This is essentially a measurement of variation in fidelity over multiple years.
Choice experiments	No	Not ethical to perform removal experiments on species of conservation concern; difficult to capture individuals and lab experiments highly unnatural.

There are five lines of inquiry that provide clear evidence for preference (Table 3.7, Robertson and Hutto 2006), although only two are currently feasible to evaluate with Rusty Blackbirds in the Northeast: site fidelity and temporal variance in population size. From 2006-2007, I determined nesting fidelity at three sites (Table 3.8) that were within 30 km of each other and did not experience obvious habitat alterations between years. In 2007, Rusty Blackbirds returned to nest in the two sites in regenerating clear-cuts, but did not return to nest in a non-regenerating fen. This limited sample supports the hypothesis that Rusty Blackbirds had suitable non-regenerating habitat available to them that they did not prefer, choosing instead to nest in regenerating clear-cuts. I recommend that

future studies determine nesting fidelity and/or temporal variance in nesting fidelity to test the hypothesis that preference for nest sites in regenerating clear-cuts is greater than or equal to preference for non-clear-cut sites. Furthermore, to facilitate studies of the distribution of dominant individuals, more research must be conducted to determine if breeding second-year Rusty Blackbirds can be reliably aged on the breeding grounds (P. Sinclair, Canadian Wildlife Service, Yukon Territory, pers. comm.), and if so, where they nest.

Table 3.8. Nest site fidelity of rusty blackbirds at three wetlands in Maine, 2006-2007.

2006 Nest Site	< 20 yr old clearcut	Detected in 2007	Nesting in 2007
Little Bog	Yes	Yes	Yes (2 depredated, 1 successful)
Seboomook	Yes	Yes	Yes (abandoned or depredated)
490 Fen	No	Yes	No

Robinson and Hutto (2006) concluded that only five studies had firmly established the existence of an evolutionary trap (Horvath et al. 1998, Kriska et al. 1998, Remes 2003, Lloyd and Martin 2005, Weldon and Haddad 2005). All five were caused by (evolutionarily) rapid anthropogenic changes, and in three, habitat alterations increased brood parasitism and/or predation, and bird nest survival was compromised (Remes 2003, Lloyd and Martin 2005, Weldon and Haddad 2005). I attributed eight of the eleven nest failures, all in regenerating clear-cuts, to predation. In regenerating clear-cuts in eastern Maine, Rudnicky and Hunter (1993) also found that predated nests differed from undisturbed nests only in the increased cover of pole-stage conifers (0 - 3 m tall). They speculated that to avoid predation themselves, small nest predators (e.g. red squirrels) may remain close to dense cover in regenerating cuts, and are therefore more likely to find nests under thick cover and relatively less volume of forest. Siepelski

(2006), found that understory nests (≤ 3 m) in northern mid-west North America were more than three times more abundant in sites without red squirrels. Gray jays, blue jays and American crows are other likely nest predators in my study areas, and the latter two tend to be more abundant in fragmented regions (Robinson et al. 1995).

Regardless of the specific predator involved, this study demonstrated that nest success was lower in regenerating clear-cuts, and that most nests failed due to predation. Although overall nest success was 61.6%, nest success in regenerating clear-cuts was only 32.7%. As conifers are a dominant life form in the boreal forest, Rusty Blackbirds undoubtedly evolved their preference for nest sites with dense pole-stage coniferous cover prior to European settlement, and thus prior to clear-cutting practices. Historical nesting sites likely included small patches of shrubby coniferous vegetation in beaver wetlands, bogs, and post-burn and post-blow-down regeneration adjacent to fens and other wetlands. The edges of beaver flowages may provide small patches of relatively un-fragmented nesting habitat, as beavers selectively remove hardwoods, which increases light gaps and encourages non-preferred trees such as spruces (Johnson and Naiman 1990). More than the nests I found were located in regenerating clear-cuts (Figure 3.3), an evolutionarily recent anthropogenic habitat type where nest predators have been found in greater numbers than in regenerating burns (Stuart-Smith and Hayes 2003, Smucker et al. 2005). The species' cue for nest site selection has probably not changed recently, but ongoing habitat alterations since European colonization and in the 1970s and 1980s, post-budworm salvage cutting (Griffith and Alerich 1996), has created a superabundance of nesting habitat for Rusty Blackbirds. Already particularly vulnerable to spruce budworm, dense stands of riparian conifers were particularly hard-hit by budworm and post-

budworm salvage efforts because no-spray buffers were imposed to protect streams from the effects of pesticides (Irland 1988). Although these large regenerating stands may mimic “natural” habitat on a small scale, the fragmentation associated with clear-cutting likely provides habitat for nest predators as well. More studies are needed to determine the extent to which management actions have mimicked natural habitat and ultimately created ecological traps (Robertson and Hutto 2007). Maladaptive behaviors can be particularly disruptive at low population densities, as individuals in a reasonably empty landscape have relative freedom to select their preferred habitats (Kokko and Sutherland 2001). Given the synchrony of the species’ range contraction in Maine (Figure 1.1) and the regeneration of post-budworm salvage cutting in the 1970s and 1980s, an ecological trap is a plausible contributor to population declines and/or range contraction of Rusty Blackbirds in Eastern North America.

3.6 Management Implications

Since the Maine Forest Practices Act was implemented in 1991, alternatives to clear-cutting have become the dominant form of silviculture in Maine, with clear-cutting now accounting for less than 5% of total harvesting volume by the late 1990s and early 2000s (Maine Forest Service 1999, McWilliams et al. 2005). Although this study showed reduced nest survival in regenerating clear-cuts, the effects of partial harvesting practices on Rusty Blackbird nest success are unknown. Furthermore, Rusty Blackbirds (males in particular) tend to use seed trees and snags as perches from which they presumably defend their breeding territories (pers. obs). However, these structures may provide perches for predators as well (Ratti and Reese 2008), and their effect on nesting success

of Rusty Blackbirds is also unknown. Abundance of predators and Rusty Blackbird nest success must be evaluated under different habitat management schemes and predator abundances.

Historically, Rusty Blackbird nests have almost always been found close to water (Kennard 1920, Avery 1995). In this study, mean distance to wetland was $7.4 \text{ m} \pm 18.7$ SD, but as far as 95 m from wetlands. In his review of nest predation, Patton (1994) found that predation was greatest less than 50m from an edge, and in Maine, Vander Haegan and Degraff (1996) found that the effects of predation extended 75 m into riparian buffers. However, Small and Hunter (1988) reported that even small tracts of unfragmented forest were less subject to nest predation if they were adjacent to water. Furthermore, many wetlands used by Rusty Blackbirds are ephemeral (e.g. vernal pools, certain wooded fens, Chapter 2), and may not contain standing water during winter or summer, the primary times for timber management. Therefore, to reduce predation on Rusty Blackbird nests, I recommend that forest practitioners maintain at least a 100 m buffer around suitable (Chapter 2) or occupied wetlands, and delineate the boundaries of wetlands during May and early June when seasonally flooded pools are more visible.

Chapter 4

HOME RANGE AND SPATIAL USE OF WETLANDS BY COLONIAL AND NON-COLONIAL RUSTY BLACKBIRDS

4.1 Chapter Abstract

Although anecdotal evidence suggests that Rusty Blackbirds can cluster nests together during the breeding season (forming “loose colonies”), there is have virtually no data with which to understand species’ social organization or spatial use of the landscape. I calculated 95% kernel density estimates of home range size for 13 individuals, eight of which were part of the first “loose colony” reported in New England. Colonial individuals had significantly larger home range and core range areas compared to non-colonial pairs, which I hypothesize is due to increased cooperative defense or increased opportunities for extra-pair fertilizations.

4.2 Chapter Introduction

Despite knowledge of the prolonged and ongoing declines in Rusty Blackbird (*Euphagus carolinus*) populations (Greenberg and Droege 1999, Sauer et al. 2004), there has been only one published study of the species’ breeding biology (Kennard 1920). It is unknown how climate change and the subsequent drying of boreal wetlands (Klein et al. 2005) or ongoing timber practices in the boreal forest are affecting Rusty Blackbirds. Understanding of how animals use the landscape is a critical step in formulating conservation strategies (Storch 1995, Caro 1999, Powell and Bjork 2004). In particular, knowledge of home range, defined as the area used by an individual during a specific

period of its life (Burt 1943), can be essential for understanding social structure, identifying habitat requirements, and evaluating the effects of habitat alterations (Bingham and Noon 1997).

Although the statistical analysis of an animal's home range has made considerable progress over the last 15 years, there remains little consensus on methods for best estimating or analyzing home range size (Laver and Kelly 2008). Despite criticisms (Powell 2000, Laver and Kelly 2008), minimum convex polygons (MCPs) continue to be a popular way to quantify home range size. Although analysis and interpretation is straightforward, MCPs are particularly sensitive to the number of locations (Seaman et al. 1999), sampling duration (Swihart and Slade 1985), sampling strategy (Börger et al. 2006), and serial autocorrelation (Swihart and Slade 1985). However, if used properly, the Kernel Density Estimator (KDE), introduced for home-range analyses by Worton (1987) is less sensitive to many of the limitations of MCPs, and has become the preferred method for analyzing animal home ranges (Börger et al. 2006, Laver and Kelly 2008). Furthermore, the strength of radio-tracking efforts can be examined with tests of sampling interval for statistical independence (Swihart and Slade 1985) and KDE asymptotes (the number of locations at which the area of individual's home range stabilizes, Laver and Kelly 2008) performed on individual home ranges.

Given the substantial population decline (Greenberg and Droege 1999) and the lack of basic biological knowledge about breeding populations of Rusty Blackbirds, there is a critical need for more information on landscape use and social organization of the species. I placed radio transmitters on 13 breeding Rusty Blackbirds and used 95% KDE to calculate home ranges for radio-marked individuals. My objectives were to (1) map

home ranges and core home ranges to examine their spatial arrangement around wetlands; (2) compare differences in spatial use of the landscape between colonial and non-colonial individuals; and, (3) provide recommendations to ornithologists interested in capturing and radiotracking the species.

4.3 Study Sites

I captured and radio-tracked Rusty Blackbirds at four sites with small wetlands adjacent to industrially managed timberland in Somerset County and Piscataquis County, Maine (Figure 4.1). The “Honey Hole Colony”, located in Township T6 R15 WELS, is bisected by a well-maintained, north-south forest road. The colony was centered on a 70 ha, 13-year-old stand of regenerating spruce (*Picea sp.*) and balsam fir (*Abies balsamae*). This stand was perforated by several small (< 0.6 ha) scrub/shrub wetlands (Cowardin et al. 1979) and many wet patches of *sphagnum sp.* A hill adjacent to the regenerating stand was covered mostly mature (< 40 yr) coniferous vegetation, many recent partial cuts regenerating to raspberry (*Rubus sp.*) brambles, and a small (1.3 ha) forested wetland dominated by standing dead cedar trees (*Thuja occidentalis*).

The “Gravel Pit” site is 10 km southwest of the honey hole adjacent to a well-maintained forest road in the Elm Stream Pond Township (Figure 4.1). Three small (0.66 ha total) and shallow (< 20 cm deep) vernal pools, barrow pits created during road construction, served as Rusty Blackbird foraging grounds. The vernal pools were classified as palustrine unconsolidated bottom (Cowardin et al. 1979) and were dominated by speckled alder (*Alnus incana*) and surrounded by an upland of red spruce

(*Picea rubens*), balsam fir (*Abies balsamea*), paper birch (*Betula papyfera*) and recent partial cuts.

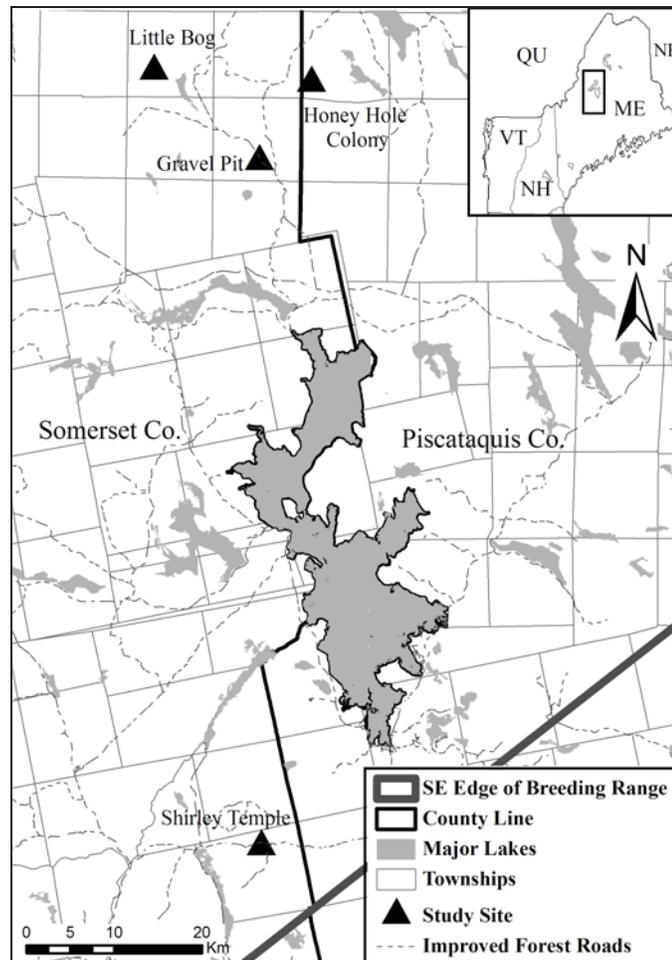


Figure 4.1. Locations of radio-tagged Rusty Blackbirds in Somerset and Piscataquis Counties, Maine, 2007. The figure is centered on Moosehead Lake.

“Little Bog” is 16 km northwest of the gravel pit in township T6R17 WELS (Figure 4.1). This site was approximately two km from a drivable road, although an overgrown logging road bisected the site. An approximately 1-m-wide creek connected a complex of terraced beaver-impounded (*Castor canadensis*) wetlands under various stages of repair. Based on its absence in satellite imagery from 2001, the primary foraging wetland, measuring approximately 0.5 ha, was impounded by beaver between

2001 and my first visit in 2006. This wetland was primarily palustrine unconsolidated bottom (Cowardin et al. 1979) with adjacent patches of palustrine scrub/shrub wetland (Cowardin et al. 1979) containing black and red spruce, speckled alder and *Sphagnum sp.* Surrounding vegetation was primarily 15-year-old regenerating spruce and fir, but there was no evidence of logging activity within three km in the last five years. Little Bog, Gravel Pit and the Honey Hole are > 30 km from the nearest town

Ninety km south of Little Bog, the “Shirley Temple” site is 16 km southeast of Moosehead Lake in East Moxie Township (Figure 4.1). This site was less remote than the other three locations, but it was still at least five km from a residence, and 10 km from the southeast edge of the Rusty Blackbird’s breeding range (Figure 4.1). A well-maintained forest road with active hauling operations bisected the two wetlands regularly used by Rusty Blackbirds. South of the road, regenerating spruce, northern white cedar and *Sphagnum sp.* dominated a 50-plus ha regenerating fen with only puddles of open water. North of the road, mature spruce, balsam fir, paper birch and many recent partial cuts surrounded a 1 ha scrub/shrub wetland.

4.4 Methods

4.4.1 Telemetry Field Methods

I gathered location data for home range analyses during 7-26 of June, 2007. I captured individuals from late May to mid June with both targeted netting techniques near nests and passive netting techniques near prime feeding wetlands (see chapter appendix). I banded eight males and seven females (United States Fish and Wildlife Service aluminum band and unique colored leg bands) and attached Holohil Systems Ltd.

model BD-2 radio-transmitters (1.6g for females, 1.9g for males; < 3 % of body weight) using a cotton thread harness designed to fall off after several months (Rappole and Tipton 1991). I waited at least 24 h before collecting location data to allow captured individuals time to adjust to the transmitter and bands.

To ensure an even representation of daytime activity, for each radio-marked individual I separated daylight hours (sunrise to sunset) into five time blocks, and randomized which block would be targeted during a given day. The sample locations based on this temporally stratified sampling design sample locations should represent an unbiased use of space during the study period, and any subsequent statistical autocorrelation should be irrelevant (Otis and White 1999). Minimum data collection for each individual was three non-consecutive days in a five-day period. Every 10 minutes, two or three technicians, each with a hand-held Yagi antenna, simultaneously recorded their individual locations using a hand-held GPS unit, and recorded a compass bearing in the direction of the strongest signal. My goal was to arrange ourselves spatially such that bearings were as close to right angles from each other as possible, and as close to the bird as possible without noticeably affecting behavior. I triangulated bearings using the program LOCATE III (Nams 2006).

I tested for observer angular error by placing a test transmitter in and around wetlands used by radio-marked Rusty Blackbirds. Naïve observers recorded bearings of the test transmitter using the same techniques used to track radio-marked birds. After eliminating one extreme outlier (likely the result of a 180 degree telemetry error), the mean absolute angular error of triangulated locations on the test transmitter was 13.2 degrees (SD = 9.0 degrees, n=38 bearings).

4.4.2 Kernel Density Estimation Technique

Home range estimates assume that individuals show site fidelity to a given area over the course of the sampling period. To meet this assumption, I visually inspected triangulated locations in chronological order to confirm that no range shifts occurred. If there was an obvious range shift during a particular point in the season, I removed those points from home range analyses. This constrained my dataset to the nesting and fledgling period (Table 4.2) and excluded data collected in early July when juveniles were more mobile and family groups had a more nomadic lifestyle (Palmer 1949). I also excluded several triangulated locations that were obviously erroneous as they were beyond the approximately 2 km maximum range of the transmitters.

I calculated 95% fixed kernel densities (“home range”) using Home Range Tools for ArcGIS (Rodgers et al. 2007). I selected fixed kernels based on Seaman and Powell’s (1996) conclusion that they outperform adaptive kernels in simulations. I used Gaussian (bivariate normal) kernel form with least-squares cross-validation for automated bandwidth selection (“smoothing”). Kernels had a grid cell resolution of 10 m, contouring was performed by volume, and I used a scaling factor of 1,000,000 and rescaled home ranges to unit variance. Prior to statistical analyses, I log-transformed response variables to meet the assumptions of equality of variance between groups and normality distributed home range areas. To test for differences in home range and core range size between colonial (i.e. individuals captured at the Honey Hole Colony) and non-colonial individuals, and between sexes, performed a t-test for equal variances in PC SAS (SAS Software 2002).

4.4.3 Core Area Delineation

Rather than defining core range at an arbitrary chosen proportion of an animal's home range (often 50%), Laver and Kelly (2008) recommended using an objective and area-independent method. Accordingly, I used ABODE for ArcGIS (Laver 2006) to calculate core areas for each individual using Powell's (2000) method. I used the same settings I used to calculate home range except grid size was set at "resolution 100" (i.e. grid size varied with size of home range). Using a kernel home range, ABODE calculated the probability of use for each cell and defined core range as the area where use was clumped (i.e. non-random). For each core area, I then plotted the probabilities and % area of home range to visually confirm, *post hoc*, that use was indeed clumped (i.e. there was a curved rather than straight line (Powell 2000)).

4.4.4 Independence and Asymptote Analysis

To address the biological independence of sampling interval, I first noted that Wood (1933) clocked Rusty Blackbirds at approximately 34 km / hr; therefore they could potentially fly at least 5.7 km during the 10-min interval. Therefore, a Rusty Blackbird could easily traverse its breeding territory many times during the sampling interval, so a 10-min sampling interval would be more than enough to ensure biological independence (Lair 1987). To determine time to statistical independence for each individual, I used Home Range Tools for ArcGIS (Rodgers et al. 2007) to calculate an index of autocorrelation (Swihart and Slade 1985), then gradually increased the sampling interval by removing data points until I reached statistical independence. For example, to increase the interval from 10 min to 20 min, I removed any points sampled within 20 min of any other point.

I calculated the home range asymptote (the number of points at which home range size stabilized) using Laver's (2005) objective method in ABODE for ArcGIS. The software automatically calculated each individual's home range after the addition of every randomly added location. I repeated this procedure ten times for each home range (10 bootstraps), and calculated the mean home range size after the addition of each point. When the entire confidence interval fell within 20% of the final home range for five consecutive points, I considered the home range to have reached an asymptote (Figure 4.1). To facilitate future studies of Rusty Blackbirds interested in a more precise stabilization of home range size, I performed asymptote analyses at the 10% and 5% thresholds as well.

4.5 Results

I captured and radio-tagged 15 adult Rusty Blackbirds and collected 25 or more triangulated locations for 13 individuals (Table 4.2). I collected most locations during the nestling and fledgling stages (Table 4.1). Eight individuals were part of the Honey Hole, the first Rusty Blackbird colony described in New England. I located eight nests at the colony, four of which successfully fledged young (Chapter 3). Of the 13 successfully radio-tracked individuals, only one individual, OrOr, did not meet the goal for equal representation of daytime activity. I radio-tracked this female throughout just one day (5:20 to 15:00), the day after her nest failed (Table 4.1). I did not observe any negative effects of transmitter attachment. One female shed her transmitter after approximately 6 weeks (the thread wore through), while the others retained their transmitters throughout the length of the study.

Table 4.1. Calender of telemetry fixes used for home range analyses of Rusty Blackbirds breeding in Maine, USA, 2007^a.

ID	Sex	Nesting		Day in June																						
		pairs ^b	Site	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26			
PkPk	M		Honey Hole	U				U	U									U			U	U	U			
YeRd	M	a	Honey Hole	I				I	I									N			N	N	X	U		
OrOr	F	a	Honey Hole																			X	U			
OrGr	F		Honey Hole						U ^c									U	U	U	U	U				
PuPu	F	b	Honey Hole					F	F									F								
RdRd	M	b	Honey Hole					F	F									F								
YeBk	M	c	Honey Hole															F	F	F	F	F				
OrPu	F	c	Honey Hole															F		F	F	F				
PuRd	M	d	Shirley Temple			N		N	N									F								
GrGr	F	d	Shirley Temple			N		N	N									F								
YeYe ^d	M		Shirley Temple			U			U														U			
RdOr	F		Gravel Pit							N								F	F							
PkYe	F	e	Little Bog															F		F	F					
RdBk	M	e	Little Bog															F		F	F					

^a Letters correspond to reproductive phase during data collection: I=Incubation, N=Nestlings, F=Fledglings, U=Unknown. X=nest failure (telemetry data not necessarily collected)

^b Individuals with the same letter were nesting pairs. If left blank, mate was not captured.

^c Abandoned nest after capture on 6/3. Renest suspected but unconfirmed.

^d Satellite male captured with nesting pair d. Breeding status unknown.

4.5.1 Independence and Asymptote Analysis

Triangulated locations for eight of 13 individuals reached statistical independence using the 10-minute sampling interval (Table 4.3). Four individuals took considerably longer to achieve statistical independence (30 min, 40 min, 120 min and 24 h sampling intervals), while the data from one individual, RdOr, did not reach statistical independence at any sampling interval. All triangulated locations were biologically independent, as home range size (Table 4.2) was indeed small enough for a Rusty Blackbird to traverse the home range many times during the ten-minute sampling interval (Lair 1987).

Table 4.2. Summary of spatial use by 13 Rusty Blackbirds in Maine, USA, June, 2007.

ID	Sex	Nesting Pairs ^a	Site	No. Locations Used	95% KDE ^b Area (ha)	No. of Wetlands in Home Range	Core Range (ha)	Core Range: % of KDE	No. of Wetlands in Core Range
PkPk	M		Honey Hole	34	172.8	5	34.81	52	1
YeRd	M	a	Honey Hole	43	60.5	4	21.36	62	2
OrOr	F		Honey Hole	31	28.3	3	7.25	56	0
OrGr	F		Honey Hole	43	71.6	4	22.66	53	1
PuPu	F	b	Honey Hole	41	22.3	2	7.67	70	1
RdRd	M	b	Honey Hole	31	25.5	2	7.76	75	2
YeBk	M	c	Honey Hole	25	13.4	1	2.23	45	1
OrPu	F	c	Honey Hole	30	19.6	1	15.66	75	1
PuRd	M	d	Shirley Temple ^c	31	12.2	4	4.31	48	1
GrGr	F	d	Shirley Temple	29	35.3	2	8.81	62	2
RdOr	F		Gravel Pit	39	17.4	4	8.04	76	4
PkYe	F	e	Little Bog	55	4.4	2	1.68	75	1
RdBk	M	e	Little Bog	61	3.8	2	1.49	75	1
			<i>mean</i>	37.9	37.5	2.77	11.06	63.38	1.39
			<i>SD</i>	10.6	45.3	1.30	9.92	11.59	0.95
			<i>SE</i>	2.95	12.57	0.36	2.75	3.22	0.26

^a Individuals with the same letter were nesting pairs. If left blank, mate was not captured.

^b KDE: Fixed kernel density estimation using Least Squares Cross Validation.

^c YeYe was excluded from home range analyses due to insufficient data ($n=11$ locations).

Nine of thirteen individuals reached a home range asymptote, defined as the point at which five consecutive points had confidence intervals fully within 20% of the final home range size (Table 4.3) (e.g. Figure 4.2). Of the four individuals that did not reach asymptotes at the 20% threshold, two were increasing in area (RdRd, OrPu), while two showed a decreasing trend (YeBk, PuRd). I collected 31, 30, 25, and 31 points, respectively, for each individual. Six birds reached asymptotes at the 10% threshold and one reached an asymptote at the 5% threshold.

Table 4.3. Summary of independence and asymptote analyses on Rusty Blackbirds captured in Maine, USA, June, 2007.

ID	Sex	Nesting Pairs ^a	Site	No. Locations Used	Independence Index ^b	Interval For Statistical Independence (min)	No. Locations to KDE Asymptote ^c		
							20% ^d	10%	5%
PkPk	M		Honey Hole	34	0.23	<10	25	32	N/A
YeRd	M	a	Honey Hole	43	1.16	1464	36	39	N/A
OrOr	F	a	Honey Hole	31	1.24	30	30	N/A	N/A
OrGr	F		Honey Hole	43	0.11	<10	35	42	N/A
PuPu	F	b	Honey Hole	41	0.29	<10	32	39	N/A
RdRd	M	b	Honey Hole	31	0.99	120	N/A	N/A	N/A
YeBk	M	c	Honey Hole	25	1.09	40	N/A	N/A	N/A
OrPu	F	c	Honey Hole	30	0.15	<10	N/A	N/A	N/A
PuRd	M	d	Shirley Temple	31	0.45	<10	N/A	N/A	N/A
GrGr	F	d	Shirley Temple	29	0.04	<10	20	N/A	N/A
RdOr	F		Gravel Pit	39	0.97	N/A	38	N/A	N/A
PkYe	F	e	Little Bog	55	0.26	<10	25	37	52
RdBk	M	e	Little Bog	61	0.56	<10	43	59	N/A
<i>Mean:</i>				38			31.6	41.3	52.0
<i>SD:</i>				11			7.3	9.3	N/A

^a Individuals with the same letter were nesting pairs. If left blank, mate was not captured.

^b Swihart-Slade index > 0.6 indicates significant autocorrelation.

^c KDE: Fixed kernel density estimation using Least Squares Cross Validation.

^d Asymptote was considered reached when 95% confidence interval ($\alpha = 0.05$) fell within 20% of final home range size for five consecutive points.

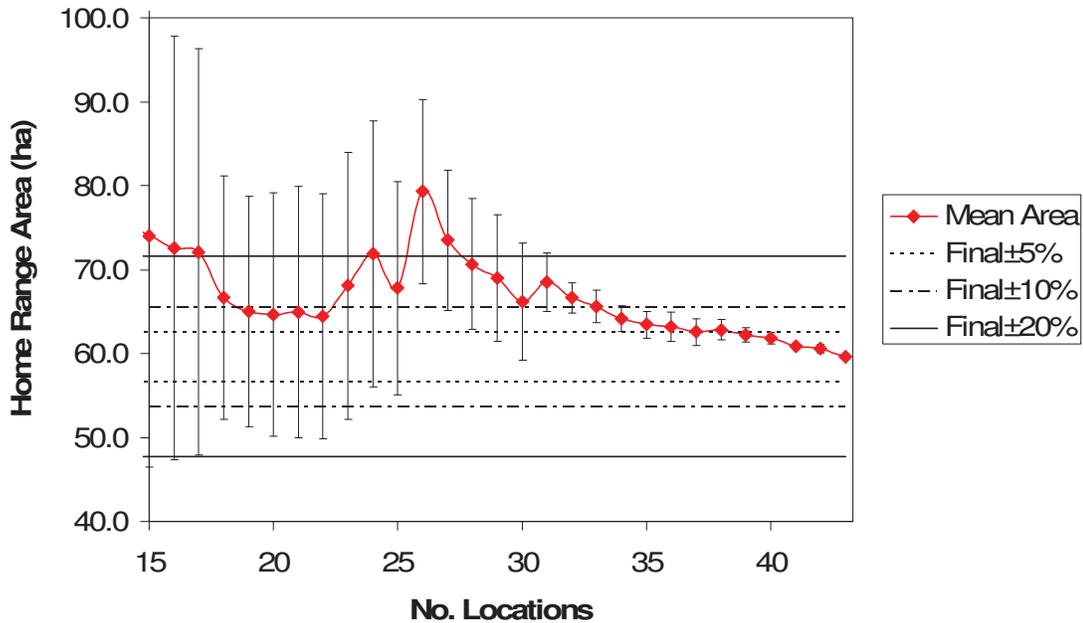


Figure 4.2. Asymptote analysis for YeRd. YeRd reached an asymptote at 36 points for at 20% threshold, 39 pts for 10%, and did not reach an asymptote for 5%. “Final” refers to the final home range area, and error bars represent the 95% confidence interval ($\alpha = 0.05$).

4.5.2 Home Range and Core Range

I collected 493 triangulated locations among the four sites and subsequently calculated home range for 13 individuals, 6 males and 7 females. Mean home range area was 37.5 ha \pm 45.3 SD, and mean core range area was 11.1 ha \pm 9.9 SD. Home range area varied widely from 3.8 ha (RdBk) to 178.8 ha (PkPk) (Table 4.2). After PkPk, the second largest home range was 71.6 ha (OrGr), less than half the size of the largest home range (map, Figure 4.3). Mean number of wetlands included in home range was 2.77 \pm 1.3 SD, while mean number of wetlands in the core range was 1.38 \pm 0.96 SD (Table 4.2). Most birds only had one or two wetlands in their core ranges, although RdOr had four. Of these four wetlands, three were small (0.66 ha total) vernal pools. Of the nine individuals that reached an asymptote (Table 4.3), mean home range size of males (79.0

ha \pm 86.0 SD) was not significantly different from mean home range size of females (29.9 ha \pm 23.0 SD) (*t*-test on log-transformed home range area, $t_{[7]} = -0.46$, $p > 0.661$). Core ranges did not differ between the sexes (*t* test on log-transformed core range area, $t_{[7]} = -0.43$, $p > 0.679$).

Although there were no significant differences between sexes, of the birds that reached an asymptote, mean home range size of colonially nesting birds (71.1 ha \pm 60.6 SD) was larger than mean home range size of non-colonial birds (15.2 ha \pm 14.8 SD) (*t* test on log-transformed home range area, $t_{[7]} = -2.68$, $p > 0.0316$). Furthermore, mean core range size of colonial birds that reached an asymptote (18.75 ha \pm 11.6 SD) was also larger than mean core range size of non-colonial birds (5.0 ha \pm 4.0 SD) (*t*-test on log-transformed core range area, $t_{[7]} = -2.63$, $p > 0.0341$). Colonial birds that reached an asymptote averaged 3.6 wetlands per home range, while non-colonial birds averaged 2.5 wetlands per home range.

At the Honey Hole colony, Rusty Blackbirds regularly visited two wetlands (i.e. each was part of the core range of four individuals, Figure 4.4). The first was a shallow 0.6 ha scrub/shrub wetland (Cowardin et al. 1979) located in the center of the colony. This wetland was in the center of a large fen that was clear-cut approximately thirteen years prior to the study. The other heavily-used wetland was a 1.3 ha forested wetland (Cowardin et al. 1979) located on a hillside 1 km northwest of the primary foraging wetland (Figure 4.4). Because of flooding by a beaver impoundment, many large, dead cedar trees filled the wetland, while both mature cedar and a regenerating hardwood/softwood mix surrounded it.

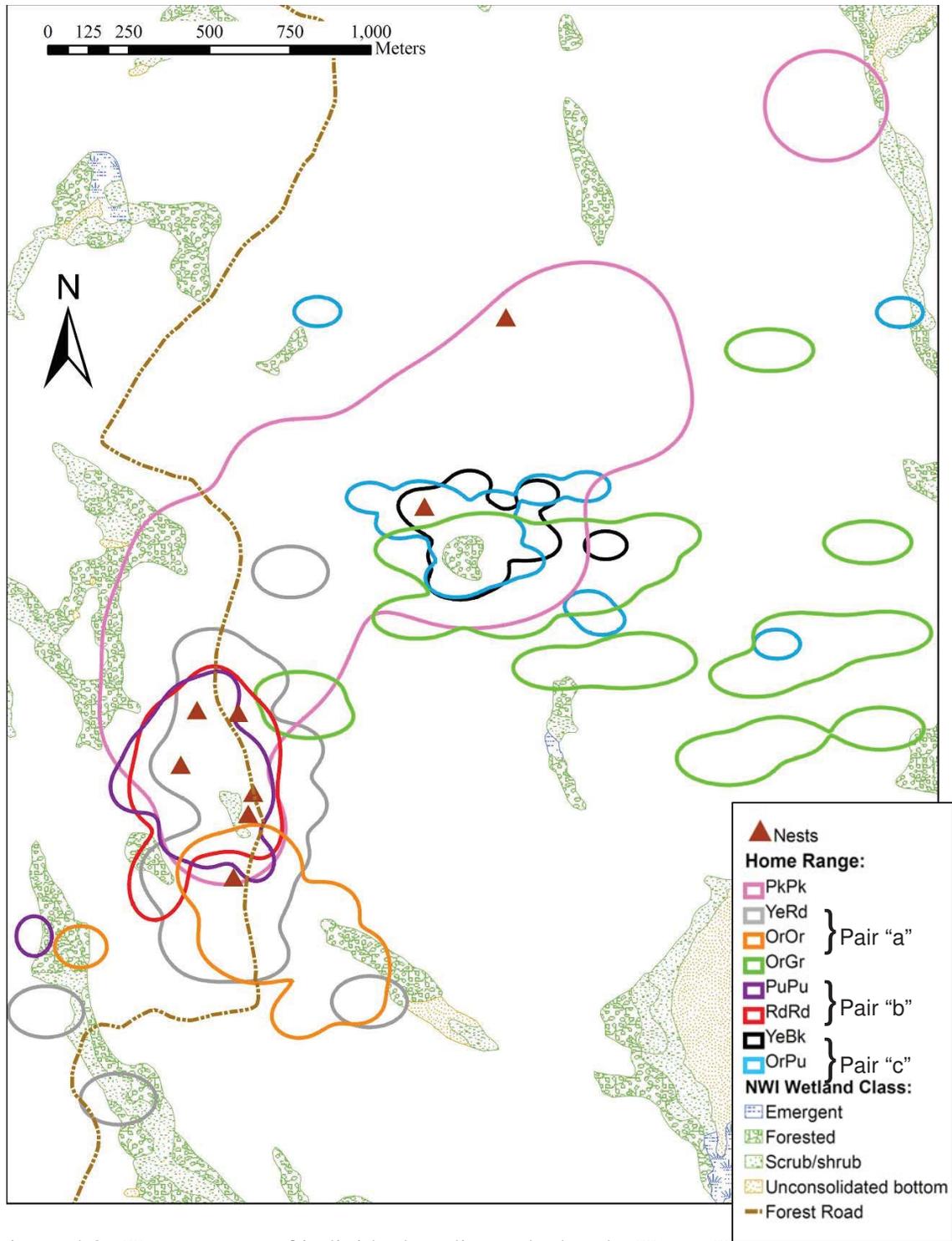


Figure 4.3. Home ranges of individuals radio tracked at the Honey Hole colony in Piscataquis County, Maine, 2007. Small pieces of two birds' home ranges (YeRd, OrGr) are off the edge of the map.

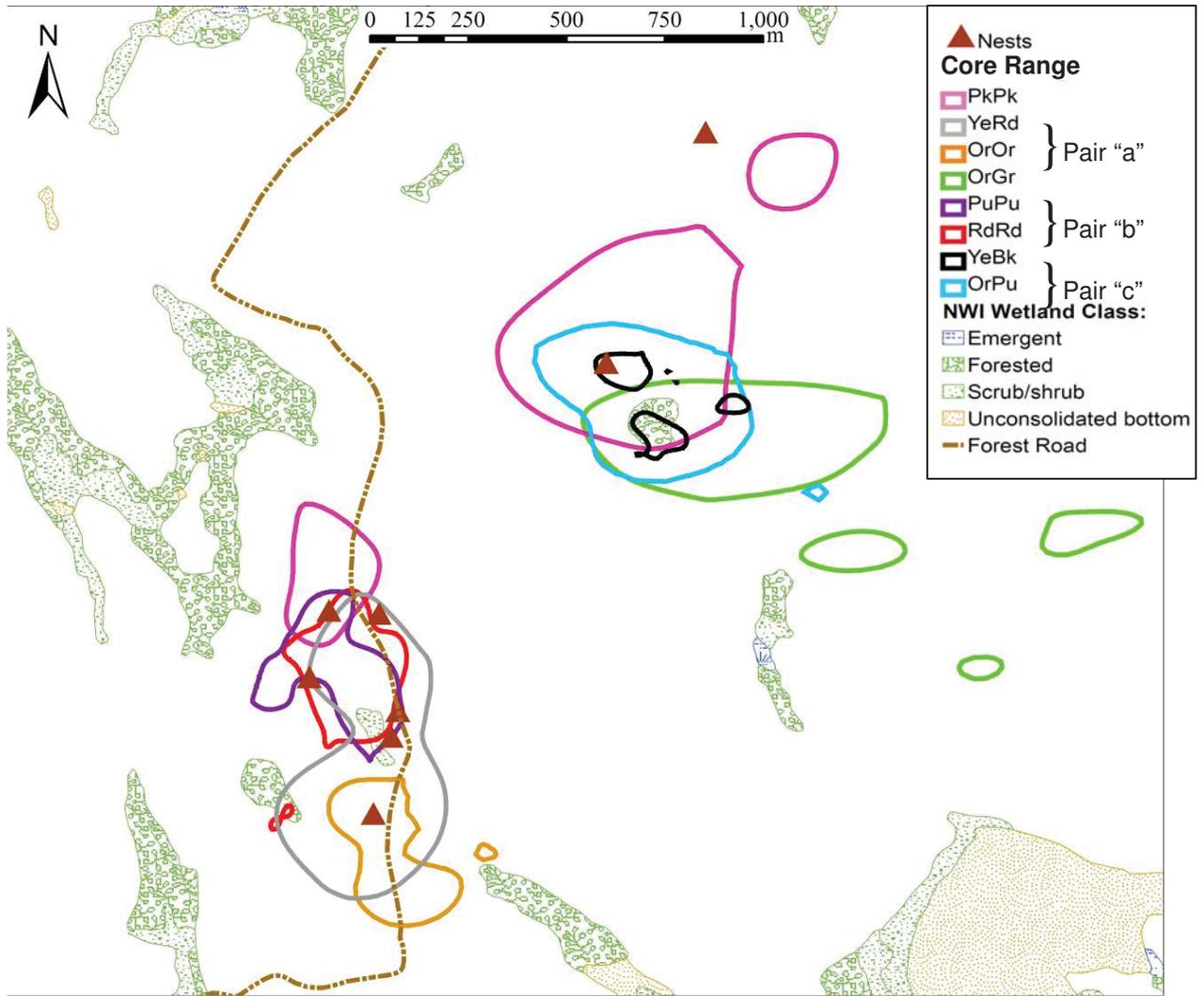


Figure 4.4. Core ranges of individuals radio tracked at the Honey Hole colony in Piscataquis County, Maine, 2007.

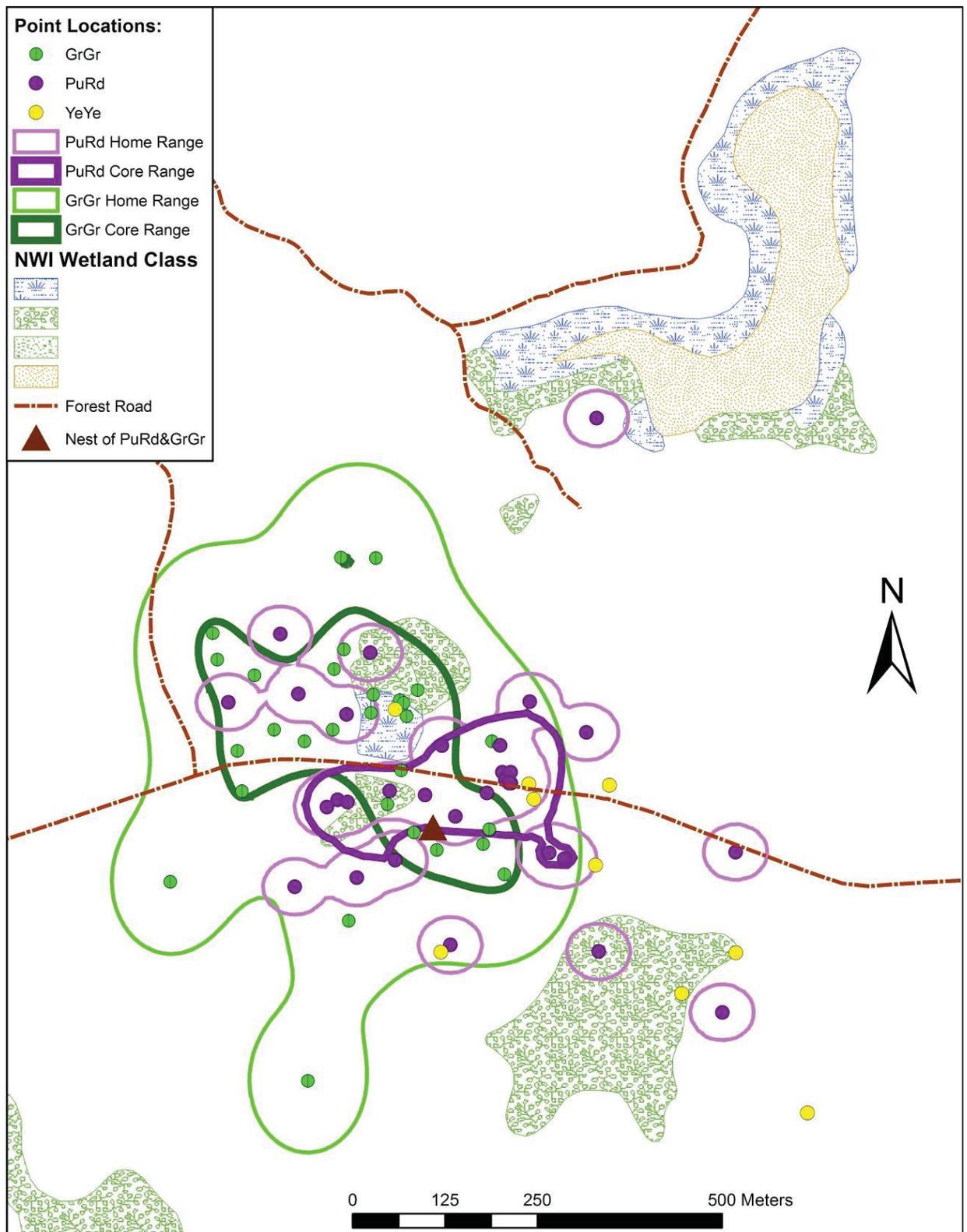


Figure 4.5. Home and core ranges of non-colonial pair “d” and a satellite male (YeYe) at the "Shirley Temple" site in Somerset County, Maine, USA, 2007.

4.6 Discussion

4.6.1 Fidelity, Independence and Asymptote Analysis

During the incubation, nestling and early fledgling periods, Rusty Blackbirds showed strong fidelity to the area near their nests and foraging wetland, but by late June and early July, fidelity became variable. When juveniles became mobile, parents remained with the young in the natal wetland, shifted to a nearby wetland, or disappeared from the area completely. In two instances, I detected only one radio-tagged parent with mobile juveniles. The ten-minute sampling interval I used was long enough for eight individuals to achieve statistical independence (Table 4.3). With the stratified random sampling design, statistical autocorrelation should be irrelevant (Otis and White 1999). However, future Rusty Blackbird home range studies that may be particularly sensitive to statistical autocorrelation should consider a sampling interval of 30-40 minutes.

To confirm that home range area has stabilized and avoid confounding subsequent analyses, it is critical to analyze asymptotes individually for each animal and perform subsequent statistical analyses only on animals that reached an asymptote (Harris et al. 1990, Laver and Kelly 2008). For nine of thirteen Rusty Blackbirds that reached an asymptote, the mean number of points to the 20% confidence interval asymptote was 32 ± 7 SD (Table 4.3). This was consistent with Seaman's (1999) recommendation of 30 to 50 points. Future studies of Rusty Blackbird home range should set a conservative a priori goal to collect at least 50 locations per individual; however individuals' asymptotes should be assessed during the study to confirm that home range stabilizes before data collection halts.

4.6.2 Home Range and Core Range

Rusty Blackbirds averaged 2.8 wetlands in their home range but only 1.4 wetlands in their core range (Table 4.1). The core ranges of nesting individuals generally encircled their nest and primary foraging wetland (Figure 4.5). Despite the limited core range, individuals of both sexes often made brief visits nearby wetlands. These visits may have been scouting trips to locate ephemeral food sources, or attempts to seek out extra-pair copulations. Regardless of their purpose, visits to nearby wetlands coupled with the occasional inability to detect radio-tracked individuals at all (transmitter range was approx. 2 km), help explain the species' relatively low detectability (0.19, Chapter 2).

Both home range and core range were significantly larger for Rusty Blackbirds at the colony compared to non-colonial individuals. The additional social interactions presented to group-living birds may help explain the larger home ranges I observed in colonial individuals. With more breeding females present in and adjacent to "loose" colonies (Figure 4.3), males may have more opportunities to attempt extra-pair fertilizations (EPFs). Despite best efforts, I was not able to locate a nest or female regularly associated with the wide-ranging male, PkPk (Figure 4.4). Interestingly, PkPk's core range was centered not on feeding wetlands, but around two active nests (those of pairs a and b) and within 100m of a third (Figure 4.5). Therefore, I suspect that PkPk was an unpaired male searching for copulations or feeding young of broods in which he may have had a paternal investment. If the desire for EPFs is indeed driving larger home ranges in colonies, one might predict that the ratio of male home range to female home range would be relatively higher in colonies (and that the difference is

exaggerated during nest-building and egg-laying, when individuals are copulating regularly).

Lack (1968) and Simpson et al. (Simpson et al. 1987) each suggested that protection from predators is the primary reason for colony formation. In 2006 and 2007 alone, Rusty Blackbirds from multiple pairs cooperatively mobbed technicians checking nests on my study areas in Maine and Vermont, and in south central Alaska and interior Alaska (D. Shaw, Alaska Bird Observatory, S. Matsuoka, U.S. Fish and Wildlife Service, Anchorage, AK, C. Fisher, Sterling College, VT, pers. comm.). In one instance, at the Honey Hole colony, a female I captured near her nest elicited distress “chucks” that appeared to summon four males to aggressively mob my capture crew. Assuming this behavior is adaptive, cooperative defense efforts, observed at both colonial and non-colonial wetlands, may aide Rusty Blackbirds to deter potential predators from nests.

Although I did not observe any predation or mortality of adults, 23% of all nests I found were predated, three of the eight nests at the colony were predated, and colonial Rusty Blackbirds had lower nest survival overall (Chapter 3). Red squirrels (*Tamiasciurus hudsonicus*) and Blue Jays (*Cyanocitta cristata*) were active at the colony and at other sites, and both are known nest predators (Siepielski 2006, Thompson 2007). If the Rusty Blackbird population in Maine has declined as it has range-wide (Greenberg and Droege 1999), then there are fewer individuals, and there is presumably more habitat available for non-colonial nesting pairs. Non-colonial pairs had higher nest survival than colonial pairs (Chapter 3); colonies may attract more predators then they can cooperatively defend against (i.e. they are below the optimal colony size). Furthermore, the Allee effect (Lande 1998) may be triggered by increased predation at low population

densities (Kenward 1978, Berg et al. 1992) if cooperative defense is less successful with fewer individuals participating. I hypothesize that with such a drastic decrease in Rusty Blackbird abundance (95% since 1966, Sauer et al. 2005), the availability of relatively isolated (i.e. less conspicuous to predators) breeding habitats with steady food supplies has increased, thus reducing the need (and opportunity) for colonial behavior.

Given that this colony is the first documented in New England, I can only speculate that these colonies were once more common. Orians (1985) describes the species as “loosely colonial” and elsewhere in the northeast (Newfoundland and Labrador), Rusty Blackbirds do tend to form small colonies (Peters and Burleigh 1951, Todd 1963). In Ontario however, the species is not known to be colonial (Flood 1978), and prior to this study, con-specific nests in New England were never reported closer than 400m (Kennard 1920, Avery 1995). Given the steep population decline in the species (Greenberg and Droege 1999), more Rusty Blackbird breeding congregations must be located and studied to determine how fitness and spatial use vary with social organization, and how habitat quality affects colony formation and reproductive success. With this information, we will be prepared to make effective management recommendations based on habitat-specific fitness.

4.7 Chapter Appendix – Capture Techniques

Although the use of a Rusty Blackbird mount or decoy with broadcast may be most effective earlier in the breeding season when males are particularly territorial, I avoided capturing during this time due to concerns about detectability (Chapter 2). I had the most success capturing during the nestling period. First, I spent time quietly

observing the parents' flight patterns as they delivered food to their nestlings. Then, depending on space availability, I set up one, two, or three 33 mm mist nets in the middle of the adults' flight path and at least 10 m from nests. I set up nets the day prior to captures to give adults time to habituate to the net poles.

Although I was successful in capturing and handling adults, I did have two instances of abandonment, possibly resulting from my capture attempts; one female abandoned two-day old chicks and a second female abandoned nine-day old eggs. Rusty Blackbirds are neophobic (i.e. innate fear of novel objects, C. Mettke-Hoffman, Smithsonian Migratory Bird Center, unpublished manuscript), and may be particularly intolerant of disturbances near their nests, especially early in nesting (Paul Meyers, U.S Forest Service, AK, pers. comm.). I recommend capturing at nesting wetlands, setting up nets in regular foraging paths as far from nests as is feasible and only after eggs have hatched, and using conspecific decoys or mounts with broadcasts in late April or early May. Furthermore, capture crews should leave nets open during processing and be prepared for other Rusty Blackbirds to respond to distress calls by captured individuals.

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BIOGRAPHY OF THE AUTHOR

Luke Losada Powell was born in Sea Cliff, NY on July 19, 1981. He grew up in Nassau County, New York and graduated from North Shore High School in 1999. He attended Tufts University in Somerville, Massachusetts and graduated in 2003 with a Bachelor of Sciences degree in Biology and Environmental Studies. Luke spent one semester abroad in Madrid, Spain through the State University of New York at Albany. After the completion of his bachelor's degree, Luke worked for University of California, Berkeley entomologist Kent Daane, studying the integrative management of invasive Argentine Ants on vineyards in California. He then returned to Long Island to work as an environmental consultant.

In 2004, Luke left the consulting industry to intern at Manomet Center for Conservation Sciences in Manomet, Massachusetts. While at Manomet, Luke learned to mist-net songbirds while helping to write the Waterbird Conservation plan for the Northeast under Dr. Kathy Parsons. Luke then served as an intern for the World Wildlife Fund's AREAS project at the Los Amigos Research Center (CICRA) in southeastern Peru. Luke became interested in parrot conservation while observing the behavior of Red and Green Macaws (*Ara chloropterus*) at various clay licks in the Peruvian Amazon. Immediately after returning from the Amazon, Luke shifted gears, working for New York City Audubon in midtown Manhattan. In addition to sporadic field work with colonial wading birds, he was project manager of the Natural Areas Program, an effort to map and document the remaining patches of wildlife habitat in New York City.

Luke returned to academia in 2005 to pursue his interests in wildlife ecology and conservation biology. He studied breeding Rusty Blackbirds for his thesis, but also

returned to Peru to collect samples of parrot clay licks in the winter of 2006-2007. His research on parrot clay licks continues to explore the benefits of soil ingestion for parrots. Luke is a candidate for the Master of Science degree in Ecology and Environmental Science from The University of Maine in August 2008.