RUSTY BLACKBIRDS IN NORTHEASTERN U.S. INDUSTRIAL FORESTS: A MULTI-

SCALE STUDY OF NEST HABITAT SELECTION AND NEST SURVIVAL

by

Shannon H. Buckley

A thesis submitted in partial fulfillment of the requirements for the Master of Science Degree State University of New York College of Environmental Science and Forestry Syracuse, New York April 2013

Approved: Department of Environmental and Forest Biology

Stacy McNulty, Major Professor

Isabel Fernandez, Chair Examining Committee

Donald Leopold, Department Chair

S. Scott Shannon, Dean The Graduate School

© 2013 Copyright S. H. Buckley All rights reserved

Acknowledgements

First, a huge thank you to my field technicians Linnea D'Amico, Sara Prussing and Joe Roy for their unflagging willingness to do whatever was required to get this project done, including a grueling schedule and enduring clouds of biting insects. Your patience, hard work and moral support made this research possible, and for that I will always be incredibly grateful. I also offer my thanks and gratitude to Luke Powell for sharing his invaluable wisdom and experience with me at the inception of this project – I get it now about the tires and the flies!

Thank you to Tim Obrey, Doug Kane, Scott McClellan, April Collins and everyone at the Greenville Inland Fisheries and Wildlife Headquarters for generously providing field accommodations in Maine. I extend my thanks and appreciation to the following people for providing land access, stand data and/or equipment: Ray Ary and Henning Stebbins at Plum Creek; Dan Hudnut, John Sobetzer and Marty Duffany at Wagner; David Dow and Scott Robinson at Prentiss and Carlisle; Todd Caldwell and Christine Hodgman at Northwoods Management and David Publicover at Appalachian Mountain Club. I thank the following organizations for providing financial support: Edna Bailey Sussman Foundation, Garden Club of America, Maine Outdoor Heritage Fund and U.S. Fish and Wildlife Service.

Thank you to my advisor Stacy McNulty and my committee members Tom Hodgman and Jonathan Cohen for providing academic, financial and moral support. I am grateful to Stacy for giving me the opportunity to pursue graduate study in the first place, and for allowing me the intellectual freedom to follow my interests and passions and create this project. I thank Jonathan for being so generous with his time, and for offering critical guidance and advice on statistical analyses. I especially want to acknowledge Tom for all he has done, both in terms of the logistical and intellectual development of this project, to make it happen. Without his hard work and dedication, none of this would have been possible. I also thank Carol Foss for sharing her knowledge of and enthusiasm for Rusty Blackbirds, as well as providing field accommodations in New Hampshire. Thanks also to Patti Newell and the NH field crews for assisting with data collection in New Hampshire.

Finally, I wish to thank my family and friends for all of the love and support they have given over the years. I am especially grateful to the love of my life, Stefan Lüpold, who has provided all manner of support, advice and encouragement throughout this process. His scientific expertise, as well as his love and patience, have been a constant source of inspiration and strength. Lastly, I thank my parents for giving me the opportunity to grow up in such a beautiful place, and for allowing me the freedom to explore and experience the natural world as a child (and beyond!). It was my awe at the beauty I perceived in nature that inspired my curiosity, my desire to understand it, and most of all my abiding love for it. It is this passion that has been my guide and given me the fortitude to continue on this path even when it seemed impossible.

"Those who contemplate the beauty of the earth find reserves of strength that will endure as long as life lasts. There is something infinitely healing in the repeated refrains of nature – the assurance that dawn comes after night, and spring after winter."

-Rachel Carson

List of Appendices Abstract Chapter 1: The Decline of the Rusty Blackbird and the Nature of Disturbance in the N England Acadian Forest Decline of the Rusty Blackbird. Rusty Blackbird Breeding Habitat. Rusty Blackbirds and the Natural Disturbance Regime of the Acadian Forest The Acadian Forest: Timber Management in the Spruce-Fir Region Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales Introduction. Methods. Description of Study Area. Bird Surveys. Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	xi xiv Vew 1 1 4 6 11 13 13 14
Abstract. Chapter 1: The Decline of the Rusty Blackbird and the Nature of Disturbance in the N England Acadian Forest Decline of the Rusty Blackbird. Rusty Blackbird Breeding Habitat. Rusty Blackbirds and the Natural Disturbance Regime of the Acadian Forest. The Acadian Forest: Timber Management in the Spruce-Fir Region. Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales. Introduction. Methods. Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements. Stand Scale Habitat Measurements	xiv New 1 1
Chapter 1: The Decline of the Rusty Blackbird and the Nature of Disturbance in the N England Acadian Forest Decline of the Rusty Blackbird. Rusty Blackbird Breeding Habitat. Rusty Blackbirds and the Natural Disturbance Regime of the Acadian Forest. The Acadian Forest: Timber Management in the Spruce-Fir Region. Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales. Introduction. Methods. Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	New 1 3 4 6 11 13 13 13 14
Decline of the Rusty Blackbird Rusty Blackbird Breeding Habitat Rusty Blackbirds and the Natural Disturbance Regime of the Acadian Forest The Acadian Forest: Timber Management in the Spruce-Fir Region Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales Introduction Methods <i>Description of Study Area</i> <i>Bird Surveys</i> <i>Nest-Tree and Nest-Patch Scale Habitat Measurements</i> <i>Stand Scale Habitat Measurements</i>	1 4 6 11 11 13 13 14
The Acadian Forest: Timber Management in the Spruce-Fir Region Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales Introduction Methods <i>Description of Study Area</i> <i>Bird Surveys</i> <i>Nest-Tree and Nest-Patch Scale Habitat Measurements</i>	11 13 13 14
Chapter 2: Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales Introduction Methods Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	11 13 13 14
Introduction Methods Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	11 13 13 14
Methods Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	13 13 14
Description of Study Area Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	13
Bird Surveys Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	14
Nest-Tree and Nest-Patch Scale Habitat Measurements Stand Scale Habitat Measurements	1 -
Stand Scale Habitat Measurements	15
	16
Home-Range Scale Habitat Measurements	17
Statistical Analyses	18
Results	20
Nest and Nest Tree Characteristics	18
Nest-Patch Scale Habitat Selection	21
Stana Scale Habitat Characteristics	
Home-Range Scale General Characteristics	23
Discussion	24 25
Nest and Nest Tree Characteristics	25
Nest-Patch Scale Habitat Selection	25
Stand Scale Habitat Characteristics	23
Home-Range Scale Habitat Selection	20
Habitat Selection and Forest Disturbance	
Conclusion	
Chapter 3: Rusty Blackbird Nest Survival, Predator Dynamics and Timber Managem in the Northeast	ent 48

Table of Contents

Methods	50
Description of Study Areas	50
Bird Surveys	50
Camera Installation and Nest Monitoring	51
Squirrel Surveys	52
Nest-Patch Scale Habitat Measurements	53
Squirrel Territory Scale Habitat Measurements	55
Rusty Blackbird Home-Range Scale Habitat Measurements	55
Statistical Analyses	56
Results	59
Nest Predators and Mast	59
Nest Survival: General and Nest-Patch Scale	61
Nest Survival: Squirrel Territory Scale and Home-Range Scale	61
Discussion	62
Nest Predators and Mast	62
Nest Survival: General and Nest-Patch Scale	66
Nest Survival: Squirrel Territory Scale	67
Nest Survival: Rusty Blackbird Home-Range Scale	68
Nest Predation, Timber Management and the Ecological Trap	70
Forest Management Recommendations and Future Research	72
Conclusion	73
Chapter 4: Using Motion-Triggered Trail Cameras to Monitor Rusty Blackbird Nests Experiences with a Forest-Dwelling, Neophobic Species	: 88
Introduction	88
Methods	89
Results	91
General Results and Camera Performance	91
Rusty Blackbird Response to Cameras	92
Discussion	93
Rusty Blackbird Response to Cameras	93
Comparison of Camera Models	94
General Thoughts on the Use of Motion-Triggered Cameras for Nest-Monitoring	95
Conclusion	97
Conclusion	103
Literature Cited	105
Curriculum Vitae	151

List of Tables

Chapter 2:

Table 2.1. Comparison of characteristics (mean ± range) of Rusty Blackbird nest sites in Maine (n=29), New Hampshire (n=43) and combined (n=72), 2011-2012	5
Table 2.2. Results of nest-patch scale habitat selection analyzed using matched-pairs logistic regression models for Rusty Blackbirds in northern New England, 2011-2012.	6
Table 2.3. Parameter estimates and odds ratios for variables used to model nest patch selection by Rusty Blackbirds in northern New England, 2011-2012	7
Table 2.4. Results of home-range scale habitat selection analyzed using logistic regression models for Rusty Blackbirds in northern New England, 2011-2012	8
Table 2.5. Parameter estimates and odds ratios for variables used to model home-range scale habitat selection by Rusty Blackbirds in northern New England, 2011-20124	0
Chapter 3:	
Table 3.1. Proportion of red squirrel surveys with positive detections in northern New England, 2011-2012	4
Table 3.2. The median of mean cones per plot (includes both nest and control plots) in northern New England, 2011-2012	4
Table 3.3. Model selection results for red squirrel detection in northern New England, 2011-2012	5
Table 3.4. Parameter estimates and odds ratios for red squirrel habitat variables in northern New England, 2011-2012	6
Table 3.5. Daily survival rate (DSR) and nest success estimates for Rusty Blackbirds in northern New England, 2011-2012	7
Table 3.6. Model selection results for survival of Rusty Blackbird nests in northern New England, 2011-2012, including nest-patch scale and temporal/control variables (n=65)	8
Table 3.7. Parameter estimates, standard errors (SE) and 95% confidence limits for nest-patch scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	0

Table 3.8. Model selection results for survival of Rusty Blackbird nests in northern NewEngland, 2011-2012, including squirrel territory scale variables (n=65)	82
Table 3.9. Model selection results for survival of Rusty Blackbird nests in northern New England in 2012, including red squirrel detection covariates (n=29)	83
Table 3.10. Model selection results for survival of Rusty Blackbird nests in northern New England, 2011-2012, including home-range scale habitat and temporal/control variables	84
Table 3.11. Parameter estimates, standard errors (SE) and 95% confidence limits for home-range scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.	86

List of Figures

Chapter 1:

 Figure 1.1. Index of abundance for Rusty Blackbirds from Christmas Bird Count (CBC) data (circles) and Breeding Bird Survey (BBS) data (diamonds) during the period 1966-2004. Solid lines represent 95% confidence limits for CBC abundance indices. Figure taken from Niven et al. 2004.
Figure 1.2. Rusty Blackbird breeding range (in red) and wintering range (in blue). Map from BirdMap Canada (http://www.bsc-eoc.org/birdmap_e.htm) 10
Chapter 2:
Figure 2.1. Map of Maine (ME) and New Hampshire (NH) study areas; Red circles indicate Rusty Blackbird nest locations in 2011 and 201241
Figure 2.2. Three distinct Rusty Blackbird nest "phenotypes" in northern New England: A. Nest in contiguous patch of live, dense conifers; B. Nest in isolated conifer(s), surrounded by relatively open space; C. Nest in snag, surrounded by water and/or alder42
Figure 2.3. Three types of canopy openings in Rusty Blackbird nest patches created through harvest activity in northern New England: <i>A</i> . Skid road (nest is between camera and tall cedar in photo center, about 5 m from skid road edge). <i>B</i> . Single tree gap (nest in trees on the left side of photo). <i>C</i> . Clearcut (nest is in remnant patch of advance regeneration)43
Figure 2.4. Mean percentage (± SE) of total wetland area composed of different wetland types for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=43) and NHRandom (n=43)), 2011 and 2012
Figure 2.5. Mean percent area (± SE) within 500-m radius covered by softwoods and hardwoods for nest and random points in Maine (MENest (n=29) and MERandom (n=29)) and in New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 201245
Figure 2.6. Mean percentage (± SE) of total softwood forest area composed of different age/size classes for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 201246
Figure 2.7. Mean percentage (± SE) of total hardwood forest area composed of different age/size classes for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 201247

Chapter 4:

Figure 4.1. A: Camera mounted on "natural" tree; B – D: Various "pole" set-ups (camera not visible in B., but behind nest tree, mounted on pole leaning against existing diagonal snag)	99
Figure 4.2. A. Blue Jay depredating nest; B. Deer depredating nest; C. Red squirrel depredating nest; D. <i>Accipiter</i> depredating nest	.100
Figure 4.3. A. Adult feeding nestlings; B. Male feeding incubating female; C. Begging nestlings; D. Both adults tending and feeding nestlings	.101
Figure 4.4. Adult feeding winged insect (A.), unknown larvae (B.), unknown worm (C.), and various invertebrates (D.) to nestlings	.102

List of Appendices

Appendix A. Landowner-Specific Stand Classification Codes	117
A.1. Plum Creek Timber Company stand code definitions and descriptions	117
A.2. Wagner Timber Company stand code definitions and descriptions	118
A.3. Northwoods Forest Management stand code definitions and descriptions	118
A.4. Prentiss and Carlisle (P and C) Forest Management stand code definitions and descriptions	119
A.5. Appalachian Mountain Club (AMC) stand code definitions and descriptions	120
Appendix B. Description of Forest Variables Used to Describe Rusty Blackbird Habitat at the Home-Range Scale	121
Appendix C: Variable Descriptions	123
C.1. Description of forest variables used to describe Rusty Blackbird habitat at the home-range scale in northern New England, 2011-2012	123
C.2. Description wetland variables used to describe Rusty Blackbird habitat at the home-range scale in northern New England, 2011-2012	124
C.3. Description of variables used to model habitat selection by Rusty Blackbirds at the nest-patch scale in northern New England, 2011-2012	125
C.4 Description of variables used to model Rusty Blackbird habitat selection at the home-range scale in northern New England, 2011-2012	126
C.5. Description of temporal/control variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	l 127
C.6. Description of variables relating to prevalence of alder (wetland indicator) around the nest	128
C.7. Description of nest-patch scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	129
C.8. Description of squirrel territory scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	130
C.9. Description of red squirrel detection variables used to model survival of Rusty Blackbird nests in northern New England in 2012	131

C.10. Description habitat variables used to model survival of Rusty Blackbird nests at the home-range scale in northern New England, 2011-2012	132
C.11. Description of habitat variables used to model red squirrel detection in northern New England, 2011-2012	132
Appendix D. Spearman Rank Correlations	133
D.1. Spearman correlation coefficients (<i>r_s</i>) and p-values between variables representing spruce-fir abundance and canopy closure around Rusty Blackbird nests in northern New England, 2011-2012	133
D.2. Spearman correlation coefficients (r_s) and p-values between variables used to mode Rusty Blackbird habitat selection at the home-range scale in northern New England, 2011-2012	1 134
D.3. Spearman correlation coefficients (r_s) and p-values between alder variables around Rusty Blackbird nest and control plots in northern New England, 2011-2012	135
D.4. Spearman correlation coefficients (r_s) and p-values for preliminary nest-patch scale variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	136
D.5. Spearman correlation coefficients (<i>r_s</i>) and p-values between home-range scale variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	137
Appendix E. Mann-Whitney U Tests	138
E.1. Results of Mann Whitney U tests for select spruce-fir and canopy variables between Rusty Blackbird nests in harvested locations (n=63) and in unharvested wetland locations (n=9) in northern New England, 2011-2012	138
E.2. Results of Mann Whitney U tests for alder variables between Rusty Blackbird nests in harvested locations (n=63) and unharvested wetland locations (n=9) in northern New England, 2011-2012	139
Appendix F. Preliminary Nest Survival Models Including Spruce-Fir and Alder Variables	140
F.1. MARK model selection results for highly correlated spruce-fir variables used to more survival of Rusty Blackbird nests in northern New England, 2011-2012	del 140
F.2. MARK model selection results for highly correlated alder variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012	141

Appendix G. Composition of Total Basal Area Variable	142
Appendix H. Nest Camera Summary	143
Appendix I. Nest Chronology and Productivity of Rusty Blackbird Nests in Northern New England, 2011-2012	145

Abstract:

S. H. Buckley. Rusty Blackbirds in Northeastern U.S. Industrial Forests: A Multi-Scale Study of Nest Habitat Selection and Nest Survival, 165 pages, 16 tables, 13 figures, 2013.

Rusty Blackbirds (*Euphagus carolinus*) declined over 85% in the past century with no clear cause. I investigated the relationship of nest habitat selection and nest success to habitat type and timber management in New England. Wetland cover drove habitat selection at the home-range scale, while dense conifers were more important at the nest-patch scale. Sixty-three of 72 nests were in harvested stands, and survival in harvested stands was not reduced. Nest success was higher in 2011 (59.4%) than 2012 (29.8%). I monitored 29 nests with passive infrared cameras and captured eight predation events. Red squirrels (*Tamiasciurus hudsonicus*) were the primary nest predators, but only in 2012 after a conifer mast event in 2011. This suggests fluctuating predator populations rather than timber harvest may be driving nest survival rates. Disturbance-dependent Rusty Blackbirds respond primarily to features at the sub-stand level, and beaver (*Castor canadensis*) can be a source of within-stand heterogeneity.

Keywords: boreal wetland, *Euphagus carolinus*, forest management, habitat selection, nest predation, passive infrared camera, red squirrels, Rusty Blackbird, spruce-fir stand

S. H. Buckley Candidate for the degree of Master of Science, April 2013 Stacy A. McNulty Department of Environmental and Forest Biology State University of New York College of Environmental Science and Forestry, Syracuse, NY Stacy A. McNulty

Chapter 1:

The Decline of the Rusty Blackbird and the Nature of Disturbance in the New England Acadian Forest

Decline of the Rusty Blackbird

Rusty Blackbirds (Euphagus carolinus) are a wetland-associated species that breeds in the North American boreal forest. Consensus among both researchers and recreational birders is that Rusty Blackbirds are much less common than they once were. Data from both the North American Breeding Bird Survey (BBS) and the Audubon Christmas Bird Count (CBC) indicate a significant decline in the species since the mid-1900's (Fig. 1.1). Based on data from the BBS, Rusty Blackbirds have declined by an average of 9.3% annually between 1966 and 2008 (Sauer and Link 2011). This equates to a range-wide cumulative decline of 93% (Greenberg and Matsuoka 2010). CBC data indicate a cumulative decline of 88% from 1965 – 2007 (Niven et al. 2004, Greenberg and Matsuoka 2010). In their analysis of historical records and anecdotal data, Greenberg and Droege (1999) found that the species appears to have been declining as far back as the turn of the 20th century, but that the rate accelerated post-1950. In view of such drastic population decreases, there has been an increased focus on this species in recent years in an effort to determine what issues are involved in their decline. There is still no consensus in terms of the causal factors, however, and many questions have yet to be resolved (Greenberg and Matsuoka 2010).

Various explanations for the decline have been suggested. Given this species' year-round dependence on wooded wetlands, the wide-spread loss and degradation of wetland ecosystems throughout North America is likely implicated. In the winter, Rusty Blackbirds inhabit the swampy, bottomland hardwoods of the southeastern United States, approximately 80% of which have been converted to agriculture since European colonization (Hefner and Brown 1984). Since

the 1950's, much of what remained of these habitats was further developed due to urbanization and the expansion of pine (*Pinus* spp.) plantations and agriculture into ever-wetter locations (Hefner and Brown 1984, Hefner et al. 1994, Twedt and Loesch 1999, Hamel et al. 2009). Indeed, patterns of Rusty Blackbird population declines in two winter locales in the southeastern United States closely resemble patterns of wetland loss (Greenberg and Droege 1999, Hamel et al. 2009).

While it is often assumed that anthropogenic impacts to the remote boreal forest are minimal, this habitat also has been altered. Northern wetlands are drying seasonally due to climate change, altering water chemistry and the abundance of aquatic macroinvertebrates (Klein et al. 2005, Riordan et al. 2006, Corcoran et al. 2009). Climate change may also be driving recently described northward retractions of the species' breeding range (Powell 2008, McClure et al. 2012). Because of their reliance on aquatic invertebrates for food, Rusty Blackbirds also are particularly susceptible to mercury accumulation and have been found to have relatively high levels of methyl mercury in blood and feathers on the breeding grounds (Edmonds et al. 2010). Finally, natural resource exploitation through logging, peat production, and oil and gas extraction has increased in recent years, particularly in the southeastern portion of the breeding range (Greenberg and Droege 1999, Savignac 2006, Greenberg et al. 2011).

CBC and BBS datasets clearly show a pattern of population decline and lack of recovery since the 1970's, but there is still uncertainty about the Rusty Blackbird's status because much of the breeding range is not sampled by either survey. Rusty Blackbirds are listed as a species of "conservation concern" by a number of government agencies and non-governmental conservation organizations, including: the IUCN's Red List of Threatened Species, the U.S. Fish and Wildlife Service's Birds of Conservation Concern and the Committee on the Status of

Endangered Wildlife in Canada's Species of Special Concern (Savignac 2006, BirdLife International 2012, U.S. Fish and Wildlife Service 2008). Despite their precipitous decline, the species has not been afforded federal protection under the Endangered Species Act. Furthermore, because of their cryptic behavior and the inaccessibility of much of their habitat, there is no range-wide, standardized monitoring program that reliably tracks this species. *Rusty Blackbird Breeding Habitat*

Rusty Blackbirds breed across the vast boreal and hemi-boreal forests of North America, from Alaska to the maritime provinces (Fig. 1.2). They usually nest in short or stunted conifers in bogs, fens and along beaver flowages, though they are known to use other nest substrates where conifers are scarce (Avery 1995, Greenberg and Droege 1999, Matsuoka et al. 2010, Powell et al. 2010). They depend on wetlands for food during the breeding season, as aquatic macroinvertebrates are the primary food source for both adults and nestlings (Ellison 1990, Avery 1995).

Given the transcontinental extent of their breeding range, it is not homogeneous throughout in terms of anthropogenic influence or ecology. Most human-caused disturbances are due to timber harvesting or energy extraction (e.g., Canadian tar sands), with some areas more heavily exploited than others. The natural disturbance regime also differs between regions, with disturbances varying in return intervals, intensities and extent across the landscape. Indeed, the mixedwood forest of the southern boreal zone (i.e., the "Acadian forest") is quite different in its ecology than the coniferous forests of the "true boreal" zone (Lorimer 1977, Seymour and Hunter 1992, Bergeron 2000, Bergeron et al. 2004). Although the Acadian forest comprises a relatively small portion of the entire Rusty Blackbird breeding range, both of my study areas are located within this region.

Rusty Blackbirds and the Natural Disturbance Regime of the Acadian Forest

The Acadian forest refers to a forest type that occurs in North America between the coniferous boreal forest and the eastern deciduous forests. It is an ecological transition zone, where temperate species at their northern limit overlap with boreal species at the southern edge of their range (Seymour and Hunter 1992). While the true boreal forest is almost entirely coniferous, dominated by black spruce (Picea nigra), jack pine (Pinus banksiana) and balsam fir (Abies balsamea), the Acadian forest supports a much more diverse assemblage of species, including northern hardwoods such as red and sugar maple (Acer rubrum and A. saccharum), American beech (*Fagus grandifolia*) and birch (*Betula* spp.). The most common conifers in the Acadian region are balsam fir and the Appalachian red spruce (*Picea rubens*), with some northern white cedar (Thuja occidentalis), tamarack (Larix laricina) and eastern white pine (*Pinus strobus*). Unlike the boreal forests further north, where natural fires burn large swaths of forest (1,000 - 10,000 ha) every 50-150 years, the natural disturbances in Acadian forests tend to cover smaller areas and are thus not completely stand-replacing (Lorimer 1977, Seymour and Hunter 1992, Bergeron 2000, Bergeron et al. 2004). Although fires occasionally occur, the most frequent natural disturbance agents in the Acadian forest are wind, insect outbreaks (primarily spruce budworm (*Choristoneura fumiferana*) and spruce bark beetle (*Dendroctonus rufipennis*)) and beaver (Castor canadensis) in riparian areas (Lorimer 1977, Seymour and Hunter 1992).

As in other parts of their breeding range, Rusty Blackbirds in the Acadian forest nest primarily in patches of short, dense conifers (Matsuoka et al. 2010a, Powell et al. 2010a), which can result from spruce budworm outbreaks (Kneeshaw and Bergeron 1998, Bouchard et al. 2006). The favored host species of spruce budworm is balsam fir, with mature trees being particularly susceptible to infestation (Bouchard et al. 2006). Outbreaks typically occur every

30-40 years, but can recur at intervals as long as 100 years in some areas (Bouchard et al. 2006). The last spruce budworm outbreak in the Acadian region occurred between 1968-1985 (Hardy et al. 1983).

Outbreaks are often regionally synchronous, which results in complete or partial mortality of fir-dominated stands across large geographic regions (Williams and Liebhold 2000, Bouchard et al. 2006). While severe spruce budworm outbreaks can lead to vast areas covered by a single age-class of young balsam fir, (Bouchard et al. 2006), often the mortality is gradual and patchy, creating relatively small canopy gaps and subsequent patches of regeneration (Lorimer 1977, Seymour and Hunter 1992, Kneeshaw and Bergeron 1998, Bouchard et al. 2006). Recruitment in these patches often follows a pattern of cyclic replacement, with balsam fir being the dominant species in the regenerating cohort (Kneeshaw and Bergeron 1998, Bouchard et al. 2006). Post-budworm regeneration following via cyclic replacement is one natural mechanism by which patches of Rusty Blackbird nesting habitat may be created.

The effects of wind disturbance are often site-specific and localized. Stands most susceptible to windthrow are shallow-rooted, pure spruce-fir forests typical of poorly drained lowlands (Lorimer 1977, Seymour 1992, Lorimer and White 2003). These are exactly the habitats often used by nesting Rusty Blackbirds. While small-scale windthrow events recur every several decades, there is a much longer rotation period for severe windstorms causing thousands of hectares of blowdown (Lorimer 1977, Lorimer and White 2003). The interval between extreme windstorms is quite variable depending on site conditions, however, ranging from 2,585 years for upland mixed spruce-hardwood sites to only 290 years for spruce-fir flats (Lorimer 1977, Lorimer and White 2003). Thus, the relatively pure spruce-fir forests favored by

Rusty Blackbirds for nesting are likely those that are especially prone to natural disturbances such as insect outbreaks and wind.

Beavers are another important natural disturbance agent in boreal and Acadian ecosystems. While their activity is restricted primarily to riparian areas, their alterations to loworder streams can have significant and lasting effects on the larger landscape (Naiman et al. 1986, Naiman et al. 1988, Johnston and Naiman 1990, Terwilliger and Pastor 1999, Martell et al. 2006). Construction of a dam across a stream results in the impoundment of water behind the dam, effectively converting what was a lotic environment to a predominantly lentic environment and increasing the area of aquatic habitat (Naiman et al. 1986, Naiman et al. 1988). Beaver selectively forage for hardwoods such as aspen (*Populus* spp.), willow (*Salix* spp.) and birch along water bodies, greatly reducing the abundance of these species within the riparian zone (Naiman et al. 1986, Naiman et al. 1988, Martell et al. 2006). This essentially "resets" succession, thereby altering the structure and composition of riparian vegetation (Little et al. 2012). Long after beaver have abandoned a site, the legacy of their activity continues, with former ponds persisting in the landscape as meadows for centuries (Naiman et al. 1986, Naiman et al. 1988, Johnston and Naiman 1990, Terwilliger and Pastor 1999). Through the processes of damming streams and selective foraging along water bodies, beaver substantially alter both the hydrological conditions as well as the vegetative composition in a manner favorable to Rusty Blackbirds (Naiman et al. 1986, Naiman et al. 1988, Martell et al. 2006).

The Acadian Forest: Timber Management in the Spruce-Fir Region

Since European settlement of New England in the 17th century, the spruce-fir forests of eastern North America have been harvested with increasing intensity (Lorimer 1977, Lorimer and White 2003). The rate and extent of harvest activity greatly increased in the 1800's, when

private ownership of large tracts of forest combined with the accelerating demand for paper and other wood products to create the industrial forest that persists in the region today (Seymour and Hunter 1992). As a result of largely unregulated logging, mature, old growth forests all but disappeared in New England (Lorimer 1977, Seymour and Hunter 1992).

Today, most eastern spruce-fir forests are managed using even-aged silvicultural methods. A typical stand might be managed as follows (taken from Seymour 1992, Seymour and Hunter 1992): First there is a complete overstory removal ("clearcut" or "one-cut shelterwood") to release or naturally regenerate a new even-aged cohort. Herbicide may be applied 2-5 years after cutting to promote conifer growth by reducing competition from early successional herbs and shrubs. As the stand matures, one or more thinnings (pre-commercial or commercial) may be done to enhance the growth of select crop trees. After 30-50 years, the overstory is removed and the process starts over again. Since the enactment of the Maine Forest Practices Act in 1989, clearcuts in the state may not exceed 250 acres in size (Maine Forest Service 2004).

The extent to which this management practice mimics the natural disturbance regime is debatable and dependent on specific local conditions (Seymour et al. 2002, Lorimer and White 2003). Regardless, however, the current age structure of the New England forest is certainly younger overall than in pre-settlement times (Seymour et al. 2002, Lorimer and White 2003). For most of the northern hardwood forests, estimates for the percent of the landscape covered by seedling-sapling forests during pre-settlement times range between 1 - 3% (Lorimer and White 2003). Seedling-sapling forests may have comprised as much as 7% of the area in spruce-fir flats, but this is still well-below the current estimate of 9-25% early successional forest in northern New England (Lorimer and White 2003).

Whether young spruce-fir forests are a result of natural or anthropogenic disturbance, the abundance and distribution of this habitat in New England directly affects Rusty Blackbirds breeding in the region. Therefore, it is important to consider how natural disturbances and their selective forces have influenced Rusty Blackbird ecology before we can begin to understand the effects of modern forest management on the species.

Figures



Figure 1.1. Index of abundance for Rusty Blackbirds from Christmas Bird Count (CBC) data (circles) and Breeding Bird Survey (BBS) data (diamonds) during the period 1966-2004. Solid lines represent 95% confidence limits for CBC abundance indices. Figure taken from Niven et al. 2004.



Figure 1.2. Rusty Blackbird breeding range (in red) and wintering range (in blue). Map from BirdMap Canada (http://www.bsc-eoc.org/birdmap_e.htm).

Chapter 2:

Nest Habitat Selection by Rusty Blackbirds at Multiple Spatial Scales Introduction

The importance of determining which habitats are selected and why is critical for the conservation of rare and declining species, as this knowledge can be used to inform conservation plans and guide land management (Caughley 1994, Jones 2001). Rusty Blackbirds (*Euphagus carolinus*) have experienced one of the most severe population declines ever recorded among North American songbirds, decreasing by approximately 95% in the last half century (Sauer et al. 2008, Greenberg and Matsuoka 2010). Researchers are still uncertain as to the cause of their declining population, and understanding how the species uses the surrounding environment during the important reproductive period is crucial, particularly in the context of increasing anthropogenic habitat changes.

An animal's choice of a particular habitat is often the result of decisions made at multiple spatial scales (Johnson 1980, Wiens 1989, Kotliar and Wiens 1990, Orians and Wittenberger 1991, Jones 2001), and in birds, it is generally described as a hierarchical process where selection at coarser scales constrains selection at finer scales (Hildén 1965, Johnson 1980, Hutto 1985, Orians and Wittenberger 1991, Jones 2001, Battin and Lawler 2006). Further, the structure of the habitat itself is hierarchical, with patches nested within patches and heterogeneity occurring across a range of spatial scales (Allen and Starr 1982, O'Neill et al. 1986, Wiens 1989, Kotliar and Wiens 1990). Given this complexity, and that habitat is perceived and therefore selected at different spatial scales, it is prudent to consider multiple scales that are relevant to the species of interest when studying habitat selection (Addicott et al. 1987, Wiens 1989, Orians and Wittenberger 1991).

Previous studies of nest habitat selection by Rusty Blackbirds, however, have focused mostly on describing the habitat at the local or nest-patch scale (5 - 20 m around the nest)(Matsuoka et al. 2010, Powell et al. 2010a). Although Matsuoka et al. (2010b) did examine nesting habitat at larger spatial scales in Alaska, all parameters were wetland-related and did not include specific non-wetland variables other than "Upland." In New England, nests are often in upland areas, and therefore the details and differences within this habitat merit consideration as well. Therefore, my first objective was to examine the landscape composition (wetland and upland forest types) within the Rusty Blackbird home range around individual nests and develop a home-range scale model and a nest-patch scale model of habitat selection for Rusty Blackbirds. At the nest-patch scale, I predicted that birds would select patches with a higher density of young conifers relative to control patches based on the results of previous studies (Matsuoka et al. 2010a, Powell et al. 2010a) as well as my own observations in the field. At the home-range scale, I predicted that birds would select locations with a higher proportion of young and/or polesized softwoods and wetlands relative to random locations because of their importance as nest sites and foraging habitat, respectively (Matsuoka et al. 2010a, Powell et al. 2010a).

A multi-scale understanding of Rusty Blackbird habitat selection may be especially informative and useful from a forest management perspective, which considers single stands as well as the arrangement of stands across the landscape. Unlike the Alaskan sites studied by Matsuoka et al. (2010a, 2010b), the landscape in northern New England is intensively managed, and even the nests in unharvested wetlands are surrounded by a matrix of managed stands at various stages of regeneration. Thus, the landscape context for nests in industrial forests is quite different from that of nests in unharvested forests and boreal wetlands and may influence habitat selection decisions. Given that much of the Rusty Blackbird boreal breeding range is now

industrial forest, it is especially important to understand how timber management influences their habitat use. A second objective, therefore, was to explicitly examine the relationship between timber harvesting and nest habitat selection by Rusty Blackbirds. Based on the same rationale described above, I predicted that most nests would be in sapling or pole-stage softwood stands.

Methods

Description of Study Areas

I researched Rusty Blackbirds in two study areas in northern New England: one in northcentral Maine around Moosehead Lake and the other north of the White Mountains in New Hampshire, near the Androscoggin River (Fig. 2.1). While both sites have roughly the same range of elevation (300 – 1,000 m) and are intensively managed for forest products, they differ in topography and in the composition of the forest matrix. In the Maine study area, broad expanses of flat, wet lowlands are interspersed with relatively isolated areas of topographic relief. In the flats, red and black spruce (*Picea rubens* and *P. mariana*) and balsam fir (*Abies balsamea*) are the dominant tree species, where they are part of a mosaic of managed softwood stands and beaver flowages. Speckled alder (*Alnus incana* sp. *rugosa*) is a common shrub in wetlands. Upland areas and slopes tend to host more hardwoods, and are characterized by the typical Acadian mixed forest of red and sugar maples (*Acer rubrum* and *A. saccharum*), quaking aspen (*Populus tremuloides*), American beech (*Fagus grandifolia*) and paper and yellow birch (*Betula papyrifera*, *B. alleghaniensis*) as well as conifers. Most of the study area is owned and managed by industrial timber companies with some held by non-profit organizations.

In contrast, the New Hampshire study area is mountainous. Although there are some low-lying flats, they account for a relatively small proportion of the landscape, which is dominated by upland forests of mixed species composition. Due to the nature of the topography,

the hydrology in this region is concentrated in river valleys between steep slopes. Here too, most of the lands are managed by industrial forest owners, but there are also significant portions managed by the Umbagog National Wildlife Refuge.

Bird Surveys

Because of differences in terrain and associated logistical constraints, methods for detecting birds at the beginning of the breeding season differed between the Maine and New Hampshire study areas. In Maine, where the target survey area was large and birds were widely dispersed across the landscape, I used the road-based survey protocol developed by Powell (2008b). I selected survey locations based on apparent habitat suitability as visible from the road. "Suitable habitat" was defined by the presence of habitat variables known to be associated with Rusty Blackbird occupancy (e.g., conifer saplings, shallow water in small pools or puddles and presence of speckled alder. Bird surveys consisted of an initial 3-min passive listening period followed by a 38-second broadcast of territorial male vocalization, and then another 5-min passive listening period (Powell 2008b). In 2012, I added a second broadcast and 5-min listening period to maximize detectability and to be consistent with the methods of a concurrent study of occupancy in the region (J. Scarl, unpubl. data).

In New Hampshire, where the target survey area was smaller and birds were concentrated along river valleys, my collaborators with New Hampshire Audubon identified potentially suitable habitat using Google Earth and stand maps (C. Foss, pers. comm.). "Suitable habitat" was defined based primarily on the presence of young conifer or conifer-dominated stands, as well as physical indicators of wet conditions (slope, hydrology, etc.). Surveys consisted of a 30min period of passive listening, without a broadcast, because of the potential for discouraging birds from settling (C. Foss, pers. comm.). The method of nest searching was the same in both study sites. Once occupied territories were located, the area was searched for nests according to recommendations of Martin and Geupel (1993).

Nest-Tree and Nest-Patch Scale Habitat Measurements

I measured nest-patch scale habitat selection by comparing habitat features between nest patches and paired random patches. Following the completion of each nesting attempt, I measured vegetation and habitat characteristics within a 5-m radius plot centered on each nest, following a protocol modified slightly from that used by James and Shugart (1970), and later by Powell (2008a). I used a 5-m radius plot because Powell (2008a) found no significant difference between results from 5-m and 11-m radius plots. I marked the location of each nest with a handheld Garmin GPS. I classified nests as "harvested" or "unharvested" at the 5-m scale because most nests were near the wetland-upland interface and the upland was all managed/harvested. Beyond this distance, all nests would be considered to be in "harvested" habitat. I confirmed the harvest history at nest sites using stand data provided by foresters and land managers. I considered an area to be harvested if the landowner identified it as a commercial, managed stand. The category "harvested" included all types of treatments (complete/partial overstory removal, thinning, etc.).

I visually estimated the percent cover of herbaceous, shrub and tree species within a 5-m radius of nests. I defined a "shrub" as any woody plant \leq 3 m tall; a "tree" was > 3 m. I measured nest height to the nearest 0.1 m and recorded the number of vertical stems supporting the nest. I recorded nest tree species, height (m) and dbh (diameter at breast height) (cm). I counted woody stems in 1-m height-class intervals every meter along 5-m transects in each cardinal direction using a 3-m PVC pole. Each branch touching the pole was traced back to its

central stem (trunk), and I counted the number of stems contributing branches that touched the pole for each species in each height interval. For vegetation > 3 m, I visually estimated the number of stems of each species above me. At these same points, I estimated canopy cover using an ocular tube (James and Shugart 1970).

I used a 10-factor prism to determine the density and diameter distribution of trees around the nest. I used a jig notched in 2-cm intervals (i.e., 0-2, 2-4, etc.) to facilitate rapid measurement of diameters ≤ 10 cm. I measured trees with a dbh > 10 cm to the nearest 0.1 cm using a diameter tape. I counted borderline trees as "half trees." I measured nest concealment in each of the four cardinal directions by placing a 1-square-foot grid (0.09 m²) centered around the nest and estimating the percent of the grid covered by vegetation when standing one meter away. Following Powell (2008), I centered control plots on a suitable nesting substrate (conifer 2-5 m tall), 50 m from the nest in a randomly selected cardinal direction.

Stand Scale Habitat Measurements

For stand scale analyses, I examined characteristics such as species composition, size/age class and area of the stand in which the nest was placed. I did not model habitat selection explicitly at the stand scale, but rather calculated summary statistics and qualitatively described nest stands (for reasons to be discussed). I obtained this information from stand attribute data provided by collaborating foresters and land managers. In most cases, a stand (identified by stand ID number) represented a single management unit that was assumed to be homogeneous in species composition and treatment history. There were a few cases, however, where portions of a given stand were managed differently. In these instances, I considered the "nest stand" to be the part of the stand that received the same treatment as the nest location and was contiguous to it. While riparian buffers certainly represent a different management history, I did not

distinguish these areas from the rest of a stand because most of the stand data sources did not delineate them separately. Because I was primarily interested in stand characteristics related to timber harvesting and of relevance to forest management, I did not examine nests in "stands" identified as "non-productive forest," such as bogs and beaver flowages at this spatial scale. *Home-Range Scale Habitat Measurements*

I used ArcGIS ArcMap version 10.0 (ESRI, Redlands, CA) to map nest locations and surrounding landscape characteristics. I calculated the percent area of different stand and wetland types within a 500-m radius of the nest. I chose this distance because of its relevance to Rusty Blackbird spatial ecology during the breeding season. The mean home-range size of 37.5 ha for Rusty Blackbirds (Powell et al. 2010b), if circular, would have a 347 m radius. Home-range sizes were quite variable, however, ranging from < 10 ha (178 m radius) to over 150 ha (691 m radius) (Powell et al. 2010b). Therefore, 500 m seemed a relevant scale at which Rusty Blackbirds might respond to landscape features. I obtained stand data including species composition, stocking level, size class and other pertinent information from forest managers.

Because each landowner used slightly different stand coding systems (Appendix A), I recoded stands into six more general categories: young softwood, young hardwood, pole-sized softwood, pole-sized hardwood, mature softwood and mature hardwood (Appendix B, C.1 in Appendix C). I then calculated the percent area encompassed by these forest types.

I obtained wetland information from the National Wetland Inventory (NWI) database available from the U.S. Fish and Wildlife Service (http://107.20.228.18/ArcGIS/services/FWS_ Wetlands_WMS /mapserver/wmsserver?). Where wetland boundaries had shifted or new wetlands had formed since the NWI data was created, I used 2011 NAIP aerial photo imagery (http://www.maine.gov/geolib/wms.htm, http://granitweb.sr.unh.edu:6080/arcgis/services

/Image-Services/NH_NAIP_ 2011_RGB/ImageServer/WMSServer) and heads-up digitizing to match conditions on the ground. In a similar manner to stands, I re-classified the various wetland types into four major categories (*sensu* Cowardin 1979): palustrine forest/scrub-shrub wetland (PFO-PSS), palustrine emergent wetland (PEM), palustrine unconsolidated bottom (PUB) and riverine (R2) (C.2, Appendix C).

For each study area, I generated a number of random control points equal to the number of nests, and calculated the percent cover of different forest- and wetland-types within 500 m. To be consistent with nest locations, all control points were within 750 m of a road.

Statistical Analyses

I developed a list of variables *a priori* that I thought might influence nest patch selection based on previous studies as well as my own field experience (C.3, Appendix C). I used matched pairs logistic regression (MPLR) analysis with a 1:1 case-control design in Program R v.2.15.2 (R Development Core Team) to determine if nest sites were associated with particular habitat variables more often than expected from chance. I performed a logistic regression on the differences between habitat measurements taken at nest points and their paired random points, which amounts to a conditional logistic regression (Hosmer and Lemeshow 1989). I examined potential correlations between habitat covariates using Spearman rank correlation coefficients (D.1, Appendix D), and did not include correlated variables ($r_S \ge 0.5$) in the same model (Booth et al. 1994). Because most of the variables of interest were related to density of conifers around the nest, they were correlated, and therefore, not combined into multivariate models or a global model. I calculated the odds ratio by taking the exponent of the model-averaged coefficient estimate (Hosmer and Lemeshow 1989). Because a one-unit change was inappropriate for basal area variables, I calculated scaled odds ratios using a unit change of 5 m²/ha. I computed standard errors for all odds ratios using the delta method (Powell 2007), and used this estimate to calculate 95% confidence limits.

For variables related to conifer density around nests (e.g., nesting substrate), I pooled spruce and fir together because both were readily used as nest trees. I distinguish between "unharvested wetland" and "harvested" because while all unharvested areas were wetlands, not all harvested areas were uplands. Despite apparent differences in habitat between nests in unharvested wetlands and harvested locations (E.1-E.2, Appendix E), I also pooled nests from harvested and unharvested sites for all habitat selection models because I had too few nests in unharvested locations (n=9) to detect a distinct pattern for this habitat. When I included unharvested wetland nests in the models, they did not strongly influence the results so I kept them in to increase statistical power. I did not include any alder variables in the nest patch selection models because few nests were associated with alder, and alder was not found to be an important factor in nest-patch selection in previous studies (Matsuoka et al. 2010a, Powell et al. 2010a). Similarly, I did not include percent cover of water in the nest-patch scale habitat selection models because over 90% of points (both nest and control) had no water within a 5-m radius.

At the home-range scale, I first calculated summary statistics for all forest- and wetlandtype variables around nests and random points, and compared means using Kruskal-Wallis tests. Although I had NWI wetland data for all 43 nests in New Hampshire, I lacked stand data for 16 of these nests, and thus my total sample size for calculating forest summary statistics in New Hampshire was only 27. Based on relevant literature as well as my own field experience, I then developed a candidate set of landscape variables (C.4, Appendix C) from this list that I thought might influence Rusty Blackbird habitat selection at the home-range scale. Given the apparent

differences in landscape physiognomy between the Maine and New Hampshire study areas (see Results), I thought it plausible that there were different patterns of habitat selection at the homerange scale. Therefore, I included study area ("Site") as a covariate and tested for interactions between Site and different habitat variables.

I modeled nest habitat selection at the home-range scale using logistic regression in Program R (Hosmer and Lemeshow 1989). I examined predictor variables for correlations using Spearman's rank correlations (D.2, Appendix D), and did not include highly correlated variables $(r_5 \ge 0.5)$ in the same model (Booth et al. 1994). I examined the variance inflation factor (c-hat) for the global model, and then corrected for minor over-dispersion (c-hat = 1.21) by using QAIC_c to compare candidate models and calculate model-averaged beta estimates. I used modelaveraged coefficient estimates to calculate odds ratios, standard errors and 95% confidence limits. I calculated standard errors for odds ratios using the delta method (Powell 2007).

Results

Nest and Nest Tree Characteristics

My collaborators and I located 72 nests (29 in Maine; 43 in New Hampshire) in 2011 and 2012. Most nests (n=68) were placed in live spruce and/or fir, occasionally in combination with northern white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*) or a snag. Only four nests were placed in vegetation that was entirely dead, and all of these were in wetlands (though not necessarily unharvested stands). All nests in snags were surrounded by water, with relatively little vegetation around the nest tree(s). Seven of the nine nests in unharvested wetlands were placed in isolated live conifers, and most of these were surrounded by alder. Of the 63 nests in harvested areas, 61 were placed in live conifers, and most had a high density of small conifers in the immediate vicinity. However, I did find a few nests in previously harvested stands that were

in snags surrounded by water due to recent flooding by beaver. I also observed five nests in harvested areas that were placed in an isolated conifer growing in the open (e.g., in the middle of an abandoned skid road or former log landing). Sixty-five percent of nests were supported by multiple (2-4) vertical stems. Mean nest heights were nearly identical in Maine and New Hampshire, at 1.78 and 1.72 m, respectively (Table 2.1). Nest tree characteristics (total height, dbh) also were similar between study areas: nest trees in Maine had a mean height of 3.35 m and mean dbh of 4.40 cm; nest trees in New Hampshire averaged 2.47 m tall with a mean dbh of 4.14 cm (Table 2.1).

Nest-Patch Scale Habitat Selection

In both Maine and New Hampshire, the majority of nests were in managed/harvested stands (n=63), with just 13% in unharvested wetlands (n=9). Eight of the nine nests in unharvested sites were in beaver-created wetlands. As noted above, however, prior harvest at a site did not preclude flooding and creation of wetlands by beaver, as I found several nests fitting this description. Indeed, one nest that was placed in two conifers growing directly out of a beaver dam was in a formerly managed stand. Regardless of management history or wetland status, over 90% of nests were placed within a few meters of an edge or interface between a more densely forested habitat and an open habitat. This "open" habitat could be a wetland, a skid road or even the canopy gap resulting from harvest or windthrow of a single large tree.

In addition to frequent proximity to edges, I noted three recurring nest "phenotypes" in my study areas (Fig. 2.2). The first, and by far the most common (n=53), was a nest in a small, live conifer surrounded by a high density of other small conifers (but usually adjacent to a more open habitat). The second was a nest in an isolated live conifer or small clump of conifers, surrounded on all sides by alder, open water and/or open space (n=15). The third and least

common (at least in my study area) was a nest in a snag surrounded by water and relatively sparse vegetation (n=4). These three phenotypes occurred in a variety of management and hydrological contexts (except for the snag nests, which were always in "wetlands").

The best-supported habitat selection model at the nest-patch scale included the covariates SFBAless10 and %Canopy (Table 2.2). With each increase of 5 m²/ha in basal area of small conifers, the probability of selection increased by 59.2% while the probability of selection decreased by 5.1% with each 1% increase in canopy cover, (Table 2.3), suggesting that Rusty Blackbirds selected locations with a high density of small conifers and lack of canopy cover. *Stand Scale Habitat Characteristics*

Across 2011 and 2012, Rusty Blackbirds selected 38 managed stands for nest sites (20 in Maine, 18 in New Hampshire). Several of these stands contained more than one nest either within the same year, between years, or both. Three of the 20 nest stands in Maine were selected twice, and six of the 18 nest stands in New Hampshire were selected multiple times (five were selected twice, one three times). The mean area of nest stands in Maine was 13.53 ha (SE=2.27, range=0.68-42.17), while the mean area of nest stands in New Hampshire was 5.43 ha (SE=0.95, range=0.42-14.55).

In Maine, 16 nests were in young softwood stands, two nests were in pole-sized softwood stands, one was in a young hardwood stand and one was in a patch of advanced regeneration (vegetation 2-3 m tall) surrounded by a recent cut (vegetation < 1 m tall). In New Hampshire, 12 nests were in young softwood stands and six nests were in young hardwood stands. The majority of nest stands in both study areas were softwood-dominated, and most were in the seedling/sapling stage. Even nests in hardwood-dominated stands (as typed by landowner) were in patches of relatively pure softwood (see Discussion).
In both Maine and New Hampshire, Rusty Blackbirds placed their nests in stands or sections of stands that had previously undergone substantial overstory removal to regenerate a new cohort. In Maine, six of the 20 nest stands had been pre-commercially thinned. None of the nests in New Hampshire were in stands that had been pre-commercially thinned. However, one nest in New Hampshire in 2012 was placed in a 4-year-old regenerating stand that had been partially clearcut in 2008. Unfortunately I did not have accurate age information for all nest stands, but of three stands in Maine and three in New Hampshire, all were 20 years old or less.

Within managed stands, I also observed a recurrent pattern of nest-patch selection. As mentioned previously, nests are often placed at or very near the edge between a more densely forested environment and an opening. In regenerating stands, this opening can be a skid road, a canopy gap due to the loss of a single tree, or even the cut itself (i.e., in an isolated patch of advanced regeneration, surrounded by a more recent clearcut) (Fig. 2.3). In addition to proximity to an edge, another common feature of nests in regenerating stands was the presence of one or more elevated perches within a few meters of the nest. These perches were often snags (typically paper birch), presumably left during the last harvest (Fig. 2.3.A and 2.3.C). I frequently observed one or both adults perching in these locations for several minutes before going to the nest to incubate and/or deliver food.

Home-Range Scale: General Characteristics

There were differences in the composition of the landscape matrix between the Maine and New Hampshire study areas. Mean percent cover of all wetlands around nests in Maine was significantly greater than New Hampshire nests: 20% and 11%, respectively (Kruskal-Wallis test, H = 16.10, df = 1, P < 0.001). In both study areas, the mean wetland cover around nests was substantially higher than random points: 11% vs. 3% in New Hampshire (Kruskal-Wallis

test, H = 29.10, df = 1, P < 0.001), 20% vs. 10% in Maine (Kruskal-Wallis test, H = 10.21, df = 1, P = 0.001). While forested/scrub-shrub wetlands were by far the most abundant type of wetland in both study areas (>70% area), the relative proportion of the other wetland types differed between study areas (Fig. 2.4). Rivers and streams were much more prevalent in New Hampshire, whereas in Maine, ponds and emergent wetlands dominated (Fig. 2.4).

My study areas also differed in terms of composition of the forest matrix. Total softwood cover (all age classes combined) was significantly greater around both nests (63%) in Maine than in New Hampshire (36%) (Kruskal-Wallis test, H = 25.42, df = 1, P < 0.001) (Fig. 2.5). Hardwoods were more prevalent around New Hampshire nests (57%) than Maine nests (23%) (Kruskal-Wallis test, H = 34.75, df = 1, P < 0.001 (Fig. 2.5). In addition to being hardwood-dominated, the forests surrounding nests in New Hampshire were also older than in Maine (Kruskal-Wallis test, H = 41.15, df = 1, P < 0.001) (Fig. 2.6 and 2.7). In both Maine and New Hampshire, nests were in locations with more young softwood stands relative to random points: 77% vs. 58% in Maine (Kruskal-Wallis test, H = 7.92, df = 1, P = 0.005).

Home-Range Scale: Habitat Selection

Patterns of habitat selection did not differ between study areas. The best-supported habitat selection at the home-range scale included percent cover of wetlands and percent cover of young softwoods (Table 2.4). With each 1% increase in the cover of wetlands, probability of selection increased by 11% (Table 2.5). With each 1% increase in young softwood cover, probability of selection increased by 3.5% (Table 2.5).

Discussion

Nest and Nest Tree Characteristics

Nest and nest tree characteristics that I observed in this study were almost identical to previous studies of Rusty Blackbirds in New England (Powell 2008, Powell et al. 2010a) and similar to studies of the species in Alaska (Matsuoka et al. 2010a). In Alaska, nest site characteristics varied significantly by study area (interior vs. coastal). Similarities with New England nests depended on individual nest characteristics. New England nests were similar to coastal Alaskan nests in that Rusty Blackbirds most often placed nests in some combination of live conifers (94% of 72 nests and 93% of 44 nests, respectively; this study, Matsuoka et al. 2010a), while nests in interior Alaska are usually in deciduous shrubs (76% of 63 nests; Matsuoka et al. 2010a). However, New England nests were more similar to the interior Alaskan nests in terms of nest height and size of the nest tree. All of the nests in Alaska (both interior and coastal sites) were located in or near (\leq 50 m) undisturbed wetlands with no timber harvest activity, while almost all of the New England nests were located in regenerating clearcuts, sometimes more than 500 m from a clearly discernible, "mappable" wetland.

Nest-Patch Scale Habitat Selection

As predicted, the best-supported habitat selection model at the nest-patch scale indicated that Rusty Blackbirds select areas with a dense cover of small conifers and lack of canopy closure for nesting. This accords well with previous studies of Rusty Blackbird nesting ecology in New England (Powell et al. 2010a) as well as in the boreal regions further north (Matsuoka et al. 2010a). Indeed, despite differences in landscape context and management, Rusty Blackbirds' preference for short, dense conifers at the nest-patch scale is consistent across breeding populations in coastal Alaska, New England and eastern, central and maritime Canada

(Matsuoka et al. 2010a, Powell et al. 2010a), differing only from interior Alaska where the birds select willow and alder (Matsuoka et al. 2010a). This is not to suggest that the microhabitat features around all nests are the same, or that the habitat cues being used to select nest sites are homogeneous across the entire population. On the contrary, given the three distinct nest phenotypes I observed in our study, it seems likely that individuals are responding to different habitat features when selecting nest sites.

These different phenotypes may represent a "bet-hedging" strategy for selecting nest sites in the presence of spatiotemporal variability in selective pressures (Chalfoun and Schmidt 2012). Given that most environments vary in space and time, the optimal nest phenotype in one place and time may not necessarily be the optimum in another place or at another time. In the case of Rusty Blackbirds, perhaps nest phenotype A is the "conservative" approach – the one that is most frequently associated with nest survival in most contexts. Given certain conditions, however, it may be that the less common nest phenotypes B or C are more successful, and that these deviations from the norm represent "diversified" or "adaptive coin-flipping" bet-hedging strategies by the species (Chalfoun and Schmidt 2012).

Preference for different nest phenotypes may not only vary between individuals but also within individuals (Olofsson et al. 2009, Chalfoun and Schmidt 2012). A single female may switch phenotypes from season to season, or even within the same season, particularly following failure of a nest (reviewed in Lima 2009). While my small sample size of nests of phenotype B or C precludes any rigorous statistical analysis or making sweeping generalizations, it is interesting to note that three of four type C nests were very likely re-nests (based on their initiation date). Although there may be different nest phenotypes that have evolved in response to environmental stochasticity, as a generalization, it appears that Rusty Blackbirds select patches of short conifers. At least in New England, this patch often borders an opening. The widespread preference for dense conifers close to open areas suggests that Rusty Blackbirds are adapted to natural disturbances that create patchy, coniferous regeneration. Fires are the most important natural disturbances in boreal forests, where they often cover thousands of hectares and are completely stand-replacing (Seymour and Hunter 1992, Hunter 1993). In Acadian forests, the dominant sources of natural disturbance are insect outbreaks (spruce budworm (*Choristoneura fumiferana*), spruce bark beetles (*Dendroctonus rufipennis*)) and windstorms (Seymour and Hunter 1992). These events typically occur every several decades, and often result in the death and subsequent regeneration of only part of the stand (Lorimer 1977, Seymour 1992, Seymour and Hunter 1992). Whether it is whole stands or isolated areas within a single stand, disturbance creates a mosaic of patches of different sizes and ages across the landscape. It is at these boundaries between contrasting patches that Rusty Blackbirds often nest.

Perhaps the most important natural disturbance agent for Rusty Blackbirds in New England is beaver. Through stream impoundment and selective removal of hardwoods, beaver create both nesting and foraging habitat for Rusty Blackbirds. Beaver use deciduous species like aspen, birch, or alder along the water's edge, thereby releasing conifers in the understory from competition (Naiman et al. 1988, Naiman et al. 1994). This creates a dense patch of young conifers at the edge of a wetland opening – the ideal combination of habitat features for nesting Rusty Blackbirds. Impoundment of water also creates a lentic habitat, which increases the overall abundance of macroinvertebrates in addition to hosting a higher proportion of species favored by Rusty Blackbirds, such as Odonates (McDowell and Naiman 1986, Naiman et al.

1988). With time, flowages become shallower with increasing amounts of emergent vegetation until they eventually become wet meadows. Unlike other openings caused by disturbance, meadows created by beaver tend not to support conifer regeneration due to the lack of ectomycorrhizae essential to root growth (Wilde et al. 1950, Iyer 1980, Terwilliger and Pastor 1999), and hence may persist in the landscape for centuries (Naiman et al. 1986, Naiman et al. 1988, Johnston and Naiman 1990, Terwilliger and Pastor 1999). Thus, beaver may create forestgraminoid ecotones (i.e., favored Rusty Blackbird nest locations) that are sustained for much longer periods of time than those created by other forms of disturbance.

Habitat characteristics around a nest are as much a reflection of local hydrological conditions as management history. That is, the harvest history of a site does not predetermine its wetland status. While all nests in unharvested locations were in wetland environments, nests in harvested areas occurred in both wetland and upland settings. My data suggest that we need not focus on "harvest history" as the defining characteristic determining differences between nest habitat attributes. Rusty Blackbird nest habitat results from a complex process of interacting disturbances that is dynamic across space and time. Most of the landscape in my study areas was harvested at some point, but this does not preclude the influence of other subsequent disturbances or imply that all regenerating stands follow the same trajectory of growth and development.

Stand Scale Habitat Characteristics

Given their preference for dense, short conifers as a nest substrate, the fact that most nests were in young softwood stands is not surprising. Although consideration of entire stands is certainly useful from a forest management perspective, Rusty Blackbirds likely do not view stands as a uniform grouping of forest cover. "Stand-level" attributes as described through forest

management are not necessarily indicative of current conditions everywhere in the stand, or more importantly, in the nest-patch specifically. Indeed, based on my observations, it seems more likely that the birds are responding to patchiness within a stand. Thus, relying only on general stand characteristics (species composition, size class, age, etc.) to determine or describe potential Rusty Blackbird habitat may be misleading. For instance, all of the nests placed in hardwooddominated stands (as typed by landowner) were in isolated patches of relatively pure spruce-fir. Similarly, I observed nests in "cut" stands (species composition undetermined) in small "islands" of advanced softwood regeneration, surrounded on all sides by a recent clearcut.

Beaver often induce another source of within-stand heterogeneity. I observed three nests in managed stands that were surrounded by water as a result of recent beaver impoundments. Two of these were in snags, and one was in a pair of live firs growing out of the beaver dam. In all of the circumstances described above, the characteristics of the individual nest patch were not representative of the majority of the stand, and the current conditions around the nest were not accurately described by the land manager's stand attribute data. This made modeling habitat selection at the stand scale problematic, and indicated that birds were responding primarily to features at the sub-stand level.

Home-Range Scale Habitat Selection

Features associated with home-range scale habitat selection – increased cover of wetlands and young softwoods – were the same in both Maine and New Hampshire. Despite their clear influence on habitat selection and the fact that Rusty Blackbirds are frequently referred to as an obligate wetland species, the proportion of area covered by wetlands around nests was relatively small. However, as I observed and Powell et al. (2010b) reported, many of the "wetlands" used for foraging by Rusty Blackbirds in New England are not "mappable" wetlands. The birds often

forage in roadside ditches and isolated ephemeral pools, neither of which are large enough to be discerned on aerial photoimagery or delineated by NWI as wetlands.

Though wetlands may not be a substantial component of the landscape around nests, they are relatively more important than forest composition in driving habitat selection at the homerange scale. Each 1% increase in wetland cover increased probability of selection by 11%, while each 1% increase in young softwood cover, the most common nesting substrate, increased selection probability by 3.5%. This suggests that there are different factors governing breeding habitat selection at different spatial scales, a phenomenon which has been described in other avian species and which accords well with the notion of habitat selection as a hierarchical process (Johnson 1980, Orians and Wittenburger 1991, Chalfoun and Schmidt 2012). Studies of breeding habitat selection in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Orians and Wittenburger 1991) and Brewer's Sparrows (*Spizella breweri*) (Chalfoun and Martin 2007) indicated that food availability was of primary importance at the territory and larger spatial scales, while the selection of a nest site was based on microhabitat features that reduced nest predation, and were independent of foraging habitat.

Decoupling of nest and foraging habitat selection cues may be especially strong for species with high mobility or large home ranges, which is the case for many blackbird species (Orians and Wittenburger 1991). Given Rusty Blackbirds have one of the largest home ranges of any blackbird (Powell et al. 2010b), they are not constrained by a requirement for spatial proximity between nesting habitat and foraging habitat. Indeed, I as well as others in New England have frequently observed birds flying hundreds of meters from the nest presumably to forage (Powell et al. 2010b, P. Newell pers. comm., S. Buckley, pers. obs.).

As previously noted in the literature (Orians and Wittenburger 1991, Boves et al. 2013), this difference in habitat selection at different scales is also interesting to consider in the context of gender. In most migratory passerines, males arrive on the breeding grounds before females, and select their home range and territories. These male settling decisions are presumably made on a relatively coarse scale, with an abundant and consistent food supply often being the primary criterion (Orians and Wittenburger 1991). Upon arrival at the breeding grounds, females choose a male (and his territory) and subsequently select a nest patch within the larger territory/home range. For Rusty Blackbirds, like in many songbirds, it is the female alone who builds the nest (though almost always closely attended by the male), and it is she who selects the specific nest location. Thus, differences in the plasticity of selection at different scales also may reflect different behavioral roles of the sexes within a species (Boves et al. 2013).

The variation between landscape features within Rusty Blackbird home ranges in Maine and New Hampshire also suggests some level of plasticity in the species - as long as certain key features are present, the structure and composition of the surrounding landscape appears of little import. Such flexibility in home-range and territory scale habitat also has been noted among Cerulean Warblers (*Setophaga cerulea*) breeding in different regions of the Appalachian Mountains (Boves et al. 2013). Indeed, the warblers exhibited even greater plasticity by selecting entirely different landscape features depending on the region, suggesting that a "onesize-fits-all" approach to habitat management is inappropriate for this species (Boves et al. 2013). In contrast, Rusty Blackbirds in different locations appear to favor the same habitat attributes, but are quite flexible in terms of the landscape matrix within which those essential features are embedded. This suggests that habitat management for the conservation of Rusty Blackbirds may be applicable across the New England region.

Habitat Selection and Forest Disturbance

Rusty Blackbirds appear to be a disturbance-adapted if not disturbance-dependent species at the southeastern edge of their range. Although there have always been some areas with naturally stunted conifers, much of the young softwood habitat in the Acadian forest was and continues to be the result of disturbance. Historically, the areas that likely attracted Rusty Blackbirds (softwood stands, wet soils) were particularly disturbance-prone (Graves 1899, Lorimer and White 2003). In contrast to the mixed Acadian forests that dominated on upland slopes, the conifer-dominated forests that prevailed in hydric or rocky soils were often relatively young and even-aged (Graves 1899, Lorimer and White 2003). The disturbance regime in these "spruce swamps" or "spruce flats" resembled that of the true boreal, characterized by larger and more frequent disturbances (Lorimer and White 2003). Because of their heightened susceptibility to both windthrow and insect outbreaks, relatively pure spruce-fir forests often died before reaching biological maturity (Graves 1899, Lorimer and White 2003). This resulted in the regeneration of new, even-aged stands ranging in size from < 1 ha to thousands of hectares (Lorimer and White 2003).

Prior to extensive timber harvesting in the Acadian forest beginning in the early 1800's (Seymour and Hunter 1992), Rusty Blackbirds and other early successional species likely depended on these unique, "boreal-like" habitats for a continuous source of nesting habitat (Lorimer and White 2003). Thus, harvesting practices that strive to mimic natural disturbances in both spatial and temporal scale should provide suitable nesting habitat for the species. Numerous studies have described forest management plans based on natural disturbance regimes for both the true boreal and Acadian forests (Hunter 1993, Bergeron et al. 1999, Harvey et al. 2002, Seymour et al. 2002, Lorimer and White 2003, Bergeron et al. 2004).

Given that different factors affected habitat selection at the nest-patch and home-range scale, the frequency with which Rusty Blackbirds nest in "non-wetland" locations and the natural disturbance regime of the region, it seems improbable that the species nested in wetlands exclusively prior to extensive timber harvesting. Rather, natural disturbances such as windthrow and insect outbreaks likely created patches of regenerating softwoods in uplands that were used as nesting habitat as well. Thus, the notion that timber harvesting alone is the cause for nesting in "non-wetland" locations is doubtful.

The relationship between timber management and Rusty Blackbirds is complex. Disturbance from harvesting often interacts with other abiotic factors (e.g., hydric soils) and disturbances (e.g., beaver) to create patchiness that would not exist were all of these conditions independent of one another. Thus, to classify nest habitats based on harvest history alone or to assume all harvested areas are alike and inherently different in structure from unharvested areas, is to overlook a rich and important complexity.

Conclusion

By examining multiple spatial scales, my study revealed several novel aspects of Rusty Blackbird nesting habitat selection. Although the range-wide preference for short, dense conifers suggests that selection at the nest-patch scale is relatively conservative, "anomalous" but recurring nest phenotypes may represent adaptations to environmental variability. As the first study to examine Rusty Blackbird nest habitat selection at the home-range scale, I show that birds in both New Hampshire and Maine favor areas with increased cover of wetlands and young softwoods. That this pattern of selection is the same despite substantial differences in landscape physiognomy between my two study areas suggests Rusty Blackbirds are quite plastic in terms of the structure of the landscape matrix around surrounding essential habitats. There also appears

to be a decoupling of habitat selection at the two spatial scales, with foraging requirements governing selection at the home-range scale and nest seclusion driving selection at the nest-patch scale. Finally, the effect of timber management on Rusty Blackbird habitat selection is multifaceted and is not independent of other forms of disturbance. Tables

Table 2.1.	Comparison	of characteristics	(mean ± range)	of Rusty	Blackbird	nest sites in
Maine (n=	29), New Han	npshire (n=43) and	l combined (n='	72), 2011-	-2012.	

Variable	ME	NH	Combined
Nest Height (m)	1.783 (0.75 – 4.00)	1.720 (0.70 - 3.55)	1.745 (0.70 - 4.00)
Nest Tree Height (m)	3.35 (2.10 - 5.35)	2.47 (0.90 - 5.50)	2.828 (0.90 - 5.50)
Nest Tree DBH (cm)	4.40 (1.70 - 8.00)	4.14 (1.35 - 11.90)	4.25 (1.35 - 11.90)
Num. of Vertical Stems	1.66 (1.00 – 4.00)	1.93 (1.00 – 4.00)	1.82 (1.00 – 4.00)

Model ^a	<i>k</i> ^b	AIC _c ^c	ΔAIC_{c}^{d}	w _i ^e	$\mathbf{L}^{\mathbf{f}}$
SFBAless10+%Canopy	2	55.14	0.00	0.998	1.000
SFBAless10	1	68.04	12.90	0.002	0.002
BAless10	1	77.15	22.00	0.000	0.000
SFBATotal	1	79.72	24.58	0.000	0.000
SFShrub	1	83.03	27.89	0.000	0.000
BATotal	1	89.26	34.12	0.000	0.000
%Canopy	1	94.75	39.61	0.000	0.000
SFStems	1	95.80	40.66	0.000	0.000
SFSum	1	96.95	41.81	0.000	0.000
Null	0	99.81	44.67	0.000	0.000
SFTree	1	99.83	44.69	0.000	0.000

Table 2.2. Results of nest-patch scale habitat selection analyzed using matched-pairs logistic regression models for Rusty Blackbirds in northern New England, 2011-2012.

^a See C.3, Appendix C for variable descriptions

^bNumber of parameters

^c Corrected Akaike's Information Criterion ^d Difference in AIC_c relative to top model ^e Model weight

^fModel likelihood based on AIC_c

Variable ^a	ß ^b	SE ^c	LCL ^d	UCL ^e	OR ^f	OR SE ^g	LCL ^h	UCL ⁱ	Unit ^j	$\mathbf{R}^{\mathbf{k}}$
SFBAless10	0.093	0.025	0.044	0.141	1.592	0.199	1.202	1.982	5	1.00
%Canopy	-0.052	0.017	-0.085	-0.018	0.949	0.016	0.918	0.981	NA	1.00
BATotal	0.024	0.008	0.009	0.039	1.129	0.045	1.014	1.218	5	0.00
SFBA	0.041	0.011	0.019	0.063	1.228	0.068	1.100	1.360	5	0.00
BAless10	0.038	0.010	0.019	0.057	1.209	0.060	1.091	1.328	5	0.00
SFSum	0.010	0.005	0.001	0.019	1.010	0.005	1.000	1.020	NA	0.00
SFShrub	0.031	0.009	0.013	0.049	1.031	0.123	1.013	1.050	NA	0.00
SFTree	-0.008	0.006	-0.019	0.003	0.992	0.006	0.980	1.004	NA	0.00
SFStems	0.020	0.009	0.003	0.038	1.020	0.009	1.002	1.038	NA	0.00

Table 2.3. Parameter estimates and odds ratios for variables used to model nest patch selection by Rusty Blackbirds in northern New England, 2011-2012.

^a See C.3, Appendix C for variable descriptions ^bCoefficient estimate

^c Standard error of coefficient

^d Lower 95% confidence limit for coefficient ^e Upper 95% confidence limit for coefficient

^fOdds ratio (scaled for BA variables)

^g Standard error of (scaled) OR

^hLower 95% confidence limit for (scaled) OR

37

ⁱUpper 95% confidence limit for (scaled) OR ^jUnit change for scaled OR

^kRelative importance value

Model ^a	k ^b	QAIC ^c		w _i ^e	$\mathbf{L}^{\mathbf{f}}$
YoungSoft+SitexTotalWet	6	117.065	0.000	0.282	1.000
YoungSoft+PoleSoft+ TotalWet+Site	6	117.786	0.721	0.196	0.697
SitexYoungSoft+TotalWet	6	118.169	1.103	0.162	0.576
YoungSoft+PoleSoft+ SitexTotalWet	7	119.005	1.939	0.107	0.379
PoleSoft+SitexYoungSoft+TotalWet	7	120.032	2.967	0.064	0.227
YoungSoft+TotalWet+ SitexPoleSoft	7	120.032	2.967	0.064	0.227
YoungSoft+PoleSoft+ TotalWet	5	121.183	4.118	0.036	0.128
PoleSoft+TotalWet	4	121.311	4.246	0.034	0.120
YoungSoft+TotalWet	4	123.528	6.463	0.011	0.039
SitexYoungSoft+ SitexPoleSoft+SitexTotalWet	9	123.610	6.544	0.011	0.038
PoleSoft+SitexTotalWet	6	123.904	6.839	0.009	0.033
Site+TotalWet	4	124.597	7.532	0.007	0.023
SitexPoleSoft+TotalWet	6	124.673	7.608	0.006	0.022
TotalWet	3	125.390	8.325	0.004	0.016

Table 2.4. Results of home-range scale habitat selection analyzed using logistic regression models for Rusty Blackbirds in northern New England, 2011-2012 (n=112; 56 nests and 56 control points).

Model ^a	<i>k^b</i>	QAIC ^c	Δ QAIC ^d	w _i ^e	$\mathbf{L}^{\mathbf{f}}$
Site*TotalWet	5	125.596	8.531	0.004	0.014
YoungSoft	3	128.580	11.514	0.001	0.003
Site+YoungSoft	4	128.919	11.854	0.001	0.003
YoungSoft+PoleSoft	4	129.908	12.843	0.000	0.002
SitexYoungSoft	5	131.076	14.011	0.000	0.001
Null	2	132.428	15.363	0.000	0.000
SitexYoungSoft+PoleSoft	6	133.035	15.969	0.000	0.000
PoleSoft	3	133.054	15.989	0.000	0.000
SitexYoungSoft+PoleSoft	6	133.285	16.220	0.000	0.000
Site	3	134.540	17.475	0.000	0.000
Site+PoleSoft	4	134.887	17.822	0.000	0.000
SitexPoleSoft	5	136.950	19.885	0.000	0.000

^a See C.4, Appendix C for variable descriptions
^b Number of parameters
^c Quasi-Akaike's Information Criterion
^d Difference in QAIC_c relative to top model
^e Model weight
^f Model likelihood based on QAIC_c

N ¹
0.584
0.698
0.465
NA
0.237
0.081
0.413

Table 2.5. Parameter estimates and odds ratios for variables used to model home-range scale habitat selection by Rusty Blackbirds in northern New England, 2011-2012.

^a See C.4, Appendix C for variable descriptions ^b Model-averaged coefficient estimate ^c Unconditional standard error of coefficient

^d Lower 95% confidence limit for coefficient

^eUpper 95% confidence limit for coefficient

^fOdds ratio

^g Standard error of OR

^h Lower 95% confidence limit for OR

ⁱUpper 95% confidence limit for OR

^jRelative importance value

Figures



Figure 2.1. Map of Maine (ME) and New Hampshire (NH) study areas; Red circles indicate Rusty Blackbird nest locations in 2011 and 2012.



Figure 2.2. Three distinct Rusty Blackbird nest "phenotypes" in northern New England: *A*. Nest in contiguous patch of live, dense conifers; *B*. Nest in isolated conifer(s), surrounded by relatively open space; *C*. Nest in snag, surrounded by water and/or alder. Arrows indicate nest location.



Figure 2.3. Rusty Blackbird nest patches in northern New England, 2011-2012, located in harvested stands with three types of canopy openings: *A*. Skid road (nest is between camera and tall cedar in photo center, about 5 m from skid road edge). *B*. Single tree gap (nest in trees on the left side of photo). *C*. Clearcut (nest is in remnant patch of advance regeneration).



Figure 2.4. Mean percentage (± SE) of total wetland area composed of different wetland types for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=43) and NHRandom (n=43)), 2011 and 2012. "PFO_PSS" refers to palustrine forested/scrub-shrub wetlands; "PEM" refers to palustrine emergent wetlands; "PUB" refers to palustrine unconsolidated bottom wetlands (ponds); "R2" refers to riverine wetlands.



Figure 2.5. Mean percent area $(\pm SE)$ within 500-m radius covered by softwoods and hardwoods for nest and random points in Maine (MENest (n=29) and MERandom (n=29)) and in New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 2012.



Figure 2.6. Mean percentage $(\pm SE)$ of total softwood forest area composed of different age/size classes for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 2012.



Figure 2.7. Mean percentage (\pm SE) of total hardwood forest area composed of different age/size classes for nests and random points in Maine (MENest (n=29) and MERandom (n=29)) and New Hampshire (NHNest (n=27) and NHRandom (n=27)), 2011 and 2012.

Chapter 3:

Rusty Blackbird Nest Survival, Predator Dynamics and Timber Management in the Northeast

Introduction

Nest predation is the most frequent cause of nest failure across a wide range of bird species, on average accounting for 80% of failed nests (Ricklefs 1969, Martin 1992, 1993a, 1993b). Therefore, nest predation can be a powerful influence on population persistence, particularly for rare or declining species, and is an important consideration in conservation planning and habitat management. Rusty Blackbirds (*Euphagus carolinus*) have declined by an average of 9.3% annually between 1966 and 2008, resulting in a range-wide cumulative decline of 93% (Sauer et al. 2008, Greenberg and Matsuoka 2010). In their analysis of historical records and anecdotal data, Greenberg and Droege (1999) found that the species appears to have been declining as far back as the turn of the 20th century, but that the rate accelerated since 1950.

Although the cause of the Rusty Blackbird decline is not yet understood, one possible contributing factor in the southeastern portion of their breeding range could be the presence of an "ecological trap." A recent study in Maine found that Rusty Blackbirds seemed to preferentially select regenerating clearcuts less than 20 years old for nest sites, where they experienced greater rates of nest predation than in older stands or undisturbed wetland habitats (Powell et al. 2010a). Rusty Blackbirds favor the dense, stunted conifers typical of boreal wetlands for nest sites (Avery 1995, Matsuoka et al. 2010a, Powell et al. 2010a, Chapter 2), and regenerating clearcuts structurally resemble this preferred habitat. However, because nests in regenerating cuts tend to be further in uplands, Powell et al. (2010a) suggested that these nests may be subject to increased rates of predation by red squirrels (*Tamiasciurus hudsonicus*), which are the most common nest predator in boreal and Acadian forests (Bayne et al. 1997, DeSanto and Willson 1998, Bayne and

Hobson 2002, Willson et al. 2003, Ball et al. 2009). Red squirrels rely on coniferous seeds, including spruce (*Picea* spp.) and balsam fir (*Abies balsamea*), as their primary food source, and therefore, their populations fluctuate drastically in accordance with conifer mast cycles (Smith 1968, Kemp and Keith 1970, Rusch and Reeder 1978, Boutin et al. 2006). Cyclical changes in predator populations could have important implications for nest predation in Rusty Blackbirds, but have not been examined to date.

My study addresses critical gaps in our understanding of nest predation in this declining species. Although Powell et al. (2010a) hypothesized that red squirrels were the primary predators of Rusty Blackbird nests, definitive identification was lacking. Further, previous studies of Rusty Blackbird nest success (Powell et al. 2010a, Matsuoka et al. 2010a) focused on local-scale habitat predictors of nest survival, and did not examine the potential influence of habitat variables at larger spatial scales that may be of relevance to predators. In their review of nest predators to habitat fragmentation, Chalfoun et al. (2002b) found that the response of nest predators to habitat features like edges is taxon-specific, and that many predator-habitat associations are more sensitive to patterns at the landscape scale (e.g., \geq 500 m radius). Thus, effective habitat management should consider the identity of nest predators as well as the landscape context in which predation occurs (Chalfoun et al. 2002b). Without this knowledge, efforts to mitigate the detrimental effects of nest predation are likely to be of limited value.

My objectives were to: 1) identify which species are the primary predators of Rusty Blackbird nests; 2) examine the relationship between red squirrels (the hypothesized primary nest predator) and habitat variables; 3) develop models relating nest success to habitat characteristics at three ecologically relevant spatial scales (nest-patch scale, squirrel territory

scale and Rusty Blackbird home-range scale), with a particular focus on timber management; and 4) explore the dynamics of nest predation, conifer mast and predator cycles.

Methods

Description of Study Areas

I researched Rusty Blackbirds in two study areas in northern New England: one in northcentral Maine around Moosehead Lake and the other north of the White Mountains in New Hampshire, near the Androscoggin River. While both of these areas are intensively managed for forest products and have a similar elevation range (300 - 1,000 m), they differ both in topography and composition of the forest matrix. Broad expanses of wet "spruce-fir flats" cover much of the Maine study area, while the New Hampshire study area is mountainous and dominated by hardwoods. In both study areas, red and black spruce (Picea rubens and P. *mariana*) and balsam fir (*Abies balsamea*) are the most common conifers, with some eastern white pine (Pinus strobus), northern white cedar (Thuja occidentalis) and tamarack (Larix *laricina*). Hardwoods present in the region include red and sugar maples (Acer rubrum and A. saccharum), quaking aspen (Populus tremuloides), American beech (Fagus grandifolia) and paper and yellow birch (Betula papyrifera, B. alleghaniensis). Due to the nature of the topography, the water in New Hampshire is concentrated in river valleys between steep slopes, while in Maine wetlands are dispersed across the landscape. Industrial timber companies own and manage the majority of the land in both study areas, with some parcels held by nongovernmental organizations.

Bird Surveys

Because of differences in terrain and associated logistical constraints, methods for detecting birds at the beginning of the breeding season differed between study areas. In Maine,

where the target survey area was quite large and birds were widely dispersed across the landscape, I used the road-based survey protocol developed by Powell (2008b). I selected survey locations based on apparent habitat suitability as visible from the road (see Chapter 2 for more detailed description). Bird surveys consisted of an initial 3-min passive listening period followed by a 38-second broadcast of territorial male vocalization, and then another 5-min passive listening period (Powell 2008b). In 2012, I added a second broadcast and 5-min listening period to maximize detectability and to be consistent with the methods of a concurrent study of occupancy in the region (J. Scarl, unpubl. data).

In New Hampshire, where the target survey area was smaller and birds were concentrated along river valleys, my collaborators with New Hampshire Audubon identified potentially suitable habitat using Google Earth and stand maps. "Suitable habitat" was defined based on the presence of young conifer stands, as well as physical indicators of wet conditions (slope, hydrology, etc.). Because of the potential for discouraging birds from settling, surveys consisted of a 30-min period of passive listening, without a broadcast, (C. Foss, pers. comm.).

The method of nest searching was the same in both study sites. Once territories were located, the area was searched for nests according to recommendations of Martin and Geupel (1993).

Camera Installation and Nest Monitoring

I installed motion-triggered, infrared cameras within 3 m of nests as habitat conditions permitted. Over two field seasons I used three different models: Reconyx Hyperfire HC600 (Reconyx Inc., Holmen, WI), Bushnell Trophy Cam (Bushnell Outdoor Products, Overland Park, KS) and Uway NightTrakker NT50B (Uway Outdoors Canada, Lethbridge, AB, Canada). When possible, I mounted cameras on adjacent natural vegetation (usually sapling or pole-stage conifers), approximately level with the nest. When there were no suitable trees for attachment in the vicinity of the nest or when the nest was too high, I mounted the camera on a "pole" created from a young, live conifer or a snag (see Chapter 4 for more detailed description of "pole" set-up).

I set cameras at the maximum sensitivity level and programmed them to take the maximum number of photos per trigger event (three or five exposures depending on the model). I attempted to avoid installing cameras until egg-laying was completed, as the disturbance of installation could result in abandonment at earlier stages in the nesting cycle (reviewed in Richardson et al. 2009). I checked cameras and nests every three to five days. During each visit, camera position and batteries were checked and adjusted as necessary, and memory cards replaced. I also examined nest contents using either binoculars or a mirror pole to assess the nesting stage and number of eggs or young present.

I deployed cameras at nests in 2011 and 2012 in Maine, but only in 2012 in New Hampshire. Camera installation at nests in New Hampshire was avoided during incubation to prevent interference with concurrent studies (see Chapter 4 for further discussion of cameras). *Squirrel Surveys*

Because of their hypothesized importance as Rusty Blackbird nest predators, I conducted broadcast surveys for red squirrels at nest sites. Given that forests with large, cone-producing trees are prime habitat for squirrels (Layne 1954, Kemp and Keith 1970, King et al. 1998, Wheatley et al. 2002, Willson et al. 2003), I surveyed select mature stands as well. Due to logistical constraints, methodologies also differed slightly between study areas and between years.

In 2011 in Maine, I conducted one survey at the conclusion of nesting at each nest. The squirrel survey consisted of a 5-min passive listening period, a 20-second broadcast of territorial calls, and then a second 5-min listening period. I noted only presence, but did not estimate abundance. I did the same at each of 12 mature forest sites. In 2011 in New Hampshire, I surveyed nest sites but not mature stands, and the survey was 10-min of passive listening without a broadcast.

In 2012, methods were identical for both study sites. I conducted 5-min listening, 20second broadcast, 5-min listening surveys to determine squirrel presence at each nest location at the conclusion of nesting and at mature forest reference points. I also estimated squirrel abundance during surveys in 2012. In association with each nest point and mature forest point survey, I conducted four "satellite" surveys, located 90 m from the nest/center points in each cardinal direction. I used 90 m because this is the diameter of an average red squirrel territory, and roughly the foraging range of red squirrels (Larsen and Boutin 1994, Fisher 1999). When survey points landed in a road or in the middle of an open water wetland with no measurable trees, I shifted the point by 45 degrees (e.g., NE instead of N). I included points that fell in a recent clearcut even when there were no measurable trees. I resurveyed all nest locations from 2011 for comparative purposes.

Nest-Patch Scale Habitat Measurements

Following the completion of each nesting attempt, I measured vegetation and habitat characteristics within 5-m radius plots around nests, following a protocol modified slightly from that used by James and Shugart (1970), and later by Powell (2008a). I used a 5-m radius plot because Powell (2008a) found no significant difference between results from 5-m and 11-m radius plots. I marked the location of each nest with a handheld Garmin GPS in the UTM

coordinate system. Because nests were often placed at the interface between a harvested stand and an unharvested wetland, I classified nests as being "cut" or "uncut" at the 5-m scale. I confirmed the harvest history at nest sites using stand data provided by collaborating foresters and land managers (Appendix A). I considered an area to be harvested if the landowner identified it as a commercial, managed stand. The category "harvested" included all types of treatments (complete/partial overstory removal, thinning, etc.).

I visually estimated the percent cover within a 5-m radius of herbaceous, shrub and tree species. I defined a "shrub" as any woody plant \leq 3 m tall; a "tree" was > 3 m. I measured nest height to the nearest 0.1 m and recorded various nest tree characteristics including the number of vertical stems supporting the nest, nest tree species, height and diameter at breast height. I counted woody stems in 1-m height class intervals every meter along 5-m transects in each cardinal direction. Each branch touching the pole was traced back to its central stem (trunk), and I counted the number of stems contributing branches that touched the pole for each species in each height interval. For vegetation > 3 m, I visually estimated the number of stems of each species above me. At these same points, I estimated canopy cover using an ocular tube (James and Shugart 1970).

I used a 10-factor prism to determine the density and diameter distribution of trees around the nest. I counted borderline trees as "half trees." I used a jig notched in 2-cm intervals (0-2, 2-4, etc.) for rapid measurement of trees with diameters ≤ 10 cm and I measured trees with a dbh > 10 cm to the nearest 0.1 cm using a 5-m diameter tape. I measured nest concealment in each of the four cardinal directions by placing a 1-square-foot grid (0.09 m²) centered around the nest and estimating the percent of the grid covered by vegetation when standing one 1 m away. To develop an index of spruce-fir cone abundance, I counted cones in each nest and control plot following a modified version of the Mountain Bird Watch protocol (Hart and Lambert 2010). Starting from the nest or plot center point, I estimated the total number of cones on the nearest cone-bearing spruce or fir in each cardinal direction. If there were no cone trees within the 5-m radius plot, I extended to 11 m. If no cone trees were located within the 11-m plot, then zero cones were recorded. When the nest tree had cones, its count replaced the cone tree furthest from the nest.

Squirrel Territory Scale Habitat Measurements

At each squirrel survey location (nests, mature forest points and all associated 90-m satellite points), I used a 10-factor prism to measure basal area of all woody vegetation breast height or taller. I used a jig to measure trees with a dbh \leq 10 cm and a diameter tape to measure trees with a dbh > 10 cm.

Rusty Blackbird Home-Range Scale Habitat Measurements

I used ArcGIS ArcMap version 10.0 (ESRI, Redlands, CA) to map nest locations and surrounding landscape characteristics. I calculated the percent area of different stand types and wetland types within a 500-m radius of the nest. I obtained stand data including species composition, stocking level, size class and other pertinent information from forest managers. Because each landowner used slightly different stand coding systems (Appendix A), I recoded stands into six more general categories: Young softwood, young hardwood, pole-sized softwood, pole-sized hardwood, mature softwood and mature hardwood. I then calculated the percent area covered by each forest type (Appendix B, C.1 in Appendix C).

I obtained wetland information from the National Wetland Inventory (NWI) database available from the U.S. Fish and Wildlife Service (http://107.20.228.18/ArcGIS/services/FWS_

Wetlands_WMS/mapserver/wmsserver?). I used 2011 NAIP aerial photo imagery for Maine and New Hampshire (http:// www.maine.gov/geolib/wms.htm, http://granitweb.sr.unh.edu:6080/ arcgis/services/Image-Services/NH_NAIP_2011_RGB/ImageServer/WMS Server) and heads-up digitizing to add recently-created wetlands or edit wetland boundaries that had shifted. I collapsed the various wetland types into four major categories (*sensu* Cowardin 1979): palustrine forest/scrub-shrub wetland (PFO-PSS), palustrine emergent wetland (PEM), palustrine unconsolidated bottom (PUB) and riverine (R2) (C.2, Appendix C). In addition to calculating the percent area of different forest and wetland types, I used ArcGIS to measure the distance from the nest to the nearest road and the nearest wetland. I considered a feature a road if a four-wheel-drive vehicle could traverse it.

Statistical Analyses

I used Program MARK (White and Burnham 1999) to model daily survival rate (DSR) as a function of different habitat variables at the nest-patch scale (5 m), squirrel territory scale (90 m) and Rusty Blackbird home-range scale (500 m). I also examined whether nest survival varied temporally, and whether there was a substantial effect of study area or year (C.5, Appendix C). I developed a set of *a priori* candidate models for each spatial scale, and then used corrected Akaike's Information Criterion (AIC_c) values to determine the best model for each spatial scale (Burnham and Anderson 2002). In accordance with previous nesting studies on the species, I calculated nest survival using 29 exposure days (Matsuoka et al. 2010, Powell et al. 2010). I used the delta method (Powell 2007) to calculate standard errors and 95% confidence limits for nest survival estimates. The season start date was standardized to May 7 for both years and both study sites. For the nest-patch scale variables, I had several general categories in which all of the variables reflected the same piece of information (e.g., all related to frequency of "spruce-fir" or "alder"). For these highly correlated variables within categories (C.3 and C.6, Appendix C, and D.1 and D.3, Appendix D), I first compared each variable separately in MARK and used AIC_c to determine their relative explanatory power (F.1-F.2, Appendix F). I selected the best among these to include as the representative variable for that category in a preliminary set of candidate models (C.7, Appendix C). I then tested for correlations between variables in this preliminary set using Spearman's correlation tests (D.4, Appendix D). For correlated variables ($r_s \ge 0.5$), I selected the one I predicted was the most representative and biologically meaningful for inclusion in the final set of candidate variables (C.7, Appendix C). I tested for interactions between habitat variables, study area and temporal variables in the final set.

I used two categories of squirrel territory scale variables to model nest survival: one based on habitat characteristics (C.8, Appendix C) and the other on audio-visual squirrel detections during surveys (C.9, Appendix C). The habitat variables were based on the hypothesis that squirrels would be more abundant in areas with more mature conifers, and that nest predation might therefore also be higher for nests with greater numbers of large conifers within 90 m. To create an index of mature conifers at this scale, I averaged the conifer basal area measurements from the four 90-m transects associated with each nest. Because of the relative scarcity of mature conifers in both study areas, and because I was unsure at what tree size there might be an effect, I tested several variables representing basal area of different-sized conifers. These variables were all subsets of one another and therefore highly correlated, so I did not combine them in multivariate models. The audio-visual red squirrel detection variables were based on the assumption that nests with more squirrels within 90 m would have higher predation risk. Because I collected data on abundance as well as presence data for red squirrels in the 2012 surveys but not in the 2011 surveys, I tested for effects of these different red squirrel metrics on DSR for the 2012 nests only.

For the Rusty Blackbird home-range scale analyses, I selected forest and wetland type variables that I thought could influence nest survival based on the ecology of red squirrels as well as parameters of general interest from a nest predation perspective (e.g., distance to the nearest road) (C.10, Appendix C). In addition, I included the variable representing percent cover of young softwood (YoungSoft) because of its importance in habitat selection (Chapter 2). I combined both pole-sized softwoods and mature softwoods into the variable MatSoft because there were so few mature (sawtimber) softwood stands in my Maine study area. "Pole-sized" softwoods were the oldest/largest softwoods in any abundance in the Maine study area, and also were strongly associated with red squirrel detections in our surveys (see Results). For all habitat variables, I tested for an interaction with year and study area (Site) because I thought there could be spatial and/or temporal variation in their relationship to nest survival. I also tested for interaction between MatSoft, representing prime squirrel habitat, and the linear and quadratic effects of date because squirrel dynamics might shift across the bird breeding season and influence nest predation. I examined Spearman rank correlations between home-range scale variables and did not include variables with $r_S \ge 0.5$ in the same model (Booth et al. 1994) (D.5, Appendix 5).

I excluded seven nests from nest survival analyses because of incomplete data. The excluded nests included two that were abandoned immediately following camera installation,
two in which no eggs were confirmed, two which were found post-fledging and one for which fledge date was unknown. Thus, my total sample size for modeling nest survival at the nest-patch scale was 65. For the home-range scale analyses, I had stand information for only 50 nests. For each covariate, I present the model-averaged beta value, standard error and 95% confidence limits.

To verify the assumption that squirrels would be more abundant in mature coniferous forests, I used logistic regression to model red squirrel detections in 2012 at 290 survey points as a function of the basal area of different sized-conifers (C.11, Appendix C). These 290 points consisted of all of the surveys at nest sites and mature reference sites, as well as the four satellite surveys associated with each nest/mature point. Logistic regressions and all other analyses except for nest survival were conducted in Program R v. 2.15.2 (R Development Core Team).

Results

Nest Predators and Mast

I monitored 29 nests with cameras: 21 total in Maine including 2011 and 2012, and 8 in New Hampshire in 2012. I documented eight predation events on camera (two in 2011, six in 2012), and identified four species of nest predators: red squirrel (*Tamiasciurus hudsonicus*), white-tailed deer (*Odocoileus virginianus*), an Accipiter spp. (*Accipiter striatus* or *A. cooperii*) and Blue Jay (*Cyanocitta cristata*). Poor image quality prevented predator identification at one nest, but given the animal's size, shape and the time of predation (21:37), it may have been the nocturnally active northern flying squirrel (*Glaucomys sabrinus*). Cameras failed to trigger during four predation events (three entire, one partial). I also failed to document a predation that occurred before I deployed a camera. Red squirrels were the most frequently observed nest predator, but only in 2012. Red squirrels accounted for 66% of all recorded predations in 2012 (n=6). However, two of the four definitive red squirrel predations were likely due to the same individual, given that they were on subsequent nests of the same pair, only 90 m apart. I did not observe any nest predation by red squirrels in 2011; the only two predators recorded were the hawk and the deer.

I documented a significant change in both the red squirrel population as well as the spruce-fir cone crop between the two years of this project (Tables 3.1 and 3.2). The proportional change in squirrel detections was almost identical at both mature stands and nest sites in Maine (Table 3.1). The estimate of the change in squirrel populations in New Hampshire (Table 3.1) is very conservative. Due to the lack of a broadcast survey in 2011 and to avoid any confounding broadcast effects, I only counted sites as occupied in 2012 if I detected squirrels pre-broadcast (the first 5 minutes of the survey). Had I included those sites where squirrels were detected postbroadcast, the number of occupied sites would have increased from four to ten, making the change across years statistically significant in New Hampshire as well. I found a sharp decrease in cone abundance in both study areas between 2011 and 2012 (Table 3.2).

Squirrels were more likely to be detected in areas with large conifers (Tables 3.3 and 3.4). The best variable for predicting red squirrel detection at a site was basal area of conifers ≥ 20 cm dbh, with the odds of detection increasing by 76% with each increase of 5 m²/ha of basal area (Tables 3.3 and 3.4). Although the odds of detection increased even more dramatically with increases in basal area of conifers ≥ 30 and ≥ 40 dbh (260% and 586%, respectively), the models including these variables received less support overall.

Nest Survival: General and Nest-Patch Scale

I located 72 nests and obtained nest survival data for 65. Nest predation increased concomitantly with the increase in red squirrels from 2011 to 2012. The nest success rate in 2012 was nearly half that of 2011 (Table 3.5). For both years combined, however, nest success was relatively high at 46.6% (Table 3.5). While nest success differed between study areas and years (Table 3.5), models accounting for these factors were not significantly better ($\Delta AIC_c \ge 2$) than the null constant survival model except when they included the covariate BATotal (Table 3.6). BATotal was an important variable overall and its effect on nest survival was positive (Table 3.7). Although the 95% confidence interval for BATotal barely encompassed zero, BATotal was in all of the top models and had a relative importance value of 0.80 (Table 3.7). While the model including both BATotal and Cut received the most support among the nest-patch scale models tested, the improvement over the univariate BATotal model was minimal ($\Delta AIC_c = 0.45$), indicating that BATotal explained most of the variation in the data.

The univariate model including Cut performed poorly, suggesting that Cut was relatively unimportant as a predictor of nest survival. The effect of Cut on nest survival was negative, but the standard estimate exceeded the β estimate (Table 3.7). All of the other habitat covariates also had a positive effect on nest survival, but models including these variables received relatively little support. None of the various models in which survival varied temporally had a substantially improved fit ($\Delta AIC_c \ge 2$) over the constant survival model (Table 3.6). *Nest Survival: Squirrel Territory Scale and Rusty Blackbird Home-Range Scale*

None of the variables describing conifer basal area at the squirrel territory scale that I tested received any support (Table 3.8). When I tested the 2012 nests for the effects of different

red squirrel detection metrics on DSR, none of the models performed better than the null model (Table 3.9).

None of the models containing either the main effect or interaction effects of study area (Site) were significantly better (AIC_c \geq 2) than the null model (Table 3.10). Thus, the apparent differences in landscape composition between the two study areas did not manifest in different patterns of nest survival. There was a strong year effect, however, as all of the best-supported models included either the main or interaction effects of year.

At the home-range scale, the model receiving the most support by far included the main effects of year, distance to road and the interaction between these two factors, which suggests there was a year-dependent effect of distance to road. Indeed, the only parameter that did not include zero in the 95% confidence interval was the interaction between distance to road and year, for which the model-averaged β estimate was 0.026 (Table 3.11). Nest survival increased with increasing distance from roads in 2011. This pattern did not hold in 2012, however, and the overall (though non-significant) effect of distance to road was negative (Table 3.11). Young softwood cover had a positive effect on nest survival and mature softwood had a negative effect, but neither was significant. Models including the effects of young or mature softwood cover received relatively little support overall.

Discussion

Nest Predators and Mast

My results support the hypothesis that red squirrels are the primary nest predator for Rusty Blackbirds, as suggested by Powell et al. (2010a). This finding concurs with other studies of both natural and artificial nests across much of North America. Red squirrels depredated over 80% of real, camera-monitored songbird nests in the alpine regions of Arizona (Martin 1988), in southeastern Alaska (Sieving and Willson 1998) and in the forests of western Canada (Ball et al. 2009). Red squirrels also were identified as the dominant nest predator of artificial nests in the industrial forests of Quebec (Darveau et al. 1997), in southeastern Alaska (Sieving and Willson 1998, Willson et al. 2003) and in central Canada (Bayne and Hobson 2002).

I found the importance of red squirrels as Rusty Blackbird nest predators, however, is highly year-dependent. Red squirrel populations fluctuate in accordance with the masting cycle of conifers, increasing substantially during a mast year and then plummeting again after a year of low cone production (Smith 1968, Kemp and Keith 1970, Rusch and Reeder 1978, Boutin et al. 2006). Annual fluctuations in squirrel numbers can be dramatic, with abundance changing by as much as 10-fold from year to year (Darveau et al. 1997). In both temperate and boreal forests, predation of songbird nests increases in years when numbers of sciurids and other small mammals are high (Rodenhouse 1986, Reitsma et al. 1990, Schmidt and Ostefeld 2003). Thus, even though I only documented a few predation events, it seems likely that the relatively high rate of nest predation I observed in 2012 was a consequence of the abundant squirrel population, which was a result of the previous year's prolific cone production.

The association I observed between red squirrels and large, cone-producing conifers is well-documented in the literature (Layne 1954, Kemp and Keith 1970, King et al. 1998, Wheatley et al. 2002, Willson et al. 2003). Given the relative paucity of mature (sawtimber-size) conifers in my study areas, however, I found the best-supported model for predicting squirrel detection included conifers with a dbh of at least 20 cm (which is generally considered pole-size rather than mature). With each 5 m²/ha increase in basal of conifers with \ge 20 cm dbh, probability of squirrel detection increased by 76%. Where they were present, however, mature

conifers (dbh \ge 30 cm) increased the probability of detecting a red squirrel by at least three-fold (detection probability increased with increasing dbh).

While all of the nest predation events by red squirrels were recorded in the Maine study area, this is likely a result of methodological rather than biological differences between the study sites. Three of the four red squirrel predations I documented in Maine were during the egg stage. Because of the risk of causing birds to abandon nests during a concurrent study in New Hampshire, my collaborators generally avoided installing cameras during incubation. Thus, I may have missed documentation of nest predations by red squirrels earlier in the nesting cycle at that study site.

Even though my collaborators did not confirm any predations by red squirrels in New Hampshire, there were other signs that the increased abundance of squirrels in 2012 altered Rusty Blackbird nesting phenology, and perhaps indirectly, nest success. In 2012, multiple nests in New Hampshire fledged several days earlier than predicted based on clutch initiation date (P. Newell, pers. comm.). This may be indicative of "force-fledging" as a result of predator disturbance or perceived predation risk by parents (Pietz and Granfors 2000, Lima 2009, Ball and Bayne 2012). Given that nestling condition is an important factor in fledgling survival, young that fledge before they are developmentally ready likely suffer higher mortality (Vitz and Rodewald 2011, Ball and Bayne 2012). Further, in a comparison of field-based fate estimates and camera evidence, Ball and Bayne (2012) found that observers often incorrectly assumed that an empty, late-stage nest was successful. This discrepancy was particularly acute when the predators were large mammals, birds and red squirrels. Thus, while documentation of nest predation events are lacking in New Hampshire, circumstantial evidence suggests a possible indirect effect of high squirrel numbers on nest success.

Given I recorded only one predation event per predator species for all other types of predators except red squirrels, it is difficult to infer their importance or impact as nest predators. Deer have been previously documented depredating grassland bird nests, as well as taking birds out of mist nests (Pietz and Granfors 2000). However, I suspect the deer predation I observed was a highly unusual occurrence. The depredated nest was an anomalous type C nest (see Chapter 2), set about a meter high in a cedar snag and with almost no concealing vegetation. Most Rusty Blackbird nests are inaccessible to deer due to their height and surrounding dense coniferous vegetation. Based on this, deer probably do not depredate Rusty Blackbird nests with enough frequency to have a significant detrimental effect.

In contrast, avian predators are much more flexible in their ability to access nests. Corvids such as Blue Jays and American Crows (*Corvus brachyrhynchos*) are common nest predators in many areas, but especially in places fragmented by agriculture and with dense human populations (Gates and Gysel 1978, Chasko and Gates 1982, Wilcove 1985, Wilcove et al. 1986, Andrén 1992, Chalfoun et al. 2002a, and many others). In heavily forested, sparsely settled landscapes, such generalist corvid predators are less common and are not the primary nest predators (Bayne and Hobson 1997, Tewksbury et al. 1998, Chalfoun et al. 2002a, Tewksbury et al. 2006). Accipiters also are common nest predators (McCallum and Hannon 2001, Schmidt and Ostfeld 2003, and others), and were widespread in both study areas (S. Buckley, pers. obs). Given that raptor populations have increased in many places since the banning of DDT in the U.S. in 1972 (Bednarz et al. 1990, Sauer et al. 2012), their importance as nest predators may have increased concomitantly (Schmidt and Ostfeld 2003).

Nest Survival: General and Nest-Patch Scale

Nest success in 2011, the year with low squirrel predation, was 59.4% and comparable to previous estimates of Rusty Blackbird nest success in Alaska (56%: Matsuoka et al. 2010a) and the Northeastern U.S. (61%: Powell et al. 2010a). Nest success plummeted to 29.8% the following year. The annual variation I observed in nest survival also was similar to the result obtained by Matsuoka et al. (2010), where nest success was at a low 21% in 2006 before rebounding to 64% in 2007 and 2008. These authors attributed 89% of the nest losses in 2006 to predation, but could not definitively link the reduced survival that year to an increase in a specific predator.

Despite such apparent differences in nest success between the two years of my study, most models with year as a covariate were not better than the null model. This is likely a function of my relatively small sample size (65), rather than a true lack of effect. With a similar magnitude of difference in nest success between years, Matsuoka et al. (2010a) noted a strong year effect on nest survival in their study of 150 Rusty Blackbird nests in Alaska. Unlike the results from the Alaska study, none of my models wherein survival varied temporally received much support using my data.

At the nest-patch scale, total basal area had a positive effect on nest survival. Although the model-averaged 95% confidence interval for total basal area did include zero, it is probable that this was also a result of my small sample size as well as the rather shallow slope ($\beta = 0.004$). All other evidence (high relative importance value, presence in all top models) points to an effect of total basal area on nest survival. Nest survival increased as total basal area increased, suggesting that the general density of vegetation around the nest, irrespective of species or size, was an important factor in determining nest success. This is contrary to what would be expected under the "potential prey site hypothesis," which contends that it is the density of the nesting substrate specifically rather than general vegetative cover that improves nest survival (Martin 1993, Chalfoun and Martin 2009). That being said, most (60-90%) of the basal area around nests was composed of softwoods and trees less than 10 cm dbh (i.e. nesting substrates) (Appendix G). Further, all of the univariate nest survival models including the highly correlated basal area variables were comparable ($\Delta AIC_c < 2$) (F.1, Appendix F). Thus, total basal area may still be indicative of the density of the nest substrate.

My nest survival results are more similar to those obtained by Matsuoka et al. (2010a) in Alaska than to Powell et al. (2010a) in New England. Powell et al. (2010a) determined that DSR was positively related to the presence of alder (a wetland indicator), but I did not find alder to be an important predictor of nest success. The univariate model including harvest history ("Cut") was one of the least-supported models (Table 3.6). The effect of increasing basal area (vegetation density) on nest survival was positive irrespective of management history. This result differs from a previous nesting study in the region, which found that the vegetation attributes associated with nest survival were dependent on the management context. While increased vegetation density around nests was generally associated with higher survival, Rudnicky and Hunter (1993) found increased cover of young conifers around nests in regenerating clearcuts was associated with higher rates of nest predation (Rudnicky and Hunter 1993). Perhaps these differences result from Rudnicky and Hunter (1993) using artificial nests on the ground, rather than natural nests in the shrub layer.

Nest Survival: Squirrel Territory Scale

Despite numerous studies documenting a correlation between predator abundance or activity and nest predation (Vickery et al. 1992, Zanette and Jenkins 2000, Schmidt et al. 2001,

2006, Vigallon and Marzluff 2005, Cain et al. 2006, Sperry et al. 2008), neither squirrel presence nor optimal squirrel habitat around the nest were good predictors of nest success in my study. This finding agrees with research indicating that the activity of red squirrels in the vicinity of the nest *per se* does not increase predation risk (Willson et al. 2003, Pelech et al. 2010). Pelech et al. (2010) found that probability of predation may increase by 150-200% when squirrels have prior experience depredating nests, and predation experience may carry over to subsequent years. This "learned" rather than "incidental" predation may in part explain the lack of correlation between indices of predator abundance/activity patterns and predation risk I and others have observed (Heske et al. 1999, Mahon and Martin 2006). It also may indicate Rusty Blackbirds could experience higher red squirrel predation during the 2013 breeding season.

Nest Survival: Rusty Blackbird Home-Range Scale

Contrary to my expectations, increased cover of mature softwoods in the surrounding landscape did not result in a significant increase in the risk of nest predation. There are biological and methodological explanations for this lack of correlation. First, this may be further corroboration of the results of Pelech et al. (2010). If squirrel activity alone is a poor predictor of nest predation, this limits the relevance of certain habitat features associated with squirrel presence (e.g., cones, mature conifers) as well. By extension, it also brings into question the capacity of habitat management to reduce predation by red squirrels (Pelech et al. 2010).

It is also possible, however, that nest predation patterns may be more closely related to the spatial arrangement of key habitat features, rather than their simple abundance as represented by percent cover. In the case of red squirrels, which generally have a summer foraging range of 100 m (Fisher 1999), a nest further than 100 m from a defended territory is unlikely to be discovered. Thus, even if much of the landscape surrounding a nest is covered by mature

softwood and occupied by squirrels, it may only be problematic if an occupied stand is in close proximity to a nest from the squirrel's perspective. An analysis of the arrangement of and proximity between forest patches (e.g., using FRAGSTATS: http://www.umass.edu/landeco/ research/fragstats/fragstats.html) would provide better resolution on the extent to which such processes may be operating.

Nest survival increased with increasing distance from a road in 2011, but not in 2012. While Small and Hunter (1988) and Askins (1994) suggested logging roads may adversely affect nest success by acting as corridors for predators, several empirical studies have not found any relationship between roads and nest predation (Yahner and Mahan 1997, King and DeGraaf 2002, Ortega and Capen 2002). Of note, all three of the non-squirrel predators identified (deer, Accipiter, Blue Jay) depredated nests within 50 m of a road. Thus, perhaps there is some association between these predators and the open habitat created by roads. I often observed hawks perched or flying along the roadside, and Blue Jays are known to prefer edges or open habitats (Chalfoun et al. 2002a). If there is an association between certain predators and roads, then it may be prudent to consider the potential effects of infrastructure associated with harvest operations rather than focusing on stand treatments exclusively.

The relationship between distance to road and nest survival may not have been apparent in 2012 because red squirrels were the dominant predators, and they tend to avoid open habitats such as clearings and roads (Bakker and Van Vuren 2004) due to their own risk of predation by raptors and mammalian carnivores. Thus, perhaps this pattern of increased depredation closer to roads is only apparent in years when red squirrel numbers are low.

Nest Predation, Timber Management and the Ecological Trap

My data do not provide clear support for the hypothesis that Rusty Blackbirds are suffering from an ecological trap as a result of timber harvesting activity. Indeed, the species seems to be adapted to and attracted to areas where disturbances create patches of short, dense conifers, and regenerating clearcuts are no exception. The relationship between Rusty Blackbird nesting ecology and timber harvest is more nuanced and complex than previous research would suggest. The distinction between wetlands and regenerating clearcuts drawn by Powell et al. (2010a, 2010b) is a false dichotomy, given that many formerly harvested sites are also "wetlands." I located nests in harvested stands that were surrounded by water several feet deep due to recent beaver impoundments. Thus, the notion that harvesting activity necessarily results in nesting further in the "upland" is incorrect given the dynamic nature of hydrological conditions in the region. Harvest history and wetland status of a nest site are not mutually exclusive.

Even if harvests do attract Rusty Blackbirds to nest in upland locations as suggested by Powell et al. (2010a), I did not find that nests in harvested stands sustained higher levels of predation than in unharvested wetlands, nor did nest survival decrease with increasing distance from wetlands. Importantly, however, this result is based on contrasting nests in a single "harvested" category, which includes all types of treatments, with nests in the "unharvested" category. Different harvest practices can have different effects on nest survival (Barber et al. 2001), and pre-commercial thinning may enhance habitat for potential nest predators such as red and northern flying squirrels (Ransome et al. 2004). Further, given that an important predictor of nest survival at the nest-patch scale was vegetation density around the nest (BATotal), forestry practices such as thinning may negatively impact Rusty Blackbird nest survival. Therefore,

although my sample sizes within specific treatment types are too small to permit analysis of individual harvest regimes, managers should be aware that stand treatments may have varied effects on nest survival. This topic is ripe for future experimental research.

Previous studies of nest success in industrial spruce-fir forests have found lower rates of nest predation in regenerating clearcuts than in mature forest (Rudnicky and Hunter 1993, Darveau et al. 1997), which is likely attributable in large part to the relative scarcity of red squirrels in early successional habitats (King et al. 1998, Boulet et al. 2003, Willson et al. 2003, Bakker and Van Vuren 2004). In their study of nest predation in the managed forests of southeast Alaska, however, DeSanto and Willson (2001) observed higher predation levels of artificial nests in clearcuts and adjacent forests (58% and 48%, respectively) relative to nests in wetland openings and the surrounding forest (20 and 23%, respectively). At this study site, however, clearcuts were surrounded by older conifers than were the wetlands. Thus, the different predation rates in clearcuts and wetlands may have been a result of differences between the matrix surrounding these two habitats rather than features of the habitats themselves (DeSanto and Willson 2001).

Given that Rusty Blackbirds often nest at or near the wetland/upland interface, however, even nests in unharvested wetlands may be susceptible to predation by red squirrels. DeSanto and Willson (2001) found that squirrels in forested wetland areas restricted their activity to the forest edge, and that predation rates were higher near wetland edges than clearcut edges (40 and 36%, respectively). Therefore, in some contexts, nest placement relative to edges *between* habitat types may be equally as relevant to predation risk as the features *within* an individual habitat type.

Forest Management Recommendations and Future Research

Regenerating clearcuts resemble the young, even-aged spruce-fir forests which historically resulted from large natural disturbances. Given that nests in regenerating clearcuts are not necessarily subject to increased predation, and that young softwood cover has a positive effect on habitat selection, maintaining some portion of the landscape as young softwood stands seems a reasonable recommendation for foresters interested in managing for Rusty Blackbird nesting habitat. Rusty Blackbird nests are often placed near an edge with an open habitat and within 10-20 m of one or more perches (often snags) that are elevated above the general canopy (Chapter 2). Therefore, the common practice of leaving behind isolated trees during a harvest appears to enhance Rusty Blackbird nesting habitat.

These young softwood stands need not be very large, as Rusty Blackbirds frequently nest in stands 10 ha or smaller (Chapter 2). Given that I observed nests in isolated patches of young conifers well below 1 ha in size, birds appear to respond to habitat features at a fine spatial scale, and structure of patches at the sub-stand level may be of even greater importance. However, because squirrels tend to avoid open and early successional habitats, regenerating cuts of larger size may create more "squirrel-free space" than isolated small cuts. Given that squirrels tend to avoid open and early successional habitats, a larger cut may provide a predator "buffer" for nests located within it. The appropriate stand harvest size should be empirically tested.

Evidence is accumulating that the ecological trap scenario is not frequent or widespread at the southeastern edge of the Rusty Blackbird breeding range. Rather, predation risk appears to be largely mediated through factors unrelated to the harvest history of a site (e.g., cyclical fluctuations in predator populations). Further, although Rusty Blackbirds may suffer from high rates of nest predation in years with an abundance of red squirrels, their overall nest survival in

the region is not chronically low, even in regenerating clearcuts (Powell et al. 2010a, S. Buckley, unpubl. data, Newell et al., in prep). Taken together, the conclusion emerging from all of the studies of breeding Rusty Blackbirds is that low productivity is not preventing recovery of this long-declining species (Greenberg and Matsuoka 2010, Matsuoka et al. 2010, Powell et al. 2010, Newell et al., in prep, S. Buckley, unpubl. data). With further range-wide declines, however, even small impediments to productivity could become limiting at local scales.

Conclusion

My results support the conclusion that the species' nest success does not appear to be chronically low, and as such is likely not the driving force behind their decline (Matsuoka et al. 2010a). While Rusty Blackbirds do suffer from high levels of nest predation in certain years, overall they have an average nest success rate between 45 and 65%, which is well within the typical range for open-cup nesting passerines (Nice 1957). Red squirrels were the principal but not sole predator of Rusty Blackbird nests. The inter-annual variation in Rusty Blackbird nest survival is likely cyclical, driven by variable cone production and mediated through the dynamic response of red squirrels to this pulsed resource. When nest predation is high, it seems to be more a result of natural increases in predator populations and less a result of anthropogenic habitat change caused by forest management.

Tables

Site	Total Number of Surveys	2011 Detections	2012 Detections	P ^a
MENests ^b	13	1	7	0.010**
MERESQ ^c	12	1	7	0.009**
NHNests ^d	24	1	4	0.160**

Table 3.1. Proportion of red squirrel surveys with positive detections in northern New England, 2011-2012.

^aP-values are from χ^2 tests comparing number of detections between years; ^b Survey at nest point in Maine; ^c Survey at mature forest point in Maine; ^d Survey at nest point in New Hampshire;

Table 3.2. The median of mean spruce and fir (combined) cones per plot (includes both n	iest
and control plots) in northern New England, 2011-2012.	

Site	2011 Number of plots	2012 Number of plots	2011 Cones	2012 Cones	P ^a
ME ^b	28	30	24.75	0.88	0.004**
NH ^c	48	38	20.63	0.50	<0.001***

^a Maine;

^bNew Hampshire;

^c P-values from Mann-Whitney U tests.

Model ^a	k ^b	AIC ^c		w _i ^e	$\mathbf{L}^{\mathbf{f}}$
Conifer20BA	2	374.24	0	0.734	1.000
Conifer10BA	2	376.31	2.06	0.262	0.357
Conifer30BA	2	384.78	10.54	0.004	0.005
Conifer40BA	2	397.65	23.41	0.000	0.000
TotalConiferBA	2	401.48	27.24	0.000	0.000
Null	1	403.69	29.45	0.000	0.000

Table 3.3. Model selection results for red squirrel detection in northern New England, 2011-2012 (n=290).

^a See C.11, Appendix C for variable descriptions
^b Number of parameters
^c Corrected Akaike's Information Criterion
^d Difference in AIC_c relative to top model
^e Model weight
^f Model likelihood based on AIC_c

Variable ^a	ß ^b	SE ^c	LCL ^d	UCL ^e	Scaled OR ^f	Scaled OR SE ^g	LCL ^h	UCL ⁱ	Unit ^j	$\mathbf{R}^{\mathbf{k}}$
Conifer20BA	0.113	0.025	0.065	0.162	1.759	0.022	1.328	2.191	5	0.734
Conifer10BA	0.062	0.013	0.036	0.088	1.363	0.089	1.190	1.537	5	0.262
Conifer30BA	0.256	0.070	0.119	0.394	3.597	1.259	1.129	6.064	5	0.004
Conifer40BA	0.385	0.156	0.080	0.691	6.855	2.742	1.481	12.230	5	0.000
TotalConiferBA	0.011	0.006	0.000	0.023	1.057	0.032	0.994	1.119	5	0.000

Table 3.4. Parameter estimates and odds ratios for habitat variables used to model red squirrel detections in northern New England, 2011-2012.

^a See C.11, Appendix C for variable descriptions ^b Coefficient estimate ^c Standard error of coefficient

^d Lower 95% confidence limit for coefficient

^e Upper 95% confidence limit for coefficient ^f Scaled odds ratio

^g Standard error for scaled OR

^h Lower 95% confidence limit for scaled OR

ⁱ Upper 95% confidence limit for scaled OR ^j Unit change for scaled OR ^k Relative importance value

Nest Group	N^{a}	DSR	SE ^b	95% CI ^c	Nest Success (%) ^d	SE ^e	95% CI ^f
All	65	0.974	0.006	0.960-0.983	46.6	0.084	30.1-63.1
ME ^g	25	0.962	0.011	0.933-0.979	32.5	0.110	10.9-54.1
NH^{h}	40	0.980	0.006	0.964-0.989	55.6	0.100	36.0-75.2
2011	29	0.982	0.006	0.966-0.991	59.4	0.105	38.8-80.0
2012	36	0.959	0.012	0.929-0.977	29.8	0.167	-2.9-62.5
Harvest	57	0.974	0.006	0.956-0.982	43.9	0.084	27.4-60.4
No Harvest	8	0.971	0.011	0.937-0.996	62.6	0.141	35.0-90.2

Table 3.5. Daily survival rate (DSR) and nest success estimates for Rusty Blackbirds in northern New England, 2011-2012.

^a Number of nests

^b Standard error for DSR estimate

^c 95% confidence interval for DSR estimate ^d Survival across entire nesting period (29 exposure days) ^e Standard error for nest success estimate

^f95% confidence interval for nest success estimate

^g Maine

^h New Hampshire

Model ^a	<i>k</i> ^b	AIC ^c		w _i ^e	$\mathbf{L}^{\mathbf{f}}$	D ^g
BATotal+Cut	3	135.22	0	0.226	1.000	129.19
BATotal	2	135.68	0.45	0.180	0.797	131.66
BATotal+Year	3	136.10	0.88	0.146	0.645	130.07
BATotal+Cut+BATotalxCut	4	137.19	1.97	0.085	0.374	129.14
BATotal+Site	3	137.46	2.24	0.074	0.327	131.43
BATotal+Year+BATotalxYear	4	137.88	2.66	0.060	0.265	129.83
BATotal+Site+BATotalxSite	4	139.35	4.12	0.029	0.127	131.30
Year+Date	3	139.71	4.48	0.024	0.106	133.68
Year	2	139.85	4.63	0.022	0.099	135.84
Year+Site	3	140.39	5.17	0.017	0.076	134.36
Year+Date+YearxDate	4	140.87	5.64	0.013	0.060	132.82
Cut+Year	3	141.10	5.87	0.012	0.053	135.07
Year+Date ² +YearxDate ²	5	141.22	5.99	0.011	0.050	131.14
Site	2	141.33	6.11	0.011	0.047	137.32
AlderTree	2	141.53	6.30	0.010	0.043	137.51
Null	1	141.54	6.32	0.010	0.043	139.54
Year+Date ²	4	141.73	6.50	0.009	0.039	133.67
Year+Age	3	141.85	6.63	0.008	0.036	135.82

Table 3.6. Model selection results for survival of Rusty Blackbird nests in northern New England, 2011-2012, including nest-patch scale and temporal/control variables (n=65).

Model ^a	<i>k</i> ^b	AIC ^c		w _i ^e	$\mathbf{L}^{\mathbf{f}}$	$\mathbf{D}^{\mathbf{g}}$
Year+Age ²	4	142.25	7.02	0.007	0.030	134.19
Year+Site+YearxSite	4	142.41	7.18	0.006	0.028	134.36
Date	2	142.87	7.64	0.005	0.022	138.85
Cut	2	142.92	7.70	0.005	0.021	138.91
NestHt	2	142.94	7.72	0.005	0.021	138.93
Cut+Year+CutxYear	4	142.97	7.74	0.005	0.021	134.92
Year+Age+YearxAge	4	143.14	7.92	0.004	0.019	135.09
NestConc	2	143.44	8.22	0.004	0.016	139.43
Age	2	143.45	8.23	0.004	0.016	139.43
Year+Age ² +YearxAge ²	5	143.96	8.73	0.003	0.013	133.88
Age ²	3	144.30	9.08	0.002	0.011	138.27
Date ²	3	144.70	9.48	0.002	0.009	138.67
BATotal+Cut+NestHt+AlderTree +NestConc+Year+Site+Age+Date	10	145.48	10.25	0.001	0.006	125.18

Table 3.6, continued:

^a See C.5 and C.7, Appendix C for variable descriptions ^bNumber of parameters ^c Corrected Akaike's Information Criterion ^d Difference in AIC_c relative to top model ^e Model weight ^f Model likelihood based on AIC_c

^g Model deviance

			95% Confidence Limits		
Parameter ^a	Estimate ^b	SE ^c	Lower ^d	Upper ^e	$\mathbf{R}^{\mathbf{f}}$
BATotal	0.004	0.003	-0.001	0.010	0.800
Cut	-0.324	0.375	-1.058	0.410	0.332
AlderTree	0.001	0.001	-0.001	0.002	0.010
NestHt	0.001	0.002	-0.003	0.006	0.005
NestConc	1.6x10 ⁻⁵	5.1x10 ⁻⁵	-8.3x10 ⁻⁵	1.2×10^{-4}	0.004
Year	0.182	0.225	-0.258	0.623	0.348
Site	-0.036	0.085	-0.202	0.130	0.137
Age	0.016	0.019	-0.021	0.052	0.016
Date	0.053	0.058	-0.061	0.167	0.042
Age ²	0.010	0.012	-0.013	0.033	0.012
Date ²	0.035	0.038	-0.039	0.110	0.022
BATotalxCut	1.7x10 ⁻⁴	9.4x10 ⁻⁴	-0.002	0.002	0.085
BATotalxYear	1.2x10 ⁻⁴	2.7x10 ⁻⁴	6.4x10 ⁻⁴	4.00x10 ⁻⁴	0.060
BATotalxSite	-5.8x10 ⁻⁵	1.3x10 ⁻⁴	3.1x10 ⁻⁴	$1.9 \mathrm{x} 10^4$	0.029
YearxSite	-3.3x10 ⁻⁴	0.005	-0.012	0.010	0.006
YearxDate	-0.001	7.3x10 ⁻⁴	-0.002	0.001	0.013

Table 3.7. Parameter estimates, standard errors (SE) and 95% confidence limits for nestpatch scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

Table 3.7, continued:

			95% Confid		
Parameter ^a	Estimate ^b	SE ^c	Lower ^d	Upper ^e	$\mathbf{R}^{\mathbf{f}}$
YearxAge	-2.4×10^{-4}	3.7x10 ⁻⁴	-0.001	4.8x10 ⁻⁴	0.004
YearxDate ²	-2.2×10^{-5}	2.4x10 ⁻⁵	-7.0x10 ⁻⁵	2.6x10 ⁻⁵	0.011
YearxAge ²	-3.0×10^{-6}	6.7x10 ⁻⁶	-1.6x10 ⁻⁵	1.0×10^{-5}	0.003

^a See C.5 and C.7, Appendix C for variable descriptions ^b Model-averaged β estimate ^c Standard error for model-averaged β estimate ^d Lower 95% limit for model-averaged β estimate ^e Upper 95% limit for model-averaged β estimate ^f Relative importance value

Model ^a	k ^b	AIC ^c	ΔAIC_{c}^{d}	w _i ^e	L^{f}	D ^g
Null	1	141.54	0.00	0.308	1.000	139.54
90BA40	2	142.69	1.15	0.173	0.563	138.67
90BATot	2	143.06	1.52	0.144	0.467	139.05
90BA30	2	143.15	1.61	0.138	0.448	139.13
90BA10	2	143.38	1.84	0.123	0.398	139.37
90BA20	2	143.52	1.98	0.115	0.372	139.50

Table 3.8. Model selection results for survival of Rusty Blackbird nests in northern New England, 2011-2012, including squirrel territory scale variables (n=65).

^a See C.8, Appendix C for variable descriptions ^b Number of parameters

^c Corrected Akaike's Information Criterion ^d Difference in AIC_c relative to top model

^e Model weight

^fModel likelihood based on AIC_c

^g Model deviance

Model ^a	<i>k</i> ^b	AIC _c ^c		w _i ^e	$\mathbf{L}^{\mathbf{f}}$	D ^g
Null	1	73.00	0.00	0.294	1.000	70.98
AvgCalls	2	74.51	1.52	0.138	0.468	70.47
AvgInd	2	74.65	1.65	0.129	0.438	70.60
NestCalls	2	74.84	1.84	0.117	0.398	70.80
AvgPres	2	74.99	2.00	0.108	0.369	70.95
NestInd	2	75.02	2.03	0.107	0.363	70.98
NestPres	2	75.03	2.03	0.107	0.363	70.98

Table 3.9. Model selection results for survival of Rusty Blackbird nests in northern New England in 2012, including red squirrel detection covariates (n=29).

^a See C.9, Appendix C for variable descriptions ^b Number of parameters

^c Corrected Akaike's Information Criterion ^d Difference in AIC_c relative to top model

^e Model weight

^fModel likelihood based on AIC_c

^g Model deviance

Model ^a	k ^b	AIC ^c	ΔAIC ^d	w_i^{e}	$\mathbf{L}^{\mathbf{f}}$	D ^g
RdDist+Year+RdDistxYear	4	103.27	0.00	0.845	1.000	95.20
WetDist+Year+WetDistxYear	4	110.13	6.86	0.027	0.032	102.06
Year	2	111.56	8.29	0.013	0.016	107.54
TotWet+Year	3	112.12	8.85	0.010	0.012	106.08
WetDist+Year	3	112.34	9.07	0.009	0.011	106.30
TotWet	2	113.01	9.74	0.006	0.008	108.99
YoungSoft+Year	3	113.05	9.78	0.006	0.008	107.01
MatSoft+Year	3	113.18	9.92	0.006	0.007	107.14
Site	2	113.19	9.92	0.006	0.007	109.17
RdDist+Year	3	113.33	10.07	0.006	0.007	107.29
TotWet+Year+TotWetxYear	4	113.36	10.09	0.005	0.006	105.29
Null	1	113.40	10.14	0.005	0.006	111.40
YoungSoft+Site+YoungSoftxSite	4	113.70	10.43	0.005	0.005	105.63
WetDist	2	113.77	10.50	0.004	0.005	109.74
YoungSoft	2	114.05	10.78	0.004	0.005	110.03
TotWet+Site	3	114.11	10.84	0.004	0.004	108.07
WetDist+Site+WetDistxSite	4	114.18	10.91	0.004	0.004	106.11
WetDist+Site	3	114.41	11.14	0.003	0.004	108.37

Table 3.10. Model selection results for survival of Rusty Blackbird nests in northern New England, 2011-2012, including home-range scale habitat and temporal/control variables (n=50).

Table	3.10,	continued:
-------	-------	------------

Model ^a	<i>k</i> ^b	AIC ^c	Δ AIC ^d	w _i ^e	$\mathbf{L}^{\mathbf{f}}$	$\mathbf{D}^{\mathbf{g}}$
Date+MatSoft+DatexMatSoft+Year	5	114.51	11.24	0.003	0.004	104.40
YoungSoft+Year+YoungSoftxYear	4	114.71	11.45	0.003	0.003	106.65
MatSoft+Year+MatSoftxYear	4	114.74	11.48	0.003	0.003	106.68
YoungSoft+Site	3	115.08	11.81	0.002	0.003	109.04
RdDist+Site	3	115.12	11.85	0.002	0.003	109.08
MatSoft+Site	3	115.12	11.86	0.002	0.003	109.08
Date	2	115.24	11.97	0.002	0.003	111.22
RdDist	2	115.30	12.04	0.002	0.002	111.28
MatSoft	2	115.37	12.10	0.002	0.002	111.35
RdDist+Site+RdDistxSite	4	115.43	12.17	0.002	0.002	107.37
MatSoft+Site+MatSoftxSite	4	115.50	12.23	0.002	0.002	107.43
TotWet+Site+TotWetxSite	4	116.01	12.74	0.001	0.002	107.94
Date ² +MatSoft+Date ² xMatSoft+Year	6	116.21	12.94	0.001	0.002	104.07
Date ²	3	116.77	13.51	0.001	0.001	110.73
Date+MatSoft	3	117.18	13.91	0.001	0.001	111.14
Date+MatSoft+DatexMatSoft	4	117.79	14.52	0.001	0.001	109.72
Date ² +MatSoft	4	118.63	15.36	0.000	0.001	110.56
Date ² +MatSoft+Date ² xMatSoft	5	119.03	15.77	0.000	0.000	108.93

^a C.5, C.10, Appendix C for variable descriptions ^b Number of parameters ^c Corrected Akaike's Information Criterion

^d Difference in AIC_c relative to top model ^e Model weight ^f Model likelihood ^g Model deviance

			95% Co			
Parameter ^a	Estimate ^b	SE ^c	Lin	R ^f		
			Lower ^d Upper ^e			
RdDistxYear	0.026	0.013	0.002	0.051	0.845	
RdDist	-0.004	0.545	-1.073	1.064	0.857	
WetDist	2.7×10^{-5}	1.5x10 ⁻⁴	-2.6×10^{-4}	3.2x10 ⁻⁴	0.047	
TotWet	-0.001	0.001	-0.002	0.001	0.027	
YoungSoft	1.6x10 ⁻⁴	0.001	-0.001	0.001	0.020	
MatSoft	-0.012	3.8x10 ⁻⁵	-0.002	0.002	0.023	
Year	-1.189	0.983	-3.116	0.737	0.938	
Site	-0.013	0.033	-0.078	0.023	0.033	
Date	1.3x10 ⁻⁴	4.8x10 ⁻⁴	-0.001	0.001	0.009	
Date ²	-2.0x10 ⁻⁶	3.1x10 ⁻⁶	-8.0x10 ⁻⁶	4.0x10 ⁻⁶	0.002	
MatSoftxYear	-7.3x10 ⁻⁵	1.3x10 ⁻⁴	-3.3x10 ⁻⁴	1.8x10 ⁻⁴	0.003	
YoungSoftxYear	-3.6x10 ⁻⁵	6.8x10 ⁻⁵	-1.7x10 ⁻⁴	9.8x10 ⁻⁵	0.003	
WetDistxYear	0.001	0.001	-0.001	0.003	0.027	
TotalWetxYear	1.8x10 ⁻⁴	2.8x10 ⁻⁴	-3.7x10 ⁻⁴	7.4x10 ⁻⁴	0.005	
MatSoftxSite	1.3x10 ⁻⁴	1.6x10 ⁻⁴	-1.9x10 ⁻⁴	4.5x10 ⁻⁴	0.002	
YoungSoftxSite	-3.4×10^{-4}	3.9x10 ⁻⁴	-0.001	4.3x10 ⁻⁴	0.005	

Table 3.11. Parameter estimates, standard errors (SE) and 95% confidence limits for home-range scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

		95% Confidence					
Parameter ^a	Estimate ^b	SE ^c	Lin	$\mathbf{R}^{\mathbf{f}}$			
			Lower ^d	Upper ^e			
WetDistxSite	-3.6×10^{-5}	4.4x10 ⁻⁵	-1.2x10 ⁻⁴	5.0x10 ⁻⁵	0.004		
TotalWetxSite	-2.2×10^{-5}	6.3x10 ⁻⁵	-1.4x10 ⁻⁴	1.0x10 ⁻⁴	0.001		
MatSoftxDate	-1.2×10^{-5}	1.4x10 ⁻⁵	-3.1x10 ⁻⁵	1.6x10 ⁻⁵	0.004		
MatSoftxDate ²	-5.6x10 ⁻⁸	-7.1x10 ⁻⁸	-1.9x10 ⁻⁷	8.2x10 ⁻⁸	0.001		

^a See C.5 and C.10, Appendix C for variable descriptions ^b Model-averaged β estimate ^c Standard error for model-averaged β estimate ^d Lower 95% limit for model-averaged β estimate ^e Upper 95% limit for model-averaged β estimate ^f Relative importance value

Chapter 4:

Using Motion-Triggered Trail Cameras to Monitor Rusty Blackbird Nests: Experiences with a Forest-Dwelling, Neophobic Species

Introduction

The use of remote surveillance cameras to monitor nests and identify nest predators has become an increasingly common method in avian field biology (reviewed in Richardson et al. 2009). Passive infrared (PIR) trail cameras, which trigger in response to movement and temperature change in the detection zone, are but one of the various options available. These cameras comprise the majority of the remote camera market, (Swann et al. 2004, Brown and Gehrt 2009) and are discussed in both the wildlife and ornithological literature (Swann et al. 2004, McKinnon and Bety 2009, Liebezeit and Zack 2010, Valdez-Juarez and Lodoño 2011). Although previous studies have used PIR trail cameras to effectively monitor bird nests, most of these have focused on ground-nesting species in relatively open habitats such as beaches and grasslands (McKinnon and Bety 2009, Valdez-Juarez and Lodoño 2011). Consequently, there is little information available on how these cameras perform in forested or densely vegetated environments, which is the primary nesting habitat for many species including my focal species – the Rusty Blackbird.

Rusty Blackbirds also are thought to be a neophobic species (Mettke-Hoffman et al. 2013), and therefore highly sensitive to novel objects in their environment. While the effects of cameras on nest success generally appear to be minimal (Richardson et al. 2009, McKinnon and Bety 2009), there is always the risk that their presence could cause the birds to abandon the nest. Understanding how neophobic species react to cameras could have implications for monitoring nest success in these species.

Given the unique circumstances in which I was using these cameras, my experiences and observations may be of interest to other researchers working in similar conditions. My objectives were to deploy PIR motion-triggered cameras to monitor Rusty Blackbird nests as a test of their performance in a novel habitat setting and also to explore the feasibility of cameramonitoring a neophobic species.

Methods

I worked in two study areas in northern New England: one in north-central Maine around Moosehead Lake and the other north of the White Mountains in New Hampshire, near the town of Errol. Both sites had a similar range of elevation (roughly 300 – 1,000 m), but the topographic relief was greater in New Hampshire. Much of the Maine study area was covered by wet "spruce-fir flats," while the New Hampshire study site was dominated by typical mixed Acadian forests of maple (*Acer* spp, American beech (*Fagus grandifolia*) and red spruce (*Picea rubens*). Industrial timber companies own and manage the majority of the land in both study areas, with some parcels held by conservation organizations (see Chapter 2 for more detailed description of study sites).

I installed PIR motion-triggered cameras within 3 m of Rusty Blackbird nests as habitat conditions permitted. Over two field seasons I used three different models: Reconyx Hyperfire HC600 (Reconyx Inc., Holmen, WI; n=4), Bushnell Trophy Cam (Bushnell Outdoor Products, Overland Park, KS; n=17) and Uway NightTrakker NT50B (Uway Outdoors Canada, Lethbridge, AB, Canada; n=2). To minimize disturbance, I only used "covert" models that did not produce a flash or emit light from the infrared LEDs. When possible, I mounted cameras on surrounding natural vegetation (usually sapling or pole-stage conifers), approximately level with the nest (1-4 m) (Fig. 4.1.A.). When there were no suitable trees for attachment in the vicinity of

the nest or when the nest was too high, I mounted the camera on a "pole" created on site from a young, live conifer or a snag (Fig. 4.1.B-D). I approximated the height of the nest using ocular estimation, and then attached the camera to the pole at the appropriate height. I did this at a location away from the nest to minimize time spent near the nest. Once the camera was mounted on the pole, I then walked into the nest area and "planted" the entire pole-mounted camera in the appropriate location and secured it to surrounding vegetation with twine.

As another precaution against disturbance, I often waited until both adults were away from the nest to install the camera (whether on pole or natural tree). I then attempted to complete the entire set-up process. During incubation, however, the female often stayed on the nest for extended periods of time. For the sake of time-efficiency, I sometimes approached the nest to install the camera while the female was still there. In 2012, however, after a nest was abandoned following the disturbance of camera installation, I avoided any camera activity at the nest while the adults were present.

I set cameras at the maximum sensitivity level and programmed them to take the maximum number of photos per triggering event (three or five exposures depending on the model). I generally used 4 GB memory cards, but in 2012 I used 8 GB cards for four installations where subsequent checks were problematic (e.g., reaching the nest was strenuous, hyper-vigilant adults, etc.). I attempted to avoid installing cameras until egg-laying was completed, as the disturbance of installation could result in abandonment at earlier stages in the nesting cycle (reviewed in Richardson et al. 2009). I checked cameras and nests every three to five days. At each visit, I checked and adjusted camera position and batteries as necessary, and replaced exposed memory cards with empty memory cards. I also observed the nest directly using either binoculars or a mirror pole to assess the nesting stage and number of eggs or young.

Unfortunately, I was unable to use cameras in New Hampshire in 2011. Further, camera installation at nests in New Hampshire was avoided during incubation to prevent interference with other concurrent studies.

Results

General Results and Camera Performance

I monitored a total of 29 nests with cameras – 21 in Maine (10 in 2011; 11 in 2012) and 8 in New Hampshire in 2012. I used Reconyx cameras to monitor six nests in 2011, Uway cameras to monitor five nests in 2011, and a Bushnell camera to monitor one nest in 2011. I used only Bushnell cameras to monitor all nests 19 nests in 2012. In 2011, I deployed a replacement camera at two nests when a camera malfunctioned, so total cameras used in 2011 exceeds number of nests.

I documented a total of eight predation events on camera, and was able to definitively identify the predator for seven of these. I identified four different predators (Fig. 4.2): red squirrel (*Tamiasciurus hudsonicus*), Accipiter (either Sharp-shinned Hawk (*Accipiter striatus*) or Cooper's hawk (*A. cooperii*)), white-tailed deer (*Odocoileus virginianus*) and Blue Jay (*Cyanocitta cristata*). I also documented an Accipiter spp. at a nest after it had been depredated by a previous (unknown) predator. I missed three entire predation events and one partial predation (four eggs and/or nestlings removed) due to failure of the camera to trigger. I obtained thousands of photos of incubation and provisioning behavior (Fig. 4.3). Some photos were even clear enough to distinguish specific types of prey (e.g., flying insect, wingless larvae, etc) (Fig. 4.4). Including all cameras combined, I obtained a total of 34,446 photos.

I found that cameras worked best when placed within approximately two meters of the nest. At further distances, cameras often did not detect movements from such small targets as

songbirds, and surrounding vegetation often obscured the view of the nest. Camera performance even within the same model also was quite variable, with some units taking no photos at all while others took thousands per day. Battery failure was never a problem using Lithium batteries, and memory cards were rarely filled between checks (3-5 days). Four GB cards were usually more than adequate to store all of the photos between nest checks. Where set-ups led to taking over 1,000 pictures per day, I replaced 4 GB cards with 8 GB cards to ensure no images would be lost. Some brands of memory cards were more reliable and/or compatible with the cameras I used. Lexar and SanDisk were the most reliable, whereas cards manufactured by PNY were less compatible.

While I received some quality photos from cameras with the "pole" set-up, this arrangement also was much more prone to problems than when cameras were attached to existing trees in the nest vicinity. First, firmly securing the pole was often difficult. Pole-mounted cameras were not as stable as a rooted tree, and were prone to being knocked over either by strong winds or animals (moose) (*Alces alces*) passing by. Because nests were often in areas with soft, saturated soils, it was even more difficult to securely anchor and stabilize poles. Second, it took longer to install pole-mounted cameras than cameras on natural trees. Because I had to remain in the nest vicinity longer, I encountered the adults more frequently. Furthermore, often poles were necessary when the nest was relatively high (≥ 2 m), and I often needed a ladder to reach the camera, which significantly increased disturbance at the nest site.

Rusty Blackbird Response to Cameras

There was a wide range in the response of the birds to the cameras. In several cases, I was able to install the camera or change SD cards without the female flushing from the nest, despite my being only a meter or two away. In 2011, none of the birds abandoned their nests in

response to the cameras. Even when they returned from foraging and I was still near the nest installing/checking the camera, they were upset initially but then calmed down once I left the immediate nest area. I rarely observed the birds responding negatively to the camera, and in those few instances when they did, they were not prolonged. Based on the 2011 results alone, I observed little evidence of neophobia.

In 2012, however, responses were different. Two nests were abandoned immediately following camera installation. While one of these incidents may have resulted from my prolonged presence around the nest during installation, the other appeared to be in response to the camera, as I was already concealed away from the nest area and observed the birds return and react to the camera. For over 20 minutes, the pair gave repeated distress calls and occasionally flew at the camera. At a third nest, I tried installing a camera on several different occasions and in various locations, but removed it each time after I observed the female appeared uneasy and would not sit in the nest on her return from foraging with the camera present. As soon as I removed the camera, she immediately went to the nest. While there were certainly instances where the birds seemed unconcerned by the camera, on average the birds appeared to be much more sensitive to the cameras in 2012 than in 2011.

Discussion

Rusty Blackbird Response to Cameras

With such a small sample, it is difficult to know whether the variability in the responses of Rusty Blackbirds to the cameras is attributable to individual variation, different installation circumstances, different predation pressures, or the most likely scenario - some combination of all of these. However, given the marked increase in red squirrels from 2011 to 2012 (Chapter 3), it seems likely that their sensitivity in 2012 was at least in part due to perceived increased predation risk. Flexibility in the breeding behavior of birds in response to changing predation risk is a widespread and well-studied phenomenon (see reviews in Lima 2009 and Martin and Briskie 2009). Nesting behavior can change as a result of prior predation experience as well. Chalfoun and Martin (2010) found that Brewer's Sparrows (*Spizella breweri*) reduced their clutch size and increased incubation times (reducing activity at the nest) after their previous nest was depredated.

There is also inherent variation in how individual birds respond to the same stressors (Cockrem and Silverin 2002, Cockrem 2007). Although some camera installations were more prolonged than others, these were not necessarily correlated with a more aggressive reaction or abandonment. Indeed, one pair abandoned their nest following what was one of the fastest and seemingly least intrusive installations. Thus, it seems probable that their reactions were at least in part a result of differences between individuals or past experiences and were not dependent on the nature of the stressor alone.

A final and often unknown factor that could have been have been influencing individual behaviors was the stage in the nesting cycle. Because of the variability in clutch sizes and the fact that I did not candle any eggs, I was not always sure of the age of nests. Females more readily abandon nests during laying and earlier stages of incubation, and adults tend to become increasingly aggressive in their defense of nests as eggs near hatching and as nestlings approach fledging (reviewed in Caro 2005).

Comparison of Camera Models

Given that all of the cameras were in different settings in terms of surrounding vegetation, exact angle and distance from the nest, etc., it is difficult to know how much of the observed variation between models is attributable to the cameras themselves versus the
environmental circumstances in which they were placed. Overall, I found the Uway models were generally less reliable than the Reconyx or Bushnell models. On two different occasions the Uway cameras began taking hundreds of photos per day, but then suddenly stopped. For one nest the camera took no photos at all. As a consequence, I missed one partial and one complete predation. Uway cameras also used compact flash (CF) rather than secure digital (SD) type memory cards.

Bushnell and Reconyx models were generally comparable in their performance, but the Bushnells were about half the price of the Reconyx and were easier to mount on small trees. Reconyx cameras, however, were far superior in the quality of the night photos. Thus, in situations where nocturnally active nest predators are prevalent, Reconyx models may be the best option. Where diurnal predators such as red squirrels or raptors are suspected, Bushnell cameras would be more cost effective.

General Thoughts on the Use of Motion-Triggered Cameras for Nest Monitoring

There were several challenges associated with using motion-triggered cameras in Rusty Blackbird nesting habitat. First, as I alluded to in the previous section, the size and shape of most trail cameras (especially Reconyx) is not well-suited to the small trees that tend to prevail around Rusty Blackbird nests. The width of the camera was almost always greater than the trunk of the tree on which it was mounted. This often required adding additional material (either Styrofoam padding or sticks) between the camera and the tree trunk to stabilize the position of the camera. Where there were two or more small trunks in close proximity, I sometimes achieved this same result by strapping the camera to multiple stems simultaneously. I suspect that for shrub-nesting species, similar problems would arise. Second, given that most nests were placed in dense vegetation and that I did not want to compromise nest concealment, it was often difficult (and sometimes impossible) to find a location for the camera with a suitably clear view of the nest. The few nests I found surrounded by open water presented yet another challenge. While concealment of the nest by vegetation was less of a problem in these situations, the general lack of trees for attachment and the fact that a pole set-up would be highly unstable sometimes precluded monitoring these nests with cameras. In addition to the logistics of installing a camera pole in these environments, the conspicuousness of such a set-up both to potential predators and to the birds themselves was a major concern. Thus, there was frequently only one feasible (and often far from ideal) option for camera placement at any given nest.

Even when there was a reasonably clear view of the nest, it was unavoidable to have at least some leaves or branches in the detection zone between the camera and the nest. This was problematic, as with each slight breeze the vegetation would move and thus cause the camera to trigger constantly. When the camera is constantly triggered, the batteries are more easily drained and the memory card fills more quickly, potentially resulting in the loss of valuable data if there are long intervals between camera checks.

While these cameras can yield qualitative data on prey type (Fig 4.4), I would not use them when the objective is to get quantitative data on the duration or rates of certain behaviors. The trigger mechanism is too variable to assume that all activity at the nest is reliably recorded. Even for distinct events like predation, there is always a risk that critical activity will be missed. There are many external factors that can influence whether or not the camera is triggered. While I tried to position the camera such that the nest was in the center of the motion-detection zone, this was not always possible. Temperature also can exert a strong influence on camera

96

performance. Cameras are often less sensitive in warmer ambient temperatures, as the thermal gradient between the target and the surrounding environment is reduced (Swann et al. 2002). The target's angle of approach also can affect triggering, as cameras are often better at picking up movement from certain directions than others (Swann et al. 2002),

Despite the variability in triggering, there are several benefits to using motion-triggered cameras for nest monitoring. First, trail cameras are easy to use and program, which minimizes time spent at the nest. Second, they are relatively inexpensive, ranging in price from about \$200 (Bushnell TrophyCam) to \$550 (Reconyx Hyperfire).

They are also relatively portable. Consisting of a box approximately 15x10x7 cm in size that contains all the necessary battery power, they are easily transported long distances by foot and across rough terrain (e.g., beaver dams). In such conditions, they have a significant advantage over systems that require large, heavy D-cell batteries or external wet cell power sources.

These cameras are designed to last up to several months in the field, and thus a nesting cycle of less than a month is easily managed without having to ever change the batteries. This is beneficial because changing the batteries takes longer than does simply replacing the memory card, which requires spending more time at the nest and increases the chances of a stressful encounter with the adults. In addition, the long battery life makes these cameras especially useful in situations where nests are remote or widely dispersed, and thus cannot be checked more than once or twice per week.

Conclusion

Use of motion-triggered trail cameras to monitor nests can yield valuable data on both nest predator identities as well as general nesting ecology. However, triggering can be variable

97

depending on set-up and environmental conditions. There are some unique challenges when employing these cameras in forested or wetland habitats. Nest concealment and difficulty in attachment present the greatest limitations to effective deployment in these conditions. Longbattery life and relatively quick set-up process, however, make these cameras especially useful in remote settings or for sensitive species where disturbance is a concern. Finally, at least for some species, it seems that sensitivity to cameras can vary widely across individuals and across years, which may require researchers to take a careful and adaptive approach to camera-monitoring of nests.

Figures



Figure 4.1. A: Camera mounted on "natural" tree; B - D: Various "pole" set-ups (camera not visible in B., but behind nest tree, mounted on pole leaning against existing diagonal snag).



Figure 4.2. A. Blue Jay depredating nest; B. Deer depredating nest; C. Red squirrel depredating nest; D. Accipiter depredating nest.



Figure 4.3. *A*. Adult feeding nestlings; *B*. Male feeding incubating female; *C*. Begging nestlings; *D*. Both adults tending and feeding nestlings.



Figure 4.4. Adult feeding winged insect (A.), unknown larvae (B.), unknown worm (C.), and various invertebrates (D.) to nestlings.

Conclusion

My examination of habitat attributes at multiple spatial scales and employment of cameras at Rusty Blackbird nests yielded valuable insight into the biological processes of nest habitat selection and nest predation in this declining species. Like other species with high mobility and large home ranges, habitat features required by breeding Rusty Blackbirds for different purposes (e.g., nesting and foraging) are not necessarily in close spatial proximity. Thus, selection of those habitats may be decoupled from one another, with foraging requirements (wetlands) being of primary importance at larger scales and microhabitat characteristics associated with reduced predation risk driving selection at the nest-patch scale.

Although spatial patterns in nest predation certainly occur as a result of predator autecology, the most salient pattern I observed in predation of Rusty Blackbirds nests was temporal in nature. Nest predation was high in 2012, when the red squirrel population was abundant, but not in 2011, when squirrel numbers were low. Nest cameras in 2011 did not capture any predations by red squirrels, but in 2012 camera data showed squirrels were the most frequent predator of Rusty Blackbird nests.

Thus, despite difficulties in deploying PIR cameras to monitor nests of a neophobic species that nests in densely vegetated habitats, the resulting photos provided important predator identification, which thereby enabled the clarification of mechanisms underlying nest predation dynamics. Nest predation rates were driven by annual fluctuations in squirrel populations, which in turn were driven by fluctuations in conifer mast production, revealing a linkage between nest predation and temporal processes in the environment. Habitat characteristics such as harvest history of a nest site were less influential on nest predation risk.

103

By explicitly investigating harvest histories of stands using both remote sensing and onthe-ground observation, my study revealed nuanced and complex relationships between Rusty Blackbirds, timber harvesting, and other forms of disturbance in New England. Forest management, although it is the dominant source of disturbance in present-day Acadian forests, does not operate in a vacuum. Natural disturbance agents such as beaver, insect outbreaks and windthrow, in addition to variable soils and hydrological conditions, continue to shape and modify forests as they have for millennia. As is often the case when studying real, ecological systems, simple, reductionist explanations of phenomena remain elusive. What emerges instead is a complexity that is daunting yet fascinating, beckoning those with a curious mind and a desire to conserve a species to go ever further, ever deeper in their search for understanding.

Literature Cited

- ADDICOTT, J. F., J. M. AHO, M. F. ANTOLIN, D. K. PADILLA, J. S. RICHARDSON, AND D. A. SALUK. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49:340-346.
- ALLEN, T. F. H., AND T. B. STARR. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, IL.
- ANDRÉN, H., P. ANGELSTAM, E. LINDSTRÖM, AND P. WIDÉN. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos 45:273-277.
- ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73:794-804.
- ASKINS, R. A. 1994. Open corridors in a heavily forested landscape: impact on shrubland and forest-interior birds. Wildlife Society Bulletin 22:339-347.
- AVERY, M. L. 1995. Rusty Blackbird (*Euphagus carolinus*). In: The birds of North America (F. B. Gill and A. Poole, eds.), no. 200. Academy of Natural Sciences, Philadelphia, PA.
- BAKKER, V. J., AND D. H. VAN VUREN. 2004. Gap-crossing decisions by the red squirrel, a forestdependent small mammal. Conservation Biology 18:689-697.
- BALL, J. R., E. M. BAYNE, AND C. S. MACHTANS. 2009. Video identification of boreal forest songbird nest predators and discordance with artificial nest studies. In: Tundra to Tropics: Connecting birds, habitats and people (T. Rich, C. Arizmendi, C. Thompson and D. Demarest, eds.), pp. 37-44. Proceedings of the 4th International Partners in Flight Conferences, McAllen, TX, 13-16 February 2008.
- BALL, J. R., AND E. M. BAYNE. 2012. Using video monitoring to assess the accuracy of nest fate and nest productivity estimates by field observation. Auk 129:438-488.
- BARBER, D.R., T. E. MARTIN, M. A. MELCHIORS, R. E. THILL, AND T. B. WIGLEY. 2001. Nesting success of birds in different silvicultural treatments in southeastern U.S. Pine Forests. Conservation Biology 15:196-207.
- BATTIN, J., AND J. T. LAWLER. 2006. Cross-scale correlations and the design and analysis of avian habitat selection studies. Condor 108:59-70.
- BAYNE, E. M., AND K. A. HOBSON. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conservation Biology 11:1418-1429.
- BAYNE, E. M., K. A. HOBSON, AND P. FARGEY. 1997. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. Ecography 20:233-239.

- BAYNE, E. M., AND K. A. HOBSON. 2002. Effects of red squirrel removal on survival of artificial songbird nests in boreal forest fragments. American Midland Naturalist 147:72-79.
- BEDNARZ, J. C., D. KLEM JR., L. J. GOODRICH, AND S. E. SENNER. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934-1986. Auk 107:96-109.
- BERGERON, Y., B. HARVEY, A. LEDUC, AND S. GAUTHIER. 1999. Basing forest management on natural disturbance: stand- and landscape-level considerations. Forestry Chronicles 75:49-54.
- BERGERON, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81:1500-1516.
- BERGERON, Y., S. GAUTHIER, M. FLANNIGAN, AND V. KAFKA. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916-1932.
- BIRDLIFE INTERNATIONAL 2012. Euphagus carolinus. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2 http://www.iucnredlist.org/apps/redlist/details/150425/0> (20 March 2013)
- BOOTH, G.D., M. J. NICCOLUCCI, AND E. G. SCHUSTER. 1994. Identifying proxy sites in multiple linear regression: An aid to better coefficient interpretation. Research Paper INT-470. U.S. Department of Agriculture, Forest Service, Ogden, UT.
- BOUCHARD, M., D. KNEESHAW, AND Y. BERGERON. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology 87:2319-2329.
- BOULET, M., M. DARVEAU, AND L. BELANGER. 2003. Nest predation and breeding activity of songbirds in riparian and nonriparian black spruce strips of central Quebec. Canadian Journal of Forest Research 33:922-930.
- BOUTIN, S., L. A. WAUTERS, A. G. MCADAM, M. M. HUMPHRIES, G. TOSI, AND A. A. DHONDT. 2006. Anticipatory reproduction and population growth in seed predators. Science 314:1928-1930.
- BOVES, T. J., D. A. BUEHLER, J. SHEEHAN, P. BOHALL WOOD, A. D. RODEWALD, J. L. LARKIN, P. D. KEYSER, F. L. NEWELL, A. EVANS, G. A. GEORGE, AND T. B. WIGLEY. 2013. Spatial variation in breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) throughout the Appalachian Mountains. Auk 130:46-59.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2nd edition. Springer-Verlag, New York.
- BROWN, J., AND S. D. GEHRT. 2009. The basics of using remote cameras to monitor wildlife. Fact Sheet: Agricultural and Natural Resources. The Ohio State University, Columbus, OH.

- CARO, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, IL.
- CAUGHLEY, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215-244.
- CHALFOUN, A. D., M. J. RATNASWAMY, AND F. R. THOMPSON III. 2002a. Nest predators in forestpasture edge and forest interior in a fragmented landscape. Ecological Applications 12:858-867.
- CHALFOUN, A. D., F. R. THOMPSON III, AND M. J. RATNASWAMY. 2002b. Nest predators and fragmentation: A review and meta-analysis. Conservation Biology 16:306-318.
- CHALFOUN, A. D., AND T. E. MARTIN. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-922.
- CHALFOUN, A. D., AND T. E. MARTIN. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. Journal of Animal Ecology 78:497-503.
- CHALFOUN, A. D., AND T. E. MARTIN. 2010. Parental investment decisions in response to ambient nest-predation risk versus actual predation on the prior nest. Condor 112:701-710.
- CHALFOUN, A. D., AND K. A. SCHMIDT. 2012. Adaptive breeding habitat selection: Is it for the birds? Auk 129:589-599.
- CHASKO, G. G., AND J. E. GATES. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. Wildlife Monographs 82:3-41.
- COCKREM, J. F., AND B. SILVERIN. 2002. Variation within and between birds in corticosterone responses of Great Tits (*Parus major*). General and Comparative Endocrinology 125:197-206.
- COCKREM, J. F. 2007. Stress, corticosterone responses and avian personalities. Journal of Ornithology 148(Supplement 2):S169-S178.
- CORCORAN, R. M., J. R. LOVVORN, AND P. J. HEGLUND. 2009. Long-term changes in limnology and invertebrates in Alaskan boreal wetlands. Hydrobiologia 620:77-89.
- COWARDIN, L. M., V. CARTER, F. C. GOLET, AND E. T. LAROE. 1979. Classification of the wetlands and deepwater habitats of the United States. U. S. Fish and Wildlife Service, Biological Services Program (FWS/OBS-79/31), Washington, D.C.

- DARVEAU, M., L. BÉLANGER, J. HUOT, E. MÉLANÇON, AND S. DEBELLEFEUILLE. 1997. Forestry practices and bird nest predation in a boreal coniferous forest. Ecological Applications 7:572-580.
- DESANTO, T. L., AND M. F. WILLSON. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. Journal of Field Ornithology 72:136-149.
- EDMONDS, S. T., D. C. EVERS, D. A. CRISTOL, C. METTKE-HOFMANN, L. L. POWELL, A. J. MCGANN, J. A. ARMIGER, O. P. LANE, D. F. TESSLER, P. NEWELL, K. HEYDEN, AND N. J. O'DRISCOLL. 2010. Geographic and seasonal variation in mercury exposure of the declining Rusty Blackbird. Condor 112:789-799.
- ELLISON, W. G. 1990. The status and habitat of the Rusty Blackbird in Caledonia and Essex counties. Vermont Fish and Wildlife Department, Woodstock, VT.
- ESRI. 2011. ArcGIS, version 10.0. Environmental Systems Research Institute, Redlands, CA.
- FISHER, J. T. 1999. The influence of landscape structure on the distribution of the red squirrel (*Tamiasciurus hudonsonicus*) in a heterogeneous boreal mosaic. M. Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada. 101 pp.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging outcome in field-forest edges. Ecology 59:871-883.
- GRAVES, H. S. 1899. Practical forestry in the Adirondacks. USDA Div. For. Bull. 26, Washington, D.C.
- GREENBERG, R., AND S. DROEGE. 1999. On the decline of the Rusty Blackbird and the use of ornithological literature to document long-term population trends. Conservation Biology 13: 553-559.
- GREENBERG, R., AND S. MATSUOKA. 2010. Rusty Blackbird: mysteries of a species in decline. Condor 112: 770-777.
- GREENBERG, R., D. W. DEMAREST, S. M. MATSUOKA, C. METTKE-HOFMANN, D. EVERS, P. B. HAMEL, J. LUSCIER, L. L. POWELL, D. SHAW, M. L. AVERY, K. A. HOBSON, P. J. BLANCHER, AND D. K. NIVEN. 2011. Understanding declines in Rusty Blackbirds. In: Boreal birds of North America: A hemispheric view of their conservation links and significance (J. V. Wells, ed.), pp. 107-126. Studies in Avian Biology 41. Berkeley, CA: University of California Press;
- HARDY, Y. J., A. LAFOND, AND L. HAMEL. 1983. The epidemiology of the current spruce budworm outbreak in Quebec. Forest Science 29:715-725.

- HAMEL, P. B., AND E. OZDENEROL. 2009. Using the spatial filtering process to evaluate the nonbreeding range of Rusty Blackbird *Euphagus carolinus*. In: Tundra to Tropics: Connecting birds, habitats and people (T. Rich, C. Arizmendi, C. Thompson and D. Demarest, eds.), pp. 334-340. Proceedings of the 4th International Partners in Flight Conferences, McAllen, TX, 13-16 February 2008.
- HART, J. A., AND J. D. LAMBERT. 2010. Mountain Birdwatch: Protocol and standard operating procedures for monitoring high-elevation landbirds in the northern Appalachian and Laurentian Regions, version 2.0. Vermont Center for Ecostudies, Norwich, VT.
- HARVEY, B. D., A. LEDUC, S. GAUTHIER, AND Y. BERGERON. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155:369-385.
- HEFNER, J. M., AND J. P. BROWN. 1984. Wetland trends in southeastern U.S. Wetlands 4:1-11.
- HEFNER, J. M., B. O. WILEN, T. E. DAHL, AND W. E. FRAYER. 1994. Southeast wetlands: status and trends, mid 1970's to mid-1980's. U.S. Fish and Wildlife Service and U.S. Environmental Protection Agency, Atlanta, GA.
- HESKE, E. J., S. K. ROBINSON, AND J. D. BRAWN. 1999. Predator activity and predation on songbird nests on forest-field edges in east-central Illinois. Landscape Ecology 14:345-354.
- HILDÉN, O. 1965. Habitat selection in birds: A review. Annales Zoologici Fennici 2:53-75.
- HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley & Sons, Inc. Hoboken, NJ.
- HUNTER, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115-120.
- HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. In: Habitat Selection in Birds (M. L. Cody, ed.), pp. 455-476. Academic Press, New York.
- IYER, J. G., R. B. COREY, AND S. A. WILDE. 1980. Mycorrhizae: facts and fallacies. Journal of Arboriculture 6:213-220.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-735.
- JOHNSON, D. H. 1980. The comparison of usage and availability of measurements for evaluating resource preference. Ecology 61: 65-71.
- JOHNSTON, C. J., AND R. J. NAIMAN. 1990. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617-1621.

JONES, J. 2001. Habitat selection studies in avian ecology: A critical review. Auk 118:557-562.

- KEMP, G. A., AND L. B. KEITH. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology 51:763-779.
- KING, D. I., C. R. GRIFFIN, R. M. DEGRAAF. 1998. Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape. Forest Ecology and Management 104:151-156.
- KING, D. I., AND R. M. DEGRAAF. 2002. The effect of forest roads on the reproductive success of forest-dwelling passerine birds. Forest Science 48:391-396.
- KLEIN, E., E. BERG, AND R. DIAL. 2005. Wetland drying and succession across the Kenai Peninsula lowlands, south-central Alaska. Canadian Journal of Forest Research 35:1931-1941.
- KNEESHAW, D. D., AND Y. BERGERON. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79:783-794.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253-260.
- LARSEN, K. W., AND S. BOUTIN. 1994. Movements, survival and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:214-223.
- LAYNE, J. N. 1954. The biology of the red squirrel, *Tamiasciurus hudonsicus loquax* Bangs, in central New York. Ecological Monographs 24: 227-267.
- LIEBEZEIT, J., AND S. ZACK. 2010. Avian habitat and nesting use of tundra-nesting birds in the Prudhoe Bay Oilfield – Long-term monitoring. 2010 Wildlife Conservation Society Interim Report. http://www.wcsnorthamerica.org/AboutUs/Publications.aspx (20 March 2013)
- LIMA, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485-513.
- LITTLE, A. M., G. R. GUNTENSPERGEN, AND T. H. ALLEN. 2012. Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. Ecoscience 19:246-257.
- LORIMER, C. G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology 58:139-148.
- LORIMER, C. G., AND A. S. WHITE. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185:41-64.

- MAHON, C. L AND K. MARTIN. 2006. Nest survival of chickadees in managed forests: Habitat, predator and year effects. Journal of Wildlife Management 70:1257-1265.
- MAINE FOREST SERVICE [ONLINE]. 2004. Maine Forest Practices Act. http://www.maine.gov/doc/mfs/pubs/pdf/FPA_04_w_history.pdf (26 April 2013)
- MARTELL, K. A., A. L. FOOTE, AND S. G. CUMMING. 2006. Riparian disturbance due to beavers (*Castor Canadensis*) in Alberta's boreal mixedwood forests: Implications for forest management. Ecoscience 13:164-171.
- MARTIN, T. E. 1988. On the advantage of being different: Nest predation and the coexistence of bird species. Proceedings of the National Academy of Sciences of the United States of America 85:2196-2199.
- MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? In: Ecology and Conservation of Neotropical Migrant Land Birds (J. M. Hagan and D. W. Johnson, eds.), pp. 455-473. Smithsonian Institution Press, Washington, DC.
- MARTIN, T. E. 1993a. Nest predation among vegetation layers and habitats: revising the dogmas. American Naturalist 141:897-913.
- MARTIN, T. E. 1993b. Nest predation and nest sites. BioScience 43:523-532.
- MARTIN, T.E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.
- MARTIN, T. E., AND J. V. BRISKIE. 2009. Predation on dependent offspring: A review of the consequences for mean expression and phenotypic plasticity in avian life history traits. The Year in Evolutionary Biology 2009: Annals of the New York Academy of Sciences 1168:201-217.
- MATSUOKA, S. M., D. SHAW, P. SINCLAIR, J. JOHNSON, R. CORCORAN, N. DAU, P. MEYERS, AND N. ROJEK. 2010a. Nesting ecology of the Rusty Blackbird in Alaska and Canada. Condor 112:810-824.
- MATSUOKA, S. M., D. SHAW, AND J. A. JOHNSON. 2010b. Estimating the abundance of nesting Rusty Blackbirds in relation to wetland habitats in Alaska. Condor 112:825-833.
- MCCALLUM, C. A., AND S. J. HANNON. 2001. Accipiter predation of American Redstart nestlings. Condor 103:192-194.
- MCCLURE, C. J. W., B. W. ROLEK, K. MCDONALD, AND G. E. HILL. 2012. Climate change and the decline of a once common bird. Ecology and Evolution 2:370-378.

- MCDOWELL, D. M., AND R. J. NAIMAN. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia 68:481-489.
- MCKINNON, L., AND J. BETY. 2009. Effect of camera monitoring on survival rates of High-Arctic shorebird nests. Journal of Field Ornithology 80:280-288.
- METTKE-HOFFMAN, C., H. WINKLER, P. B. HAMEL, AND R. GREENBERG. 2013. Migratory New World blackbirds (icterids) are more neophobic than closely-related resident icterids. PLoS ONE 8:e57565. Doi:10.1371/journal.pone.0057565. (9 March 2013)
- NAIMAN, R. J., J. M. MELILLO, AND J. E. HOBBIE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor Canadensis*). Ecology 67:1254-1269.
- NAIMAN, R. J., C. A. JOHNSTON, AND J. C. KELLEY. 1988. Alteration of North American streams by beaver. BioScience 38:753-762.
- NAIMAN, R. J., G. PINAY, C. A. JOHNSTON, AND J. PASTOR. 1994. Beaver influences on the longterm biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905-921.
- NEWELL, P., C. FOSS, N. NIBBELINK, R. COOPER AND R. GREENBERG. Rusty Blackbird landscape use and productivity during breeding and post-breeding in northern New Hampshire. *In prep.*
- NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305-321.
- NIVEN D.K., J. R. SAUER, G. S. BUTCHER, AND W. L. LINK. 2004. Christmas Bird Count provides insight into population change in land birds that breed in the boreal forest. American Birds 58:10-20.
- OLOFSSON, H., J. RIPA, AND N. JONZÉN. 2009. Bet-hedging as an evolutionary game: The trade-off between egg size and number. Proceedings of the Royal Society of London, Series B 276:2963-2969.
- O'NEILL, R. V., D. L. DEANGELIS, J. B. WAIDE, AND T. F. H. ALLEN. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ.
- ORIANS, G. H., AND J. F. WITTENBURGER. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137(Supplement):50-66.
- ORTEGA, Y. K., AND D. E. CAPEN. 1999. Effects of forest roads on habitat quality for ovenbirds in a forested landscape. Auk 116:937-946.
- PELECH, S. A., J. N. M. SMITH, AND S. BOUTIN. 2010. A predator's perspective of nest predation: predation by red squirrels is learned, not incidental. Oikos 119:841-851.
- PIETZ, P. J., AND D. A. GRANFORS. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71-87.

- POWELL, L. A. 2007. Approximating variance of demographic parameters using the delta method: A reference for avian biologists. Condor 109:949-954.
- POWELL, L. L. 2008a. Habitat occupancy, status, and reproductive ecology of Rusty Blackbirds in New England. M. Sc. Thesis, University of Maine, Orono, ME.
- POWELL, L. L. 2008b. Long term monitoring plan for Rusty Blackbirds in the Atlantic Northern Forest, version 1.8. University of Maine, Orono, ME.
- POWELL, L. L., T. P. HODGMAN, W. E. GLANZ, J. D. OSENTON, AND C. M. FISHER. 2010a. Nest-site selection and nest survival of the Rusty Blackbird: Does timber management adjacent to wetlands create ecological traps? Condor 112:800-809.
- POWELL, L. L., T. P. HODGMAN, AND W. E. GLANZ. 2010b. Home ranges of Rusty Blackbirds breeding in wetlands: How much would buffers from timber harvest protect habitat? Condor 112:834-840.
- PRICE, K., K. BROUGHTON, S. BOUTIN, AND A. R. E. SINCLAIR. 1986. Territory size and ownership in red squirrels: response to removals. Canadian Journal of Zoology 64:1144-1147.
- R CORE DEVELOPMENT TEAM. 2012. R version v. 2.15.2: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://cran.r-project.org
- RANSOME, D. B., P. M. F. LINDGREN, D. S. SULLIVAN, AND T. P. SULLIVAN. 2004. Long-term responses of ecosystems components to stand thinning in young lodgepole pine forest. I. Population dynamics of northern flying squirrels and red squirrels. Forest Ecology and Management 202:355-367.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: An artificial nest experiment. Oikos 57:375-380.
- RICHARDSON, T. W., T. GARDALI, AND S. H. JENKINS. 2009. Review and meta-analysis of camera effects on avian nest success. Journal of Wildlife Management 73:287-293.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.
- RIORDAN, B., D. VERBYLA, AND A. D. MCGUIRE. 2006. Shrinking ponds in subarctic Alaska based on 1950-2002 remotely sensed images. Journal of Geophysical Research 111:G04002.
- RODENHOUSE, N. L. 1986. Food limitation for forest passerines: Effects of natural and experimental food reductions. Ph.D. Dissertation, Dartmouth College, Hanover, NH.

- RUDNICKY, T. C., AND M. L. HUNTER. 1993. Avian nest predation in clearcuts, forests, and forest edges in a forest-dominated landscape. Journal of Wildlife Management 57:358-364.
- RUSCH, D. A., AND W. G. REEDER. 1978. Population ecology of Alberta red squirrels. Ecology 79:400-420.
- SAUER, J. R., J. E. HINES AND J. FALLON [online]. 2008. The North American Breeding Bird Survey, results and analysis 1966-2007. Version 5.15.2008. U. S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD. http://www.mbr-pwrc.usgs.gov/bbs/
- SAUER, J. R., AND W. LINK. 2011. Analysis of the North American breeding bird survey using hierarchical models. Auk 128:87-98.
- SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI, JR., AND W. A. LINK. 2012. The North American Breeding Bird Survey, results and analysis 1966-2011. Version 12.13.2011. U. S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/bbs/>
- SAVIGNAC, C. 2006. COSEWIC assessment and status report on the Rusty Blackbird (*Euphagus carolinus*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON.
- SCHMIDT, K. A., J. R. GOHEEN, AND R. NAUMANN. 2001. Incidental nest predation in songbirds: behavioral indicators detect ecological scales and processes. Ecology 82:2937-2947.
- SCHMIDT, K. A., AND R. S. OSTFELD. 2003. Songbird populations in fluctuating environments: Predator responses to pulsed resources. Ecology 84:406-415.
- SCHMIDT, K. A., R. S. OSTFELD, AND K. N. SMYTH. 2006. Spatial heterogeneity in predator activity, nest survivorship and nest site selection two forest thrushes. Oecologia 148:22-29.
- SEYMOUR, R. S. 1992. The red spruce-balsam fir forest of Maine: Evolution of silvicultural practice in response to stand development patterns and disturbances. In: The ecology and silviculture of mixed-species forests: A Festschrift for David M. Smith (M. J. Kelty, B. C. Larson, and C. D. Oliver, eds.), pp. 217-244. Norwell, MA, Kluwer Publishers.
- SEYMOUR, R. S., AND M. L. HUNTER. 1992. New forestry principles in eastern spruce-fir forests: principles and applications to Maine. Maine Agricultural Experiment Station Misc. Pub. 716. University of Maine, Orono, ME.
- SEYMOUR, R. S., A. S. WHITE, AND P. G. DEMAYNADIER. 2002. Natural disturbance regimes in northeastern North America evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management 155:357-367.
- SIEVING, K. E., AND M. F. WILLSON. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79:2391-2402.

- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia 76:62-64.
- SMITH, M. C. 1968. Red squirrel response to spruce cone failure in interior Alaska. Journal of Wildlife Management 32: 305-317.
- SPERRY, J. L., R. G. PEAK, D. A. CIMPRICH, AND P. J. WEATHERHEAD. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379-383.
- SWANN, D. E., C. C. HASS, D. C. DALTON, AND S. A. WOLF. 2004. Infrared-triggered cameras for detecting wildlife: An evaluation and review. Wildlife Society Bulletin 32:357-365.
- TEWKSBURY, J. T., S. J. HEJL, AND T. E. MARTIN. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.
- TEWKSBURY, J. T., L. GARNER, S. GARNER, J. D. LLOYD, V. SAAB, AND T. E. MARTIN. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87:759-768.
- TERWILLIGER, J., AND J. PASTOR. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83-94.
- TWEDT, D. J., AND C. R. LOESCH. 1999. Forest area and distribution in the Mississippi Alluvial Valley: implications for breeding bird conservation. Journal of Biogeography 26:1215-1224.
- U. S. FISH AND WILDLIFE SERVICE [online]. 2008. Birds of conservation concern 2008. U. S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, VA. <http://library.fws.gov/Bird_Publications/BCC2008.pdf> (20 March 2013)
- VALDEZ-JUAREZ, S. O., AND G. A. LONDOÑO. 2011. Nesting of the Pectoral Sparrow (*Areemon taciturnus*) in southeastern Peru. The Wilson Journal of Ornithology 123:808-813.
- VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281-288.
- VIGALLON, S. M. AND J. M. MARZLUFF. 2005. Is nest predation by Stellar's jays (*Cyanocitta stelleria*) incidental or the result of a specialized search strategy? Auk 122:36-49.
- VITZ, A. C., AND A. D. RODEWALD. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. Condor 113:400-411.
- WHEATLEY, M., K. L. LARSEN, AND S. BOUTIN. 2002. Does density reflect habitat quality for North American red squirrels during a spruce-cone failure? Journal of Mammalogy 83:716-727.

- WHITTAKER, J. 1984. Model interpretation from the additive elements of the likelihood function. Applied Statistics 33:52-64.
- WHITE, G. C., AND K. P BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement):S120-S139.
- WIENS, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.
- WILCOVE, D. S., C. H. MCLELLAN, AND A. P. DOBSON. 1986. Habitat fragmentation in the temperate zone. In: Conservation biology. The science of scarcity and diversity (M. E. Soulé, ed.), pp. 237-256. Sinauer Associates, Sunderland, MA.
- WILDE, S. A., C. T. YOUNGBERG, AND J. H. HOVIND. 1950. Changes in the composition of groundwater, soil fertility, and forest growth produced by the construction and removal of beaver dams. Journal of Wildlife Management 14:122-128.
- WILLIAMS, D. W., AND A. M. LIEBHOLD. 2000. Spatial synchrony of spruce budworm outbreaks in eastern North America. Ecology 81:2753-2766.
- WILLSON, M. F., T. L. DE SANTO, AND K. E. SIEVING. 2003. Red squirrels and predation risk to bird nests in the northern forests. Canadian Journal of Zoology 81:1202-1208.
- YAHNER, R. H., AND C. G. MAHAN. 1997. Effects of logging roads on depredation of artificial ground nests in a forested landscapes. Wildlife Society Bulletin 25:158-162.
- ZANETTE, L., AND B. JENKINS. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117:445-454.

Appendix A: Landowner-Specific Stand Classification Codes

Species composition	Size/Age Class	Canopy Stocking	Modifiers
S: \geq 75% canopy softwood	1: Regeneration, < 15 ft (5 m) tall	A: >90%	r: Harvest leading to regeneration (<40% canopy cover)
SH: 50 -74% canopy softwood	2: Sapling, 15-29 ft tall ^a	B: 70-90%	t: Thinning
HS: 50 -74% canopy hardwood	3: Pulpwood, > 30 tall, < 50% canopy sawtimber-size	C: 40-70%	x: Pre-commercial thinning
H: ≥75% canopy hardwood	4: Sawtimber, > 50 ft tall ^b	D: 20-40%	w: Wet
I: ≥75% canopy hardwood, intolerant		E: <20%	b: Patch retention
NF: non-productive forest			g: Group selection

A.1. Plum Creek Timber Company stand code definitions and descriptions.

^a Or \ge 30 ft tall but without 50% of Crowns large enough for pulpwood

^b Or < 50 ft tall but with \geq 59% Crowns large enough for sawtimber

A.2. Wagner Timber Company stand code definitions and descriptions.

Species Composition	Size/Age Class	Canopy Stocking
S: \geq 75% canopy softwood	1: Seedlings and saplings	A: 80-100%
M: 26 -74% canopy hardwood	2: Pole-sized	B: 50-79%
H: \geq 75% canopy hardwood	3: Sawtimber	C: 20-49%
		D: 0-19%

A.3. Northwoods Forest Management stand code definitions and descriptions.

Species Composition	Size/Age Class	Canopy Stocking
S: Softwood	0: 0-3 feet tall	A: 80-100%
M: Mixedwood	1: 3-10 feet tall	B: 50-80%
H: Hardwood	2: 10-30 feet tall	C: 20-50%
C: Cut	3: 30-45 feet tall	D: 5-20%
	4: 45-60 feet tall	E: 0-5%
	5: \geq 60 feet tall	

Species Composition	Size/Age Class	Canopy Stocking	Modifiers
S: >75% canopy softwood	R: Regeneration, 0-5 feet tall	A: 80-100%	Il: inoperable site
SH: 50-75% softwood	1: Saplings, 5-20 feet tall, 1-3 in dbh	B: 60-79%	S: Wet
M: 25-75% softwood	2: Small Pole, 20-40 feet tall, 3-5 in dbh	C: 30-59%	
HS: 25-50% softwood	3: Pole/pulp, 40-55 feet tall, <10 in dbh	D: 0-29%	
H: >75% hardwood	4: Sawlog, >55 ft tall, >10 in dbh		

A.4. Prentiss and Carlisle (P and C) Forest Management stand code definitions and descriptions.

A.5. Appalachian Mountain Club (AMC) stand code definitions and descriptions.

Species Composition	Size/Age Class	Canopy Stocking
M: Mixedwood	1: Seedling	A: >80%
O: Other softwood	2: Sapling (1-4 in. dbh)	B: 60-80%
I: Intolerant Hardwood	3: Pole (5-10 in. dbh)	C: 20-60%
S: Softwood	4: Saw (>10 in dbh)	D: <20%
T: Tolerant Hardwood		

Appendix B: Description of forest types and stands included in each type for landscape analyses of Rusty Blackbird habitat in northern New England, 2011-2012.

Stand	Types	Included
-------	-------	----------

Category	Description	Plum Creek	Wagner	Northwoods	P and C	AMC
Young Softwood	Includes softwood and softwood-dominated seedling and sapling stands	S1, S2, SH1, SH2	S1, M1 ^b	S0, S1, S2, M0 ^c , M1 ^c , M2 ^c	SR, S1, SHR, SH1, S2, SH2, MR°, M1°, M2°	S1, S2, M1 ^b , M2 ^b , O1, O2
Young Hardwood	Includes hardwood and hardwood- dominated seedling and sapling stands	H1, H2, HS1, HS2	H1, M1 ^b	H0, H1, H2, M0 ^c , M1 ^c , M2 ^c	HR, HSR, H1, HS1, H2, HS2, MR ^c , M1 ^c , M2 ^c	M2 ^b , T2, I2
Pole-sized Softwood	Includes softwood and softwood-dominated pole-sized/pulpwood stands	S3, SH3	S2, M2 ^b	S3, M3 ^c	S3, SH3, M3 [°]	S3, O3, M3 ^b
Pole-sized Hardwood	Includes hardwood and hardwood- dominated pole-sized/pulpwood stands	H3, HS3	H2, M2 ^b	H3, M3 ^c	H3, HS3, M3 ^c	T3, I3, M3 ^b
Mature Softwood	Includes softwood and softwood-dominated saw timber stands	S4, SH4	S3, M3 ^b	S4, M4 ^c	S4, SH4, M4 ^c	S4, O4, M4 ^b
Mature Hardwood	Includes hardwood and hardwood- dominated saw timber stands	H4, HS4	H3, M3 ^b	H4, M4 ^c	H4, HS4, M4 ^c	M4 ^b , T4, I4

^aSee Appendix A for landowner-specific stand definitions and descriptions

^bReclassified as "softwood-dominated" or "hardwood-dominated" based on predominate species as indicated in stand attribute data "Reclassified as "softwood-dominated" or "hardwood-dominated" based on predominate species as interpreted from aerial photos

Appendix C: Variable Descriptions

Variable	Description ^a
YoungSoft	Softwood and softwood-dominated (≥50%) seedling and sapling stands
PoleSoft	Softwood and softwood-dominated (≥50%) pole-sized stands
MatureSoft	Softwood and softwood-dominated (≥50%) mature/saw timber stands
TotalSoft	Softwood and softwood-dominated (≥50%), all size/age classes
YoungHard	Hardwood and hardwood-dominated (≥50%) seedling and sapling stands
PoleHard	Hardwood and hardwood-dominated (≥50%) pole-sized stands
MatureHard	Hardwood and hardwood-dominated (≥50%) mature/saw timber stands
TotalHard	Hardwood and hardwood-dominated (≥50%), all size/age classes

C.1. Description of forest variables used to describe Rusty Blackbird habitat at the home-range scale in northern New England, 2011-2012.

^a Measured as percent cover within a 500-m radius of nest/center point.

C.2. Description of wetland variables used to describe Rusty Blackbird habitat at the home-range scale in northern New England, 2011-2012.

Variable	Description ^a
R2	Stream/river (Lower perennial riverine wetlands, usually unconsolidated bottom (UB) or streambed (SB))
PUB	Pond (Palustrine unconsolidated bottom)
PEM	Palustrine emergent wetland
PFO_PSS	Palustrine forested/scrub-shrub wetland
TotalWet	All wetlands combined

^a Measured as percent cover within a 500-m radius of nest/center point

Variable	Description
BATotal	Total basal area (all species)
BAless10	Total basal area ≤ 10 cm dbh
SFBATotal	Basal area of spruce-fir
SFBAless10	Basal area of spruce-fir ≤ 10 cm dbh
SFStems ^a	Frequency of spruce-fir ≤ 5 m tall
SFShrub ^b	Percent cover spruce-fir ≤ 3 m tall
SFTree ^b	Percent cover spruce-fir > 3 m tall
SFSum ^b	Total percent cover spruce-fir
Canopy	Percent canopy cover ^c

C.3. Description of variables used to model habitat selection by Rusty Blackbirds at the nest-patch scale in northern New England, 2011-2012.

^a Stems measured as "hits" in 1-m-height intervals on PVC pole.

^b All percent cover values based on ocular estimation.

^c Averaged across four directions.

C.4. Description of variables used to model habitat selection by Rusty Blackbirds at the home-range scale in northern New England, 2011-2012.

Variable	Description ^a
YoungSoft	Softwood and softwood-dominated (250%) seedling and sapling stands
PoleSoft	Softwood and softwood-dominated (≥50%) pole-sized stands
TotalWet	All wetlands combined

^a Measured as percent cover within a 500-m radius of nest/center point.

C.5. Description of temporal/control variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

Variable	Description
Site	Maine (ME) or New Hampshire (NH)
Year	2011 or 2012
Date	Date of the nesting season
Age	Age of the nest
Date ²	Quadratic effect of date
Age ²	Quadratic effect of age

C.6. Description of variables relating to prevalence of	of alder
(wetland indicator) around the nest.	

Variable	Description
AlderTree ^a	Percent cover alder > 3 m tall
AlderSum ^a	Total percent cover alder
AlderBA	Basal area of alder
AlderShrub ^a	Percent cover alder ≤ 3 m tall
AlderStems ^b	Frequency of alder stems

^aAll % cover values based on ocular estimation

^b All Percent cover values based on ocular estimation.

Variable	Description
BATotal	Total basal area (all species)
AlderTree	% cover alder > 3 m tall
NestHt	Nest height (m)
NestConc ^a	Mean % concealment of nest by vegetation
Cut	Nest in harvested or unharvested area
NestTreeHt ^b	Nest tree height (m)
Cones ^b	Mean number of cones per plot
RESQ ^b	Red squirrel presence ^c

C.7. Description of nest-patch scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

^aAveraged across four directions

^b Preliminary variable – not included in final candidate set

^c Defined as "0" or "1" based on detection during 10-min. survey

C.8. Description of squirrel territory-scale habitat variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

Variable	Description
90BATot	Basal area of all conifers averaged across four plots 90 m from nest (N,S,E,W)
90BA10	Basal area of all conifers with dbh \ge 10 cm, averaged across four plots 90 m from nest (N,S,E,W)
90BA20	Basal area of all conifers with dbh \ge 20 cm, averaged across four plots 90 m from nest (N,S,E,W)
90BA30	Basal area of all conifers with dbh \ge 30 cm, averaged across four plots 90 m from nest (N,S,E,W)
90BA40	Basal area of all conifers with dbh \ge 40 cm, averaged across four plots 90 m from nest (N,S,E,W)
C.9. Description of squirrel territory-scale detection variables used to model survival of Rusty Blackbird nests in northern New England, 2011-2012.

Variable	Description
AvgCalls	Mean number of calls heard, averaged across 5 survey points: nest point, 90 m to the N, S, E and W
AvgInd	Mean number of individuals detected, averaged across 5 survey points: nest point, 90 m to the N, S, E and W
AvgPres	Mean number of surveys with squirrels present, averaged across 5 survey points: nest point, 90 m to the N, S, E and W
NestCalls	Number of calls heard during the nest point survey
NestInd	Number of individuals detected during the nest point survey
NestPres	Squirrel presence at the nest

C.10. Description of habitat variables used to model survival of Rusty Blackbird nests at the home-range scale in northern New England, 2011-2012.

Variable	Description
RdDist	Distance from the nest to the nearest road (in m)
WetDist	Distance from the nest to the nearest wetland (in m)
TotalWet	Percent cover of all wetland types within a 500 m radius of the nest
YoungSoft	Percent cover of young softwood forest within 500 m radius of the nest
MatSoft	Percent cover of mature softwood forest within 500 m radius of the nest

C.11. Description of habitat variables used to model red squirrel detection in northern New England, 2011-2012.

Variable	Description
TotalConiferBA	Basal area of all conifers
Conifer10BA	Basal area of conifers > 10 cm dbh
Conifer20BA	Basal area of conifers ≥ 20 cm dbh
Conifer30BA	Basal area of conifers \geq 30 cm dbh
Conifer40BA	Basal area of conifers ≥ 40 cm dbh

Appendix D: Spearman Correlations

D.1. Spearman correlation coefficients (*r_s*) and p-values between variables representing spruce-fir abundance and canopy closure around Rusty Blackbird nests in northern New England, 2011-2012 (n=144; 72 nest sites and 72 control sites).^{a,b}

	BATotal	BAless10	SFBATotal	SFBAless10	SFStems	SFSum	SFShrub	SFTree	Canopy
BATotal		0.905***	0.770***	0.717***	0.430	0.335	0.216	0.204	0.300
BAless10	<0.001***		0.742**	0.801**	0.447	0.362	0.281	0.162	0.173
SFBATotal	0.011**	0.004**		0.943***	0.682	0.557	0.414	0.282	0.212
SFBAless10	0.019*	0.004**	<0.001***		0.664	0.547	0.483	0.214	0.106
SFStems	0.782	0.642	0.128	0.139		0.567	0.452	0.328	0.364
SFSum	0.587	0.872	0.522	0.398	0.301		0.696**	0.401	0.049*
SFShrub	0.857	0.797	0.396	0.228	0.320	0.005**		-0.045	-0.250***
SFTree	0.290	0.200	0.257	0.164	0.560	0.698	0.094		0.380
Canopy	0.822	0.490	0.303	0.155	0.680	0.015*	0.001***	0.262	

^a See C.3, Appendix C for variable descriptions

* Significant at α =0.05

** Significant at α =0.01

^b Entries above the diagonal are r_s values, **boldface** font indicates significance at $\alpha = 0.05$; Entries below the diagonal are p-values.

*** Significant at α=0.001

D.2. Spearman correlation coefficients (r_s) and p-values between variables^a used to model Rusty Blackbird habitat selection at the home-range scale in northern New England, 2011-2012 (n=112; 56 nest sites and 56 control sites).^b

	YoungSoft	PoleSoft	TotalWet
YoungSoft		-0.052	0.255
PoleSoft	0.130		0.299
TotalWet	0.063	0.001***	

^a See C.4, Appendix C for variable descriptions

^b Entries above the diagonal are r_S values, **boldface** font indicates significance at $\alpha = 0.05$; Entries below the diagonal are p-values.

- * Significant at α =0.05
- ** Significant at α =0.01
- *** Significant at α =0.001

	,				
	AlderSum	AlderShrub	AlderTree	AlderBA	AlderStems
AlderSum		0.890	0.695	0.690	0.871
AlderShrub	0.115		0.408	0.695	0.829
AlderTree	0.766	0.156		0.407	0.555
AlderBA	0.988	0.452	0.066		0.774
AlderStems	0.214	0.108	0.256	0.328	

D.3. Spearman correlation coefficients (r_S) and p-values between alder variables^a around Rusty Blackbird nest and control plots in northern New England, 2011-2012 (n=144; 72 nest sites and 72 control sites).^b

^a See C.6, Appendix C for variable descriptions

^b Entries above the diagonal are r_s values, **boldface** font indicates significance at $\alpha = 0.05$; Entries below the diagonal are p-values.

* Significant at α =0.05

** Significant at α =0.01

*** Significant at α =0.001

D.4. S ₁	earman correlation coefficients (<i>r_s</i>) and p-values for preliminary nest-patch scale variables used to mod	lel survival of
Rusty	Blackbird nests in northern New England, 2011-2012 (n=65). ^a	

	Site	Year	Cut	BATotal	AlderTree	NestHt	NestTreeHt	Canopy	NestConc	RESQ	Cones
Site		-0.054	-0.185*	-0.299*	0.088	-0.055	-0.044	0.012	0.0632	0.242*	0.186*
Year	0.670		0.041	0.314**	-0.001	0.235	0.186	-0.155	-0.125	-0.463***	0.551***
Cut	0.023*	0.748		0.267**	-0.327*	-0.005	0.121	-0.192	-0.036	-0.128	0.006
BATotal	0.015*	0.014**	0.010**		-0.020	0.270	0.073	0.188	0.103	-0.171	0.101
AlderTree	0.095	0.378	0.019*	0.960		0.086	-0.060	0.245	0.289	0.154	0.045***
NestHt	0.842	0.275	0.556	0.520	0.557		0.660***	0.629***	0.130	-0.260	0.205
NestTreeHt	0.666	0.105	0.613	0.943	0.570	<0.001***		0.332*	-0.008	-0.125	0.165
Canopy	0.903	0.182	0.465	0.197	0.091	<0.001***	0.017*		0.277**	0.001	0.0625
NestConc	0.816	0.399	0.246	0.487	0.099	0.070	0.943	0.011**		0.266*	-0.051
RESQ	0.052*	<0.001***	0.309	0.165	0.481	0.246	0.251	0.792	0.049*		-0.077
Cones	0.017*	<0.001***	0.256	0.720	<0.001***	0.220	0.250	0.302	0.917	0.958	

^a See C.5 and C.7, Appendix C for variable descriptions ^b Entries above the diagonal are r_s values, **boldface** font indicates significance at $\alpha = 0.05$; Entries below the diagonal are p-values.

* Significant at α =0.05

** Significant at α =0.01

*** Significant at α=0.001

	Site	Year	YoungSoft	MatSoft	TotalWet	WetDist	RdDist
Site		-0.122	0.614*	-0.246	0.581*	-0.541*	0.162
Year	0.353		-0.142	0.075	-0.243	-0.035	-0.044
YoungSoft	0.029*	0.391		-0.542*	0.144	-0.211	0.231
MatSoft	0.219	0.686	0.016*		0.033	-0.066	0.052
TotalWet	0.032*	0.220	0.392	0.764		-0.414*	0.097
WetDist	0.020*	0.812	0.290	0.868	0.042*		-0.019
RdDist	0.692	0.533	0.531	0.798	0.855	0.757	

D.5. Spearman correlation coefficients (r_s) and p-values between home-range scale variables^a used to model survival of Rusty Blackbird nests in northern New England, 2011-2012 (n=50).^b

^a See C.10, Appendix C for variable descriptions

^b Entries above the diagonal are r_s values, **boldface** font indicates significance at $\alpha = 0.05$; Entries below the diagonal are p-values.

* Significant at α =0.05

** Significant at α =0.01

*** Significant at α =0.001

Appendix E: Mann Whitney U Tests

	Mee	dian	Mean			
Variable ^a	Cut	Uncut	Cut	Uncut	U	Р
BATotal	49.31	27.52	52.21	27.78	148	0.021*
BAless10	49.31	16.06	50.59	19.88	107	0.003**
SFBATotal	35.55	8.03	38.70	14.78	116.5	0.005**
SFBAless10	34.40	4.59	38.17	11.21	101.5	0.002**
SFStems	37.00	14.00	36.51	20.11	118.5	0.005**
SFSum	75.00	25.00	73.89	31.00	106	0.003**
SFShrub	35.00	5.00	48.30	5.78	66.5	<0.001***
SFTree	15.00	15.00	22.57	23.56	271.5	0.844
Canopy	26.30	40.45	28.42	41.28	393	0.063

E.1. Results of Mann Whitney *U* tests for select spruce-fir and canopy variables between Rusty Blackbird nests in harvested locations (n=63) and in unharvested wetland locations (n=9) in northern New England, 2011-2012.

^a See C.3, Appendix C for variable descriptions

E.2. Results of Mann Whitney *U* tests for alder variables between Rusty Blackbird nests in harvested locations (n=63) and unharvested wetland locations (n=9) in northern New England, 2011-2012.

Median		Median		Mean			
Cut	Uncut	Cut	Uncut	U	Р		
0.00	30.00	6.92	52.78	488.5	<0.001***		
0.00	25.00	3.51	38.89	504	<0.001***		
0.00	5.00	3.41	13.89	400	0.003		
0.00	0.00	2.42	3.31	356	0.076		
0.00	25.00	3.21	21.56	495	<0.001***		
	Me Cut 0.00 0.00 0.00 0.00 0.00	Median Cut Uncut 0.00 30.00 0.00 25.00 0.00 5.00 0.00 0.00 0.00 25.00	Median M Cut Uncut Cut 0.00 30.00 6.92 0.00 25.00 3.51 0.00 5.00 3.41 0.00 0.00 2.42 0.00 25.00 3.21	Median Mean Cut Uncut Cut Uncut 0.00 30.00 6.92 52.78 0.00 25.00 3.51 38.89 0.00 5.00 3.41 13.89 0.00 0.00 2.42 3.31 0.00 25.00 3.21 21.56	Median Mean Cut Uncut Cut Uncut U 0.00 30.00 6.92 52.78 488.5 0.00 25.00 3.51 38.89 504 0.00 5.00 3.41 13.89 400 0.00 0.00 2.42 3.31 356 0.00 25.00 3.21 21.56 495		

^a See C.6, Appendix C for variable descriptions

Model ^a	k ^b	AIC ^c	∆AIC _c ^d	w _i ^e	$\mathbf{L}^{\mathbf{f}}$	D ^g
BATotal	2	135.68	0	0.317	1	131.66
BAless10	2	136.20	0.52	0.244	0.772	132.18
SFBATotal	2	136.64	0.96	0.196	0.619	132.62
SFBAless10	2	136.84	1.16	0.177	0.559	132.83
Null	1	141.54	5.86	0.017	0.053	139.54
SFStems	2	142.36	6.69	0.011	0.035	138.35
SFShrub	2	143.46	7.78	0.006	0.020	139.44
SFTree	2	143.48	7.80	0.006	0.020	139.46
SFSum	2	143.53	7.85	0.006	0.020	139.51

Appendix F: Preliminary Nest Survival Models Including Spruce-Fir and Alder Variables

F.1. MARK model selection results for highly correlated spruce-fir variables used to model

survival of Rusty Blackbird nests in northern New England, 2011-2012 (n=65).

^a See C.3, Appendix C for variable descriptions ${}^{b}k$ is the number of parameters in the model

^c AIC_c is Akaike's Information Criterion corrected for small sample size ${}^{d}\Delta AIC_{c}$ is the difference in AIC_c between a given model and the top model

^e w_i is the model weight

^fL is the model likelihood

^gD is the model deviance

Model	<i>k</i> ^b	AIC ^c	Δ AIC ^d	w _i ^e	$\mathbf{L}^{\mathbf{f}}$	D ^g
AlderTree	2	141.53	0	0.275	1	137.51
Null	1	141.54	0.01	0.278	0.993	139.54
AlderStems	2	143.01	1.48	0.131	0.476	139.00
AlderSum	2	143.21	1.68	0.118	0.431	139.20
AlderBA	2	143.47	1.95	0.104	0.378	139.46
AlderShrub	2	143.55	2.025	0.100	0.363	139.54

F.2. MARK model selection results for highly correlated alder variables^a used to model survival of Rusty Blackbird nests in northern New England, 2011-2012 (n=65).

^a See C.6, Appendix C for variable descriptions ${}^{b}k$ is the number of parameters in the model

 κ is the number of parameters in the model ^c AIC_c is Akaike's Information Criterion corrected for small sample size ^d Δ AIC_c is the difference in AIC_c between a given model and the top model ^e w_i is the model weight ^fL is the model likelihood

^gD is the model deviance





Mean percentage of total basal area composed of spruce-fir and ≤ 10 cm dbh basal area variables (±SE) at Rusty Blackbird nest and control plots in Maine (MENest (n=29)) and MEControl (n=29)) and New Hampshire (NHNest (n=43) and NHControl (n=43)) in 2011 and 2012.

NestID	Year	Site	Brand	Unit ^a	Photos	Fate
RB01	2011	ME	Uway, Reconyx	1, 4	816	Successful
RB02	2011	ME	Reconyx	5	30	Failed
RB03	2011	ME	Uway	2	190	Successful
RB05	2011	ME	Uway	1	1,610	Successful
RB07	2011	ME	Reconyx	4	1,416	Successful
RB08	2011	ME	Reconyx	3	710	Successful
RB09	2011	ME	Uway, Reconyx	2, 4	1,400	Successful ^b
RB10	2011	ME	Reconyx	5	835	Failed
RB11	2011	ME	Bushnell	7	651	Failed
RB12	2011	ME	Uway	1	0	Failed
BEBK2	2012	ME	Bushnell	7	7	Failed
SIHI	2012	ME	Bushnell	5	6,011	Failed
SIHI2	2012	ME	Bushnell	9	5.416	Successful
TOFL	2012	ME	Bushnell	6	558	Failed
LOJA2	2012	ME	Bushnell	8	181	Successful
CHPO	2012	ME	Bushnell	9	564	Failed
PAST	2012	ME	Bushnell	11	117	Successful

Summary of camera information for	r all camera-monitored	Rusty Blackbird nests in
northern New England, 2011-2012.		

NestID	Year	Site	Brand	Unit ^a	Photos	Fate
CHPOB	2012	ME	Bushnell	11	4,120	Failed
ROCCOS	2012	ME	Bushnell	12	783	Failed
SIHI3	2012	ME	Bushnell	13	3,285	Successful
BISP	2012	ME	Bushnell	10	96	Successful
ABHA12	2012	NH	Bushnell	NA	3,213	Successful
BEND12	2012	NH	Bushnell	NA	291	Failed
CLSP	2012	NH	Bushnell	NA	1,315	Successful
EHFL	2012	NH	Bushnell	NA	288	Successful
HITP12	2012	NH	Bushnell	NA	129	Successful
MI1412B	2012	NH	Bushnell	NA	57	Failed
MOLL312	2012	NH	Bushnell	NA	225	Successful
OWPA	2012	NH	Bushnell	NA	132	Failed

^aIdentifies the unit number which I assigned to each camera; Unit numbers were not assigned to cameras in NH.

^bNest was likely partially depredated since originally 4 eggs but ultimately only one nestling (which fledged)

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
4MILE	NH	2011	13-May	30-May	Unknown	Fledged	11-Jun
ABHA11	NH	2011	9-May	26-May	Unknown	Fledged	7-Jun
ABHA12	NH	2012	4-May	21-May	Unknown	Fledged	2-Jun
ABHW11	NH	2011	9-May	26-May	Unknown	Fledged	7-Jun
ABHW12	NH	2012	4-May	21-May	Unknown	Fledged	2-Jun
BEBK	NH	2011	8-May	25-May	Unknown	Fledged	6-Jun
BEBK2	ME	2012	28-Apr	15-May	5	Depredated	23-May – 27 -May ^f
BEND11	NH	2011	16-May	2-Jun	Unknown	Depredated	10-Jun – 11 -Jun ^f
BEND12	NH	2012	4-May	21-May	Unknown	Depredated	23-May – 24 -May ^f
BISP	ME	2012	20-May	6-Jun	5	Fledged	18-Jun
CEDS12	NH	2012	2-May	19-May	Unknown	Fledged	31-May
CESR11	NH	2011	15-May	1-Jun	Unknown	Fledged	13-Jun

Appen	dix I: Nest Ch	ronology a	nd Productivitv	of Rusty	y Blackbird Nests in	northern New	England , 2011-2	2012
				•				

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
СНРО	ME	2012	6-May	NA	4	Depredated	19-May, 20-May ^g
CHPOB	ME	2012	22-May	NA	4	Depredated	4-Jun – 11 -Jun ^f
CLHI	NH	2012	24-Apr	11-May	Unknown	Fledged	23-May
CLSP	NH	2012	24-Apr	11-May	Unknown	Fledged	23-May
COBK	NH	2011	13-May	30-May	Unknown	Fledged	11-Jun
COCH	NH	2011	13-May	30-May	Unknown	Fledged	11-Jun
DIXI11	NH	2011	10-May	27-May	Unknown	Fledged	8-Jun
DIXI12	NH	2012	23-Apr	10-May	Unknown	Fledged	22-May
DIXN	NH	2011	10-May	27-May	Unknown	Depredated	4-Jun – 11 -Jun ^f
EHFL	NH	2012	18-Apr	5-May	Unknown	Fledged	8-Jun
HITP11	NH	2011	3-May	20-May	Unknown	Fledged	17-May
HITP12	NH	2012	22-Apr	9-May	Unknown	Fledged	1-Jun

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
HORN11	NH	2011	11-May	28-May	Unknown	Fledged	21-May
INTE	NH	2012	23-Apr	10-May	Unknown	Depredated	22-May
KEBK	NH	2011	14-May	31-May	Unknown	Fledged	12-Jun
LOJA	ME	2012	29-Apr	16-May	Unknown	Depredated	14-May - 15-May ^f
LOJA2	ME	2012	23-Apr	10-May	4	Fledged	22-May
MI12	NH	2012	24-Apr	11-May	Unknown	Fledged	23-May
MI1311A	NH	2011	15-May	1-Jun	Unknown	Abandoned	17-May – 20-May
MI1311B	NH	2011	23-May	9-Jun	Unknown	Fledged	21-Jun
MI1312	NH	2012	25-Apr	12-May	Unknown	Fledged	24-May
MI1411	NH	2011	10-May	27-May	Unknown	Depredated	26-May – 1-Jun ^f
MI1412A	NH	2012	1-May	18-May	Unknown	Depredated	24-May – 27 -May ^f
MI1412B	NH	2012	26-May	NA	Unknown	Depredated	8-Jun ^g

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
MILE10.8	NH	2011	12-May	29-May	Unknown	Fledged	7-Jun
MOBK	NH	2011	10-May	27-May	Unknown	Fledged	7-Jun
MOLL11	NH	2011	9-May	26-May	Unknown	Fledged	10-Jun
MOLL311	NH	2011	12-May	29-May	Unknown	Depredated	18-May – 27-May ^f
MOLL312	NH	2012	22-Apr	9-May	Unknown	Fledged	23-May
MUDH	NH	2011	12-May	29-May	Unknown	Fledged	10-Jun
NPJU11	NH	2011	12-May	29-May	Unknown	Fledged	10-Jun
NPJU12	NH	2012	11-May	28-May	Unknown	Depredated	25-May – 1-Jun ^f
OWPA	NH	2012	1-May	18-May	Unknown	Depredated	26-May – 27 -May ^f
PAST	ME	2012	27-Apr	14-May	2+	Fledged	26-May
RB01	ME	2011	8-May	25-May	Unknown	Fledged	5-Jun
RB02	ME	2011	10-May	27-May	5	Depredated	2-Jun ^g

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
RB03	ME	2011	7-May	24-May	2+	Fledged	5 Jun
RB04	ME	2011	7-May	24-May	3+	Fledged	5-Jun
RB05	ME	2011	9-May	26-May	4	Fledged	7-Jun
RB06	ME	2011	4-May	21-May	2+	Fledged	2-Jun
RB07	ME	2011	14-May	31-May	3+	Fledged	12-Jun
RB08	ME	2011	18-May	4-Jun	5	Fledged	16-Jun
RB09	ME	2011	23-May	9-Jun	5	Fledged ^g	21-Jun
RB10	ME	2011	9-Jun	26-Jun	3	Depredated	$2\text{-Jul}-7\text{-Jul}^{\rm f}$
RB11	ME	2011	26-May	12-Jun	4	Depredated	11-Jun ^g
RB12	ME	2011	23-May	9-Jun	5	Depredated	15-Jun – 19-Jun ^f
RB13	ME	2011	11-May	28-May	2+	Fledged	9-Jun
ROCCOS	ME	2012	18-May	4-Jun	Unknown	Depredated	4-Jun ^g

NestID ^a	Site ^b	Year	Start Date ^{c,d}	Hatch Date ^d	Clutch Size ^e	Fate	Fledge/Fail Date ^d
SIHI	ME	2012	29-Apr	16-May	2	Depredated	23-May, 24-May ^g
SIHI2	ME	2012	5-May	22-May	4	Fledged	3-Jun
SIHI3	ME	2012	24-May	10-Jun	3	Fledged	23-Jun
TOFL	ME	2012	25-Apr	12-May	Unknown	Depredated	19-May ^g
WTNC	NH	2011	19-May	5-Jun	Unknown	Fledged	17-Jun

^a Nest identification code

^b ME = Maine; NH = New Hampshire

^g Predation date(s) determined exactly by camera

^h Partially depredated prior to fledging

^c Clutch initiation date (first egg laid)

^d Estimated based on nest checks in the field at 3-5 day intervals, 29-day nesting period (Matsuoka et al. 2010a, Powell et al. 2010a) and camera data (when possible)

^e + indicates minimum clutch size – exact size unknown (e.g., 2+ means at least two eggs/nestlings)

```
^{\rm f} Date interval between nest checks during which predation occurred – exact date unknown
```

150

Curriculum Vitae Shannon H. Buckley

Education:

- B.A. in Biology and Spanish from Willamette University in Salem, Oregon: May 2009
- M.S. in Conservation Biology from SUNY College of Environmental Science and Forestry in Syracuse, NY: May 2013

Professional Experience:

- Graduate Teaching Assistant (General Biology and Animal Behavior) at SUNY ESF in Syracuse, NY: January 2011 May 2012
- Cerulean Warbler Project Field Crew Leader in Athens, OH: April August 2010
- Naturalist Intern at Aullwood Audubon Center and Farm in Dayton, OH: August December 2009
- Southwestern Willow Flycatcher Research Field Technician at Southern Sierra Research Station in Weldon, CA: May–August 2009
- Webber Scholar with the Willamette Science Outreach Program
- Independent research project "Selecting Avian Indicator Species to Monitor Riparian Restoration in the Deer Creek Watershed, California:" May–November 2007
- May–Aug. 2006, 2007, 2008: Intern/volunteer with Friends of Deer Creek in Nevada City, CA