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ECOLOGY OF RUSTY BLACKBIRDS WINTERING IN LOUISIANA: SEASONAL
TRENDS, FLOCK COMPOSITION AND HABITAT ASSOCIATIONS

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
In partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by
Emma E. DeLeon
B.S., University of Pittsburgh, 2006
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ABSTRACT

With an estimated population loss of at least 5% annually and a 100-year history of decline, Rusty Blackbirds (*Euphagus carolinus*) are one of the fastest declining bird species in North America. Determining cause of decline is important, both for conserving the species and for identifying threats to the wooded wetland ecosystems they use on their boreal breeding-grounds and their wintering-grounds in the southeastern United States.

One hypothesis is that loss of wintering ground habitat, possibly in conjunction with competition or disease, is causing Rusty Blackbird decline. To determine contribution of wintering ground conditions, it is important to understand the behaviors and habitat requirements that make these birds prone to decline. My research objectives were to develop survey strategies for detecting and quantifying Rusty Blackbird presence, to examine inter- and intraspecific associations for potential competition, and to determine habitat requirements at spatial scales appropriate to foraging movements. The present study uses data from 550 survey occasions and 163 independently collected birder observations to examine survey methods and seasonal trends over two winters. Occupancy modeling was used to investigate flocking behavior and habitat associations (at 25 m and 100 m scales) at 74 unique sites (naïve occupancy = 0.82, average occupancy by survey round = 0.51).

Results indicate that Rusty Blackbirds may be less dependent on forested habitat than previously thought, but show strong a strong relationship to availability of wet ground. Range-wide alterations in hydrological processes, due to drainage or flood control, could lead to decreased quality or availability of shallow-water habitat and aquatic food resources. Rusty Blackbirds frequently flock with other blackbird species, and show similarities in use of open habitats. Competition cannot be ruled out and could worsen with use of degraded habitat.

Overall results suggest that wintering behavior and habitat changes are likely contributors to long-term and continuing Rusty Blackbird decline.

CHAPTER 1. INTRODUCTION/OVERVIEW

1.1 Rusty Blackbird Status and Trends

Birds have traditionally been used as indicators of environmental health, and studying the cause of rapid or persistent population declines in a particular species can often lead to the discovery of underlying issues affecting whole ecosystems. With an estimated population decline of at least 88% in the past 40 years, and a continuing yearly decrease of at least 5%, Rusty Blackbirds (*Euphagus carolinus*) are currently one of the fastest declining bird species in North America (Niven et al. 2004, Greenberg and Matsuoka 2010). Additionally, it is estimated that the Rusty Blackbird population has been decreasing steadily over the past 100 years (Greenberg and Droege 1999). As a result, Rusty Blackbirds are currently considered a species of concern by conservation organizations including the International Union for Conservation of Nature (2012), The United States Fish and Wildlife Service (2008), Partners in Flight and Canada's Committee on the Status of Endangered Wildlife (Rich et al. 2004, Savignac 2006). The International Rusty Blackbird Technical Working Group was formed in 2005 with the goal of directing research efforts to determine causes of Rusty Blackbird decline. Current research focuses on both preserving the species and determining whether underlying causes for decline pose a broader threat to ecosystems in any part of the species' range.

Despite recent efforts, scientists have been unable to determine a definite cause for decreasing Rusty Blackbird populations. There are a variety of hypotheses currently under consideration, most of which could indicate large-scale habitat problems and threats shared with other species. Determining the causes of Rusty Blackbird decline is important, not only for developing a conservation strategy before populations become critically low, but also for

identifying potential threats to wooded wetland ecosystems throughout North America. In order to determine underlying reasons for the decrease in Rusty Blackbird populations, it is important to first understand the basic behaviors and habitat requirements that could make these birds particularly prone to decline.

1.2 Natural History

Knowledge of basic natural history, behavior, and habitat requirements of Rusty Blackbirds has improved greatly over the past few years, but the species has still not been studied extensively. Most recent focus has been on testing theories of the species' decline, with less in-depth investigation of basic ecology and resource requirements (Greenberg and Matsuoka 2010). Until recently, the only publication focused exclusively on Rusty Blackbird natural history was a 1920 study of nesting habits (Kennard 1920). Breeding and nesting habitat requirements have been studied in more depth over the past five years (Powell 2008, Matsuoka et al. 2010 a, b, Powell et al. 2010), but while wintering ground requirements and behavior are also being investigated, only one study has been published (Luscier et al. 2010). The reason Rusty Blackbirds have been studied so little and their decline has escaped notice for so long is largely due to challenges posed by the very behaviors and habitat requirements that require more investigation. Inaccessible habitat and unpredictable behavior make Rusty Blackbirds difficult to study on both the breeding and wintering grounds, while assumed similarities to more common blackbird species have caused them to be overlooked for many years. Many conclusions about Rusty Blackbird behavior, habitat, and food requirements, especially on the wintering grounds, are still based on informal narratives and accounts.

Rusty Blackbirds breed in wet boreal forests and bogs in the far northeastern United States, Alaska, and Canada, where they forage in shallow water and nest along wetland edges and in forest openings in conifer-dominated habitats (Ellison 1990, Avery 1995, Matsuoka 2010a, Powell et al. 2010). Rusty Blackbirds winter in the southern United States, predominantly along the east coast and throughout the Mississippi River Valley. Primary wintering habitat is traditionally considered to be flooded bottomland forest, but may also include less heavily forested areas. Birds are routinely seen foraging in flooded forest, open pastures, swamp edges, and along creeks or bayous (Meanly 1972, Avery 1995, Lusnier et al. 2010).

On both breeding and wintering grounds, Rusty Blackbirds forage in leaf litter and shallow water for insects, spiders, snails, crawfish and other aquatic invertebrates, as well as small fish, and frogs (Matsuoka et al. 2010 a, Greenberg et al. 2011). Even in tall, mature forest wintering habitat, birds tend to forage on or near the ground (Dickson and Noble 1978). Rusty Blackbirds use a characteristic leaf flipping technique to pull invertebrates out from under wet leaf litter. They also probe in shallow water, mud and occasionally rotting wood (Avery 1995). Birds often wade directly into shallow water or forage from floating vegetation or debris over deeper water (Avery 1995, Greenberg et al. 2011). Several observers have noted that Rusty Blackbirds forage more like shorebirds than like typical blackbirds (Forbush 1927, Todd 1940). Tree mast, including pine seeds, acorn mast, other nuts, and some fruit also make up part of their winter diet (Avery 1995, Mettke-Hofmann et al. 2008, Edmonds et al. 2010). Birds have been observed eating acorns from a variety of small-seeded oaks, as well as pecans and larger acorns that have been crushed either by grackles, on roads, or by harvesting machinery (Avery 1995, Newell 2009, Greenberg et al. 2011, Mettke- Hofmann pers. com.). There are occasional reports

of predation on grain crops, but less so than other blackbird species, and with minimal commercial impact (Beal 1900, Dolbeer 1978, Avery 1995). Dietary studies, jaw musculature and bill structure indicate a largely insectivorous diet (Beal 1900, Beecher 1951).

Rusty Blackbirds appear to be sensitive to transient environmental conditions, changing the timing and limits of their yearly migration range as well as foraging nomadically over large distances throughout the winter and even over the course of a day (Mettke-Hofmann et al. 2008, Hamel and Ozdenerol 2009, Greenberg and Matsuoka 2010). Variation in weather, water levels and mast production are all possible reasons for yearly adjustments to migration patterns. For example, site occupancy by Rusty Blackbirds in Mississippi and Arkansas was lower in years where regional water levels were higher (Luscier 2009). Rusty Blackbirds generally forage over a range of approximately 1.6 km on a daily basis and return each night to roost sites up to 11 km away, providing a range of habitat choices for foraging (Mettke-Hofmann et al. 2008, pers. com.). Short-term variation in foraging site selection and resource use may also depend on transient variables such as water level at sites or weather conditions (R. Greenberg pers. com.).

Rusty Blackbirds may migrate as either mixed or single species flocks and often forage and roost as part of mixed flocks during the winter (Avery 1995, Greenberg et al. 2011). Some sources suggest that single-species flocks are predominant or that association with other species is weak, but others note that Rusty Blackbirds are often found in mixed flocks consisting mainly of Red-Winged Blackbirds (*Agelaius phoeniceus*), Common Grackles (*Quiscalus quiscula*), European Starlings (*Sturnus vulgaris*) and Brown-headed Cowbirds (*Molothrus ater*) (Avery 1995, Greenberg and Matsuoka 2010). Recent studies suggest that co-occurrence in foraging habitat with Common Grackles is common and may indicate important competitive or cooperative interactions (Luscier 2009). Despite association with other blackbird species, and

some overlap in habitat and prey, Rusty Blackbirds seem to fill a slightly different niche than other North American blackbirds: In general, Rusty Blackbirds are less gregarious, more neophobic, more insectivorous, and more dependent on wooded wetland habitat (Avery 1995, Greenberg and Droege 1999, Mettke-Hofmann 2006).

According to the *Birds of North America* species account, there is no evidence to suggest segregation of age or sex classes during migration, and there is no discussion of habitat partitioning on the wintering grounds (Avery 1995). However, preliminary evidence from studies in Mississippi suggests that wintering Rusty Blackbirds may segregate by age and sex with females and young birds wintering further south, a general pattern noted in many species of bird including other blackbirds (Dolbeer 1982, Cristol et al. 1999, C. Mettke-Hofmann pers. comm.). Studies in Mississippi, Georgia and South Carolina have indicated males and older birds may forage at higher food-availability sites, while females and young birds are found feeding in lower quality habitat (Mettke-Hofmann et al. 2008). In some bird species where division of the sexes occurs on the wintering ground, behavioral dominance results in intraspecific competition; larger, more aggressive individuals, often males, tend to occupy higher quality habitat (Marra 2000). Imbalances on the wintering ground may affect condition and survivorship and effects can carry over to migration and breeding (Marra and Holmes 2001). Preliminary results of another study indicate that larger flocks in nutrient rich habitats in South Carolina are more evenly balanced between males and females (Newell 2009). It is also unknown whether flock partitioning occurs throughout the wintering range.

1.3 Population Decline

Increased awareness of declining migratory bird populations and habitat problems in North America, combined with recent use of citizen science databases, have revealed long-term trends in the population status of many species (Sullivan et al. 2009, North American Bird Conservation Initiative 2011, Sauer et al. 2011). Because Rusty Blackbirds were not studied until recently, much of what is known about their decline is based on compilations of historical data from Christmas Bird Counts, Breeding Bird Surveys, and regional species checklists (Greenberg and Droege 1999). Breeding Bird Surveys from 1966-2008 indicate a total population decline of 93% with losses of 9.3% per year (Sauer et al 2004, Sauer and Link 2011). Christmas Bird Count data from 1965-2003 estimate yearly loss at 5.1% and overall loss through 2007 at 88% (Niven et al. 2004, Greenberg and Matsuoka 2010). The highest rate of loss by region was detected in the Mississippi Alluvial Valley at an estimated 6.5% per year (Niven et al. 2004). Decline appeared to be worst during the 1970s (Figure 1.1) (Niven et al. 2004, Sauer et al. 2004, Greenberg and Droege 1999). Greenberg and Droege (1999) used regional checklist rankings, the migration card program, field notes, historical accounts and questionnaires to track Rusty Blackbird decline back as far as the mid 1800s. Rate of decline appears to have been steadily increasing, with the steepest trend of decline beginning around the 1950s and agreeing with the steep decline showed from the 1950s through the 1970s in Breeding Bird Survey and Christmas Bird Count data (Figure 1.2) (Greenberg and Droege 1999). Most recent estimates suggest that between 88 and 93% of the population has been lost since the mid-1960s. While the species may still be relatively common, with up to two million birds remaining in the population, more than 11 million birds have already been lost (Niven et al 2004, Greenberg and Matsuoka

2010). Today, annual decline seems to have leveled off but remains serious at 5-10% per year (Figure 1.1) (Niven et al. 2004, Greenberg and Droege 1999).

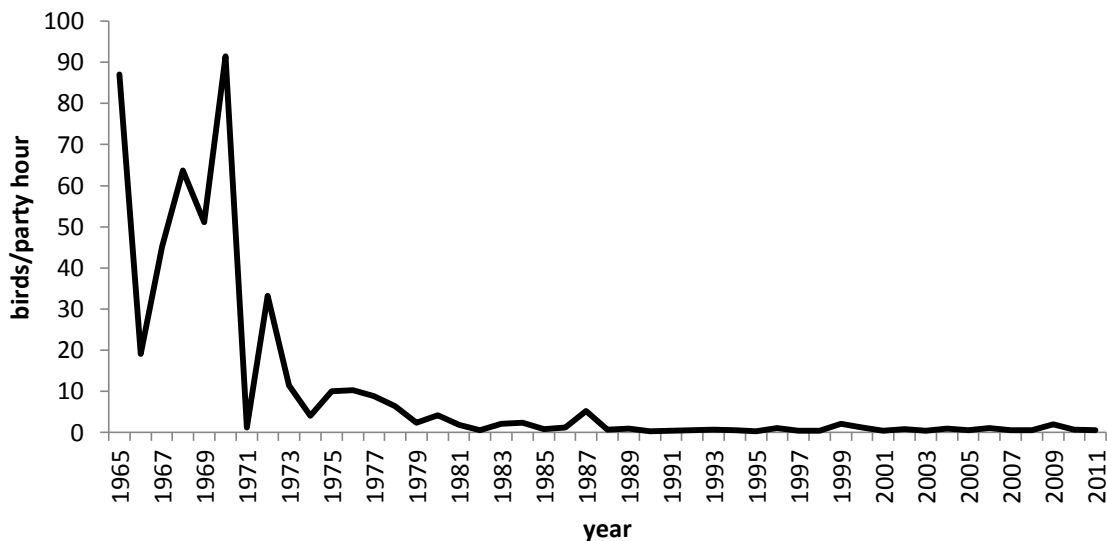


Figure 1.1. Rusty Blackbird decline since 1965 based on Christmas Bird Count data. Data was obtained from National Audubon Society 2010 but only results from 1965 forward are shown based on analysis presented in Sauer et al. (2004), Niven et al. (2004) and Greenberg and Droege (1999).

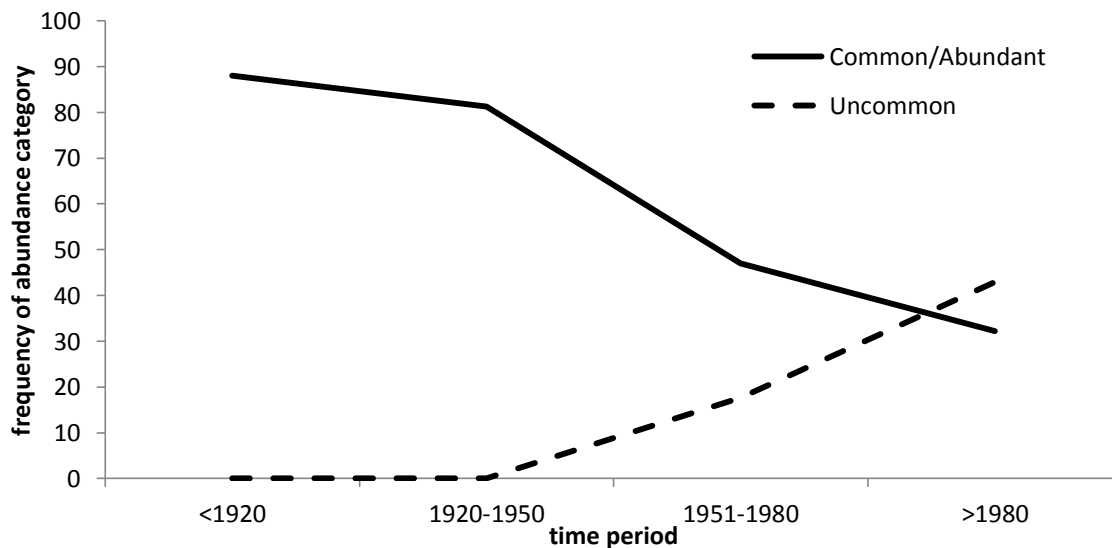


Figure 1.2. Long-term decline of Rusty Blackbird populations. Frequency of abundance category measures the number of state checklists in a given time period which rank Rusty Blackbirds as “uncommon”, “fairly common”, “common” or “abundant” (n= 25, 16, 17, 28 for time periods). Data from Greenberg and Droege 1999.

1.4 Hypotheses to Explain Decline

Hypotheses to explain the observed pattern of Rusty Blackbird population decline must address the long-term trend since the 1800s as well as the increased rate during the 1950s through the 1970s and the present-day continuation of decline. The most parsimonious explanation for long term population loss seems to be habitat destruction on the wintering grounds. At the time Rusty Blackbird decline started, there was very little human impact in the boreal forest, but deforestation and wetland drainage in the southern United States for agricultural use had already begun as far back as the 1600s and 1700s (Dahl and Allord 1997). Habitat destruction intensified over time, and it is estimated that 57% of wetlands in the Mississippi Alluvial Valley and 46% of wetlands along the mid-Atlantic and Atlantic coastal plain were lost between the 1780s and the 1980s (Hamel et al. 2009). The peak of freshwater wetland loss between the 1950s and the 1980s corresponds to the peak in Rusty Blackbird decline, with the highest deforestation rates slightly later in the 1970s and 80s (Hamel et al. 2009). The leveling off of Rusty Blackbird decline from the late 1980s through current times corresponds with decreased rates of wetland loss due to legislation, such as Swampbuster and the Emergency Wetland Resources Act, and programs such as the Wetland Reserve Program and the Conservation Reserve Program, put in place in the 1980s (Dahl and Allord 1997, Leininger and Hamel 2007, Hamel et al 2009). Experimental reforestation plots have successfully attracted Rusty Blackbirds, and it is possible that reforestation and wetland regeneration efforts are producing new habitat and slowing decline (Hamel 2003, Hamel et al. 2009). Despite restoration efforts, development continues to destroy wetlands nationwide, and many of the original alterations remain in place, so rapid population recovery would not be expected. Despite qualitative similarities in the trends, both land use data and Rusty Blackbird data are from a

variety of unstandardized sources, and direct quantitative comparison has not been possible (Hamel et al. 2009). Even qualitative trends are not completely parallel, with Rusty Blackbird decline appearing to be steeper than can be explained by rates of forested wetland loss alone (Leininger and Hamel 2007, Hamel et al. 2009). Comparisons of Rusty Blackbird population decline and habitat loss patterns between regions of the southeast show similar rates of decline but, deforestation trends of different magnitude and conversion type (i.e. agriculture, silviculture, etc.), which could indicate other causes for decline (Hamel et al. 2009).

There are a variety of explanations that could account for mismatched rates of deforestation and Rusty Blackbird decline. For example, since the greatest converted acreage was in states where large concentrations of Rusty Blackbirds winter, the overall impact on populations may have been intensified (Leininger and Hamel 2007). The progressively more fragmented nature of the remaining forest could also have caused an increasingly steep rate of decline in Rusty Blackbird populations through the 1970s. Studies in bottomland hardwood forest have shown negative impacts of habitat fragmentation on both breeding and wintering forest-dependent birds (Burdick et al. 1989). Habitat changes could also have resulted in interspecific competition for the best habitat or may have placed Rusty Blackbirds in more direct competition with other blackbird species. Additionally, many blackbird species are seen as crop pests in the Southern United States, and efforts to reduce populations by poisoning at roost sites may also impact Rusty Blackbirds that use multi-species roosts. Blackbird control, however, is not thought to be a major cause of Rusty Blackbird decline because other more targeted species have shown only slight population declines over the same time period (Greenberg and Droege 1999).

Shallow water and prey availability in wintering habitat may impact Rusty Blackbird populations more directly than changes in forested wetlands alone. Clearing for urbanization and agriculture usually progresses from drier, more easily manageable land to wetter and more flood-prone areas, and wetland conversion may have impacted Rusty Blackbirds with increasing severity as the process continued (Leininger and Hamel 2007, Hamel et al. 2009). Agriculture has lead to increased use of pesticides, concentration of water in runoff ditches and contamination of water sources which could have impacted birds, through decreasing availability of aquatic prey or bioaccumulation of toxins, especially during the 1940s through 1960s (Edwards 1993, Fry 1995, Relyea 2005). In addition, much of the southern United States, and the Mississippi River Valley in particular, underwent a series of large-scale flood control projects, primarily from the 1930s through the 1950s (Dahl and Allord 1997, Fredrickson 1997, Hupp 2000). Prior to levee, dam and channelization projects, river bottomlands consisted of ponds and sloughs scattered through wooded areas and were connected to rivers of varying sizes and depths. Such rivers were free to meander, and flood vast areas. Today most major river systems in the southeast are controlled: natural flooding is very limited, rivers are channelized, and availability of temporary or shallow water has been greatly reduced (Fredrickson 1997, King and Keeland 1999, Hupp 2000). Reduced connectivity with larger bodies of water, and changes in hydroperiod alter abundance and diversity of organisms able to live in temporary pools (Tockner 2002, Williams 2005). Channelization changes sediment deposition and lowers water tables which can result in drier more topographically and environmentally homogeneous floodplains (Hupp 2000, Franklin et al. 2009, Pierce and King 2011). Changes in floodplain geomorphology have been shown to impact other bird species and anecdotal evidence suggests that surface mosaic of shallow water and wet soil may be important to Rusty Blackbird foraging

(Hoover 2009, Greenberg et al. 2011, Benson et al. 2011, Pierce and King 2011). Altering the region-wide hydrologic system from a dynamic system that maintains standing water of varying depths to one that permanently divides dry ground from deep water sources could drastically limit shallow water foraging areas and prey species available to Rusty Blackbirds. While progress has been made in reforestation efforts, regional hydrologic function is difficult or impossible to restore, and topography and water dynamics may not be taken into account during reforestation projects (Fredrickson 1997, King and Keeland 1999). Changes in water depth and availability across a wide range of wetland habitats might show a similar but stronger trend than deforestation of floodplain forests alone, and could account for the continuing decline in Rusty Blackbird populations.

Since the most precipitous drop in Rusty Blackbird populations did not occur until the 1950s through the 1970s, decline could also correlate with changes on breeding ground habitat. By this time, boreal forests were beginning to be logged, mined and polluted by downwind industrial activities. Logging and drainage removes coniferous forest nesting habitat and wetland foraging habitat, and evidence from Powell et al. (2010) shows that regenerating clear-cuts may actually act as ecological traps where Rusty Blackbird nest success is especially low (Matsuoka et al. 2010 a, b, Powell et al. 2010). Range contractions in the northeastern portion of their breeding range also indicate potential habitat problems (Powell et al. 2010). Mercury pollution is another possible cause of decline. Bioaccumulation of environmental mercury pollution is especially problematic for species that forage on aquatic prey, and Rusty Blackbirds mainly eat aquatic insects and invertebrates on the breeding grounds (Edmonds et al. 2010). Rusty blackbirds forage in acidic boreal wetlands where mercury is easily methylated to MeHG (methylmercury), an especially available and toxic form (Edmonds et al. 2010). Edmonds et al.

(2010) showed that blood levels of mercury were higher on the breeding grounds than on the wintering grounds, but levels differed by region, being highest in the northeast. It seems likely that regional and even local mercury exposure varies greatly and may be impacting some portions of the population far more than others, suggesting that this is not the main driver of range-wide Rusty Blackbird decline. However, mercury levels found were high enough to imply detrimental effects on reproductive success and behavior of at least some sub-populations of Rusty Blackbirds (Edmonds et al. 2010).

Another suggested hypothesis for Rusty Blackbird decline is disease or parasites. Barnard et al. (2010) found high levels of hematozoa infection in Rusty Blackbirds in several regions of the breeding ground as well as in Arkansas and Mississippi. *Leucocytozoon*, the most commonly detected parasite in their study, is transmitted via insect vectors and is known to cause weight loss, anemia and mortality in juveniles (Bennett et al. 1993, Barnard et al. 2010). In the case of most bird species, hematozoa infection rates are low on the wintering grounds, but high rates of infection (49%) were observed among Rusty Blackbirds (Barnard et al. 2010). It is possible that warm wintering ground conditions allow for transmission year round, but limited studies suggest that a relapse of latent infection is more likely (Barnard et al. 2010). Usually relapse is triggered by breeding stresses, and while offseason relapse is not well understood, Barnard et al. (2010) suggest that stress from competition and/or poor habitat on the wintering grounds could be causing relapses of parasitic infection in Rusty Blackbird populations. In concert with wintering ground scenarios involving habitat loss, changes in shallow water availability, and inter or intraspecific competition, stress or disease could lower survivorship on the wintering grounds or result in poor condition and loss of fitness upon return to the breeding grounds.

Pressures during all three main life stages (breeding, migration, and wintering) are probably contributing to current Rusty Blackbird decline, and it is likely that anthropogenic change has played a large role. Given the similarities in timing between the trend of Rusty Blackbird population decline and trends of destruction, conversion, and control of wetlands in the southeast United States, it seems likely that habitat alterations on the wintering grounds, and perhaps along migration pathways, have negatively impacted Rusty Blackbird populations. Increased rates of decline may further depend on issues such as breeding ground destruction, competition, or disease.

1.5 Study Objectives

Results of prior and ongoing studies indicate that loss or alteration of wetland habitat could be causing or contributing to Rusty Blackbird decline. The present study focuses on investigating Rusty Blackbird wintering habitat requirements and flocking behavior. Currently available sources provide contradictory or ambiguous information on behavior and habitat use. My three main research objectives were: 1) Develop effective and replicable survey strategies for detecting and quantifying Rusty Blackbird presence; 2) Quantify inter- and intraspecific associations for evidence of potential competition; and 3) examine habitat associations at spatial scales reflecting typical foraging movements of individual birds. Ultimately, the goal of this study is to provide background data and working methods on which to base further investigation of the role wintering ground conditions may play in the range-wide decline of Rusty Blackbirds.

CHAPTER 2. SURVEY TECHNIQUES FOR STUDYING RUSTY BLACKBIRDS IN LOUISIANA

2.1 Introduction

Rusty Blackbirds are most accessible for study on their wintering grounds, but there are still a variety of challenges associated with surveying for the species in winter (Luscier 2008, Greenberg et al 2011). Rarity, poor understanding of habitat requirements, large range of daily movement, complex or secretive behaviors, and variability in timing and extent of yearly migration all make detection and abundance estimation of these birds problematic (Luscier 2009, Greenberg et al. 2009, 2011). There is a need for reliable and efficient methods for standardized study of this species.

While still a relatively common species, Rusty Blackbirds are rare enough that large sample sizes, even via stratified random point selection, are difficult to obtain without extensive effort (Luscier 2009). Rusty Blackbirds are not evenly distributed across the landscape, and are generally associated with difficult-to-access flooded forest or wetlands; Specific habitat indicators are poorly understood, and in some areas birds use habitats as diverse as forest and suburban lawns. The species seems to use a broad range of habitats, yet in specific locations based on characteristics or spatial characteristics we do not yet understand. As such, locating birds can be very challenging.

Rusty Blackbirds can even be difficult to detect at sites where they have been found regularly. Birds forage over a large area on any given day and may or may not be present at small defined survey locations when an observer is at a site. Birds are generally thought to be relatively shy and neophobic; they forage low to the ground, and are not particularly vocal (Dickson and Noble 1978, Greenberg et al. 1999, Mettke-Hofmann 2006). While both males and

females do sing on the wintering ground, in addition to producing a variety of other vocalizations, singing does not begin until late winter, and birds do not respond well to playback (Avery 1995, Lusnier 2009). Flocking behavior also complicates detection, as different flock sizes and species compositions may be more or less obvious, and large flocks can make abundance estimation difficult. Mixed flocks with more common blackbirds may improve chances of locating birds, but may also increase chances of missing or miscounting any Rusty Blackbirds in the flock. All of these factors mean that survey methods should attempt to account for imperfect detection.

Finally, in addition to difficulties with locating and detecting birds in any given season, Rusty Blackbirds seem to be highly variable in extent and timing of yearly migration. Timing of arrival and departure, at least in Louisiana, may vary by weeks in different years. Concentration of birds in a given region is also highly variable. Only a few regions of the Atlantic Coastal Plain and some inland river valleys show predictably high numbers of birds (Hamel and Ozdenerol 2009, Greenberg and Matsuoka 2010). The Christmas Bird Count, commonly used for study of Rusty Blackbirds, may actually occur too early in the wintering season to consistently detect the southernmost range of wintering populations (Hamel and Ozdenerol 2009). Long-term monitoring is important, and any short-term study should be adaptable to differences in timing and population from year to year.

A variety of techniques are available for improving study of rare or secretive species. Surveying at non-random sites, increasing time or range of survey coverage, and using playback, are all methods commonly used to improve detectability during avian surveys (Edwards et al. 1981, Ralph et al 1995, Gibbons and Gregory 2006, Jones 2011). Additionally, citizen science data sets, collected by organized volunteer programs, have been used successfully to improve

sample sizes and increase spatial and temporal scope of bird studies (Sauer 2004, Greenberg 2009, Sullivan 2009, Dickinson and Bonney 2012). It has been noted, however, that some citizen science approaches, such as Christmas Bird Counts, may be unreliable when applied to rare, flocking, or seasonally variable species or to species restricted to inaccessible habitats (Bock and Root 1981, Hamel and Ozdenerol 2009, Lusnier 2009). In this chapter I test the above approaches for applicability to the study of wintering Rusty Blackbirds and make recommendations to aid future studies in accounting for the variability in Rusty Blackbird behavior while maximizing survey efficiency. Specific objectives were to compare occupancy rates at sites selected using a stratified random approach versus sites where birds had been previously detected by local birders; to assess the suitability of citizen science data for looking at variation in seasonal timing, population fluctuation, flock size and sex ratios; and to assess timing and use of stationary point counts and area searches. I used all available data to examine yearly variation in population size, flock size and sex ratios, checking for any drastic changes, imbalances or evidence of intraspecific competition.

2.2 Methods

2.2.1 Citizen Science Data and Site Selection

I compiled a citizen science database of detailed sighting information from birders statewide throughout the winters of 2009-2010 and 2010-2011. Citizen science data was used to select survey sites and seasonal and flock trends were compared between citizen science and survey data sets. Citizen science data was collected using LABIRD, a Louisiana birding listserv run by the Louisiana State University Museum of Natural Science (Louisiana Bird Resource Office 2011 a). I solicited information from list members starting in November of each year, and

corresponded with observers of Rusty Blackbirds for more detail. Louisiana was conducting a state-wide winter bird atlas project during both years of my study, which contributed to birder activity throughout the state and to regular bird list postings (Louisiana Bird Resource Office 2011 b). I also used eBird, a national data portal managed by Cornell Lab of Ornithology, to obtain several sighting locations, but only included points if I was able to contact the observer to confirm an exact location. Citizen science information included 49 birder reports at 47 locations in the first season and 114 reports from 106 locations in the second season (Figure 2.1). Reports were only included if information on flock size and point location was provided. I also compared survey and detailed observer reports to the larger, but coarser scale, data set available through eBird which included 610 reports over the two years (eBird 2011). Despite efforts to standardize across seasons, it is possible that differences in my data collection efforts could have resulted in more Rusty Blackbird detections the second year, so I also compared data against eBird records from Louisiana. Many observers who provided data for this project also cross posted on eBird, but a large number of observers post on eBird alone, and the data base also includes many observations that did not provide enough spatial detail to be included in my study; therefore I considered this a semi-independent source of seasonal trend data.

I selected survey points using two methods: stratified random sampling and based on citizen science reports. During the first winter, I selected 18 survey sites in easily accessible public land in or near bottomland forest in southeastern Louisiana, and selected 35 additional sites in the same region where birders had located Rusty Blackbirds earlier in the season. In the second winter, I surveyed 23 sites known to have been occupied in the previous winter and added 21 new birder-reported sites. A total of 97 site/seasons and 74 independent sites were surveyed over the two years (Figure 2.1).

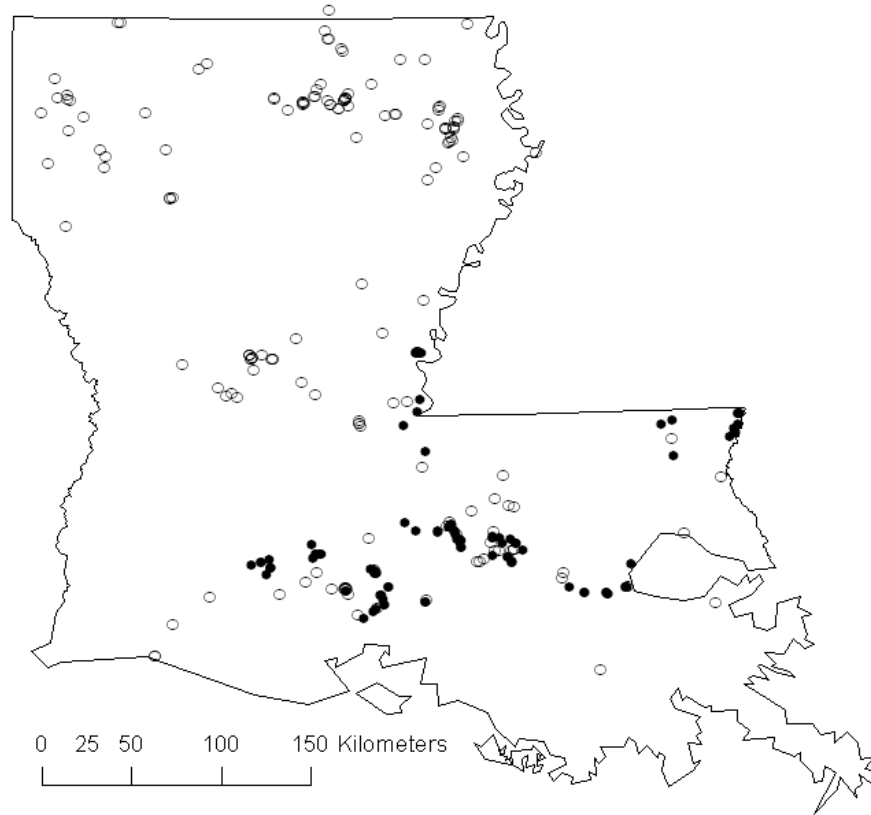


Figure 2.1. Points I surveyed (black) and reported by birders (white) throughout Louisiana during November through March 2009-2010 and 2010-2011.

2.2.2 Survey Timing

I conducted repeated surveys for Rusty Blackbirds in southeastern Louisiana during the winters of 2009-2010 and 2010-2011. I began surveys in December during the first season, but these data were subsequently eliminated due to low detection rates and inconsistencies with later methods. I began surveys in early January and ended in early March, to capture the peak of Rusty Blackbird presence in the region while avoiding periods of migration in and out of the area (Lowrey 1974, Luscier 2009). Each site was surveyed during three, roughly monthly, rounds. In 2010, rounds overlapped slightly: round one was January 5 through February 14; round two was

February 2 through March 10; and round three was March 7 through March 23. In the second year there was no overlap between rounds: round one was January 6 through January 30; round two was February 2 through February 24; and round three was February 25 through March 13.

2.2.3 Avian Surveys

I designed a survey protocol based on techniques previously used to study Rusty Blackbird populations in the central and lower Mississippi Alluvial Valley (Luscier 2009). I surveyed from 30 minutes after sunrise until one hour before sunset in order to maximize survey time while avoiding roost-related movements at dawn and dusk (Avery 1995, Luscier 2009). I avoided surveying on days with heavy wind and rain, as recommended by most survey protocols; however, I frequently observed birds during light to moderate rainfall, so I continued to survey under these conditions (Ralph et al. 1995). I used a combination of 15- minute stationary point count surveys within 200 m radius count circles and 30-minute extended searches of the area up to 1.6 km away.

Point counts consisted of a two-minute settling time, a ten-minute passive point count, and two minutes of playback followed by one minute of silence. During the second year, survey time remained 15 minutes but no playback was used. I noted date, time, cloud cover, precipitation and wind-speed (based on the Beaufort scale). I recorded number of Rusty Blackbirds detected, time into point count of first detection, and male to female ratio. I noted whether birds were perched, foraging, or vocalizing and whether detection was aural, visual or both. I also recorded number and species of any other blackbird species as well as American Robins (*Turdus migratorius*) present within the 200 m radius survey circle. If no Rusty

Blackbirds were detected, I still recorded data on other species. I did not include flyover birds of any species in final point count totals.

Extended searches were bounded by a 30-minute time limit and by a 1.6 km distance limit, based on the approximate daily range of a flock of foraging Rusty Blackbirds (Mettke-Hofmann pers. com.). I attempted to cover as much ground as possible, either by foot or by vehicle during the 30-minute search. Due to differences in site accessibility, most searching was focused within 600 m of the original point. I recorded distance and time to first and last Rusty Blackbird detection, number and sex ratio of birds, and number and species of any associated blackbirds and American Robins. If additional birds were found more than 400 m from the original sampling point and in a visibly different habitat type, I created a new survey point.

2.2.4 Data Analysis

First, I assessed methods of site selection by comparing naïve occupancy rates at sites selected randomly, based on citizen science reports, and based on occupied status in the previous year. Second, I examined number of birds detected, seasonal timing, flock size and sex ratios of flocks in both survey years comparing citizen science and survey results. To conservatively estimate number of birds detected by repeated surveys, I summed the maximum number of birds seen at once at each site during each round (birds per site/round). Citizen science totals were the number of birds reported in correspondence with local birders or reported on eBird. I examined seasonal trends between years by comparing arrival timing and dates by which 25, 50, 75 and 100% of birds seen in a season were detected, and compared seasonal offsets according to birder and citizen science data sets. I determined survey dates and data collection methods that would best capture either peak Rusty Blackbird population or migration in and out of the region.

Information on size of individual flocks was not available via eBird, but detailed local birder data was compared with surveys in both years using Wilcoxon Rank Sum tests. Due to the variability in skill level, effort, and estimation techniques of the many observers contributing citizen science data, I was not able to base any conclusions about Rusty Blackbird sex ratios on these data, and used survey data only to look for evidence of unbalanced sex ratios or intraspecific competition. I used a Wilcoxon Rank Sum test to search for region-wide difference in number of males and females counted on surveys, and used a Chi-square Goodness of Fit test to determine if observed number of males in each flock was significantly different from the number expected if flock ratios were balanced. Finally, I examined the success of survey techniques based on naïve occupancy rates, and compared the efficiency of point counts and extended area searches. Point count and extended survey efficiency were assessed by comparing proportions of total birds detected across time and distance bands. Rates of response to playback and discovery due to aural or visual detection were also assessed.

2.3 Results/Survey Method Assessment

2.3.1 Site Selection

Results indicate that stratified random sampling of suitable habitat was less effective for locating reliable Rusty Blackbird survey locations than citizen science. My surveys were likely to detect Rusty Blackbirds at points where birders had previously located birds the same winter. Of the 21 birder-located points surveyed, 13 (62%) were occupied on at least one survey occasion later the same winter. Points where birds had been located the previous year were also likely to have birds the second year: 16 out of 23 (67%) previously surveyed points were occupied again the second year, showing some site fidelity between years, for the species if not

for individual birds. Conversely, semi-random point selection, placing points near or within bottomland forest areas assumed to be suitable habitat, only yielded birds at 6 of 18 (33%) sites. A true random selection technique would presumably have an even lower success rate. Based on the low occupancy rate for random sites, I did not use this point selection method during the second year.

2.3.2 Seasonal Trends and Timing

There were more birds detected in the second season than in the first according to both birder data and surveys. In season one, 21 individual birders contributed 49 reports for a total of 638 birds. In season two, 23 birders submitted 114 reports of 5504 birds. The number of reported birds per survey was significantly higher in the second year (Wilcoxon Rank Sum Test $W = 1825$, $p < 0.001$). My surveys mirrored the same basic trend. In season one, 1222 birds were detected over 94 site/rounds. In season two, 2362 birds were detected over 112 site/rounds. Raw detection rate of birds per survey hour was also significantly higher in year two (Wilcoxon rank sum test $W = 30577.5$, $p < 0.001$). Between November 2009 and March 2010, 236 eBird checklists reported a total of 7842 Rusty Blackbirds while between November 2010 and March 2011, 374 checklists reported 11808 birds. Numbers of Rusty Blackbirds reported in year two were greater, but posting rates to eBird also increased. Between November and March an average (\pm SE) of 313.6 ± 23.0 lists per week were submitted in 2009-2010 and 377.0 ± 22.3 in 2010-2011. All three data sources did indicate larger numbers of Rusty Blackbirds in the region during 2011, and both survey and birder observations directly related to Rusty Blackbirds showed significant increases in regional population.

The two years of my study show different seasonal timing, with the second season offset towards later arrival, peak and departure dates. This trend is apparent in both citizen science and survey data sets (Figure 2.2). Both seasons started with low numbers of birds until early January, then ended abruptly in late February or early March with departure of all birds. Based on the average (\pm SE) offset of the dates when 25, 50, 75 and 100% of total birds detected over a season had been located, the first season is offset a similar 12.5 ± 4.2 days later than the second season according to birder data, 9.5 ± 3.8 days later according to eBird data, and 8.8 ± 3.7 days later according to survey data (Appendix I). Based on averaging data from citizen science and survey data for two years, the seasonal peak (from the end of the 1st quartile through the end of the 3rd quartile) lasts 31.3 ± 2.5 days in length and falls somewhere between January 1 and February 28 with seasonal tails extending from early November through late March.

Flock size was generally low in both years, according to both birder and citizen science data. Both data sources showed similar average flock sizes for 2010, but differed in 2011. According to my survey data, average flock size ((median) \pm SE) in 2010 was $20.6(6.5) \pm 3.4$ and in 2011 was $19.7(7.2) \pm 3.5$. There was no significant difference in flock size by year (Wilcoxon Rank Sum Test $W = 7744$, $p = 0.54$). Birder data did show a difference in flock size by year (Wilcoxon Rank Sum Test $W = 1825$, $p < 0.001$), with an average flock size of $14.7(7.0) \pm 3.0$ in 2010 and $49.6(15.5) \pm 8.1$ in 2011. In the first year, birder-observed and surveyed flock sizes were not significantly different from each other (Wilcoxon Rank Sum Test $W = 2103.5$, $p = 0.92$), but in the second year birder-observed flock sizes were significantly larger than surveyed flocks (Wilcoxon Rank Sum Test $W = 7652.5$, $p < 0.001$).

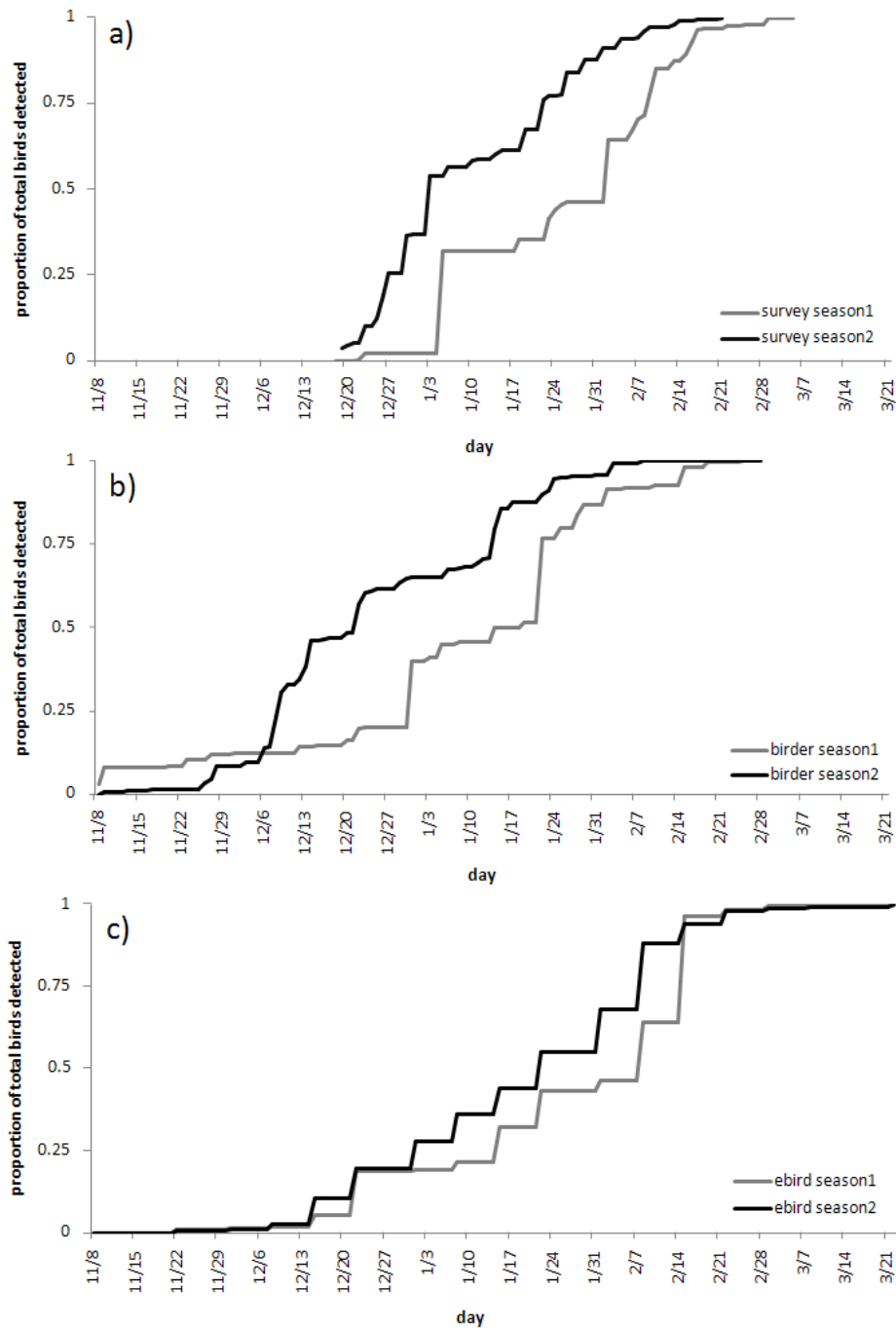


Figure 2.2. Seasonal timing over two winters based on survey and citizen science data. Timing is expressed as proportion of total birds found in a given season detected as of each date. For survey data (a) totals are based on the sum of the maximum number of birds seen per site per survey round. Citizen science totals from independently collected birder observations (b) and eBird (c) are the total number of birds detected in each season. Season1 is the winter of 2009-2010 and season2 is 2010-2011.

I examined sex ratios of Rusty Blackbird flocks in both years using my survey data set, but did not compare results to citizen science data sets. Only 44% of detailed reports collected from birders included information on sex of any birds in the reported flock. Of the total birds in the birder data set, 61% were of unidentified sex. Many observers also noted that sex ratios provided were uncertain or estimated. My survey data involved only one observer and exact numbers of birds were counted whenever possible. Only 3% of surveys had no information on sex ratio and only 12% of birds were of unidentified sex. Of 4740 birds that could be identified by sex, 48% were male and 52% were female. Survey data showed no significant difference in the number of males and females present in the region in year one (Wilcoxon Rank Sum test, $W = 26146$, $p = 0.89$) or in year two (Wilcoxon Rank Sum test, $W = 53655$, $p = 0.38$). There was also no trend indicating that individual flocks had male to female sex ratios substantially different from 1:1. On average (\pm SE), flocks had 4.1 ± 0.5 males and 4.5 ± 0.6 females. All single bird observations were removed from the dataset prior to examining flock ratios more closely. However, neither sex appears more likely to be solitary; in year one there were four single males and seven single females and in year two there were 14 single males and eight single females. Chi-squared Goodness of Fit tests, of observed number of male birds compared to expected number if flock ratios were even, indicated that the null hypothesis of a 1:1 sex ratio within flocks could not be rejected in the study-wide data set ($\chi^2 = 174.38$, $df = 187$, $\alpha = .05$, $p = 0.74$) or in the year two data set ($\chi^2 = 96.32$, $df = 127$, $\alpha = .05$, $p = 0.98$). In year one, the final chi-square value was approximately equal to that required for rejection ($\chi^2 = 78.05$, $df = 59$, $\alpha = .05$, $p = 0.05$), but does not provide any strong evidence that flocks ratios were unbalanced.

2.3.3 Point Counts and Extended Searches

Rusty Blackbird naïve detection rate over the two study years was relatively high (0.35): birds were detected on 191 of 550 survey occasions. The majority of detections were due to both vocal and visual cues. I heard vocalizations at 48% of surveys, but only 1% of detections, on either point or extended counts, were due to aural detection alone, as opposed to 52% visual only detections.

The naïve detection rate for stationary point count surveys was 25%, with Rusty Blackbirds detected on 135 of the 550 point counts. Of the 5403 total birds detected 2238 (41%) were detected on point counts. The average (SE) time into point count of the first detection was 3.4 minutes \pm 0.2; however 60% of detections occurred within less than one minute of starting the point count (Figure 2.3). Adding more point count time seems to result in a slow increase in detections, as the majority (80%) of detections occurred within the first five minutes of starting a point count (Figure 2.3). Point counts were also supplemented with playback surveys of Rusty Blackbird calls, song and mixed flock vocalizations (in that order). Playback was attempted on 206 survey occasions during the first season. However, there were only four occasions where birds seemed to directly respond to recordings (i.e., were not detected until during the last three minutes of the survey in which there was a two minute playback followed by one minute of silence). Due to this low (2%) response rate, playback was not considered to contribute significantly to overall birds detected and was eliminated during the second season.

Distance to birds detected during point counts was not well documented, but birds were detected from 0 m to 200 m. Large flocks, especially when accompanied by other more vocal species, were much more detectable at greater distances than smaller flocks or pure Rusty

Blackbird flocks. Ability to detect birds from a stationary point could be impacted by habitat type, flock size and flock species composition. These factors were analyzed in an occupancy modeling framework in Chapter 3.

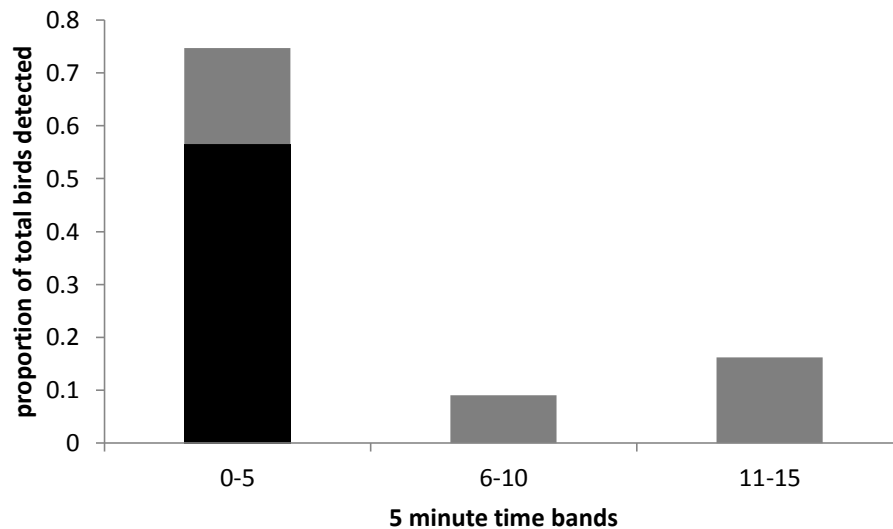


Figure 2.3. Proportion of first point count detections occurring in each five minute time band; black bar indicates detections within the first minute.

The naïve detection rate for extended area searches was 31%; Rusty Blackbirds were detected on 170 of 550 surveys. The proportion of total birds located due to extended searches was 60% (3165 of the total 5403 birds). The same bird was never included in both point count and extended count totals. Average (\pm SE) time to first extended search detection was 8.9 minutes \pm 0.7, and average time until last detection of a previously undetected bird was 12.8 \pm 1.0. Most first detections occurred during the first 10 minutes of the extended search with steadily fewer detections in each subsequent 10-minute time band (Figure 2.4). Last detections occurred within the first 10 minutes of the extended count on 50% of occasions, with fewer detections occurring in subsequent time bands; however, the proportion detected is steady between the last 20 minutes and the last 30 minutes, and was still close to 30% in each band (Figure 2.4).

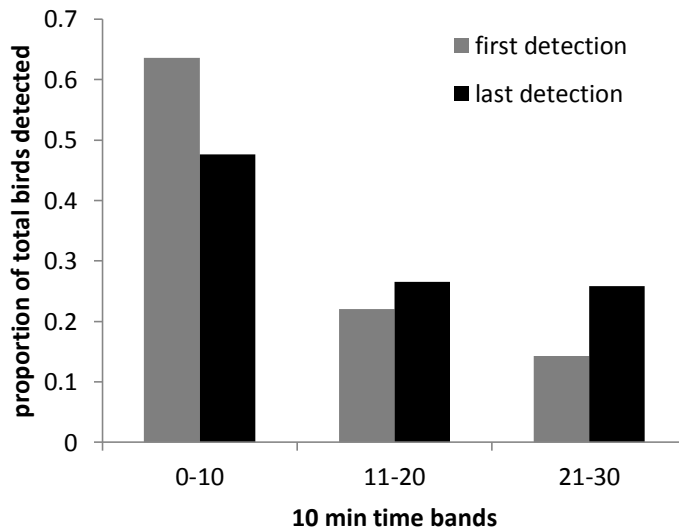


Figure 2.4. Proportion of total extended search detections occurring during each 10 minute time band. Gray bars indicate first extended count detection and black bars indicate last extended count detection.

Although the primary limit imposed upon extended area surveys was the 30 minute time limit, surveys were also restricted by a 1.6 km distance limit. Because the distance limit was not reached on most surveys, the proportion of birds detected in further distance bands is expected to be lower. Average (\pm SE) distance to first extended search detection was 188.96 m \pm 15.15 m and average to last extended search detection was 187.5 m \pm 15.3. Most (50%) detections were within 200 m of the original point, but detection remains high (40%) between 200 and 400 m. Only 9% of birds were detected at distances greater than 400 m (Figure 2.5). Even considering only the proportion of extended survey birds found within 400 m, 54% of total birds were detected on area searches. Stationary counts alone accounted for only 41% of total birds.

As expected, distance to detection on extended searches was correlated with time of detection (Spearman rank test $\rho=0.54$ for time and distance to first detection $\rho=0.57$ for time and

distance to last detection). Increasing the time and area covered, in the form of extended searching, improved survey success from 25% to 35%. The detection rate (at least one bird per survey) on extended searches (31%) was slightly higher than for point counts (25%), and the overall number of birds detected due to extended searches was significantly higher than number of birds detected on point counts (Wilcoxon Signed Rank test paired by survey occasion, $V=9815.50$, $p = 0.0006$).

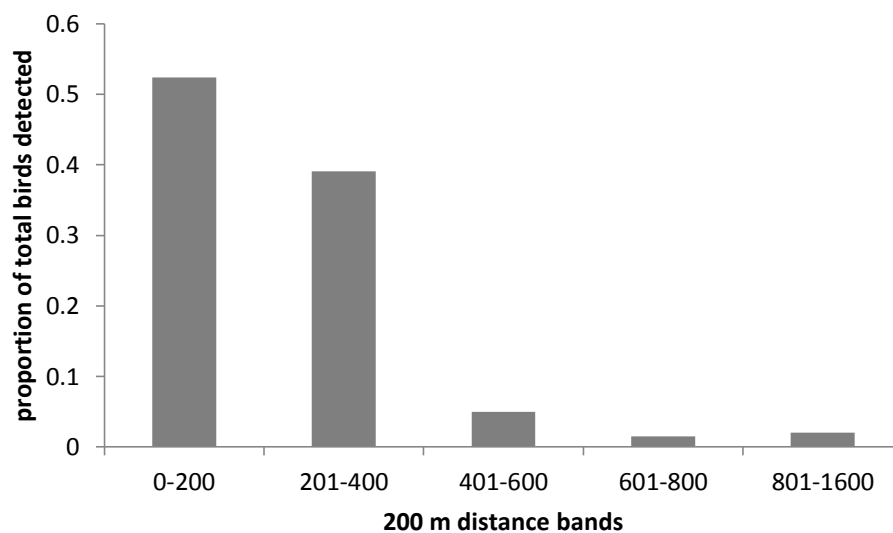


Figure 2.5. Proportion of total birds detected in each 200 m distance band.

2.4 Discussion/Recommendations

Use of citizen science data proved a successful method for locating sites occupied by Rusty Blackbirds. This non-random site selection technique is not suitable for modeling overall regional population levels, but is appropriate for site-by-site analysis of habitat characteristics and for looking at dynamic changes in occupancy or abundance status at the same sites over time (MacKenzie et al. 2006). Using sites known to have been occupied at some point is a reliable method for locating Rusty Blackbirds, and ensured enough occupied sites for use in analysis,

which can be difficult when working with rare or difficult to detect species like Rusty Blackbirds. Naïve occupancy over the full set of all sites in all seasons was 66%, which is suitable for occupancy modeling and ultimately allowed for analysis of 61 unique sites where birds were detected on at least one survey round. Since Rusty Blackbirds use a wide range of habitat types, such a small sample might not have been sufficient to describe typical site characteristics. Rusty Blackbirds are only reliably common every year in a few regions and, while it may make analysis more challenging, non-random point selection is a practical approach (Dawson 1981, Mackenzie et al. 2006, Hamel and Ozdenerol 2009, Jones 2011).

Surveys, detailed birder data and eBird data all indicated higher numbers of Rusty Blackbirds found in 2011 than in 2010, but citizen science efforts focused specifically on Rusty Blackbirds had results more similar to survey data than eBird data. After standardizing for effort, eBird data showed no significant difference in number of birds per year; however, increased posting rates would not be directly related to Rusty Blackbird effort so number of Rusty Blackbirds reported may not have increased proportionally to the total number of checklists submitted. Both survey and birder observations directly related to Rusty Blackbirds showed significant increases in regional population when standardized by detection rates. Standardization of citizen science efforts specifically for Rusty Blackbirds may be important for tracking population fluctuation.

Trends in yearly timing were consistent between citizen science data and more intensive repeated surveys. Both data sets showed the same patterns of seasonal timing in a given year and indicated differences in timing between the two years of the study. Tendency towards variation in extent and timing of migration is congruent with what is known about Rusty Blackbird wintering behavior and is most likely due to habitat or weather conditions, such as temperature,

precipitation, flooding, or tree mast production, both in Louisiana and further north (Hamel and Ozdenerol 2009, Lusnier et al. 2010). Such variation suggests that precautions should be taken when planning a survey season so as to properly detect either the tails or the peak of any season. In order to account for peak bird populations in this region, surveys should be focused in early January through late February. To account for migration into and out of wintering grounds in Louisiana, data should be collected from early November through late March. Use of citizen science data could be extremely helpful in looking at the beginnings and ends of seasons, eliminating the need to perform intensive surveys over long periods of time.

Birder data and survey data indicated similar average flock sizes in 2010 and relatively small flock sizes throughout the study, but in 2011 birders observed significantly larger flocks than indicated by my results. Larger flock sizes in 2011 would agree with trends indicating a larger regional population in the second winter. It is unclear whether non-standardized estimation of flock sizes among birders could have influenced results, but discrepancy in flock size results alone does not indicate strong overall differences between survey and citizen science approaches. Birder data was insufficient to draw conclusions about sex ratios, but no evidence of imbalances in regional or flock by flock ratios was observed in survey data.

Both point count and extended area searches were effective methods for detecting Rusty Blackbirds, but the detection rate due to extended searching was slightly higher than for stationary counts, and the overall number of birds detected due to extended searches was significantly higher than number of birds detected on point counts. Adding extended area searching to standard point counts improved detection rates and helped with detection of this highly mobile species. Both aural and visual detections were important, but visual detection rates were actually higher than aural detection rates, and playback had little effect. Survey

techniques that allow an observer to see the entire survey circle or to cover more area visually could improve survey results. Survey methods were adequate for detecting birds at occupied locations, but efficiency could be improved by using shorter, smaller radius, stationary point counts accompanied by extended searches of a standardized area that can be covered on foot in a reasonable amount of time. An alternate approach would be to arrange sets of relatively short, small-radius point counts in transects or grids over each area of interest.

Both citizen science and more detailed survey methods are important for studying rare and declining species like the Rusty Blackbird (Greenberg and Matsuoka 2010, Dickson and Bonney 2012). Citizen science is a useful method for locating occupied sites and for time and cost efficient monitoring of Rusty Blackbirds and other species over large areas and long time periods (Dickson and Bonney). Additional study over long time spans would be needed to accurately describe the typical variation in Rusty Blackbird population size and migration timing in the region, but my results show that seasonal fluctuations in population size and migration timing are similar between citizen science and more intensive survey efforts. Detailed birder observations collected specifically for this study were more congruent with survey data than was eBird data, and a species-specific approach to gathering citizen science data is likely better suited to the study of Rusty Blackbirds and other rare species. Providing participants with detailed protocols and information about the species would likely produce more consistent data in future studies, but could also limit participation (Dickson and Bonney 2012). Data on flock composition, and in some cases flock size and exact spatial location, were difficult to gather from citizen science, and surveys are a better approach for collecting detailed information. Future studies of Rusty Blackbirds or other species with large foraging ranges, limited aural detectability, or imperfect detectability in general, should avoid using standard point count

procedures designed for breeding birds, or more common species and should focus on coverage of larger spatial areas. Overall my approach of blending citizen science data with detailed surveys was effective for detecting and studying a rare and unpredictably located species.

CHAPTER 3. USING OCCUPANCY ESTIMATION TO MODEL RUSTY BLACKBIRD HABITAT ASSOCIATION AND CO-OCCURRENCE WITH OTHER SPECIES

3.1 Introduction

Despite the suspicion that long-term and large-scale habitat destruction of wooded wetlands on the wintering grounds could have impacted the historical decline of Rusty Blackbirds, relatively little research has been done on actual habitat preferences (Greenberg et al. 2010). Accounts vary as to the extent to which birds associate with wooded wetland, and there are inconsistencies in the correlation of region-wide trends of deforestation and Rusty Blackbird decline (Hamel et al. 2009, Luscier et al. 2010). It has been suggested that the compound effects of deforestation, drainage of wetlands and water control could account for some of these differences (Hamel et al. 2009, Greenberg et al. 2010). The importance of these effects has been difficult to examine because of the patchy and unpredictable occurrence of Rusty Blackbirds. Louisiana is on the southern edge of the wintering range where all usable sites are unlikely to be saturated with birds even in years of high regional occupancy but has a relatively reliable wintering population and a variety of wetland habitats (Lowrey 1974, Hamel and Ozdenerol 2009). This should allow models to reflect birds' choice of preferred sites. Luscier et al. (2009, 2010) attempted to analyze habitat associations at a small scale, but had limited success in identifying important traits within an 11.3 m habitat circle. It is not surprising perhaps, that habitat preferences were difficult to identify at such a small scale, as Rusty Blackbirds move over a large daily foraging range and individuals or flocks can cover several hundred meters within minutes.

Luscier (2009) found that Rusty Blackbirds and Common Grackles co-occurred more often than would be expected if birds were occupying sites independently; various other sources

have also proposed that there may be some relationship, either cooperative or competitive, between Rusty Blackbirds and other more common species (Avery 1995, Barnard et al. 2010, Greenberg et al. 2010). Field observation and raw data trends in my study also indicated co-occurrence between Rusty Blackbirds, Red-winged Blackbirds and Common Grackles. Habitat conditions can impact co-occurrence and co-detection, but no previous studies have explicitly looked at co-occurrence of these species after accounting for habitat characteristics (Richmond et al. 2010).

Occupancy models account for imperfect detectability, and are often used for rare or secretive species like the Rusty Blackbird (MacKenzie et al. 2006, Luscier 2009). In basic occupancy modeling, repeated survey occasions allow for estimation of probability of site occupancy (Ψ) which is modeled simultaneously with probability of detection (P). The technique is based on the assumption that occupancy is closed (no changes in status) throughout a given span of time, so any observed variation during this period must be due to detectability. This allows the model to account for individuals that may be present but not detected. Detectability and occupancy can also be modeled as functions of site or survey-specific covariates. The logistic functions, transformed via the logit link for each combination of occupancy and detectability covariates, are compared using a maximum-likelihood procedure. Results can be evaluated using AIC (Akaike's Information Criterion) ranking to determine which set of covariates most parsimoniously explains the observed pattern of occupancy rates (Mackenzie et al. 2002, MacKenzie et al. 2006, Donovan and Hines 2007). A variety of expansions of the basic occupancy modeling structure are possible, including multi-season models, which modify closure assumptions to allow for examination of dynamic changes in

occupancy over time, and two-species models, which describe co-occupancy (MacKenzie et al. 2006). Parameterizations for these two variations are described in the methods section.

Rusty Blackbirds are relatively rare, and due to a variety of complex flocking and foraging behaviors, can be difficult to detect (Chapters 1, 2). One problem is that birds are highly mobile, traveling several kilometers a day while moving between foraging and roost sites. Given these behaviors, it is possible that naïve occupancy might be low when birds are using a site, but are not detected at the time of a survey either due to temporary movement away from the survey point or because of cryptic behavior. Occupancy modeling accounts for issues of non-detection and allows for adjusted calculation of estimated site use. While the case of nomadic behavior might appear to violate closure assumptions, it seems reasonable to assume that birds are using the same set of sites within a larger-scale habitat, over at least short spans of time. Non-detection at a small survey site would then account for cases where birds are present at the site at some point during each day of the closure period, but not necessarily during the survey. Luscier (2009) assumed 4-5 day closure at 200 m sites for Rusty Blackbirds and throughout the course of my study (assuming 3-6 day closure) birds were frequently found at sites on both the first and last survey day. Of 78 closed survey sets where birds were detected on the first day, 45% had no permanent status change, even without accounting for detectability so birds were consistently present during the assumed closure period. Closed system estimation techniques in mark recapture studies are robust to temporary emigration within a sampling period as long as movements are random with respect to status on consecutive surveys (i.e. non-markovian) and similar assumptions have been made in previous occupancy based studies (Kendall 1999, Kéry et al. 2009). Because Rusty Blackbirds return to roost sites each night, there is no reason to suspect any temporal non-independence of surveys on consecutive days. The modified definition of

closure used in my study (i.e. no non-random status changes at sites within a consistently occupied area during a 3-6 day span), does not violate closure assumptions necessary for occupancy modeling. Accounting for non-detection allows for more accurate estimation of site occupancy based on habitat characteristics than if raw observations of birds were used.

My specific objectives were to examine the relationship of Rusty Blackbirds to their foraging habitat and to determine if they were more likely to occur alone or with other common blackbird species in different habitat types. I hypothesized that Rusty Blackbirds were targeting shallow water sources, which can be highly transient, so I used multi-season occupancy models to compare the dynamic patterns of changes in occupancy status to changes in habitat conditions at sites. I expected that occupancy rates would be higher and transience rates lower at wet, forested sites that retain shallow water throughout the winter, and that this relationship would be true at both 25 m and 100 m spatial scales. I used two-species occupancy models to relate occupancy and detectability of Rusty Blackbirds to that of Red-winged Blackbirds and Common Grackles under varying habitat conditions. I predicted that Rusty Blackbirds would associate more often with Common Grackles and Red-winged blackbirds than they would if the species were choosing sites or being detected independently, and that these associations would be stronger for less forested habitats where several blackbird species are commonly found foraging in mixed flocks.

3.2 Methods

I surveyed for Rusty Blackbirds and habitat characteristics in southeastern Louisiana from 1 January through early March in 2010 and 2011. Sites were surveyed for birds a maximum of nine times each year, following the avian survey protocol outlined in Chapter 1. I

conducted three bird surveys in each of three monthly rounds. I attempted to survey on three successive days in order to best meet the assumption of closure required for occupancy modeling (Mackenzie 2006), but due to weather and timing problems, I extended the closure assumption to include surveys conducted within a six day span. Habitat surveys were conducted within 25 m and 100 m habitat circles once during each round. I used an occupancy modeling approach to compare importance of various habitat and species covariates while accounting for imperfect detectability.

3.2.1 Habitat Surveys (100 m and 25m)

I conducted one habitat sample within a 100 m radius of each point during each round. I visually estimated percent of ground covered by water, leaf-litter, short grass/lawn, leafy vegetation, woody vegetation or debris, and an “other” category including any habitat type not fitting into one of the previous categories. I then visually estimated percentage of the available water that was shallow (< 5 cm) and percentage of the available leaf litter that was wet. It was not possible to quantitatively describe habitat at the 100 m habitat level, so I also did a 25 m microhabitat sample around each point during each round. I measured the distance to the nearest water and tree cover and took a series of measurements at the central observation point and at points 12.5 m and 25 m from the center (Appendix II.1). I measured water depth and litter depth (either depth to ground or to water in the case of dense floating vegetation), and categorized ground cover as dry, damp, saturated, or under water (water deeper than 5 cm). I also measured canopy cover (using a GRS densitometer), estimated canopy height, and determined whether canopy was leafy or bare. I used a modified vegetation pole to measure visual obstruction at a height of 1 m. This was done by placing the pole at each point and then sighting back at the 1 m mark on the pole from a level height 5 m away, in 4 directions 45 degrees from the original

cardinal direction transects. I walked each 25 m cardinal direction transect and used a Biltmore stick to tally trees and stems >1 cm DBH (diameter at breast height) within 2 m of transects. I identified trees to species whenever possible. DBH and tree species were only measured once at each site rather than on each round.

While birds were often seen multiple times at the same site, they were not always detected again within the same 100 m or 25 m habitat circle. To better describe the area birds were using, and to help account for between-round changes that might allow birds to use the same general area, I also took measurements at sub-points. I created sub-points based on distance from original point, habitat type and bird behavior (Appendix II.2). On subsequent visits, the original points were always re-surveyed for habitat, but sub-points were only re-surveyed if birds were detected again. New sub-points could be added at any time. For occupancy analysis with 200 m avian survey data, I averaged the habitat values of any habitat points falling within 200 m of the original point on a given round.

3.2.2 Occupancy Model Parameterizations

I used two variations on the basic occupancy modeling structure to examine Rusty Blackbird occupancy and detectability patterns: multi-season occupancy models and two-species occupancy models. All models were run in the program PRESENCE 4.0 (Hines 2006). I adjusted the effective sample-size to equal the number of sites used in the analysis, and used resulting AICc scores to account for small sample-size in relation to number of estimated parameters when ranking models (Burnham and Anderson 2002). I considered any models within $\Delta 2$ AICc of the top score to have substantial model support (Burnham and Anderson 2002). I used weighted model averaging to compare importance of individual detectability or

habitat parameters when several models received substantial support. Model averaged weights for covariates were calculated by weighting within-model parameter estimates for each covariate by the AIC weight (relative likelihood) of the model in which they occurred, then summing adjusted weights across the top models. Parameters estimates are untransformed estimates of covariate coefficients used in the logit transformed function. (Burnham and Anderson 2002). Model fit was tested using Chi-Square Goodness-of-Fit tests for the top habitat models, to confirm results were an accurate reflection of observed patterns (MacKenzie et al. 2006). I compared the observed number of non-detections to an expected number calculated using top model estimates of Ψ and P applied over the number of visits and rounds that were actually conducted. I compared observed and expected values by site rather than by detection history and used numbers of non-detections rather than occupancy to obtain numerically reasonable expected cell values for Chi-Square tests.

In multi-season models, occupancy is no longer held constant throughout the entire study. Occupancy is only assumed to be constant within each season, several of which may be included in the model parameterization. This relaxation of the closure assumption allows estimation of two additional parameters: colonization (γ) and extinction (ϵ). As compared with use of static occupancy patterns, this allows for stronger inferences about the relationship between changes in occupancy status and habitat characteristics (MacKenzie et al. 2006). For modeling purposes, I considered each of the three rounds to be a “season,” and used the default parameterization offered in PRESENCE4.0, which directly estimates original Ψ from survey data and derives subsequent site-based occupancies based on habitat ϵ and γ rates in a given time period. I allowed original Ψ and ϵ between all rounds to vary based on habitat covariates, but held γ constant because there were too few instances of colonization in the data set to sufficiently

model this parameter (5 occasions as opposed to 32 occasions of extinction). Although a parameterization that directly models occupancy and extinction based on habitat covariates for each season is possible, models did not meet convergence criteria due to small sample sizes, and the default parameterization was interpreted to be more numerically stable (MacKenzie et al. 2006). I was more interested in the underlying process of transience and the habitat variables driving it than in exact occupancy probabilities for individual sites, and most sites began as occupied or were known to have been occupied at some previous point, so the default parameterization is appropriate (MacKenzie et al. 2006, Donovan and Hines 2007).

Two-species models estimate several additional parameters for the co-occurrence of two species (Appendix VI.1). I used two sets of single-season two-species models to look at co-occupancy and co-detectability of Rusty Blackbirds with Common Grackles and Red-winged Blackbirds. The parameterization I used accounted for the presence of a more common species (either Common Grackles or Red-winged Blackbirds), and the conditional presence of Rusty Blackbirds, given the presence of the other species. The conditional parameterization is more numerically stable than when species occurrence is modeled separately, and allows for better model convergence when habitat covariates are included (Hines 2006, Richmond et al. 2010). This parameterization is also recommended for use when one species (in this case Red-Winged Blackbirds or Common Grackles) is suspected to be dominant or more prevalent (Richmond et al 2010). Multi-species multi-season models do exist but are highly parameterized, and require very large sample sizes. Since I was more interested in static co-occurrence and detectability than in colonization and extinction patterns for this section of analysis, I used single-season models to simplify parameterization.

3.2.3 Data Estimation and Selection

Data in year one were sparse (i.e. missing survey occasions and large numbers of non-detections), so complex and highly parameterized models did not meet convergence criteria when seasons were considered separately. I was more interested in the effect of habitat on dynamic occupancy and transience rates, which should be driven by similar habitat variables across years, than in comparing occupancy in different years, so I combined data from both years into a single data set. Because Rusty Blackbird abundance in Louisiana is variable from year to year, comparing site use from one year to the next at the same site might actually be misleading. The overall number of birds in the region may result in differences in site use not directly related to actual habitat conditions. For example, a site may change occupancy status from year to year, not because of any change in habitat characteristics, but due to a change in bird saturation of the overall region. Within a year, however, subtle changes in available habitat should influence site selection by a relatively constant regional pool of birds. I modeled round-to-round differences within a season to examine the patterns driving site selection, but accounted for between year differences by modeling year as a detectability covariate.

I modeled detectability in a separate analysis prior to constructing habitat or co-occupancy models. A larger data set was available to examine detectability alone than detectability modeled together with occupancy, and separate modeling allowed for testing a larger number of parameters (e.g. Powell 2008, Richmond et al. 2010). I examined detectability using the full 200 m avian survey data set, which included all birds detected within 200 m by either survey method, at all 97 sites (618 survey occasions) surveyed in either year. All but one detectability parameter varied on a survey-by-survey basis, so sites monitored in both years were considered to be independent for this part of the analysis.

For 100m habitat analysis, I used data from only one year at each site, to avoid potential pseudoreplication of habitat characteristics. Data were selected based on completeness of survey history and by presence of birds in at least one round. If all else was equal, data from one year was chosen randomly. Because survey sites were selected based on prior knowledge of bird presence, and then selected for inclusion in the data set based on number of surveys and presence of birds, the majority of sites were occupied, especially during the first round. As a result, multi-season models had difficulty estimating initial occupancy. I included 16 randomly selected survey sites from year one to use in estimating initial occupancy. In year two, no random sites were surveyed, but some of the sites chosen based on having birds the previous year were now unoccupied during the first round. The final data set used for multi-season models consisted of surveys from 73 unique sites and the corresponding habitat data. Twenty-five meter habitat data was only measured in 2011, so only 39 sites were available for microhabitat models. Two-species occupancy models were run as separate single-season models where round was still considered to be equivalent to season, so all unique sites surveyed in the first round (63) and all sites surveyed in the second round (72) were used. The third round was eliminated due to sparse data. I would not expect results from these rounds to be different, since detectability and occupancy in the first two rounds were fairly similar.

In some cases habitat data were not taken on all rounds. Sites were only included in final analysis if habitat data were available for at least two of the three rounds and could be estimated for the missing round (necessary for use in multi-season models). Estimated data were based on the average of first and last round values in the case of missing round two data, and were based on the previous or subsequent round in the case of missing first or last round data respectively.

This is a conservative approach which, if anything, would weaken any habitat relationship trends rather than assuming any directional change.

3.2.4 Detectability Analysis

I used a multi-season framework to account for potential detectability differences based on survey round. I held occupancy (Ψ) colonization (γ) and extinction (ϵ) constant, and allowed detectability (P) to vary. There were greater differences in raw occupancy and detectability rates between round three and any other round in both years than there were between rounds one and two in 2010 and 2011. Therefore I re-parameterized round in the model structure, so detectability during rounds 1 and 2 was calculated with the same intercept, but round 3 was calculated separately (Appendix III). To account for any potential differences among years, I also included year as a detectability parameter. Occupancy itself may have also varied by round or season, but to focus on the impact of habitat in later models, I modeled detectability as a nuisance parameter.

Prior to building detectability model sets, I eliminated survey-specific variables that seemed to lack biological significance, had little variability between surveys, or were highly correlated (Spearman Rank Correlation Test $p \geq 0.5$) with other variables that would explain the same effect (Appendix IV.1). Nine variables were retained (Table 3.1). I log-transformed the variables flock, RWBL and COGR to approximate a situation where larger numbers of birds have more impact on Rusty Blackbird detectability than smaller, but the influence asymptotes as accompanying flock size increases. Only flock size and the two individual species variables were highly correlated, so I avoided including these variables in the same model. I transformed all variables to have values between zero and three for use in PRESENCE, and built an *a priori*

set of 25 models to test detectability variables at the 97 sites surveyed in either season, and 22 models to test detectability variables at the 44 sites surveyed in 2011 (Appendix IV.2,3).

Table 3.1. Variables included in detectability modeling. Variables were measured within a 200 m radius of the point count site* and within the 15-minute point count and 30-minute extended area search.

variable	description	type**	correlations
year	year surveyed (2010 =1 or 2011=2)	site	-
round	survey from rounds 1 and 2 (=0) or round 3 (=1)	structural	-
weather	sunny =1, partly cloudy =2, overcast =3, rain =4	survey	-
wind	wind speed 1-5 on the Beaufort scale (season 2 only)	survey	-
prior	RUBL previously detected within 200 m	survey	-
flock	log (# other blackbirds + AMRO) on point count and or associated with RUBLS within 200 m	survey	COGR, RWBL
COGR	log (# COGR) present on point count and or associated with RUBLS within 200 m	survey	Flock, RWBL
RWBL	log (# RWBL) on point count and or associated with RUBLS within 200 m	survey	Flock, COGR
open	amount of grassy area averaged over all rounds (approximates amount of open space)	site	-

AMRO = American Robin, COGR = Common Grackle, RUBL = Rusty Blackbird, and RWBL = Red-winged Blackbird

*variable open measured within a 100 m radius habitat sampling circle

** Site-specific variables remained the same throughout a survey year and have only one measurement. Survey-specific variables were measured on each survey occasion. Structural variables are incorporated into the model structure using intercepts.

3.2.5 Multi-season Habitat Association Analysis

I modeled the relationship of Ψ and ϵ , based on 200 m avian survey data, with 100 m and 25 m habitat data. Colonization (γ) was held constant, and P was based on previous analysis. For habitat covariates that varied by round, initial Ψ at each site was based on habitat conditions in round one; ϵ between rounds one and two was based on habitat conditions in round two; and ϵ between rounds two and three was based on habitat conditions in round three (ϵ based on conditions at time $t+1$). Prior to building habitat occupancy models, I eliminated variables which

seemed to lack biological significance (based on raw data trends and field observations), had very little variability between surveys, or were highly correlated (Spearman rank correlation test $\rho \geq 0.5$) with another variable that would explain the same effect (Appendix V.1, 2). Five 100 m variables and seven 25 m variables were retained (Table 3.2, 3.3). Several retained variables were highly correlated but had different biological interpretations. No correlated variables were placed together in the same model. All variables were transformed to values from 0-3 for use in PRESENCE. I built an *a priori* set of 27 models to test 100 m habitat variables at 73 independent sites and 26 models to test 25 m habitat variables at 39 sites (Appendix V3, 4).

In addition to the standard occupancy models, I ran a 100 m model set in which occupancy was adjusted to include only sites used by relatively large flocks of Rusty Blackbirds. It seems likely that abundance could be an important indicator of site quality in a flocking species like the Rusty Blackbird. The median flock size at occupied sites was seven birds, so I considered a site to be occupied on a given survey occasion only if a flock of seven or more birds was detected. Data were too sparse to also test 25 m models for flock occupancy.

Table 3.2. Large-scale (100 m) habitat variables included in occupancy models. Variables were estimated within a 100 m radius sampling circle*.

variable	description	type**	correlations
water	% ground covered by water	round	shallow, grass, toforest
shallow	% ground covered by shallow water	round	water, wetlitter
grass	% ground covered by short vegetation or lawn	round	water, toforest
wetlitter	% ground covered by wet leaf-litter	round	shallow
toforest	average distance to nearest substantial tree cover	site	water, grass

* Toforest was paced out or measured by GPS to the appropriate distance from the primary point regardless of sampling circle

**Site-specific variables remained the same throughout a survey-year and have only one measurement. Variables that vary by round were entered as three separate site-specific variable columns and then assigned to the correct parameter within PRESENCE.

Table 3.3. Small scale (25 m) habitat variables included in occupancy models. Variables were measured within a 25 m radius sampling circle*.

variable	description	type	correlations
towater	distance to water of any kind	round	water
water	water depth	round	towater
litter	litter depth	round	toforest, visobs
visobs	average visual obstruction at 1 m height	site	litter
trees	number of trees or stems >1 cm DBH	site	toforest, visobs
DBH	average DBH	site	-
toforest	average distance to nearest substantial tree cover	site	toforest, visobs

* Towater and toforest were paced out or measured by GPS to the appropriate distance from the primary point regardless of sampling circle

**Site-specific variables remained the same throughout a survey year and have only one measurement. Variables that vary by round were entered as three separate site-specific variable columns and then assigned to the correct parameter within PRESENCE.

3.2.6 Two-species Co-occurrence Analysis

I modeled the co-occurrence of Rusty Blackbirds with Common Grackles and with Red-winged Blackbirds, using 200 m survey data and 100 m habitat variables to account for possible habitat affects that could be driving occupancy or detectability. I compared models where Rusty Blackbird Ψ or P was modeled independently from a more prevalent species (unconditional models) with models where Rusty Blackbird Ψ and P are conditional on Ψ and P of the other species. In conditional occupancy models, the probability of detecting Rusty Blackbirds given presence of species A (Ψ_{AB}) is modeled separately, and allowed to differ from the probability that Rusty Blackbirds occupy the site alone (Ψ_{Ba}). Similarly, detectability (r in co-occurrence models) can be modeled conditionally such that the probability of detecting Rusty Blackbirds when both species are detected (r_{BA}) is modeled separately and allowed to differ from the probability of detecting Rusty Blackbirds alone (r_{Ba}) (Table 3.4, Appendix VI.1).

Table 3.4. Variables used in two-species model sets and the model parameters to which they apply. Conditional and unconditional variables are structural variables coded for using different arrangements of model intercepts (Appendix VI.1).

variable(s)	parameter	description
conditional	Ψ	$\Psi_{BA} \neq \Psi_{Ba}$, no habitat affect
conditional +conditional habitat	Ψ	$\Psi_{BA} \neq \Psi_{Ba}$, habitat affects Ψ_{BA} differently from Ψ_{Ba}
conditional +unconditional habitat	Ψ	$\Psi_{BA} \neq \Psi_{Ba}$, habitat affects Ψ_{BA} and Ψ_{Ba} in the same way
unconditional	Ψ	$\Psi_{BA} = \Psi_{Ba}$, no habitat affects
unconditional +unconditional habitat	Ψ	$\Psi_{BA} = \Psi_{Ba}$, habitat affects Ψ_{BA} and Ψ_{Ba} in the same way
conditional	P	$r_{BA} \neq r_{Ba}$, no habitat affect
conditional +unconditional habitat	P	$r_{BA} \neq r_{Ba}$, habitat affects r_{BA} and r_{Ba} in the same way
unconditional	P	$r_{BA} = r_{Ba}$, no habitat affect
unconditional +unconditional habitat	P	$r_{BA} = r_{Ba}$, habitat affects r_{BA} and r_{Ba} in the same way
habitat = shallow	Ψ	Occupancy is affected by % ground cover of shallow water.
habitat = open	Ψ or P	Detectability or occupancy is affected by amount of open space (average % grassy cover).

Rusty Blackbirds may associate with other species differently in different habitat types, and failure to account for effects of habitat on occupancy and detectability can result in misleading results, so I also incorporated detectability and habitat variables into analysis (Richmond et al. 2010). Variables were allowed to either impact both species in the same way or to vary, in conditional models (Table 3.4). I included shallow water and grassy cover as habitat variables. Shallow water was most likely to be important to Rusty Blackbird occupancy based on 100 m analysis (see Results), and I wanted to test the hypothesis that interactions with other

species were different in grassy/open habitat. Detectability variables included were also slightly different from previous models where flock-size, round, and year were used. I ran separate model sets for each round, with years combined, and because flock size correlated with the presence of grackles or Red-winged Blackbirds, so this variable was eliminated. Models did not meet convergence criteria when year was used as a detectability covariate, due to small sample sizes, so this variable was also dropped. I re-tested open space as a detectability covariate, since it had some model support in season two and could be more important for detection of other blackbirds than for Rusty Blackbirds alone. I allowed habitat variables to affect occupancy by species differently in conditional models, but assumed that open space would have the same impact on detectability of all species (Table 3.4, Appendix VI.1). I tested a set of 27 *a priori* models for Rusty Blackbirds and Common Grackles, and for Rusty Blackbirds with Red-winged Blackbirds in round one and in round two using combinations of the variables described in table 3.4 (Appendix VI.2).

3.3 Results

3.3.1 Detectability Models

Two detectability models received substantial model support (within $\Delta 2$ AICc) and accounted for 86% of available model weight (Table 3.5). After model averaging, the most important variable was log flock size of other species (Figure 3.1). Log of flock size was positively associated with detectability, indicating that generally, larger flocks of other species lead to more Rusty Blackbird detections. Year was not significantly different in importance than flock, and indicated higher detectability in 2011 as expected. Round was also important, and confirmed lower detectability in the third round but was significantly less important than year or flock (Figure 3.1).

Table 3.5. Top eight detectability models accounting for 95% of available model weight* plus the null model. AIC model weight is the relative likelihood that the model fits the original data. AICc is adjusted for small sample size (k). Models (within $\Delta 2$ AICc were included in model averaging). Detectability is negatively related to round, time since sunrise and cloud cover and positively related to flock size, year and open space.

model	AICc	Δ AICc	AIC weight	k	-2log likelihood
$\Psi(.)\gamma(.)\epsilon(.)P(\text{year}+\text{flock})$	634.34	0.00	0.4924	6	621.41
$\Psi(.)\gamma(.)\epsilon(.)P(\text{round}+\text{year}+\text{flock})$	634.91	0.57	0.3703	7	619.65
$\Psi(.)\gamma(.)\epsilon(.)P(\text{round}+\text{flock})$	639.53	5.19	0.0368	6	626.60
$\Psi(.)\gamma(.)\epsilon(.)P(\text{flock})$	639.86	5.52	0.0312	5	629.20
$\Psi(.)\gamma(.)\epsilon(.)P(\text{flock}+\text{time})$	640.28	5.94	0.0253	6	627.35
$\Psi(.)\gamma(.)\epsilon(.)P(\text{global}^{**})$	641.09	6.75	0.0168	11	615.98
$\Psi(.)\gamma(.)\epsilon(.)P(\text{flock}+\text{open})$	641.78	7.44	0.0119	6	628.85
$\Psi(.)\gamma(.)\epsilon(.)P(\text{flock}+\text{weather})$	641.94	7.60	0.0110	6	629.01
$\Psi(.)\gamma(.)\epsilon(.)P(.)$	674.61	40.72	0.0000	4	666.18

*16 additional models were tested but had model weight <1% (Appendix IV.4)

**global = $P(\text{year}+\text{round}+\text{time}+\text{weather}+\text{prior}+\text{flock}+\text{open})$

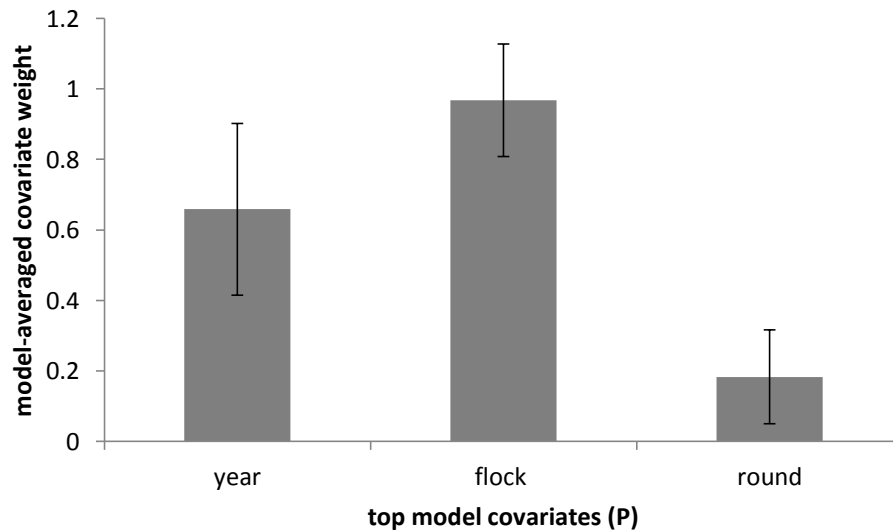


Figure 3.1. Model averaged covariate weights associated with detectability (P) in the model set testing detectability for all 97 site/seasons. Model averaged covariate weights are the absolute values of the sums of model weighted parameter estimates from all models (within $\Delta 2$ AICc). Model averaged weights with original signs \pm SE are as follows: flock 0.97 ± 0.16 , year 0.66 ± 0.24 and round -0.18 ± 0.13 .

I also tested detectability in season two alone, to confirm results and to see if the variable wind, which was only measured in 2011, had significant model support. Six models had some support (Appendix IV.4, 5). After model averaging, log flock size and the highly correlated log number of Red-winged Blackbirds appeared to be the most important variables. Open space received a similar amount of model support, which could indicate some importance as a detectability variable. Because open space was not important in the overall data set, and because I wanted to test the highly correlated variable grassy cover as an occupancy variable, it was not included in multi-season habitat models. Round had some model support, but significantly less weight than other variables. Wind also received some model support, but less model-averaged weight than any of the other parameters.

Overall results of 2011 detectability models were congruent with combined-year models, and it is unlikely that excluding wind as a variable in the overall data set would change overall results (Appendix IV.5). Prior to incorporating top detectability variables into habitat occupancy models, I also retested the detectability model set on the reduced data set of 73 independent sites used in 100 m habitat models. The same two detectability models received substantial model support as in the full data set, and accounted for 93% of total available model weight. Flock, year and round all received similar and significant model weights (Appendix IV.6). Based on results of detectability models, the final variables selected for incorporation into multi-season habitat models were flock, year and round. Open space was included in habitat models as an occupancy variable (grass) and was later re-tested for importance as an occupancy or detectability variable in single-season, two-species occupancy models.

3.3.2 Habitat Association Models

Four top habitat models (within $\Delta 2$ AICc) explained relationships of Rusty Blackbird occupancy and transience at sites with 100 m habitat variables and accounted for 57% of available model weight (Table 3.6, Appendix V.5). The best model showed good fit (Chi-square Goodness-of-Fit test, $\chi^2 = 33.64$, $df = 61$, $\alpha = .05$, $p = 0.99$), indicating that model results are not significantly different from the observed pattern of occupancy, and that model set results should be an adequate description of real relationships.

Table 3.6. Top six 100 m occupancy/transience models (accounting for 70% of available model weight)* plus the null models**. AIC model weight is the relative likelihood that the model fits the original data. AICc is adjusted for small sample size (k). Models within $\Delta 2$ AICc were included in model averaging for habitat covariates. Models were tested on the set of 73 independent sites. For all models except null $P = (\text{season} + \text{round} + \text{flock})$. Occupancy is positively related to shallow water, grass and wet litter and negatively related to water cover. Extinction is negatively related to shallow water, wet litter and grass and positively related to water cover.

model	AICc	Δ AICc	AIC weight	k	-2log likelihood
$\Psi(\text{shallow} + \text{grass})\gamma(.)\epsilon(\text{shallow} + \text{grass})$	464.95	0.00	0.2126	11	438.62
$\Psi(\text{wetlitter} + \text{grass})\gamma(.)\epsilon(\text{wetlitter} + \text{grass})$	465.60	0.65	0.1536	11	439.27
$\Psi(\text{water})\gamma(.)\epsilon(.)$	466.33	1.38	0.1066	8	448.08
$\Psi(\text{grass})\gamma(.)\epsilon(\text{grass})$	466.42	1.47	0.1019	9	445.56
$\Psi(\text{water})\gamma(.)\epsilon(\text{water})$	467.15	2.20	0.0708	9	446.29
$\Psi(\text{grass})\gamma(.)\epsilon(.)$	467.87	2.92	0.0494	8	449.62
$\Psi(.)\gamma(.)\epsilon(.)$	469.43	4.48	0.0226	7	453.71
$\Psi(.)\gamma(.)\epsilon(.)P(.)$	17.86	52.91	0.0000	4	509.27

*19 additional models were tested but had model weight <5% (Appendix V.5)

** Due to correlated variables, it was not possible to build a true global model. The most parameterized models had 11 parameters and ranked 1st, 2nd, 7th 8th and 10th in the overall set (Appendix V.5).

After model averaging, wet litter and shallow water received about the same amount of model support. Grass received significantly less support than wet litter but was within the range

of error for shallow water. Water received some model support but significantly less than any of the other variables (Figure 3.2). The relationship between Rusty Blackbird occupancy and amount of wet litter and shallow water was positive, as expected. Of 82 occupied survey rounds, 77 (93%) corresponded to sites having at least some shallow water or wet litter present.

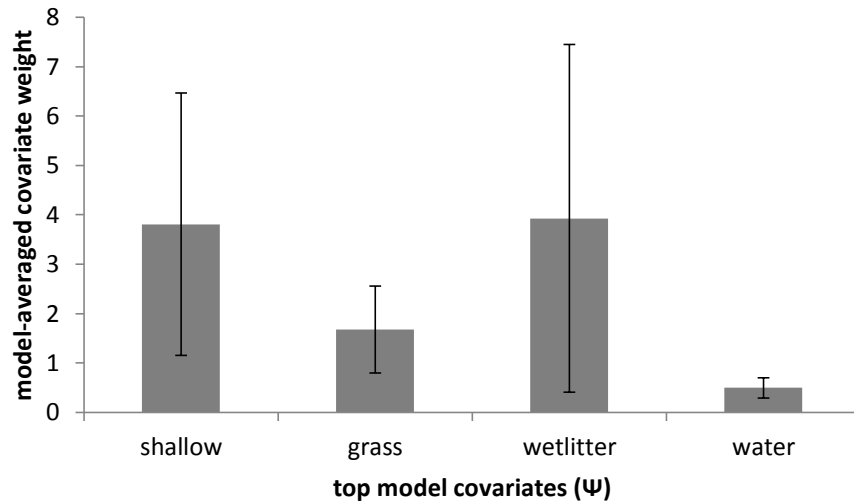


Figure 3.2. Model averaged covariate weights associated with the occupancy parameter Ψ in top 100 m habitat models. Model averaged covariate weights are the absolute values of the sums of model weighted parameter estimates from all models (within $\Delta 2$ AICc). Model averaged weights with original signs \pm SE are as follows: shallow 3.81 ± 2.66 , wet litter 3.93 ± 3.52 , grass 1.66 ± 0.88 , and water -0.50 ± 0.21

However, these ground cover types were common overall and 81 of 105 (77%) unoccupied rounds also occurred at sites with wet litter or shallow water. Only 29 of 187 habitat surveys had no shallow water or wet leaf-litter present, but of these, 24 (83%) corresponded to an unoccupied survey round. Average (\pm SE) percent of ground covered by wet litter and shallow water combined was higher (13.2 ± 1.6) at occupied sites than at unoccupied sites (9.0 ± 1.1).

However, the relationship between Rusty Blackbird occupancy and overall water cover was negative and the relationship between occupancy and grassy groundcover was unexpectedly positive.

After model averaging for transience (extinction), the shallow water variable received the most model support, followed by grass and wet litter (Figure 3.3). Wet litter is slightly less significant than shallow water, but error bars of both overlap with grass cover. As expected, transience was negatively related to shallow water and wet litter, with extinction between rounds lower at sites retaining wet ground cover. However the relationship between grassy groundcover and transience was also negative. To ensure that higher transience between the second and third round (see Appendix III) was not driving habitat trends, I also tested the same model set on rounds one and two alone, and found similar results. Two and three round model sets had the same two top-ranked models and shallow water and wet litter variables received the most model averaged support in both sets (Appendix V.6).

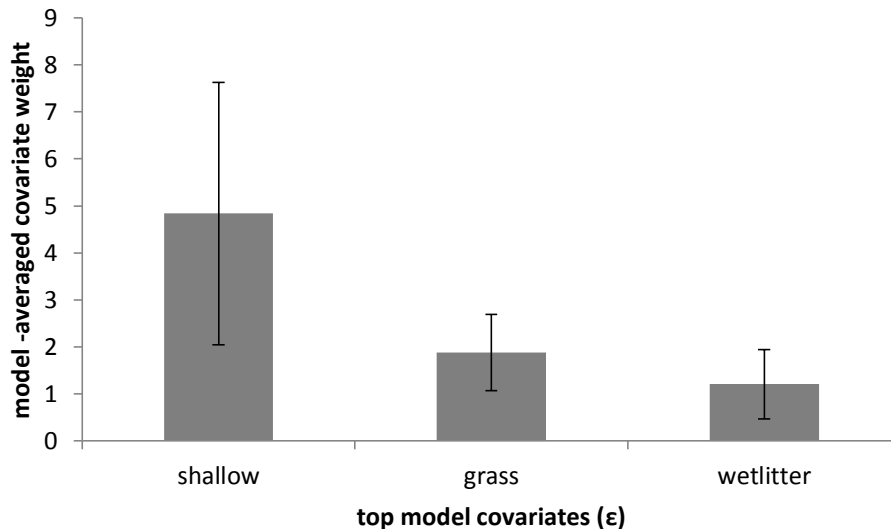


Figure 3.3. Model averaged covariate weights associated with the transience parameter ϵ (local extinction) in top 100 m habitat models. Model averaged covariate weights are the absolute values of the sums of model weighted parameter estimates from all models (within $\Delta 2$ AICc). Model averaged weights with original signs \pm SE are as follows: shallow -4.84 ± 2.79 , grass -1.88 ± 0.81 and wet litter -1.21 ± 0.74 .

After adjusting occupancy to equal median flock size of seven birds and running the same 100 m habitat model set, only one model had substantial support (Table 3.7, Appendix V.7). This model accounted for 74% of total available model weight. The model showed good fit (Chi-Square Goodness-of-Fit test, $\chi^2 = 13.50$, $df = 61$, $\alpha = .05$, $p > 0.99$). Wet litter and water received support as occupancy and transience variables, with wet litter receiving significantly more model weight for both parameters (Figure 3.4, 3.5). The relationship between occupancy and amount of wet leaf litter was positive, and the relationship with overall amount of water cover remained negative. The relationship between transience and wet leaf-litter was negative, as expected, and the relationship with overall water cover was positive.

Table 3.7. Top five 100 m abundance-adjusted occupancy/transience models (accounting for 98% of available model weight)*, plus the null models.** AIC model weight is the relative likelihood that the model fits the original data. AICc is adjusted for small sample size (k). Models within $\Delta 2$ AICc were included in model averaging for habitat covariates. Models were tested on the set of 73 independent sites. For all models except null $P =$ (season+round+flock). Occupancy is positively related to wet litter, and grass and negatively related to water cover. Extinction is negatively related to wet litter and positively related to water cover.

model	AICc	Δ AICc	AIC weight	k	-2log likelihood
$\Psi(\text{wetlitter}+\text{water})\gamma(.)\epsilon(\text{wetlitter}+\text{water})$	314.01	0.00	0.7362	11	287.68
$\Psi(\text{wetlitter}+\text{grass})\gamma(.)\epsilon(\text{wetlitter}+\text{grass})$	317.80	3.79	0.1107	11	291.47
$\Psi(\text{water})\gamma(.)\epsilon(\text{wetlitter})$	318.32	4.31	0.0853	9	297.46
$\Psi(\text{grass})\gamma(.)\epsilon(\text{wetlitter})$	319.90	5.89	0.0387	9	299.04
$\Psi(\text{water})\gamma(.)\epsilon(.)$	323.42	9.41	0.0067	8	305.17
$\Psi(.)\gamma(.)\epsilon(.)$	327.05	13.04	0.0011	7	311.33
$\Psi(.)\gamma(.)\epsilon(.)P(.)$	352.65	38.64	0.0000	4	344.06

*20 additional models were tested but had model weight <1% (Appendix V.7)

** Due to correlated variables it was not possible to build a true global model. The most parameterized models had 11 parameters and ranked 1st, 2nd, 18th, 24th and 25th in the overall set (V.6).

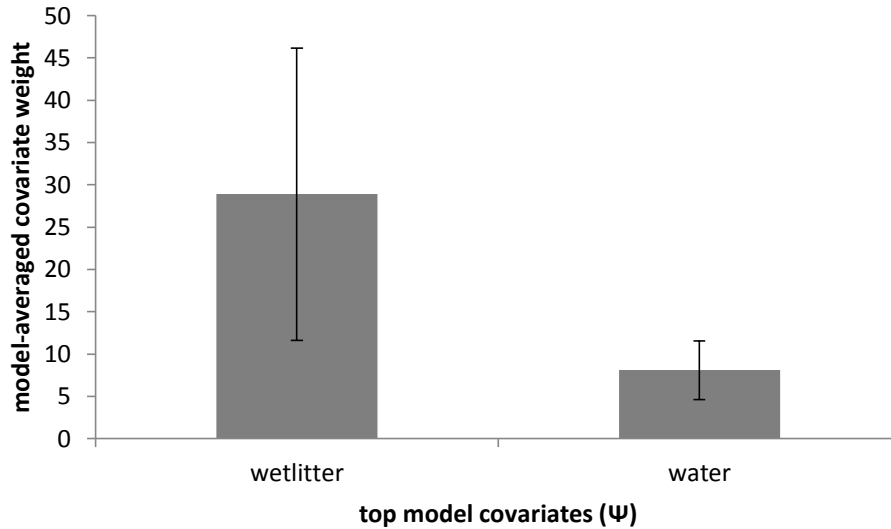


Figure 3.4. Model averaged covariate weights associated with the parameter Ψ in top 100 m habitat models estimating occupancy by a flock of at least seven birds. Model averaged covariate weights are the absolute values of the sums of model weighted parameter estimates from all models (within $\Delta 2$ AICc). Model averaged weights with original signs \pm SE are as follows: wet litter 28.89 ± 17.26 and water -8.10 ± 3.47 .

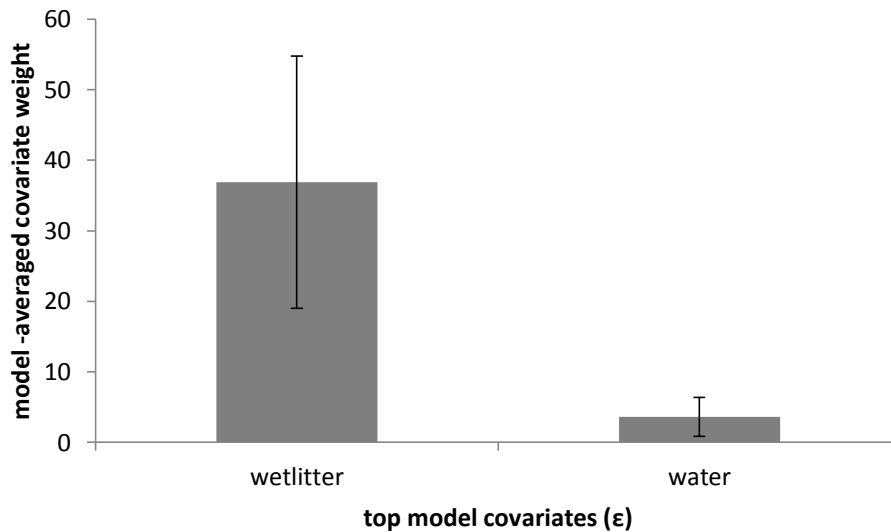


Figure 3.5. Model averaged covariate weights associated with the parameter ϵ (local extinction) in top 100 m habitat models estimating transience in flocks of at least seven birds. Model averaged covariate weights are the absolute values of the sums of model weighted parameter estimates from all models (within $\Delta 2$ AICc). Model averaged weights with original signs \pm SE are as follows: wet litter -36.88 ± 17.87 , and water 3.63 ± 2.76 .

For multi-season models where habitat was measured at the 25 m scale, there were two models with support within $\Delta 2$ AICc, accounting for 52% of available model support (Table 3.8,

Appendix V.8). Model fit for the top model was good (Chi-Square Goodness-of-Fit test $\chi^2 = 19.50$, $df = 31$, $\alpha = .05$, $p = 0.95$). Only visual obstruction received support as an occupancy variable, and only distance to nearest water received model support as a transience variable. Post hoc testing indicated that open understory was more important as an occupancy variable than as a detectability variable (Appendix V.8). Occupancy was negatively related to visual obstruction, and extinction was negatively related to distance to water. Data were too sparse for models in the 25 m habitat set to converge when occupancy was adjusted to model flocks of seven birds or more.

Table 3.8. Top five 25 m occupancy/transience models (accounting for 73% of available model weight)* plus the null and global models**. AIC model weight is the relative likelihood that the model fits the original data. AICc is adjusted for small sample size (k). Models within $\Delta 2$ AICc were included in model averaging for habitat covariates. Models were tested on a set of 39 sites sampled in 2011. For all models except null $P = (\text{round} + \text{flock})$. Occupancy is negatively related to visual obscurity and litter depth and positively related to distance to forest. Extinction is negatively related to distance to water and water cover.

model	AICc	Δ AICc	AIC weight	k	-2log likelihood
$\Psi(\text{visobs})\gamma(.)\epsilon(.)$	327.66	0.00	0.3735	7	310.05
$\Psi(\text{visobs})\gamma(.)\epsilon(\text{towater})$	329.53	1.87	0.1466	8	308.73
$\Psi(\text{visobs})\gamma(.)\epsilon(\text{water})$	330.68	3.02	0.0825	8	309.88
$\Psi(\text{toforest})\gamma(.)\epsilon(.)$	330.69	3.03	0.0821	7	313.08
$\Psi(\text{litter})\gamma(.)\epsilon(.)$	331.81	4.15	0.0469	7	314.20
$\Psi(.)\gamma(.)\epsilon(.)$	335.49	7.83	0.0074	7	317.88
$\Psi(\text{global})^1$	344.81	17.15	0.0004	12	308.81
$\Psi(\text{global})^2$	345.99	18.33	0.0001	12	309.99
$\Psi(.)\gamma(.)\epsilon(.)P(.)$	358.55	38.64	0.0000	4	349.37

*16 additional models were tested but had model weight <5% (Appendix V.8)

** Due to correlated variables it was not possible to build a true global model. The most parameterized models were global¹ $\Psi(\text{towater} + \text{toforest} + \text{DBH})\gamma(.)\epsilon(\text{towater} + \text{toforest} + \text{DBH})$ and global² $\Psi(\text{water} + \text{toforest} + \text{DBH})\gamma(.)\epsilon(\text{water} + \text{toforest} + \text{DBH})$.

3.3.3 Two-species Models

Modeling association between Rusty Blackbirds and Red-winged Blackbirds with incorporated habitat covariates resulted in the same top model in both rounds. This model indicates that detectability of Rusty Blackbirds is conditionally related to detection of Red-winged Blackbirds (detection together is more likely than independent detection of both species), and that occupancy of a site by Rusty Blackbirds is conditionally dependent on occupancy by Red-winged Blackbirds (occupancy together is more likely than if species were selecting sites independently), with occupancy of both species being impacted in the same way by amount of open grassy ground cover at a site (Table 3.9). However, both rounds had additional model

Table 3.9. Co-detection and co-occupancy between Red-winged Blackbirds and Rusty Blackbirds during round 1(a) and round 2(b). The top three models in both rounds received substantial model support (within $\Delta 2$ AICc) and accounted for 60% of model weight in round one and 62% of model weight in round two. Also shown are models with at least 10% of AIC weight, null and global (most parameterized) models. Occupancy and detectability are positively related to grass and shallow water. See Appendix VI.3 and VI.4 for additional models.

a)

model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
$\Psi(\text{cond}+\text{grass}),p(\text{cond})$	416.57	0.00	0.2559	1.0000	7	400.53
$\Psi(\text{uncond}),p(\text{cond}+\text{grass})$	417.17	0.60	0.1896	0.7408	6	403.67
$\Psi(\text{cond}),p(\text{cond}+\text{grass})$	417.53	0.96	0.1583	0.6188	7	401.49
$\Psi(\text{uncond}+\text{shallow}),p(\text{uncond})$	419.02	2.45	0.0752	0.2938	5	407.97
$\Psi(\text{uncond}+\text{grass}),p(\text{cond})$	419.18	2.61	0.0694	0.2712	6	405.68
$\Psi(\text{uncond}+\text{shallow}),p(\text{cond}+\text{grass})$	419.54	2.97	0.0580	0.2265	7	403.50
$\Psi(\text{cond}+\text{condshallow}),p(\text{cond}+\text{grass})$	423.67	7.10	0.0074	0.0287	10	399.44
$\Psi(.),p(.)$	427.20	10.63	0.0013	0.0049	2	423.00

b)

$\Psi(\text{cond}+\text{grass}),p(\text{cond})$	500.56	0.00	0.2339	1.0000	7	484.81
$\Psi(\text{cond}+\text{grass}),p(\text{uncond})$	500.75	0.19	0.2127	0.9094	6	487.46
$\Psi(\text{uncond}+\text{grass}),p(\text{cond})$	500.99	0.43	0.1886	0.8065	6	487.70
$\Psi(\text{uncond}+\text{grass}),p(\text{uncond})$	502.64	2.08	0.0827	0.3535	5	491.73
$\Psi(\text{cond}+\text{condgrass}),p(\text{cond})$	502.98	2.42	0.0697	0.2982	9	482.08
$\Psi(\text{cond}+\text{condgrass}),p(\text{uncond})$	503.12	2.56	0.0650	0.2780	8	484.83
$\Psi(.),p(.)$	509.15	8.59	0.0032	0.0136	2	504.98
$\Psi(\text{cond}+\text{condshallow}),p(\text{cond}+\text{grass})$	513.81	13.25	0.0003	0.0013	10	490.20

support for competing models (Table 3.9). Four of the top six models (within $\Delta 2$ AICc in either round) supported conditional occupancy, and five of the six indicated conditional detectability. Amount of grassy cover appeared as a variable increasing either occupancy or detectability of both species in all six models. None of the top ranked models indicated both unconditional occupancy and detectability so results seem to indicate that detection and or occupancy of Rusty Blackbirds may be related to presence of Red-winged Blackbirds.

Modeling association between Rusty Blackbirds and Common Grackles with habitat covariates resulted in the same top model in both rounds. This model indicated that detectability of Rusty Blackbirds is conditionally related to detection of Common Grackles (detection together is more likely than independent detection of species), but that occupancy of a site by Rusty Blackbirds is independent of occupancy by grackles, with occupancy of both species being impacted in the same way by amount of open grassy ground cover at a site (Table 3.10).

Table 3.10. Co-detection and co-occupancy between Common Grackles and Rusty Blackbirds during round 1(a) and round 2(b). The top two models in round one and the top three models in round two received substantial model support (within $\Delta 2$ AICc), and accounted for 93% of model weight in round one and 74% of model weight in round two. Also shown are models with at least 10% of AIC weight, null and global (most parameterized) models. Occupancy and detectability are positively related to grass and shallow water. See Appendix VI.5 and VI.6 for additional models.

a)

model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
$\Psi(\text{uncond}+\text{grass}),p(\text{cond})$	369.7	0.00	0.6025	1.0000	6	356.20
$\Psi(\text{cond}+\text{grass}),p(\text{cond})$	370.9	1.20	0.3306	0.5488	7	354.86
$\Psi(\text{cond}+\text{condshallow}),p(\text{cond}+\text{grass})$	388.68	18.98	0.0000	0.0001	10	364.45
$\Psi(.),p(.)$	399.85	30.15	0.0000	0.0000	2	395.65

b)

$\Psi(\text{uncond}+\text{grass}),p(\text{cond})$	456.54	0.00	0.3655	1.0000	6	443.25
$\Psi(\text{uncond}+\text{grass}),p(\text{uncond})$	457.05	0.51	0.2832	0.7749	5	446.14
$\Psi(\text{cond}+\text{grass}),p(\text{cond})$	458.95	2.41	0.1095	0.2997	7	443.20
$\Psi(\text{cond}+\text{grass}),p(\text{uncond})$	459.24	2.70	0.0947	0.2592	6	445.95
$\Psi(.),p(.)$	461.74	5.20	0.0271	0.0743	2	457.57
$\Psi(\text{cond}+\text{condshallow}),p(\text{cond}+\text{grass})$	473.07	16.53	0.0001	0.0003	10	449.46

However, round one models had some convergence problems, and both rounds had additional model support for competing models (Table 3.10, Appendix VI.4). Results linking co-occupancy and co-detection of Common Grackles and Rusty Blackbirds are inconclusive.

3.4 Discussion

3.4.1 Detectability

Flock size of other species accompanying Rusty Blackbirds, survey year, and survey round were consistently supported as important detectability variables. Wind and open space received limited support as detectability variables. In the full set of all surveys over both years, in year two alone, and in the data set used for habitat occupancy models, log of flock size was the most important variable, with larger flocks of accompanying species increasing Rusty Blackbird detectability. In future studies, all these variables should be considered for impact on detectability.

Seasonal timing, regional population of birds, flock size, distribution throughout a region or flocking behavior could all differ within or between survey years, and could potentially change Rusty Blackbird occupancy or detectability. While considered nuisance variables in this study and modeled as detectability variables, it is important to realize that seasonal variation needs to be accounted for in any study of Rusty Blackbirds. Similarly, it is important to remember that detectability estimation is needed to account for intrinsic problems of daily nomadic behavior.

Log flock size was modeled to approximate a relationship in which presence in flocks with more common, highly vocal species makes Rusty Blackbirds more detectable, but in which increasing flock size no longer pays off after some point. The strong positive correlation

between detectability and log flock size seen in models indicates that this relationship is reasonable. Detectability analysis of season two data shows that log number of Red-winged Blackbirds, the most commonly detected species, has a significant positive effect on Rusty Blackbird detectability similar to overall log flock size. This may suggest that interactions with Red-winged Blackbirds are more important than previously thought, or may simply reflect how common Red-winged Blackbirds are in similar habitats in Louisiana. Log number of Common Grackles, the second most common species, received no model support. While previous studies have noted co-occurrence with Common Grackles, none have examined interactions with Red-winged Blackbirds. Co-occurrence with other species may have implications beyond accounting for detectability. Understanding Rusty Blackbird interactions with other species could be important to understanding population decline. I further investigated Rusty Blackbird detectability, occupancy and habitat when associated with Common Grackles and Red-winged Blackbirds, using two-species occupancy models.

Wind speed received some model support although significantly less than other variables. It has been noted that detectability decreases with higher wind, either due to changes in foraging and flying behavior or due to interference with observer ability to hear calls and wind was shown to be an important detectability variable in a previous study (Ralph et al. 1995, Powell 2008). However, in this study Rusty Blackbirds birds seemed to forage mainly on the ground away from the influence of all but heavy winds and were detected visually in most cases (Chapter 2). Wind may have less effect upon detectability of this species on the wintering grounds. Wind data was only recorded in season two, so the variable was not included in final occupancy models, but its exclusion should not have greatly impacted model results.

Open space was a difficult variable to interpret. Although this variable did not have any model support in the combined-season models, it is possible that birds are more detectable in open areas. Open space did receive significant model support in season two alone, although the standard error on the model-weighted estimate was larger than for any other variable. It also received model support in two-species models with Red-winged Blackbirds. Because this variable is actually the average of amount of open lawn space during each round, it could also be included as a habitat variable. Grassy area ranked low in model sets as a detectability variable but high as an occupancy variable and models including visual obstruction as a detectability variable had less support than models including it as a habitat variable for occupancy. It seems as though open space is better tested as an occupancy variable, but unexpectedly high occupancy rates and lower transience at open grassy sites could still reflect some confounding effects of higher detectability at these sites.

3.4.2 Habitat Association

As predicted, wet ground cover and shallow water were important indicators of site occupancy, bird abundance, and persistence at sites. There is some indirect evidence that forested habitat may be important to abundance and to persistence of larger flocks, but the relationship is not as strong as predicted, and birds actually seem to associate more consistently with sites that have open space and little understory cover. Despite being less quantitative, 100 m habitat models seem to be more informative than 25 m models, which may indicate that birds are selecting habitat at larger spatial scales and/or that the degree of habitat variability at larger scales is more conducive to modeling.

At the 100m level, shallow water and wet leaf-litter receive nearly equal model support as positive predictors of occupancy. This could indicate that shallow water, regardless of underlying substrate or overall habitat type, may be just as important as more forest-specific wet leaf-litter substrate. Additionally, the significant positive relationship between occupancy and grassy ground cover and the lack of importance of distance to forest seem to indicate that forested habitat is not particularly important at this spatial scale. While further distances to forest were negatively related to occupancy this variable was very weak in all models. Birds were frequently observed foraging in wet flooded lawns, especially immediately after rain or when standing water puddles were present. Perhaps the positive relationship with open grassy area is also driven by ground moisture. Supporting this hypothesis, model sets pairing grass with water or wet litter ranked higher than grass alone. Throughout the study, birds were observed feeding in a variety of substrates including woody debris, floating vegetation, gravel, and quite frequently grass, but usually in the presence of water. Most occupied sites had shallow water or wet leaf-litter while most unoccupied sites did not.

Water cover also received some model support as a predictor of occupancy, although a less significant amount than any other variable. While overall water and shallow water are highly correlated, their relationships to occupancy are opposite. The negative relationship between occupancy and water cover makes sense, because large areas of water may be deeper, or have proportionally less edge space available for foraging. The amount of shallow water or wet ground cover present at a site is more important to Rusty Blackbird occupancy than the overall amount of water cover. General negative response to amount of overall ground covered by water could lead birds to avoid large bodies of water like lakes and impoundments, while the stronger

positive response to amount of shallow water could indicate selection of puddles and shallow more temporary pools for foraging.

Transience at sites shows a similar relationship with 100 m habitat variables to that of occupancy. Birds are more likely to persist at sites with more shallow water, wet litter or grass cover. Relationship between transience and wet litter is slightly less significant than with shallow water, but SE of both variables overlap with grass cover. While originally I had predicted that transience at more open grassy sites might be higher than in flooded forest sites, due to faster evaporation of puddles or more limited food resources, this hypothesis was not supported by models. However, grassy cover is not exclusive of shallow water or wet litter. It is possible that as long as a grassy site maintains shallow standing water, birds are in fact less likely to leave. Models combining grassy cover + shallow water and grassy cover + wet litter ranked higher than grass alone when explaining transience, and were the only explanations of transience to rank better than the null (constant rate of transience at all sites). Overall water cover was again less important than shallow water cover and had the opposite relationship, with transience more likely at sites with high water cover. Lack of importance of distance to forest and lower transience at grassy sites seem to indicate that forest cover may not be especially important to maintaining birds at sites. Shallow water, regardless of habitat type, seems to be the most important predictor of persistence of birds at sites.

Rusty Blackbirds are a flocking species, and ultimately abundance may be a more meaningful metric to describe habitat quality than occupancy. Once basic habitat requirements are better understood and birds can be more reliably located, focus on sites able to support large flocks may be most useful for conservation and monitoring. Sites that originally had large flocks but later have only a few birds may represent changes in habitat quality, so including flock-size

when examining population processes is also important. When considering 100 m occupancy and persistence at sites by at least one bird, shallow water is more important than overall water, and presence of some type of wet ground cover is more important than any specific substrate. Distance to forest seemed to be unimportant in determining occupancy or transience. After adjusting occupancy to describe a flock of seven birds or more, wet leaf-litter is the most important predictor of occupancy and transience. This model still supports positive importance of wet ground cover, but presence of leaves implies some indirect importance of trees or forest. Distance to forest was still not a good predictor of flock occupancy or transience. The difference in predictors of occupancy and transience for at least one bird vs. continued occupancy by a flock of at least seven birds seems to indicate that while birds can and frequently do use open grassy habitats, or in fact any habitat with shallow water, these sites may not be as ideal for maintaining larger flocks as sites with at least some leaf litter.

I also measured habitat associations at a 25 m scale to quantify habitat characteristics more precisely. Habitat variables measured at the 100 m scale were based largely on visual estimation, and dealt mostly with ground cover. It was possible to get real measurements of ground cover variables and more feasible to test forest variables at a smaller scale. At the 25 m habitat scale, only amount of visual obstruction at 1 m height had model support as a negative predictor of Rusty Blackbird occupancy. Results are congruent with 100 m results where grassy sites, which would have little or no understory vegetation, were positively correlated with occupancy. Often forested bottomland sites with flooded or very wet ground also have an open understory. While not significant, relationships between occupancy and persistence were positively related to small numbers of trees and large DBH. These traits could describe mature forest with large trees and little shrubby understory. Forest with open understory would also

agree with 100 m results of association with shallow water and wet litter. Based on field observations, birds did not seem to use forested sites with heavy understory vegetation. However, visual obstruction is difficult to interpret because it is impossible to distinguish truly open grassy sites from forested sites with clear understory. It is not possible to conclude whether birds had a preference for open understory in forest or for sites that were not forested at all. As in 100 m models, it appears that birds are not avoiding open areas at the 25 m scale. Only distance to water had influence as a transience variable. Rusty Blackbirds were more likely to stay present at sites that had shorter distances to water. This agrees with the importance of wet ground cover seen in 100 m models, but the variable encompasses any type of water regardless of depth. Neither the actual water depth variable nor any combination of litter depth and water depth were important at the 25 m level. It is possible that within 25 m of where birds were seen foraging there was not enough real variation in water depth to indicate any avoidance of deep water.

Measuring the available variation within a habitat and modeling response by a study organism must take place at a scale at which the organism is making habitat choices for results to be meaningful (Weins 1989). I examined relationship of Rusty Blackbirds and foraging habitat characteristics at both 100 m and 25 m levels because birds move quickly over large areas while foraging, but precise quantitative measurement of habitat characteristics is only possible at smaller scales. While not at odds with 100 m results, data at the 25 m spatial scale seems less representative of field observations than 100 m data. Birds readily moved greater than 25 m while foraging and were often relocated within a few hundred meters on repeated survey rounds, but were seldom seen in the exact same location. Despite the more accurate quantitative measurements possible at small spatial scales, occupancy and especially site transience, may not

be as directly coupled to habitat characteristics as at larger scales. Birds could easily be present at a site within a few hundred meters of the original point during several rounds but using slightly different microhabitat. A temporary pool may dry up or water line may recede, so although birds are still present within the survey, their actual site-use no longer reflects the original 25 m habitat zone around a point. I attempted to account for this by averaging in new 25 m habitat sub-point measures for each site as the season progressed, but it was not practical to create a new point every time birds were seen more than 50 m away from an existing point so not all newly utilized areas could be included (Appendix II.2). Habitat effects may have also been suppressed by averaging new 25 m circles with the original survey circles. It may be meaningful that the only variable indicating persistence was distance to water, which was not restricted to within 25 m. The risk of decoupling bird presence and microhabitat at small spatial scales, of 25 m or less, indicates that Rusty Blackbird foraging habitat associations would be better measured at larger spatial scales.

The only other published study of Rusty Blackbird wintering habitat associations found some evidence of increased occupancy by individuals or flocks with increased tree density, canopy cover and forested habitat type (Luscier 2009, et. al 2010). While these results were not consistent across years, relationships with forest-based variables seem to be somewhat contradictory to the results of the present study. However, the two studies did vary in methodology, year and region. It is possible that my use of citizen science data for site selection may have skewed sites towards more open and accessible habitat than was found in the refuges, parks and wildlife management areas used by Luscier (2009), but a range of forested and non-grassy sites were still included in my study. The survey point itself was centered in forest at 48% of sites and 23% of sites had no grass cover at all within 100 m. Luscier (2009) used a

much smaller (11.3 m) habitat scale and did not specifically test the shallow water and ground cover variables which came to the top of most model sets in my study. Ultimately, Lusnier et al. (2010) concluded that wintering Rusty Blackbirds were not as specialized in site-use as often reported by general observations, and that use may vary by year or region. Recent summaries from unpublished data also suggest that Rusty Blackbirds use a variety of habitats and that presence or type of shallow water, or specific mast items may be more important than distance to forest or understory vegetation (Greenberg et al. 2011). Conclusions from other studies and observations do correspond to model results and field observations from my study, suggesting that Rusty Blackbirds make use of a variety of forested and non-forested habitats with shallow water.

In all habitat models in the present study, ground moisture variables such as water, shallow water and wet litter appear to have an important role in determining site occupancy or persistence. The importance of wet leaf-litter in 100 m models, especially when abundance is considered, does indicate indirect importance of forested habitat, but more direct forest indicators such as overall amount of leaf litter and distance to tree cover had no model support at this spatial scale. Grassy cover and low visual obstruction had positive relationships with occupancy and/or persistence at sites, indicating that open areas are at least used, if not preferred. It is possible that complications with detectability, use of forest with open understory, or use of edge habitat may have influenced results. It seems that, at the scale of foraging habitat, having access to wet ground cover or shallow water is the most important factor for Rusty Blackbird presence, abundance and persistence. It is likely that Rusty Blackbirds are capable of using a wide variety of habitats, as long as some shallow water or wet ground cover is available for foraging.

3.4.3 Co-occurrence with Other Species

Multi-species model results were inconclusive as to whether Rusty Blackbird occupancy at sites is conditional on or independent from occupancy of Red-winged Blackbirds or Common Grackles. There is slightly more support for co-occupancy with Red-Winged Blackbirds than with Common Grackles, and at least some evidence that Rusty Blackbirds may be more likely to occupy sites with either species than if they were selecting sites independently of the others. Evidence of co-detection of Rusty Blackbirds with other species seems to be more consistent than evidence for co-occupancy. Other species flock size also showed up as the strongest variable in Rusty Blackbird detectability model sets. It may be that Rusty Blackbirds are simply more detectable when in mixed flocks, but frequent mixed flocking in and of itself does imply possibility for non-neutral interspecific interactions. All three species also react similarly to grassy ground cover, with increased occupancy and or detectability at sites with a greater percentage of this cover type. Proportion of ground covered by shallow water was the most important variable in predicting Rusty Blackbird presence in habitat models, but was not important in describing co-occupancy with other species. It is possible that any co-occupancy between the species is more likely in more open habitat, or that other birds are not as dependent on the presence of shallow water as Rusty Blackbirds. It is also possible that mixed flocks are more common and/or more detectable in open habitat. Detection and occurrence in mixed flocks at the same sites and similar reactions to habitat variables suggest the potential for competition and should be studied in more depth.

CHAPTER 4. CONCLUSIONS AND FUTURE RESEARCH

4.1 Recommendations for future research

There is need for efficient and standardized methods for long term study of Rusty Blackbirds over a wide area. As already shown in previous studies, leading to the discovery of decline, citizen science data is excellent for examination of long term trends (Greenberg and Droege 1999, Niven et al. 2004, Sauer et al. 2001, 2004). A study linking seasonal variation with habitat and climate covariates, similar to that suggested in Hamel and Ozdenerol (2009), could be especially informative. The span of data in the present study was insufficient to look at extent of yearly variation in timing and migration into the region, but the two years showed definite variation in seasonal timing, and possible differences in regional population size. This study also suggests that citizen science data show seasonal timing and flock trends similar to those observed using a more labor-intensive survey scheme. Available Rusty Blackbird Blitz data and eBird data could provide good sources for large scale and long term analysis linking habitat and climate to seasonal variation. Rigorous small scale studies are also needed. Results of this study suggest that the importance of shallow water and food availability, and the potential for competition involved with mixed flocking, should be further investigated. Adaptation of survey techniques to focus on occupied habitat and to efficiently assess population and habitat over larger spatial scales is recommended over standard point count procedures and small habitat survey circles.

Evidence from habitat models suggests that shallow-water availability could be the driving force behind Rusty Blackbird wintering habitat selection. While drainage and deforestation of bottomland hardwood forests are highly correlated, historical changes in relation

to water availability may be more likely to have impacted Rusty Blackbird populations than changes in forest cover alone. Birds seem to be able to use a variety of habitat types, are fully capable of moving over large areas of fragmented habitat on a daily basis and seem to be less directly affiliated with forest than with water, all of which suggest these birds are not as sensitive to deforestation as previously suggested. However, results do suggest that foraging substrate, particularly shallow standing water and wet leaf litter, is important. While shallow-water resources were once provided in large part by seasonal flooding, rainfall may now determine availability and location of these resources and may make seasonal water availability unpredictable. Change from flood driven to precipitation driven water sources could have impacted availability of invertebrate food sources for Rusty Blackbirds. Determining the extent to which Rusty Blackbirds rely on ephemeral, especially rain-fed, water sources is important in advance of climate change that may further alter precipitation patterns. Rusty Blackbirds would be especially vulnerable in the event of regional drying trends.

In concert with more detailed studies of Rusty Blackbird reliance on shallow water, there is a need to look more carefully at foraging microhabitat and food availability. Food availability data were collected as part of this project but only preliminary analysis has taken place. During the course of this study, birds were observed foraging on fruit (*Celtis laevigata*, *Ligustrum sinense*, and *Sapium sebifera*) and small (*Quercus nigra* and *Quercus phellos*) or crushed acorns, however the majority of foraging seemed to be related to probing and leaf flipping in wet leaf-litter, shallow water and wet lawn; presumably targeting live prey. It was difficult to identify live prey items in birds' bills but snails, small fish or tadpoles and a variety of insect-like prey items were observed. On average, more live prey items than mast items were found in food availability samples from 25 m habitat circles (Appendix VII.1). Mast availability was similar

between most substrates but, more live prey items and higher diversity was found in leaf litter and woody debris (with some shallow water on average) and in floating vegetation than in lawns or in deep water (Appendix VII. 1, 2). Based on observations and preliminary data, it seems possible that even on the wintering ground, live aquatic prey may be the main food source, at least in regions warm enough to have open shallow water year round.

While this study showed no evidence of intraspecific competition or imbalanced sex ratios in flocks, comparative studies with other regions where imbalances have been detected could provide further insights. Data does suggest potential for interspecific competition. While model results did not conclusively show that occupancy or detectability of Rusty Blackbirds with Red-winged Blackbirds or Common Grackles was higher than if species were behaving independently, this study did indicate co-occurrence and similar use of grassy habitat. Raw data, detectability models, and multi-species models indicated that co-detection and co-occupancy with other species of blackbird, especially Red-winged Blackbirds, was possible, and all species were positively associated with grassy habitat. Limited resources or changes in the location of shallow water habitat could lead to Rusty Blackbird competition with other species more common or better adapted to open habitats. Comparative studies of Rusty Blackbirds and other blackbird species in a variety of habitats would be useful.

4.2 Conclusions

Results of my study provide evidence that habitat changes on the wintering ground could be contributing to both long term and intensified shorter term decline of Rusty Blackbird populations. Rusty Blackbirds seem to be less specific in terms of use of forested habitat than previously thought, but there does seem to be strong dependence on availability of wet ground

and most likely on accompanying invertebrate prey. Changes in regional hydrological processes across much of the wintering grounds could have decreased quality or availability of habitat. Currently available water sources may be more limited, more ephemeral, or may maintain lower prey diversity or abundance than traditional flooded habitat. Disease or interspecific competition could also easily worsen a situation where birds are using poor or limited habitat. There is some evidence of shared habitat and mixed flocking with other blackbirds. The nature of these relationships is unknown but could indicate competition for resources. While other hypotheses can certainly not be ruled out at this point, wintering ground behavior and habitat are likely important factors in Rusty Blackbird decline. Understanding the connection between Rusty Blackbird habitat use on their wintering grounds and the species' decline could help guide efforts to manage and restore wetland habitat in the southeastern United States in a manner which would benefit Rusty Blackbirds and other wetland-dependant species.

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APPENDIX I. SEASONAL TREND CALCULATIONS

Table I. Seasonal quartile analysis: dates at which 25%, 50%, 75% and 100% of total birds* found in a season were detected. S1 = season one (2009-2010), S2 = season two (2010-2011). Offsets are the number of days by which season two precedes season one. Average offset is \pm (SE).

quartile	survey S1	survey S2	survey offset	birder S1	birder S2	birder offset	ebird S1	eBird S2	eBird offset
25	1/24	1/15	9	1/19	12/28	22	1/15	1/1	14
50	2/21	2/21	0	2/2	1/10	23	2/8	1/22	17
75	2/28	2/10	18	2/10	2/2	8	2/15	2/8	7
100	3/20	3/12	8	3/16	3/19	-3	3/22	3/22	0
average offset			8.75			12.50			9.50
(SE)			(3.68)			(4.19)			(3.80)

* Total birder and eBird detections include the sum of all available reports. Total survey detections are the sum of the maximum number of birds seen at one time at each point in each round.

APPENDIX II. SITE SELECTION AND HABITAT SAMPLING PROTOCOLS

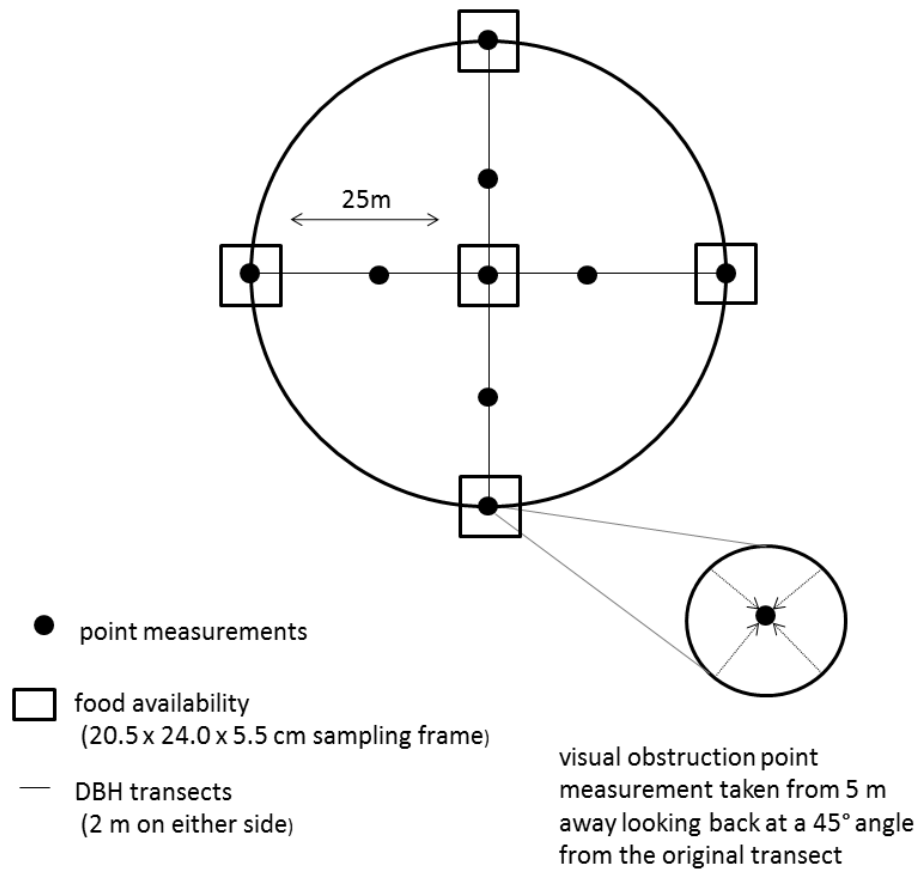


Figure II.1 Diagram of 25 m habitat and food availability sampling locations (figure not to scale).

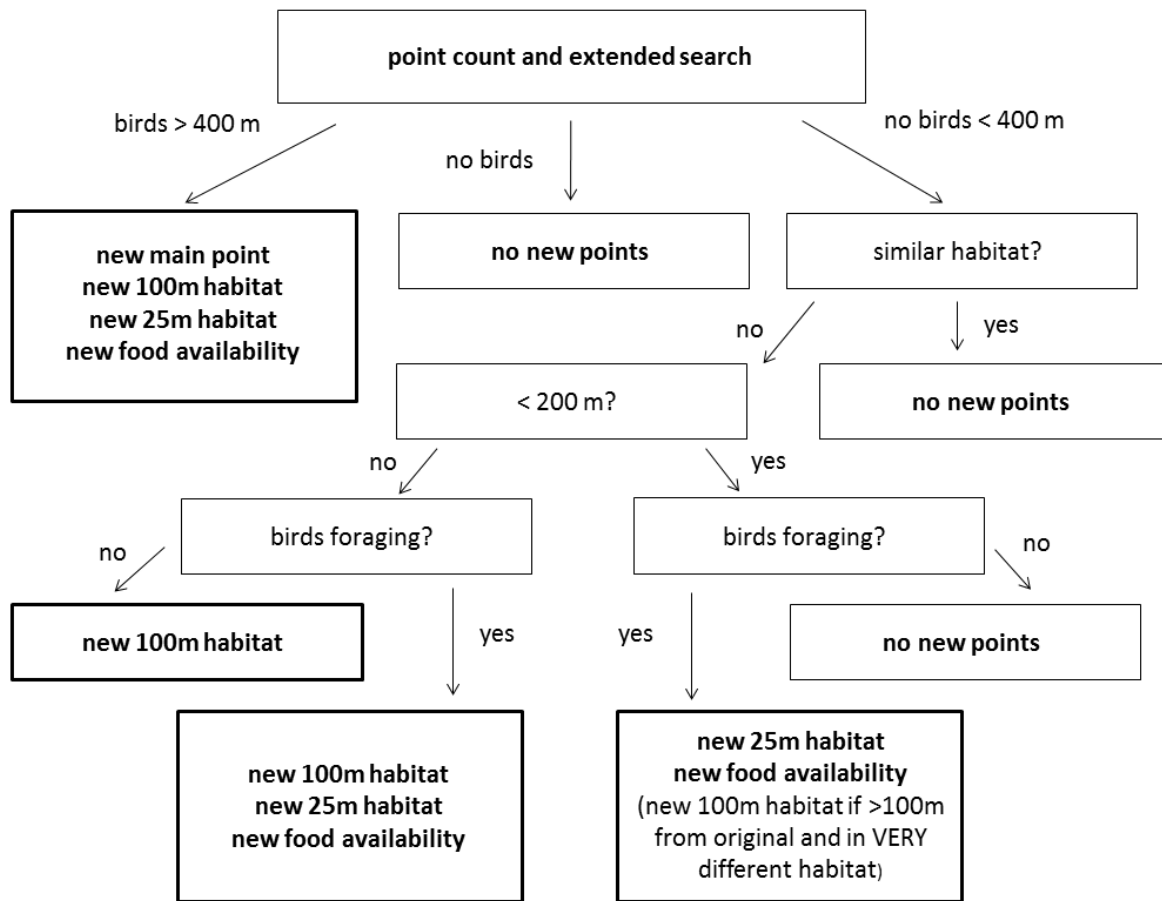


Figure II.2 Flow chart for decision to create a new 200 m survey point, 100 m habitat point, 25 m microhabitat or food availability point. New sub-points were never created within 100m of another point measured on the same round. "Very different" habitat was considered to be an entirely different habitat type or to have different water coverage.

APPENDIX III. DIFFERENCES IN SURVEY RATES BY ROUND AND YEAR

Table III. Naïve occupancy, detectability and transience rates by survey round and season. Rates from the same round are generally more similar across years than are rates from different rounds within the same year.

year	round	occupancy rate	detectability rate	transience rate*
2010	1	0.52	0.34	-
	2	0.64	0.41	0.33
	3	0.20	0.26	0.45
	2010 average	0.45	0.34	0.39
2011	1	0.71	0.38	-
	2	0.61	0.31	0.27
	3	0.39	0.35	0.44
	2011 average	0.57	0.35	0.36
combined	overall average	0.51	0.34	0.38

*Transience rate is average rate at which sites change occupancy status between rounds 1 and 2 and between rounds 2 and 3.

APPENDIX IV. DETECTABILITY VARIABLES AND MODELS

Table IV.1. All potential detectability variables collected. Some variables were eliminated prior to building model sets due to high correlation with other variables (spearman rank correlation test $\rho \geq .5$), codependence on other variables, or lack of biological importance. Retained variables (indicated by -) were used to construct detectability model sets in chapter 3.

variable	description	reason if eliminated
year	year surveyed (2010 or 2011)	-
round	round surveyed (1, 2 or 3)	-
weather	sunny = 1, partly cloudy = 2, overcast = 3, rain = 4	-
wind	wind speed 1-5 on the Beaufort scale	-
prior	RUBLs previously detected within 200 m? (yes/no) 1=yes	-
flock	log (# other blackbirds + AMRO) on point count and or associated with RUBLs within 200 m	-
COGR	log (# COGR) present on point count and or associated with RUBLs within 200 m	-
RWBL	log (# RWBL) on point count and or associated with RUBLs within 200 m	-
open	amount of grassy area averaged over all rounds (approximates amount of open space)	-
observer	person who did the point count	97% of surveys by same observer
date	julian date	highly correlated with round
vocalization	birds vocalizing when found? (yes/no)	codependent on detection of birds
temperature	temperature (°F)	no logical association with detectability

COGR = Common Grackle, RUBL = Rusty Blackbird and RWBL = Red-winged Blackbird

Table IV.2. Detectability model set for full set of 97 site/seasons. Due to small number of colonization events, standard errors on the estimated parameter values for the γ parameter were unusually large in two cases. All models converged to within at least 6.51 significant digits.

model	p	Ψ	ϵ	γ	parameter SEs	converged
1	ok	yes
2	year	.	.	.	ok	yes
3	round	.	.	.	ok	yes
4	time	.	.	.	ok	yes
5	weather	.	.	.	ok	yes
6	prior	.	.	.	ok	yes
7	flock	.	.	.	large γ	yes
8	COGR	.	.	.	ok	yes
9	RWBL	.	.	.	ok	yes
10	open	.	.	.	ok	yes
11	round+flock	.	.	.	ok	yes
12	round+prior	.	.	.	ok	yes
13	round+year	.	.	.	ok	yes
14	round+weather	.	.	.	ok	6.72
15	year+flock	.	.	.	ok	yes
16	year+weather	.	.	.	ok	yes
17	round+year+flock	.	.	.	ok	yes
18	round+year+weather	.	.	.	ok	yes
19	flock+time	.	.	.	large γ	6.26
20	flock+weather	.	.	.	ok	yes
21	flock+open	.	.	.	ok	6.51
22	COGR+open	.	.	.	ok	6.87
23	RWBL+open	.	.	.	ok	yes
24	flock+weather+open	.	.	.	ok	6.31
25	season+round+time+weather+prior+flock+open	.	.	.	ok	yes

Table IV.3. Detectability model set for 44 sites measured in 2011. Wind was not measured in 2010, but was shown to be an important variable in previous studies (Powell 2008) so this model incorporates wind into 3 models but does not include year. Standard errors on all β estimates were small and all models converged to within at least 5.94 significant digits.

model	p	Ψ	ϵ	γ	parameter SEs	converged
1	ok	yes
2	round	.	.	.	ok	yes
3	time	.	.	.	ok	yes
4	weather	.	.	.	ok	6.52
5	prior	.	.	.	ok	yes
6	flock	.	.	.	ok	yes
7	COGR	.	.	.	ok	yes
8	RWBL	.	.	.	ok	yes
9	open	.	.	.	ok	yes
10	wind	.	.	.	ok	yes
11	round+flock	.	.	.	ok	yes
12	round+prior	.	.	.	ok	yes
13	round+weather	.	.	.	ok	6.70
14	flock+time	.	.	.	ok	yes
15	flock+weather	.	.	.	ok	yes
16	flock+open	.	.	.	ok	yes
17	flock+wind	.	.	.	ok	yes
18	COGR+open	.	.	.	ok	yes
19	RWBL+open	.	.	.	ok	yes
20	wind+open	.	.	.	ok	yes
21	flock+weather+open	.	.	.	ok	yes
22	round+time+weather+prior+flock+open+ wind	.	.	.	ok	5.94

Table IV. 4. Detectability results from PRESENCE 4.0 for full set 97 site/seasons. For all models occupancy colonization and extinction were held constant $\Psi(.), \gamma(.), \epsilon(.)$

rank	model	AICc	$\Delta AICc$	AIC wgt	likelihood	k	-2log likelihood
1	p(year+flock)	634.34	0.00	0.4924	1.0000	6	621.41
2	p(round+year+flock)	634.91	0.57	0.3703	0.7520	7	619.65
3	p(round+flock)	639.53	5.19	0.0368	0.0746	6	626.60
4	p(flock)	639.86	5.52	0.0312	0.0633	5	629.20
5	p(flock+time)	640.28	5.94	0.0253	0.0513	6	627.35
6	p(global)*	641.09	6.75	0.0168	0.0342	11	615.98
7	p(flock+open)	641.78	7.44	0.0119	0.0242	6	628.85
8	p(flock+weather)	641.94	7.60	0.011	0.0224	6	629.01
9	p(flock+weather+open)	643.94	9.60	0.0041	0.0082	7	628.68
10	p(RWBL)	650.19	15.85	0.0002	0.0004	5	639.53
11	p(RWBL+open)	652.10	17.76	0.0001	0.0001	6	639.17
12	p(COGR)	664.72	30.38	0.0000	0.0000	5	654.06
13	p(COGR+open)	666.68	32.34	0.0000	0.0000	6	653.75
14	p(round+prior)	669.98	35.64	0.0000	0.0000	6	657.05
15	p(prior)	670.00	35.66	0.0000	0.0000	5	659.34
16	p(round+year)	673.42	39.08	0.0000	0.0000	6	660.49
17	p(year)	673.68	39.34	0.0000	0.0000	5	663.02
18	p(round)	673.97	39.63	0.0000	0.0000	5	663.31
19	p(time)	674.10	39.76	0.0000	0.0000	5	663.44
20	p(.)	674.61	40.27	0.0000	0.0000	4	666.18
21	p(round+year+weather)	675.73	41.39	0.0000	0.0000	7	660.47
22	p(year+weather)	675.83	41.49	0.0000	0.0000	6	662.90
23	p(open)	675.85	41.51	0.0000	0.0000	5	665.19
24	p(round+weather)	676.24	41.90	0.0000	0.0000	6	663.31
25	p(weather)	676.78	42.44	0.0000	0.0000	5	666.12

*global = p(year+round+time+weather+prior+flock+open)

Table IV.5. Detectability results from PRESENCE 4.0 for 44 sites surveyed in 2011. For all models occupancy colonization and extinction were held constant $\Psi(\cdot), \gamma(\cdot), \epsilon(\cdot)$. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support. Model averaged parameter weights (\pm SE) for variables in top models are as follows: Flock $.60 \pm .13$, RWBL $.52 \pm .12$, open $.39 \pm .21$, round $.06 \pm .05$, and wind $.05 \pm .04$.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	p(RWBL+open)	362.33	0.00	0.2367	1.0000	6	348.06
2	p(flock)	362.93	0.60	0.1754	0.7408	5	351.35
3	p(flock+wind)	363.61	1.28	0.1248	0.5273	6	349.34
4	p(RWBL)	364.03	1.70	0.1012	0.4274	5	352.45
5	p(round+flock)	364.07	1.74	0.0992	0.4190	6	349.80
6	p(flock+open)	364.23	1.90	0.0916	0.3867	6	349.96
7	p(flock+time)	364.74	2.41	0.0709	0.2997	6	350.47
8	p(flock+weather)	364.86	2.53	0.0668	0.2822	6	350.59
9	p(flock+weather+open)	366.30	3.97	0.0325	0.1374	7	349.19
10	p(global)*	373.91	11.58	0.0007	0.0031	11	343.66
11	p(COGR)	378.93	16.60	0.0001	0.0002	5	367.35
12	p(COGR+open)	379.55	17.22	0.0000	0.0002	6	365.28
13	p(wind+open)	386.95	24.62	0.0000	0.0000	6	372.68
14	p(open)	387.72	25.39	0.0000	0.0000	5	376.14
15	p(.)	388.46	26.13	0.0000	0.0000	4	379.43
16	p(wind)	388.84	26.51	0.0000	0.0000	5	377.26
17	p(time)	389.54	27.21	0.0000	0.0000	5	377.96
18	p(prior)	389.54	27.21	0.0000	0.0000	5	377.96
19	p(round)	390.63	28.3	0.0000	0.0000	5	379.05
20	p(weather)	390.88	28.55	0.0000	0.0000	5	379.30
21	p(round+prior)	391.98	29.65	0.0000	0.0000	6	377.71
22	p(round+weather)	393.11	30.78	0.0000	0.0000	6	378.84

*global =p(round+time+weather+prior+flock+open+wind)

Table IV.6. Detectability results from PRESENCE 4.0 for set of 73 independent sites used in habitat modeling. For all models occupancy colonization and extinction were held constant $\Psi(.), \gamma(.), \epsilon(.)$. Models within $\Delta 2AICc$ were considered to have substantial model support. Model averaged parameter weights (\pm SE) for variables in top models are as follows: year $1.36 \pm .34$, Flock $1.30 \pm .21$, round $1.03 \pm .43$.

rank	model	AICc	$\Delta AICc$	AIC wgt	likelihood	k	-2log likelihood
1	p(round+season+flock)	466.55	0.00	0.7303	1.0000	7	450.80
2	p(season+flock)	469.19	2.64	0.1951	0.2671	6	455.90
3	p(global)*	471.20	4.65	0.0714	0.0978	11	444.80
4	p(round+flock)	478.85	12.30	0.0016	0.0021	6	465.56
5	p(flock)	480.47	13.92	0.0007	0.0009	5	469.56
6	p(flock+time)	481.25	14.7	0.0005	0.0006	6	467.96
7	p(flock+weather)	482.83	16.28	0.0002	0.0003	6	469.54
8	p(flock+open)	482.85	16.30	0.0002	0.0003	6	469.56
9	p(flock+weather+open)	485.29	18.74	0.0001	0.0001	7	469.54
10	p(RWBL)	488.46	21.91	0.0000	0.0000	5	477.55
11	p(RWBL+open)	489.38	22.83	0.0000	0.0000	6	476.09
12	p(COGR)	504.06	37.51	0.0000	0.0000	5	493.15
13	p(COGR+open)	505.39	38.84	0.0000	0.0000	6	492.10
14	p(round+season)	507.85	41.30	0.0000	0.0000	6	494.56
15	p(season)	509.86	43.31	0.0000	0.0000	5	498.95
16	p(round+season+weather)	510.05	43.50	0.0000	0.0000	7	494.30
17	p(season+weather)	511.50	44.95	0.0000	0.0000	6	498.21
18	p(round)	512.63	46.08	0.0000	0.0000	5	501.72
19	p(.)	513.55	47.00	0.0000	0.0000	4	504.95
20	p(round+prior)	513.67	47.12	0.0000	0.0000	6	500.38
21	p(time)	513.77	47.22	0.0000	0.0000	5	502.86
22	p(open)	514.00	47.45	0.0000	0.0000	5	503.09
23	p(prior)	514.07	47.52	0.0000	0.0000	5	503.16
24	p(round+weather)	514.94	48.39	0.0000	0.0000	6	501.65
25	p(weather)	515.46	48.91	0.0000	0.0000	5	504.55

*global = p(season+round+time+weather+prior+flock+open)

APPENDIX V. HABITAT VARIABLES AND MODELS

Table V.1. Habitat variable selection: All potential 100 m habitat variables collected. Percent ground cover measurements are within the 100 m survey circle, distance to forest was measured regardless of circle boundaries. Some variables were eliminated prior to building model sets due to high correlation with other variables (Spearman rank correlation test $\rho \geq .5$), uncertainty of field measurements, or lack of biological importance. Retained variables (indicated by -) were used to construct habitat association model sets in Chapter 3.

variable	description	reason if eliminated
water	% ground covered by water	-
shallow	% ground covered by shallow water	-
grass	% ground covered by short vegetation or lawn	-
wetlitter	% ground covered by wet leaf-litter (damp + saturated litter categories)	-
toforest	average distance to nearest substantial tree cover	-
litter	% ground covered by leaf litter	highly correlated with more specific wetlitter variable
leafy	% ground covered by leafy vegetation	not measured consistently in field*
woody	% ground covered by woody vegetation or debris	not measured consistently in field*
other	% other ground cover (impervious surface etc)	not a biologically meaningful category

*There was some overlap in which plants were considered leafy or woody and woody debris was not noted consistently in the first year

Table V.2. All potential 25 m habitat variables collected. Some variables were eliminated prior to building model sets due to high correlation with other variables (Spearman rank correlation test $\rho \geq .5$), uncertainty of field measurements, or lack of biological importance. Retained variables (indicated by -) were used to construct habitat association model sets in Chapter 3.

variable	description	reason if eliminated
towater	distance to water of any kind	-
water	water depth	-
litter	litter depth	-
visobs	average visual obstruction at 1 m height using vegetation pole	-
trees	number of trees or stems >1 cm DBH	-
DBH	average DBH	-
toforest	average distance to nearest substantial tree cover	-
canopy height	visual estimate of height (ft or m)	not measured accurately, correlated with DBH, less biologically important*
canopy cover	coverage at points using GRS densitometer	highly correlated with toforest, trees, and visobs, less biologically important*
leaf cover	if canopy was covered were trees leafed out	Less biologically important, changes due to season already accounted for in detectability*
ground moisture	Dry = 1, damp = 2, saturated = 3, under water = 4	not a quantitative measurement, already examined categorically at 100m level and highly correlated with 25 m quantitative measures towater and water.

*Canopy structure variables were considered less important, especially when correlated with variables relevant at all vertical levels, since Rusty Blackbirds are primarily ground foragers.

Table V.3. Model set 100 m habitat association for full set of 97 site/seasons for standard occupancy data (at least 1 bird = occupied) and abundance adjusted (adj) data (flock ≥ 7 birds = occupied). Standard errors on the estimated parameter values (param. SE) were reasonably small and all models converged to within at least 6.09 significant digits for the standard occupancy set and to within 2.32 significant digits for the abundance adjusted data set.

model	Ψ	ϵ	γ	P*	param. SEs	converged	converged (adj)
1	ok	yes	5.96
2	.	.	.	year+round+flock	ok	yes	yes
3	water	.	.	year+round+flock	ok	yes	5.17
4	shallow	.	.	year+round+flock	ok	yes	4.55
5	wetlitter	.	.	year+round+flock	ok	yes	yes
6	grass	.	.	year+round+flock	ok	yes	6.62
7	toforest	.	.	year+round+flock	ok	yes	5.83
8	shallow	shallow	.	year+round+flock	ok	yes	yes
9	wetlitter	wetlitter	.	year+round+flock	ok	6.53	yes
10	grass	grass	.	year+round+flock	ok	6.80	3.90
11	toforest	toforest	.	year+round+flock	ok	6.84	6.05
12	water	water	.	year+round+flock	ok	yes	2.32
13	water	wetlitter	.	year+round+flock	ok	6.78	5.25
14	wetlitter	water	.	year+round+flock	ok	yes	6.49
15	shallow	grass	.	year+round+flock	ok	6.72	6.75
16	shallow	toforest	.	year+round+flock	ok	yes	6.42
17	wetlitter	toforest	.	year+round+flock	ok	6.16	3.61
18	grass	wetlitter	.	year+round+flock	ok	yes	4.96
19	grass	shallow	.	year+round+flock	ok	yes	6.55
20	wetlitter	grass	.	year+round+flock	ok	6.09	6.38
21	toforest	shallow	.	year+round+flock	ok	yes	6.37
22	toforest	wetlitter	.	year+round+flock	ok	yes	yes
23	shallow+grass	shallow+grass	.	year+round+flock	ok	yes	3.43
24	shallow+toforest	shallow+toforest	.	year+round+flock	ok	6.82	yes
25	wetlitter+grass	wetlitter+grass	.	year+round+flock	ok	yes	6.38
26	water+wetlitter	water+wetlitter	.	year+round+flock	ok	yes	6.02
27	wetlitter+toforest	wetlitter+toforest	.	year+round+flock	ok	yes	yes

*In the adjusted set there were no flocks with at least 7 birds in round three so these data were not included and year+flock was used to estimate detectability.

Table V.4. Model set 25 m habitat association for 39 sites measured in 2011. Due to small sample size standard errors on the estimated parameter values (param. SE) for the Ψ parameter were unusually large in four cases. However none of the top ranked models had large SE of individual parameters and removing models with large SE does not change order of remaining models. All models converged to within at least 6.10 significant digits.

model	Ψ	ε	γ	p	param. SE	converged
1	ok	yes
2	.	.	.	round+flock	ok	yes
3	toforest	.	.	round+flock	large Ψ	yes
4	towater	.	.	round+flock	ok	6.63
5	water	.	.	round+flock	ok	6.46
6	visobs	.	.	round+flock	ok	yes
7	DBH	.	.	round+flock	ok	yes
8	trees	.	.	round+flock	ok	yes
9	litter	.	.	round+flock	ok	yes
10	DBH+trees	.	.	round+flock	ok	yes
11	water+litter	.	.	round+flock	ok	6.81
12	toforest	toforest	.	round+flock	large Ψ	yes
13	towater	towater	.	round+flock	ok	yes
14	water	water	.	round+flock	ok	6.36
15	water+litter	water+litter	.	round+flock	ok	6.93
16	toforest	towater	.	round+flock	large Ψ	yes
17	toforest	water	.	round+flock	large Ψ	6.94
18	towater	toforest	.	round+flock	ok	yes
19	water	toforest	.	round+flock	ok	6.76
20	visobs	towater	.	round+flock	ok	yes
21	visobs	water	.	round+flock	ok	6.88
22	DBH+trees	towater	.	round+flock	ok	yes
23	DBH+trees	water	.	round+flock	ok	yes
25	towater+toforest+DBH	towater+toforest+DBH	.	round+flock	ok	6.10
25	water+toforest+DBH	water+toforest+DBH	.	round+flock	ok	6.73
26*	.	.	.	round+flock+visobs	ok	yes

*Model 26 is a *post-hoc* test with visobs affecting detectability instead of occupancy.

Table V.5. Occupancy model results from PRESENCE 4.0 for 100 m habitat modeling. Colonization was held constant $\gamma(\cdot)$ and detectability was $p(\text{year}+\text{round}+\text{flock})$ for all models except the null. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{shallow}+\text{grass}), \varepsilon(\text{shallow}+\text{grass})$	464.95	0.00	0.2126	1.0000	11	438.62
2	$\Psi(\text{wetlitter}+\text{grass}), \varepsilon(\text{wetlitter}+\text{grass})$	465.60	0.65	0.1536	0.7225	11	439.27
3	$\Psi(\text{water}), \varepsilon(\cdot)$	466.33	1.38	0.1066	0.5016	8	448.08
4	$\Psi(\text{grass}), \varepsilon(\text{grass})$	466.42	1.47	0.1019	0.4795	9	445.56
5	$\Psi(\text{water}), \varepsilon(\text{water})$	467.15	2.20	0.0708	0.3329	9	446.29
6	$\Psi(\text{grass}), \varepsilon(\cdot)$	467.87	2.92	0.0494	0.2322	8	449.62
7	$\Psi(\text{toforest}), \varepsilon(\cdot)$	468.17	3.22	0.0425	0.1999	8	449.92
8	$\Psi(\text{water}), \varepsilon(\text{wetlitter})$	468.49	3.54	0.0362	0.1703	9	447.63
9	$\Psi(\text{shallow}), \varepsilon(\text{grass})$	468.54	3.59	0.0353	0.1661	9	447.68
10	$\Psi(\text{wetlitter}), \varepsilon(\text{grass})$	469.26	4.31	0.0246	0.1159	9	448.40
11	$\Psi(\cdot), \varepsilon(\cdot)$	469.43	4.48	0.0226	0.1065	7	453.71
12	$\Psi(\text{grass}), \varepsilon(\text{shallow})$	469.58	4.63	0.0210	0.0988	9	448.72
13	$\Psi(\text{toforest}), \varepsilon(\text{shallow})$	469.64	4.69	0.0204	0.0958	9	448.78
14	$\Psi(\text{grass}), \varepsilon(\text{wetlitter})$	469.81	4.86	0.0187	0.0880	9	448.95
15	$\Psi(\text{toforest}), \varepsilon(\text{wetlitter})$	469.87	4.92	0.0182	0.0854	9	449.01
16	$\Psi(\text{toforest}), \varepsilon(\text{toforest})$	470.14	5.19	0.0159	0.0746	9	449.28
17	$\Psi(\text{wetlitter}), \varepsilon(\text{water})$	470.86	5.91	0.0111	0.0521	9	450.00
18	$\Psi(\text{water}+\text{wetlitter}), \varepsilon(\text{water}+\text{wetlitter})$	471.08	6.13	0.0099	0.0467	11	444.75
19	$\Psi(\text{shallow}), \varepsilon(\cdot)$	471.40	6.45	0.0085	0.0398	8	453.15
20	$\Psi(\text{wetlitter}), \varepsilon(\cdot)$	471.94	6.99	0.0065	0.0303	8	453.69
21	$\Psi(\text{shallow}), \varepsilon(\text{shallow})$	473.31	8.36	0.0033	0.0153	9	452.45
22	$\Psi(\text{shallow}), \varepsilon(\text{toforest})$	473.76	8.81	0.0026	0.0122	9	452.90
23	$\Psi(\text{wetlitter}), \varepsilon(\text{wetlitter})$	473.83	8.88	0.0025	0.0118	9	452.97
24	$\Psi(\text{wetlitter}), \varepsilon(\text{toforest})$	474.29	9.34	0.0020	0.0094	9	453.43
25	$\Psi(\text{shallow}+\text{toforest}), \varepsilon(\text{shallow}+\text{toforest})$	474.30	9.35	0.0020	0.0093	11	447.97
26	$\Psi(\text{wetlitter}+\text{toforest}), \varepsilon(\text{wetlitter}+\text{toforest})$	474.86	9.91	0.0015	0.0070	11	448.53
27	$\Psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	517.86	52.91	0.0000	0.0000	4	509.27

Table V.6. Occupancy model results from PRESENCE 4.0 for 100 m habitat modeling in rounds one and two only. Colonization was held constant $\gamma(.)$ and detectability was $p(\text{year} + \text{flock})$ for all models except the null. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support. Model averaged β parameter weights for variables in top models \pm SE are as follows: for Ψ ; wetlitter 12.82 ± 9.14 , shallow 12.43 ± 6.56 , grass 3.69 ± 1.43 , and for ϵ ; shallow 11.92 ± 7.69 , grass 3.39 ± 0.94 , wetlitter 2.44 ± 1.80 . Results are similar to 100 m models including all three rounds (Table V.5).

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{shallow}+\text{grass}),\epsilon(\text{shallow}+\text{grass})$	410.02	0.00	0.4683	1.0000	10	386.64
2	$\Psi(\text{wetlitter}+\text{grass}),\epsilon(\text{wetlitter}+\text{grass})$	410.65	0.63	0.3417	0.7298	10	387.27
3	$\Psi(\text{grass}),\epsilon(\text{grass})$	415.61	5.59	0.0286	0.0611	8	397.46
4	$\Psi(\text{grass}),\epsilon(.)$	415.64	5.62	0.0282	0.0602	7	399.99
5	$\Psi(\text{toforest}),\epsilon(.)$	416.57	6.55	0.0177	0.0378	7	400.92
6	$\Psi(\text{grass}),\epsilon(\text{shallow})$	417.22	7.20	0.0128	0.0273	8	399.07
7	$\Psi(\text{water}),\epsilon(.)$	417.46	7.44	0.0113	0.0242	7	401.81
8	$\Psi(\text{shallow}),\epsilon(\text{grass})$	417.58	7.56	0.0107	0.0228	8	399.43
9	$\Psi(\text{grass}),\epsilon(\text{wetlitter})$	417.71	7.69	0.0100	0.0214	8	399.56
10	$\Psi(\text{toforest}),\epsilon(\text{shallow})$	417.80	7.78	0.0096	0.0204	8	399.65
11	$\Psi(\text{wetlitter}),\epsilon(\text{grass})$	418.12	8.10	0.0082	0.0174	8	399.97
12	$\Psi(\text{water}),\epsilon(\text{water})$	418.61	8.59	0.0064	0.0136	8	400.46
13	$\Psi(\text{toforest}),\epsilon(\text{wetlitter})$	418.63	8.61	0.0063	0.0135	8	400.48
14	$\Psi(\text{shallow}),\epsilon(.)$	418.94	8.92	0.0054	0.0116	7	403.29
15	$\Psi(\text{water}+\text{wetlitter}),\epsilon(\text{water}+\text{wetlitter})$	418.95	8.93	0.0054	0.0115	10	395.57
16	$\Psi(.)\epsilon(.)$	419.03	9.01	0.0052	0.0111	6	405.81
17	$\Psi(\text{toforest}),\epsilon(\text{toforest})$	419.07	9.05	0.0051	0.0108	8	400.92
18	$\Psi(\text{shallow}+\text{toforest}),\epsilon(\text{shallow}+\text{toforest})$	419.35	9.33	0.0044	0.0094	10	395.97
19	$\Psi(\text{water}),\epsilon(\text{wetlitter})$	419.74	9.72	0.0036	0.0078	8	401.59
20	$\Psi(\text{wetlitter}+\text{toforest}),\epsilon(\text{wetlitter}+\text{toforest})$	420.40	10.38	0.0026	0.0056	10	397.02
21	$\Psi(\text{shallow}),\epsilon(\text{shallow})$	420.82	10.80	0.0021	0.0045	8	402.67
22	$\Psi(\text{shallow}),\epsilon(\text{toforest})$	421.05	11.03	0.0019	0.0040	8	402.90
23	$\Psi(\text{wetlitter}),\epsilon(.)$	421.28	11.26	0.0017	0.0036	7	405.63
24	$\Psi(\text{wetlitter}),\epsilon(\text{water})$	421.30	11.28	0.0017	0.0036	8	403.15
25	$\Psi(\text{wetlitter}),\epsilon(\text{toforest})$	423.38	13.36	0.0006	0.0013	8	405.23
26	$\Psi(\text{wetlitter}),\epsilon(\text{wetlitter})$	423.49	13.47	0.0006	0.0012	8	405.34
27	$\Psi(.),\gamma(.),\epsilon(.),p(.)$	450.21	40.19	0.0000	0.0000	4	441.65

Table V.7. Occupancy model results from PRESENCE 4.0 for habitat modeling when a flock of seven or more birds was required for a site to be considered occupied on any round. Colonization was held constant $\gamma(\cdot)$ and detectability was $p(\text{year}+\text{round}+\text{flock})$ for all models except the null. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{wetlitter}+\text{water}), \epsilon(\text{wetlitter}+\text{water})$	314.01	0.00	0.7362	1.0000	11	287.68
2	$\Psi(\text{wetlitter}+\text{grass}), \epsilon(\text{wetlitter}+\text{grass})$	317.80	3.79	0.1107	0.1503	11	291.47
3	$\Psi(\text{water}), \epsilon(\text{wetlitter})$	318.32	4.31	0.0853	0.1159	9	297.46
4	$\Psi(\text{grass}), \epsilon(\text{wetlitter})$	319.90	5.89	0.0387	0.0526	9	299.04
5	$\Psi(\text{water}), \epsilon(\cdot)$	323.42	9.41	0.0067	0.0090	8	305.17
6	$\Psi(\text{toforest}), \epsilon(\text{wetlitter})$	325.07	11.06	0.0029	0.0040	9	304.21
7	$\Psi(\text{shallow}+\text{grass}), \epsilon(\text{shallow}+\text{grass})$	325.41	11.40	0.0025	0.0033	11	299.08
8	$\Psi(\text{wetlitter}+\text{toforest}), \epsilon(\text{wetlitter}+\text{toforest})$	325.43	11.42	0.0024	0.0033	11	299.10
9	$\Psi(\text{wetlitter}), \epsilon(\text{wetlitter})$	325.68	11.67	0.0022	0.0029	9	304.82
10	$\Psi(\text{shallow}+\text{toforest}), \epsilon(\text{shallow}+\text{toforest})$	325.79	11.78	0.0020	0.0028	11	299.46
11	$\Psi(\text{water}), \epsilon(\text{water})$	325.96	11.95	0.0019	0.0025	9	305.10
12	$\Psi(\text{grass}), \epsilon(\text{shallow})$	326.16	12.15	0.0017	0.0023	9	305.30
13	$\Psi(\text{grass}), \epsilon(\cdot)$	326.31	12.30	0.0016	0.0021	8	308.06
14	$\Psi(\cdot), \epsilon(\cdot)$	327.05	13.04	0.0011	0.0015	7	311.33
15	$\Psi(\text{wetlitter}), \epsilon(\cdot)$	327.96	13.95	0.0007	0.0009	8	309.71
16	$\Psi(\text{shallow}), \epsilon(\cdot)$	328.46	14.45	0.0005	0.0007	8	310.21
17	$\Psi(\text{grass}), \epsilon(\text{grass})$	328.69	14.68	0.0005	0.0006	9	307.83
18	$\Psi(\text{wetlitter}), \epsilon(\text{grass})$	328.99	14.98	0.0004	0.0006	9	308.13
19	$\Psi(\text{toforest}), \epsilon(\cdot)$	329.17	15.16	0.0004	0.0005	8	310.92
20	$\Psi(\text{shallow}), \epsilon(\text{shallow})$	329.33	15.32	0.0003	0.0005	9	308.47
21	$\Psi(\text{wetlitter}), \epsilon(\text{water})$	329.43	15.42	0.0003	0.0004	9	308.57
22	$\Psi(\text{toforest}), \epsilon(\text{shallow})$	329.55	15.54	0.0003	0.0004	9	308.69
23	$\Psi(\text{shallow}), \epsilon(\text{grass})$	329.88	15.87	0.0003	0.0004	9	309.02
24	$\Psi(\text{wetlitter}), \epsilon(\text{toforest})$	330.36	16.35	0.0002	0.0003	9	309.50
25	$\Psi(\text{shallow}), \epsilon(\text{toforest})$	330.84	16.83	0.0002	0.0002	9	309.98
26	$\Psi(\text{toforest}), \epsilon(\text{toforest})$	331.33	17.32	0.0001	0.0002	9	310.47
27	$\Psi, \gamma(\cdot), \epsilon(\cdot), p(\cdot)$	352.65	38.64	0.0000	0.0000	4	344.06

Table V.8. Occupancy model results from PRESENCE 4.0 for 25 m habitat modeling. Colonization was held constant $\gamma(\cdot)$ and detectability was $p(\text{round}+\text{flock})$ for all models except the null and model 15*. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{visobs}),\varepsilon(\cdot)$	327.66	0.00	0.3735	1	7	310.05
2	$\Psi(\text{visobs}),\varepsilon(\text{towater})$	329.53	1.87	0.1466	0.3926	8	308.73
3	$\Psi(\text{visobs}),\varepsilon(\text{water})$	330.68	3.02	0.0825	0.2209	8	309.88
4	$\Psi(\text{toforest}),\varepsilon(\cdot)$	330.69	3.03	0.0821	0.2198	7	313.08
5	$\Psi(\text{litter}),\varepsilon(\cdot)$	331.81	4.15	0.0469	0.1256	7	314.20
6	$\Psi(\text{DBH}+\text{trees}),\varepsilon(\cdot)$	332.28	4.62	0.0371	0.0993	8	311.48
7	$\Psi(\text{toforest}),\varepsilon(\text{towater})$	332.38	4.72	0.0353	0.0944	8	311.58
8	$\Psi(\text{DBH}),\varepsilon(\cdot)$	332.45	4.79	0.0341	0.0912	7	314.84
9	$\Psi(\cdot),\varepsilon(\cdot)$	332.56	4.90	0.0322	0.0863	6	317.93
10	$\Psi(\text{trees}),\varepsilon(\cdot)$	332.79	5.13	0.0287	0.0769	7	315.18
11	$\Psi(\text{DBH}+\text{trees}),\varepsilon(\text{towater})$	333.71	6.05	0.0181	0.0486	9	309.50
12	$\Psi(\text{toforest}),\varepsilon(\text{toforest})$	333.81	6.15	0.0173	0.0462	8	313.01
13	$\Psi(\text{toforest}),\varepsilon(\text{water})$	333.87	6.21	0.0167	0.0448	8	313.07
14	$\Psi(\text{water}+\text{litter}),\varepsilon(\cdot)$	334.67	7.01	0.0112	0.03	8	313.87
15	$\Psi(\cdot),\varepsilon(\cdot),p(\text{round}+\text{flock}+\text{visobs})$	335.49	7.83	0.0074	0.0199	7	317.88
16	$\Psi(\text{towater}),\varepsilon(\cdot)$	335.5	7.84	0.0074	0.0198	7	317.89
17	$\Psi(\text{water}),\varepsilon(\cdot)$	335.51	7.85	0.0074	0.0197	7	317.90
18	$\Psi(\text{DBH}+\text{trees}),\varepsilon(\text{water})$	335.68	8.02	0.0068	0.0181	9	311.47
19	$\Psi(\text{towater}),\varepsilon(\text{towater})$	336.98	9.32	0.0035	0.0095	8	316.18
20	$\Psi(\text{towater}),\varepsilon(\text{toforest})$	338.63	10.97	0.0015	0.0041	8	317.83
21	$\Psi(\text{water}),\varepsilon(\text{toforest})$	338.64	10.98	0.0015	0.0041	8	317.84
22	$\Psi(\text{water}),\varepsilon(\text{water})$	338.69	11.03	0.0015	0.004	8	317.89
23	$\Psi(\text{water}+\text{litter}),\varepsilon(\text{water}+\text{litter})$	341.55	13.89	0.0004	0.001	10	313.69
24	$\Psi(\text{towater}+\text{toforest}+\text{DBH}),\varepsilon(\text{towater}+\text{toforest}+\text{DBH})$	344.81	17.15	0.0001	0.0002	12	308.81
25	$\Psi(\text{water}+\text{toforest}+\text{DBH}),\varepsilon(\text{water}+\text{toforest}+\text{DBH})$	345.99	18.33	0	0.0001	12	309.99
26	$\Psi(\cdot),\gamma(\cdot),\varepsilon(\cdot),p(\cdot)$	358.55	30.89	0	0	4	349.37

*Model 15 is a *post-hoc* test of the top model where visual obstruction is tested as a detectability rather than an occupancy covariate.

APPENDIX VI. TWO-SPECIES VARIABLES AND MODELS

Table VI. 1. Two-species model parameters: Definition of all two-season model parameters estimated in the multi-species model parameterization used for this study. Conditional and unconditional columns show the difference in how model intercepts are coded for each parameter depending on conditional or unconditional model structure. Within each model, all combinations of $\Psi_{\text{conditional}}$ or $\Psi_{\text{unconditional}}$ with P conditional or P unconditional are allowed. Habitat variables can also vary with conditional Ψ or remain the same for all parameter intercepts. In the analysis presented here habitat was assumed to have the same affect on all detectability intercepts regardless of model structure. For further information on multi-season model construction and parameterization see Richmond et al. 2010 and Donovan and Hines 2007.

parameter	definition	conditional	unconditional
Ψ_A	presence of species A	1 0 0	1 0
Ψ_{BA}	presence of species B given A is present	0 1 0	0 1
Ψ_{Ba}	presence of species B given A is absent	0 0 1	0 1
PA	probability of detecting A given absence of B	1 0 0	1 0
PB	probability of detecting B given absence of A	0 1 0	0 1
rA	probability of detecting A given presence of B	1 0 0	1 0
rBA	probability of detecting B given detection of A	0 0 1	0 1
rBa	probability of detecting B given A is present but not detected	0 1 0	0 1
habitat (same)	habitat covariate impacts all Ψ or P parameters (above) the same way.	H	H
habitat (differs)	Habitat covariate impacts all Ψ parameters (above) differently.	H 0 0 0 H 0 0 0 H	NA

Table VI. 2. Model set for association of Rusty Blackbirds with Red-winged Blackbirds (RWBL) or Common Grackles (COGR) with habitat covariates accounted for. This model set was run for 63 independent sites surveyed in round one and 72 in round two and for each combination of Rusty Blackbirds with COGR and RWBL. Models had small SEs on parameter estimates and converged to at least 4.85 significant digits, except for round one models for COGR (COGR1) which had large SEs in six models two of which did not converge.

model	Ψ	P	param. SE	converged
1	.	.	ok	yes
2	conditional	conditional	ok	yes
3	conditional	conditional+grass	Ba(COGR1)	yes
4	conditional	unconditional	ok	yes
5	conditional	unconditional+grass	Ba(COGR1)	5.82(COGR1)
6	unconditional	conditional	ok	yes
7	unconditional	conditional+grass	ok	yes
8	unconditional	unconditional	ok	yes
9	unconditional	unconditional+grass	$\Psi A(COGR1)$	yes
10	conditional+grass	conditional	ok	yes
11	conditional+conditional grass	conditional	ok	yes
12	conditional+grass	unconditional	ok	yes
13	conditional+conditional grass	unconditional	ok	yes
14	unconditional+grass	conditional	ok	yes
15	unconditional+grass	unconditional	ok	yes
16	conditional+shallow	conditional	ok	yes
17	conditional+conditional shallow	conditional	ok	yes
18	conditional+shallow	conditional+grass	Ba(COGR1)	4.86(COGR1), 5.32(RWBL1)
19	conditional+conditional shallow	conditional+grass	-	no (COGR1)
20	conditional+shallow	unconditional	ok	yes
21	conditional+conditionalshallow	unconditional	ok	yes
22	conditional+shallow	unconditional+grass	ok	yes
23	conditional +conditionalshallow	unconditional+grass	-	no(COGR1)
24	unconditional+shallow	conditional	ok	4.85(RWBL1)
25	unconditional+shallow	conditional+grass	ok	yes
26	unconditional+shallow	unconditional	ok	yes
27	unconditional+shallow	unconditional+grass	ok	5.70(RWBL1)

Table VI.3. Model results from PRESENCE 4.0 for co-occurrence of Rusty Blackbirds and Red-Winged Blackbirds, with habitat covariates accounted for, during round one. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{cond})$	416.57	0.00	0.2559	1.0000	7	400.53
2	$\Psi(\text{uncond}),\text{p}(\text{cond}+\text{grass})$	417.17	0.60	0.1896	0.7408	6	403.67
3	$\Psi(\text{cond}),\text{p}(\text{cond}+\text{grass})$	417.53	0.96	0.1583	0.6188	7	401.49
4	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{uncond})$	419.02	2.45	0.0752	0.2938	5	407.97
5	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{cond})$	419.18	2.61	0.0694	0.2712	6	405.68
6	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	419.54	2.97	0.0580	0.2265	7	403.50
7	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	420.15	3.58	0.0427	0.1670	8	401.48
8	$\Psi(\text{cond}),\text{p}(\text{cond})$	420.24	3.67	0.0408	0.1596	6	406.74
9	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{uncond})$	420.80	4.23	0.0309	0.1206	6	407.30
10	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{cond})$	421.61	5.04	0.0206	0.0805	9	400.21
11	$\Psi(\text{uncond}),\text{p}(\text{cond})$	422.70	6.13	0.0119	0.0467	5	411.65
12	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond})$	422.78	6.21	0.0115	0.0448	7	406.74
13	$\Psi(\text{cond}),\text{p}(\text{uncond}+\text{grass})$	423.52	6.95	0.0079	0.0310	6	410.02
14	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{cond}+\text{grass})$	423.67	7.10	0.0074	0.0287	10	399.44
15	$\Psi(\text{cond}),\text{p}(\text{uncond})$	424.93	8.36	0.0039	0.0153	5	413.88
16	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond})$	425.15	8.58	0.0035	0.0137	6	411.65
17	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{uncond})$	425.73	9.16	0.0026	0.0103	8	407.06
18	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	426.05	9.48	0.0022	0.0087	7	410.01
19	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{conditional})$	426.45	9.88	0.0018	0.0072	9	405.05
20	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{uncond})$	426.63	10.06	0.0017	0.0065	5	415.58
21	$\Psi(.),\text{p}(.)$	427.20	10.63	0.0013	0.0049	2	423.00
22	$\text{psi}(\text{cond}+\text{shallow}),\text{p}(\text{uncond})$	427.36	10.79	0.0012	0.0045	6	413.86
23	$\Psi(\text{uncond}),\text{p}(\text{uncond}+\text{grass})$	428.03	11.46	0.0008	0.0032	5	416.98
24	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{uncond}+\text{grass})$	429.63	13.06	0.0004	0.0015	9	408.23
25	$\text{psi}(\text{uncond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	430.47	13.90	0.0002	0.0010	6	416.97
26	$\text{psi}(\text{cond}+\text{condshallow}),\text{p}(\text{uncond})$	431.05	14.48	0.0002	0.0007	8	412.38
27	$\text{psi}(\text{uncond}),\text{p}(\text{uncond})$	431.55	14.98	0.0001	0.0006	4	422.86

VI.4. Model results for co-occurrence of Rusty Blackbirds and Red-Winged Blackbirds, with habitat covariates accounted for, during round two. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{cond})$	500.56	0.00	0.2339	1.0000	7	484.81
2	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{uncond})$	500.75	0.19	0.2127	0.9094	6	487.46
3	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{cond})$	500.99	0.43	0.1886	0.8065	6	487.70
4	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{uncond})$	502.64	2.08	0.0827	0.3535	5	491.73
5	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{cond})$	502.98	2.42	0.0697	0.2982	9	482.08
6	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{uncond})$	503.12	2.56	0.0650	0.2780	8	484.83
7	$\Psi(\text{uncond}),\text{p}(\text{cond})$	505.65	5.09	0.0184	0.0785	5	494.74
8	$\Psi(\text{uncond}),\text{p}(\text{cond}+\text{grass})$	505.77	5.21	0.0173	0.0739	6	492.48
9	$\Psi(\text{cond}),\text{p}(\text{cond})$	505.77	5.21	0.0173	0.0739	6	492.48
10	$\Psi(\text{cond}),\text{p}(\text{uncond})$	506.03	5.47	0.0152	0.0649	5	495.12
11	$\Psi(\text{cond}),\text{p}(\text{cond}+\text{grass})$	506.85	6.29	0.0101	0.0431	7	491.10
12	$\Psi(\text{cond}),\text{p}(\text{uncond}+\text{grass})$	507.17	6.61	0.0086	0.0367	6	493.88
13	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond})$	507.35	6.79	0.0078	0.0335	6	494.06
14	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	507.41	6.85	0.0076	0.0325	7	491.66
15	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond})$	507.48	6.92	0.0074	0.0314	7	491.73
16	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{uncond})$	507.51	6.95	0.0072	0.0310	6	494.22
17	$\Psi(\text{uncond}),\text{p}(\text{uncond})$	507.85	7.29	0.0061	0.0261	4	499.25
18	$\Psi(\text{uncond}),\text{p}(\text{uncond}+\text{grass})$	508.19	7.63	0.0052	0.0220	5	497.28
19	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	508.52	7.96	0.0044	0.0187	8	490.23
20	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	508.59	8.03	0.0042	0.0180	7	492.84
21	$\Psi(.),\text{p}(.)$	509.15	8.59	0.0032	0.0136	2	504.98
22	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{uncond})$	509.27	8.71	0.0030	0.0128	5	498.36
23	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	509.54	8.98	0.0026	0.0112	6	496.25
24	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{uncond})$	512.44	11.88	0.0006	0.0026	8	494.15
25	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{cond})$	512.54	11.98	0.0006	0.0025	9	491.64
26	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{uncond}+\text{grass})$	513.72	13.16	0.0003	0.0014	9	492.82
27	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{cond}+\text{grass})$	513.81	13.25	0.0003	0.0013	10	490.20

Table VI.5. Model results for co-occurrence of Rusty Blackbirds and Common Grackles, with habitat covariates accounted for, during round one. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support. Two models, $(\Psi(\text{cond}+\text{condshallow}),p(\text{cond}+\text{grass}))$ and $\Psi(\text{cond}+\text{condshallow}),p(\text{uncond}+\text{grass})$, did not converge and were removed from the set. Models 3, 7, 13, and 22 had large SE on parameter B estimates which can be an indicator of unreliable model results. Removing the problematic models from the set does not change the ranking order or model likelihood of the remaining top models and only changes AIC weight in the fourth decimal place.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{cond}+\text{grass}),p(\text{cond})$	416.57	0.00	0.2579	1.0000	7	400.53
2	$\Psi(\text{uncond}),p(\text{cond}+\text{grass})$	417.17	0.60	0.1910	0.7408	6	403.67
3	$\Psi(\text{cond}),p(\text{cond}+\text{grass})$	417.53	0.96	0.1596	0.6188	7	401.49
4	$\Psi(\text{uncond}+\text{shallow}),p(\text{uncond})$	419.02	2.45	0.0758	0.2938	5	407.97
5	$\Psi(\text{uncond}+\text{grass}),p(\text{cond})$	419.18	2.61	0.0699	0.2712	6	405.68
6	$\Psi(\text{uncond}+\text{shallow}),p(\text{cond}+\text{grass})$	419.54	2.97	0.0584	0.2265	7	403.50
7	$\Psi(\text{cond}+\text{shallow}),p(\text{cond}+\text{grass})$	420.15	3.58	0.0431	0.1670	8	401.48
8	$\Psi(\text{cond}),p(\text{cond})$	420.24	3.67	0.0412	0.1596	6	406.74
9	$\Psi(\text{cond}+\text{grass}),p(\text{uncond})$	420.80	4.23	0.0311	0.1206	6	407.30
10	$\Psi(\text{cond}+\text{condgrass}),p(\text{cond})$	421.61	5.04	0.0207	0.0805	9	400.21
11	$\Psi(\text{uncond}),p(\text{cond})$	422.70	6.13	0.0120	0.0467	5	411.65
12	$\Psi(\text{cond}+\text{shallow}),p(\text{cond})$	422.78	6.21	0.0116	0.0448	7	406.74
13	$\Psi(\text{cond}),p(\text{uncond}+\text{grass})$	423.52	6.95	0.0080	0.0310	6	410.02
14	$\Psi(\text{cond}),p(\text{uncond})$	424.93	8.36	0.0039	0.0153	5	413.88
15	$\Psi(\text{uncond}+\text{shallow}),p(\text{cond})$	425.15	8.58	0.0035	0.0137	6	411.65
16	$\Psi(\text{cond}+\text{condgrass}),p(\text{uncond})$	425.73	9.16	0.0026	0.0103	8	407.06
17	$\Psi(\text{cond}+\text{shallow}),p(\text{uncond}+\text{grass})$	426.05	9.48	0.0023	0.0087	7	410.01
18	$\Psi(\text{cond}+\text{condshallow}),p(\text{conditional})$	426.45	9.88	0.0018	0.0072	9	405.05
19	$\Psi(\text{uncond}+\text{grass}),p(\text{uncond})$	426.63	10.06	0.0017	0.0065	5	415.58
20	$\Psi(.),p(.)$	427.20	10.63	0.0013	0.0049	2	423.00
21	$\Psi(\text{cond}+\text{shallow}),p(\text{uncond})$	427.36	10.79	0.0012	0.0045	6	413.86
22	$\Psi(\text{uncond}),p(\text{uncond}+\text{grass})$	428.03	11.46	0.0008	0.0032	5	416.98
23	$\Psi(\text{uncond}+\text{shallow}),p(\text{uncond}+\text{grass})$	430.47	13.90	0.0002	0.0010	6	416.97
24	$\Psi(\text{cond}+\text{condshallow}),p(\text{uncond})$	431.05	14.48	0.0002	0.0007	8	412.38
25	$\Psi(\text{uncond}),p(\text{uncond})$	431.55	14.98	0.0001	0.0006	4	422.86

Table VI.6. Model results for co-occurrence of Rusty Blackbirds with Common Grackles, with habitat covariates accounted for, during round two. Models within $\Delta 2\text{AICc}$ were considered to have substantial model support.

rank	model	AICc	ΔAICc	AIC wgt	likelihood	k	-2log likelihood
1	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{cond})$	500.56	0.00	0.2339	1.0000	7	484.81
2	$\Psi(\text{cond}+\text{grass}),\text{p}(\text{uncond})$	500.75	0.19	0.2127	0.9094	6	487.46
3	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{cond})$	500.99	0.43	0.1886	0.8065	6	487.70
4	$\Psi(\text{uncond}+\text{grass}),\text{p}(\text{uncond})$	502.64	2.08	0.0827	0.3535	5	491.73
5	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{cond})$	502.98	2.42	0.0697	0.2982	9	482.08
6	$\Psi(\text{cond}+\text{condgrass}),\text{p}(\text{uncond})$	503.12	2.56	0.0650	0.2780	8	484.83
7	$\Psi(\text{uncond}),\text{p}(\text{cond})$	505.65	5.09	0.0184	0.0785	5	494.74
8	$\Psi(\text{uncond}),\text{p}(\text{cond}+\text{grass})$	505.77	5.21	0.0173	0.0739	6	492.48
9	$\Psi(\text{cond}),\text{p}(\text{cond})$	505.77	5.21	0.0173	0.0739	6	492.48
10	$\Psi(\text{cond}),\text{p}(\text{uncond})$	506.03	5.47	0.0152	0.0649	5	495.12
11	$\Psi(\text{cond}),\text{p}(\text{cond}+\text{grass})$	506.85	6.29	0.0101	0.0431	7	491.10
12	$\Psi(\text{cond}),\text{p}(\text{uncond}+\text{grass})$	507.17	6.61	0.0086	0.0367	6	493.88
13	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond})$	507.35	6.79	0.0078	0.0335	6	494.06
14	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	507.41	6.85	0.0076	0.0325	7	491.66
15	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond})$	507.48	6.92	0.0074	0.0314	7	491.73
16	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{uncond})$	507.51	6.95	0.0072	0.0310	6	494.22
17	$\Psi(\text{uncond}),\text{p}(\text{uncond})$	507.85	7.29	0.0061	0.0261	4	499.25
18	$\Psi(\text{uncond}),\text{p}(\text{uncond}+\text{grass})$	508.19	7.63	0.0052	0.0220	5	497.28
19	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{cond}+\text{grass})$	508.52	7.96	0.0044	0.0187	8	490.23
20	$\Psi(\text{cond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	508.59	8.03	0.0042	0.0180	7	492.84
21	$\Psi(.),\text{p}(.)$	509.15	8.59	0.0032	0.0136	2	504.98
22	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{uncond})$	509.27	8.71	0.0030	0.0128	5	498.36
23	$\Psi(\text{uncond}+\text{shallow}),\text{p}(\text{uncond}+\text{grass})$	509.54	8.98	0.0026	0.0112	6	496.25
24	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{uncond})$	512.44	11.88	0.0006	0.0026	8	494.15
25	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{cond})$	512.54	11.98	0.0006	0.0025	9	491.64
26	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{uncond}+\text{grass})$	513.72	13.16	0.0003	0.0014	9	492.82
27	$\Psi(\text{cond}+\text{condshallow}),\text{p}(\text{cond}+\text{condgrass})$	513.81	13.25	0.0003	0.0013	10	490.20

Appendix VII. PRELIMINARY FOOD AVAILABILITY DATA

Table VII.1. Abundance of potential food items (mast and live prey) by groundcover substrate categories. Average abundances are \pm (SE). Five 20.5 x 24.0 x 5.5 cm samples were taken within each 25 m habitat circle (at the center and at 25 m in each cardinal direction). Food availability samples were associated with water depth measurements taken at the same locations during habitat sampling. At occupied points, sampling took place the same day birds were located.

substrate	#samples	av. water depth	total mast	av. mast/site	total live	av. live/site
impervious surface	29	0.0 (0.0)	55	2.0 (0.9)	0	0.0 (0.0)
water	103	26.8 (2.6)	44	0.4 (0.3)	56	0.6 (0.3)
grass	135	0.2 (0.1)	39	0.3 (0.1)	89	0.7 (0.2)
woody-debris	43	5.3 (2.1)	20	0.5 (0.2)	48	1.1 (0.2)
leaf litter	781	1.3 (0.1)	346	0.4 (0.1)	1004	1.3 (0.1)
floating vegetation	149	36.1 (2.1)	4	0.0 (0.0)	276	1.2 (0.2)

Table VII.2. Classifications of potential mast (a), and live prey (b) food items and associated ground-cover substrates. Classification is to class or order whenever possible. Food items were sampled from five 20.5 x 24.0 x 5.5 cm locations within each 25 m habitat circle (at the center and 25 m away in each cardinal direction). At occupied points sampling took place the day birds were located.

a)

classification	total	impervious surface	grass	woody debris	leaf-litter	floating vegetation	water
<i>Carya aquatica</i>	5				x		
<i>Carya illinoensis</i>	68		x	x	x		x
<i>Celtis laevigata</i>	102			x	x		
<i>Ligustrum sinense</i>	22			x	x	x	
<i>Pinus</i> sp.	3				x		
<i>Quercus lyrata</i>	4				x		
<i>Quercus nigra</i>	123	x	x		x		
<i>Quercus nuttallii</i>	1				x		
<i>Quercus phellos</i>	8				x		
<i>Quercus</i> sp.	1				x		
<i>Quercus virginiana</i>	1				x		
<i>Sapium sebifera</i>	45				x		
<i>Taxodium</i>							
<i>distichum</i>	184		x		x	x	x
unidentified mast	29		x	x	x	x	

b)

classification	total	impervious surface	grass	woody debris	leaf-litter	floating vegetation	water
Actinopterygii	48				x	x	x
Amphipoda	116				x	x	
Anura	4					x	x
Araneae	42		x	x	x	x	
Chilopoda	9				x		
Clitellata	97		x	x	x	x	
Coleoptera	113		x	x	x	x	x
Collembola	242		x		x		
Decapoda	8				x	x	
Diploda	3				x		
Diptera	5				x		
Gastropoda	104		x	x	x	x	
Hemiptera	6				x	x	
Hymenoptera	83		x	x	x	x	x
Isopoda	287		x	x	x	x	
Lepidoptera	14		x		x	x	
Odonata	10					x	
Orthoptera	1				x		
Patellologastropoda	24				x	x	
Stylommatophora	40		x		x	x	
Veneroida	99			x	x	x	
unknown							
grub/larva	118		x	x	x		
unidentified live	68		x	x	x	x	

VITA

Emma DeLeon was born in 1984 in Buffalo, New York and grew up with birdwatcher parents who encouraged her love of nature. She attended the University of Pittsburgh, where after a brief foray into plant genetics, she re-discovered her interest in birds through an ornithology class and began an internship at Powdermill Avian Research Center. Emma completed her undergraduate studies in 2006 with a double degree in Ecology and Evolution and in Anthropology. After deciding to pursue ecology, she continued to work as a technician at Powdermill for several years, where she helped to develop a program to monitor migrants using nocturnal flight calls and learned to band birds in her spare time. After experimenting with a variety of field jobs in Arizona, Illinois, Louisiana, Nevada and Pennsylvania, Emma returned to school in 2009 to begin a Masters degree at Louisiana State University. After graduation in the summer of 2012, Emma hopes to continue to travel, enjoy nature, and study birds while pursuing a career in conservation ecology.