WINTER ECOLOGY OF THE RUSTY BLACKBIRD (EUPHAGUS CAROLINUS)

by

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(Under the Direction of Robert Cooper and Russell Greenberg)

ABSTRACT

The Rusty Blackbird (*Euphagus carolinus*) is the fastest declining songbird in North America likely due to loss, modification, and conversion of wetland habitat in their winter range in the southeastern United States. The species uses suburban landscapes for wintering habitat, although forested bottomland wetlands historically provided the necessary resources for wintering. Suburban landscapes used by Rusty Blackbirds are composed of a mosaic of patches including forested wetlands, residential lawns, and pecan groves. The patches act together to provide Rusty Blackbirds with pre-opened mast that includes both small-seeded red oak (*Quercus* spp.) acorns and pecans (*Carya illinoinensis*), terrestrial non-native earthworms (*Lumbricus* spp.), aquatic wetland worms (*Tubifex* spp.), and invertebrates other than worms like snails, dragonfly (Odonata) and fly (Diptera) larvae, and Isopods. This is the first study that documents significant worm-use by Rusty Blackbirds.

Current and short-term past and future weather, and particularly precipitation, largely drives patch use, body mass regulation, and incorporated diet items, indicating habitat-use is likely driven by invertebrate availability in suburban landscapes. Therefore, managing water fluctuations in wetlands used by Rusty Blackbirds may be an important

technique to increase invertebrate abundance and availability during the winter and especially during times when invertebrates have low availability during periods of drought. This research is the first to document precipitation as a driver of habitat use and food incorporation for songbirds during winter.

Rusty Blackbirds use mast to overcome times when invertebrates have low availability such as during current and future cold weather and times without precipitation. Red oak trees in wetlands and residential areas provide mast and habitat for suburban gray squirrels (*Sciurus carolinensis*), which are an important facilitator in providing pre-opened nuts throughout the winter. Small-seeded red oak trees in residential areas and wetlands also provide leaf litter for cover and forage of terrestrial and aquatic worms. Rusty Blackbirds also use abandoned pecan orchards extensively during cold weather. Providing all components in the landscape is necessary for successful management of the species. Managing Rusty Blackbirds in suburban landscapes may be complex because the diet in the eastern population consists of non-native components (i.e., pecan and non-native terrestrial earthworms).

INDEX WORDS: Rusty Blackbird, *Euphagus carolinus*, Winter, Telemetry, Patch-use, Diet isotopes, Body mass, Precipitation, Temperature, Barometric pressure

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M.S., The Louisiana State University, 2008

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial

Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2013

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DEDICATION

This dissertation is dedicated to my parents; David Murray Newell and Jean

Cecile Newell. They have been the biggest supporters in everything I do and have raised

me to think for myself. They taught me I am capable of anything I put my mind to.

ACKNOWLEDGEMENTS

I would like to acknowledge the important people and institutions that helped make this work possible. Russell Greenberg brought the plight of the Rusty Blackbird to the ornithology world, conceived of this research, found funding, and selected me to spend about half my graduate years following the blackbird around from South Carolina to New Hampshire. I am very grateful to have been able to be challenged with this project. I am also grateful to have been able to work with such a great mind in ornithology. I would also like to thank Bob Cooper for taking me as a student after my previous advisor left the university. I had always wanted to work with Dr. Cooper and I was very fortunate to be a part of his high quality lab. Thanks for supporting me and encouraging me through sometimes difficult times, you are a true mentor.

The Cooper lab provided an excellent learning environment and their assistance and advice was important to me. Thanks to Sarah Brown, Joanna Hatt, Mason Cline, Cathy Ricketts, Anna Joy Lehmicke, Bryan Nuse, Brett Maley, Abby Sterling, Ali Leggett, Kirk Stodola, and Clark Jones. I would also like to thank my committee members Mike Conroy, John Maerz, and Sara Schweitzer for advice and help throughout my time at the University of Georgia. I am grateful for Dr. Conroy who was patient as I learned Bayesian statistics from him. I was fortunate to have had him take me under his wing and get as much one-on-one learning as I did. John Maerz opened my eyes to the world of teaching. It is easy to be inspired by his passion for teaching. I had not considered my aptitude for being a good teacher, but through John, I learned that teaching

providing teaching assistantships that gave me the opportunity to develop teaching skills and my approach to teaching through interactions with students.

My parents have always inspired me to take my life where I want to, and although uneducated in the traditional sense, are some of the most intelligent and interesting people I know. I would also like to thank my husband Michael Wohner for supporting me through one of the most difficult periods of my life.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

THE DECLINE

The Rusty Blackbird (*Euphagus carolinus*) is reported to be the fastest declining songbird

species in North America (Niven et al. 2004, Sauer et al. 2005, Greenberg et al. 2011).

Based on isotopic analysis of feathers, there are two distinct populations, one that winters

west of the Appalachians and breeds in Alaska and western and central Canada, and one

that winters east of the Appalachians and breeds in New England and eastern Canada

(Fig. 1.1; Hobson et al. 2010). Both eastern and western populations of Rusty Blackbird

have experienced an estimated 85-95% decline continent-wide with similar accelerated

rates of population decline since at least the 1960s (Fig. 1.2; Greenberg and Droege 1999,

Savignac 2006, Greenberg and Matsuoka 2010, Greenberg et al. 2011). The species was

thus declared a focal species of conservation concern of the USFWS (2008) and

considered vulnerable to extinction by the IUCN Red List (2010).

After more than a decade of research on this species, the reason for the decline

still remains unclear (Greenberg and Matsuoka 2010). Potential hypotheses include loss

and modification of high quality winter wetland habitat, loss of migration stopover

habitat, and modification of breeding ground habitat due to acid rain or forest

management (Avery 1995, Greenberg and Droege 1999, Hamel et al. 2009, Greenberg

and Matsuoka 2010, Greenberg et al. 2011). It is commonly thought that loss and

modification of winter wetland habitat in the southeastern United States is the most

plausible explanation for the decline. Winter wetland systems have been disappearing

most quickly and match the blackbird population decline trend (Hamel et al. 2009,

Greenberg and Matsuoka 2010). The peak of freshwater wetland loss between the 1950s

and the 1980s also corresponds to the peak in Rusty Blackbird decline (Hamel et al.

2009). Nest success across the breeding range indicates Rusty Blackbirds perform as well

as, or better than, other songbird species (~75-95%; Matsuoka et al. 2010, P. Newell

Wohner and C. Foss *unpub. data*). In addition, although wetlands on the breeding

grounds of Alaska and Canada have been impacted by global climate change (Corcoron

et al. 2009), the wintering grounds are more heavily impacted (Nagy et al. 2011).

Further evidence the decline is caused by factors on the wintering ground is

populations of other blackbirds including the Red-winged Blackbird (*Agelaius

phoeniceus*) and Common Grackle (*Quiscalus quiscula*), that overlap the Rusty Blackbird

core wintering range in the Southeast, are also experiencing rapid declines compared to

their overall decline (Fig. 1.3; Blackwell and Dolbeer 2001, USGS 2011). The concurrent

decline indicates a similar story among these native eastern North American blackbird

species. In Georgia, South Carolina, Mississippi, and Alabama, Red-winged Blackbird

population trends were -3.5, -5.0, -2.1, and -4.0 %/year, respectively, and were -3.9, -3.4,

-4.8 and -3.6 %/year for Common Grackles (USGS 2011). These blackbird trends

compare to the overall trend across the United States of -0.9%/year and -1.6 %/year from

1965 to 2010 for Red-winged Blackbirds and Common Grackles, respectively (USGS

2011). The fact that blackbird decline is much greater in blackbirds wintering in the

Southeast than overall trends across the United States supports the premise that habitat

loss on the wintering ground is likely responsible for Rusty Blackbird decline. Thus, research focusing on the wintering ground could be of paramount importance.

Habitat use, occupancy, and body condition studies have previously been conducted on wintering Rusty Blackbirds from the western population (Luscier et al. 2010, DeLeon 2012, C. Mettke-Hofmann *unpub. data*); however, winter ecology appears to be different in the eastern population. For instance, sexual segregation and smaller flock sizes were much more prevalent in research on Rusty Blackbirds from the western population. My research was conducted on the eastern population of Rusty Blackbird and documents several aspects of winter ecology including landscape use, body mass regulation, and diet incorporation as it relates to winter weather factors such as precipitation, temperature, and barometric pressure.

LANDSCAPE USE

Rusty Blackbirds are gregarious during the non-breeding season, occurring in flocks that are found in landscapes composed of various patch types that provide a combination of invertebrates and tree mast. Wintering ground research indicates this species extensively uses suburban habitats that include bottomland hardwood stands, moist soil impoundments, pecan (*Carya illinoinensis*) orchards and groves, and residential lawns (Luscier et al. 2010, DeLeon 2012, P. Newell Wohner *unpub. data*, C. Mettke-Hofmann *unpub. data*). Rusty Blackbird use of suburban landscapes indicates the species is not limited to forested wetlands and has adapted to changing land use practices.

Within these various patch types in the suburban landscape, Rusty Blackbirds consume a variety of small-size red oak (*Quercus* spp.) acorns such as willow oak (*Q. phellos*) and water oak (*Q. nigra*), as well as pecan nuts. Tree mast is relatively high in

high-energy lipids compared to many invertebrate sources and may be included in the winter diet to help birds endure extreme winter temperatures and/or to compensate for times of low invertebrate availability (Fredrickson and Reid 1988, Smith and Scarlett 1987). Even within a 60-minute period, Rusty Blackbirds venture back and forth from various suburban patch-types accumulating various food resources. Pecans are acquired from abandoned pecan groves where there is a crushing mechanism. Pre-opened small-seeded red oak acorn mast are eaten in residential areas and wetlands. Terrestrial non-native earthworms (*Lumbricus* spp.) are taken from lawns and wetland margins. Aquatic worms and other invertebrates such as snails, Odonata and Diptera larvae, and spiders (Araneae) come from wetlands. Daily patch choices within the landscape are likely governed by short-term past, present, and future weather conditions.

BODY MASS REGULATION

North-temperate zone wintering songbirds are most food-limited during winter when food resources are lower and more unpredictable and the need for increased resources is higher due to increased metabolism to compensate for colder weather (Sherry et al. 2005). Species dependent on wetlands for food resources may be even more limited because periods of drought severely limit invertebrate abundance and activity in wetlands (Sherry et al. 2005). In addition, low early morning temperature, and extreme temperature and precipitation events can limit wetland invertebrate availability frequently throughout the winter (Neckles et al. 1990, Batema et al. 2005, Corcoran et al. 2009).

In the North-temperate zone, songbirds compensate for food shortages by storing fat for protection against food scarcity and unpredictability, and are generally heavier during winter (Rappole 1995, Newton 1998). Fat reserves are usually a compromise

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between risk of starvation and predation (Newton 1998, Rogers 2005). While increased fat reserves result in reduced flight efficiency (Metcalf and Ure 1995, Newton 1998), temperate-zone wintering birds with higher fat stores are usually associated with higher physiological condition (Koivula et al. 1995, Stevenson and Woods 2006, Danner *in prep.*).

Rusty Blackbirds are temperate-zone wintering songbirds that contend with periods of extreme weather on their wintering grounds. Thus, they may regulate body mass adaptively, storing less fat when resources are more predictable or available and storing more fat when resources are less available. Because temperature and precipitation affect wetland invertebrate availability, body mass regulation is likely related to weather events (Rogers 1995).

DIET

The wintering diet of Rusty Blackbirds is cited in recent studies to include snails, insects, spiders, and crayfish (Luscier et al. 2010, DeLeon 2012, Greenberg et al. 2011); however, these citations are based largely on accounts from Beal (1900) who could only sample ten stomachs during wintering (December to February) and from unknown populations. Considering the timing of the most rapid decline, beginning ~1965, that began well after the last reports of this species' wintering diet, it seems instructive to elucidate the current diet of this species.

Researchers have hypothesized the importance of tree mast and especially pecan for wintering Rusty Blackbirds; however, the function and importance of tree mast in the diet are still unknown. Because pecans have much higher levels of lipid (~72%) than acorns (~20%), and are also more reliably available throughout the winter, they may be a

superior food source to both acorns and invertebrates for enduring periods of extreme weather (Fredrickson and Reid 1988, Kaminski et al. 2003). Alternatively, pecan mast availability may only be important when invertebrate resources are not available due to extreme weather.

Recent techniques in bird diet studies use isotopic information from bird consumers to estimate dietary proportions in the diet of source items available in the environment (Kelly 2000, Phillips 2001, Podlesak et al. 2005, Inger and Bearhop 2008). Stable isotope diet analysis provides a picture of food items or groups that are incorporated into animal tissue (Inger and Bearhop 2008). In most isotopic studies, the naturally occurring heavy and light stable isotopes of carbon and nitrogen are used in a ratio to develop a signature unique to individual organisms (Kelly 2000, Phillips 2001, Inger and Bearhop 2008). The ratio of heavy isotopes to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) compared to a standard is represented by $\delta^{13}C$ and $\delta^{15}N$ (Kelly 2000, Phillips 2001).

Signatures from different tissues of an animal yield information about diet incorporation over varying time and spatial scales (Podlesak et al. 2005, Inger and Bearhop 2008). Blood plasma and red blood cells indicate diet composition within the past ~1-3 days and ~10-30 days, respectively, in passerines (Bearhop et al. 2003, Pearson et al. 2003, Podlesak et al. 2005, Sabat et al. 2013). The variation in temporal scale of different tissues of an animal occurs because tissue replacement occurs at varying intervals depending on the tissue type (Inger and Bearhop 2008). Carbon and nitrogen isotopic signatures of the consumers and their diet sources, as well as source concentrations and discrimination factors, are used in Bayesian mixing models to

determine proportions of dietary items in short and mid-term diet (Bearhop et al. 2003, Podlesak et al. 2005, Koenig et al. 2008). Discrimination factors must be incorporated into diet mixing-models to account for the predictable shift from ingestion, digestion, and assimilation to the actual source signatures.

Rusty Blackbirds are difficult to observe foraging, and it is no longer acceptable to sacrifice rare and declining bird species, thus, the technique of using isotopic information to elucidate short and mid-term winter diet of Rusty Blackbirds is desirable. Individual bird diets can then be related to short-term weather variables at the time of capture to determine potential causes of diet shifts and fluctuations.

NON-NATIVE EARTHWORMS AND SUBURBAN AREAS

Although non-native earthworms appear to have a detrimental effect on some populations of native songbirds in northern forests (Loss et al. 2012), they have also been found to have a positive influence on other native songbirds such as American Robin (*Turdus migratorius*; Cameron and Bayne 2012), especially in heavily disturbed sites. Non-native earthworm species are only likely to occur in high abundance in extremely disturbed sites such as suburban sites (Hendrix et al. 2006). Suburban landscapes may, therefore, place stress on surrounding forest ecosystems. Disturbed land such as gardens, lawns, and refuse sites are often hypothesized to be ideal for populations of non-native earthworms to prosper and expand (James and Hendrix 2004, Szlavecz et al. 2006, Szlavecz et al. 2011). However, in a review of many studies of exotic earthworms across the southeast and the world, Hendrix et al. (2006) found high abundances of exotic earthworms occurred only in severely disturbed forest sites, whereas native earthworms occurred in undisturbed to slightly disturbed sites, sometimes in association with exotics.

Exotics most often fail to disperse into undisturbed landscapes even decades after introduction (Hendrix et al. 2006).

The presence of predominately non-native earthworms in suburban areas may have consequences for management of Rusty Blackbird flocks occurring in suburban landscapes. Rusty Blackbird flocks in suburban areas may be exposed to higher densities of, if not exclusive, populations of non-native earthworm taxa while blackbirds in undisturbed landscapes may not. Studies have found native bird populations are affected positively by the abundance of non-native earthworm prey in heavily disturbed sites (Rodriguez 2006, Cameron and Bayne 2012). Rodriguez (2006) reviewed the facilitative effects of non-native species on native species in 61 studies. In many cases, non-native species tend to facilitate native species (Rodriguez 2006). The facilitative impacts of non-native earthworms may present management dilemmas in conservation and restoration efforts (Rodriguez 2006). However, if suburban habitats exclusively contain non-native earthworms, then despite the controversial nature of their presence, they would seem to be a resource that could be managed for wildlife under certain scenarios.

DISSERTATION OBJECTIVES AND STRUCTURE

Although Rusty Blackbirds are in precipitous decline, there are still up to an estimated two million birds remaining and it may not be too late to stop and reverse further decline (Greenberg et al. 2011). While previous wetland loss in the southeastern United States in both the recent past (1950s-1990s) and since colonization (<1920s) was predominately due to agriculture and the forest products industry (Pinder et al. 1999, Koneff and Royle 2004), future wetland loss will be due, in large part, to urbanization (Nagy et al. 2011). Because of the projected increase in urbanization, and Rusty Blackbird flocks seem to

persist in suburban landscapes, I studied wintering blackbirds in suburban southeastern landscapes. I attempted to understand how eastern populations of Rusty Blackbird use the landscape, regulate body mass, and incorporate invertebrate and tree mast resources into their diet in relation to current and short-term winter weather variation. Last, I attempted to provide managers of public and private lands, such as nature parks and residential communities, with recommendations for conservation of this species.

There has been very little research conducted on wintering Rusty Blackbirds thus far, and none on the winter ecology of the eastern population. The core wintering area with the most persistent flocks of Rusty Blackbirds in the eastern population consists of portions of the Piedmont Plateau and Atlantic Coastal Plain (Fig. 1.4; Hamel and Ozdenerol 2009). I therefore studied flocks in these two physiognomic regions (Fig. 1.5).

This dissertation includes four manuscripts preceded by an introduction and literature review, and followed by a conclusion with major findings and conservation recommendations. In Chapter 2, I examine patch use within suburban landscapes on the Piedmont Plateau during winters 2011 and 2012 using a multiple logistic regression analysis of radio-telemetry location data. Blackbirds in four sites were followed throughout the day as they ventured back and forth between residential lawns, pecan groves, and nature-park wetlands. Weather variables were created for each hour blackbirds were observed from the nearest weather station and included present, and short-term past and future precipitation, temperature, and barometric pressure. I then found relationships between patch use and short-term weather variables. This telemetry study emphasizes the need to consider Rusty Blackbird patch-use at the landscape scale and I will emphasize this throughout the dissertation.

In Chapter 3, I use Bergstrom and Sherry's (2008) regression equation to estimate total, lipid, and lean body mass of blackbirds captured in sites on the Piedmont Plateau and Atlantic Coastal Plain from 2007 to 2012. I then use scaled body mass (Peig and Green 2010) to determine how mass components change with precipitation, temperature, and barometric pressure. Others have found short-term weather variables influence body mass (Mandin and Vezin 2012). I reason if birds are operating with food limitation below a critical threshold, body mass should be related to events associated with increased food availability such as precipitation and temperature, with increased body mass occurring under warmer temperatures and more precipitation. Alternatively, if birds operate above the threshold, body mass should not be positively related to short-term temperature or precipitation.

In Chapter 4, I determine carbon and nitrogen discrimination factors (Δ^{13}C and Δ^{15}N) from a large dataset of plasma, red blood cells (RBC), and claw tips of Rusty Blackbirds from the Piedmont Plateau and Atlantic Coastal Plain from 2009 to 2012. Typically, researchers using Bayesian stable-isotope mixing models to estimate dietary proportions use an average value for $\Delta\delta^{13}$C and Δ^{15}N for songbirds; however, many factors can influence discrimination factors and an average value may result in highly erroneous results (Caut et al. 2009, Bond and Diamond 2011). Output from isotopic mixing models is highly sensitive to variation in discrimination factors (Bond and Diamond 2011). Because I had a large sample size of isotopic data from various sites with varying source signatures, I was able to estimate discrimination factors without the use of a captive study normally required. I first determined RBC discrimination factors using the R package SIAR by systematically modeling diet proportions with potential

combinations of $\Delta^{13}C$ and $\Delta^{15}N$ within the known range for songbirds (Caut et al. 2009).

I then found the best solutions compatible with known food source availability

information by site and year. I was able to estimate Rusty Blackbird RBC specific

discrimination factors through use of a decision table to eliminate nonsensical

combinations of discrimination factors. I then determined $\Delta^{13}C$ and $\Delta^{15}N$ values of

plasma and claw tips by back-adjusting signatures to plot over RBC values over the same

time frame. Because plasma represents diet over ~1-3 days and RBC over the past three

weeks to a month, and blackbirds exhibit site-fidelity (determined through the telemetry

study in Chapter 2), I reasoned that plasma values should overlay RBC values for the

same time-frame plasma was sampled in the same site. I used similar logic to determine

discrimination factors for claw tips.

In Chapter 5, I evaluate the short and mid-term diet of Rusty Blackbirds with

Bayesian isotopic mixing models based on plasma and RBC signatures and using

discrimination factors determined in Chapter 4. I estimate median values of posterior

distributions from SIAR for proportions of six groups of potential food items (i.e.,

pecans, acorns, worms, and trophic levels with nitrogen signatures of 3‰, 6‰, and 9‰)

that were collected in sites Rusty Blackbirds were observed foraging via telemetry.

Precipitation is the most important factor governing availability of invertebrates

(Fredrickson and Batema 1992, Batema et al. 2005); thus, I also relate diet proportions to

short-term weather. I test two hypotheses: (1) that blackbirds incorporate pecans over

invertebrates because invertebrate resources in wetlands are limited, or (2) to prepare for

extreme weather (Delestrade 1999, Cuthill et al. 2000, Danner et al. *in prep*.).

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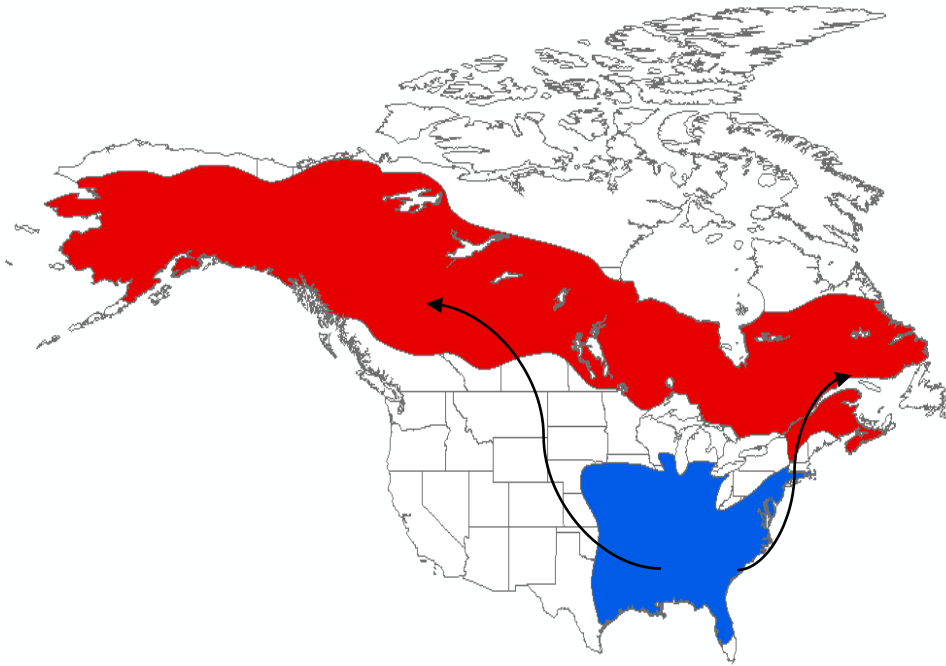
Figure 1.1. Breeding (red) and wintering range (blue) of the Rusty Blackbird in North America. Arrows represent general migration pathways from the wintering ground to the breeding ground of the eastern and western populations of the species.
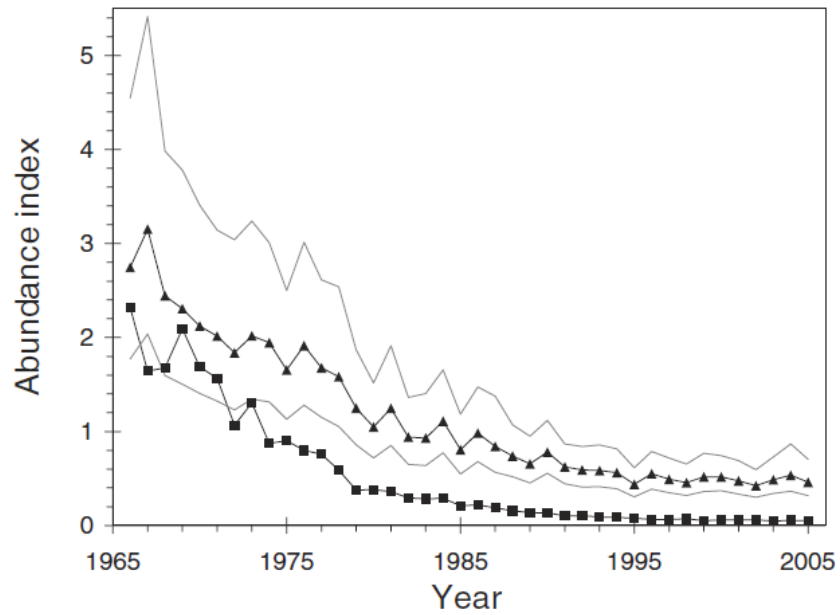
Figure 1.2. Trends in the abundance index of Rusty Blackbirds from 1966 to 2005 as estimated from the Christmas Bird Count (triangles with 97.5% credible interval in gray) and North American Breeding Bird Survey (squares; Sauer et al. 2005). Reproduced with permission from Greenberg et al. (2011).
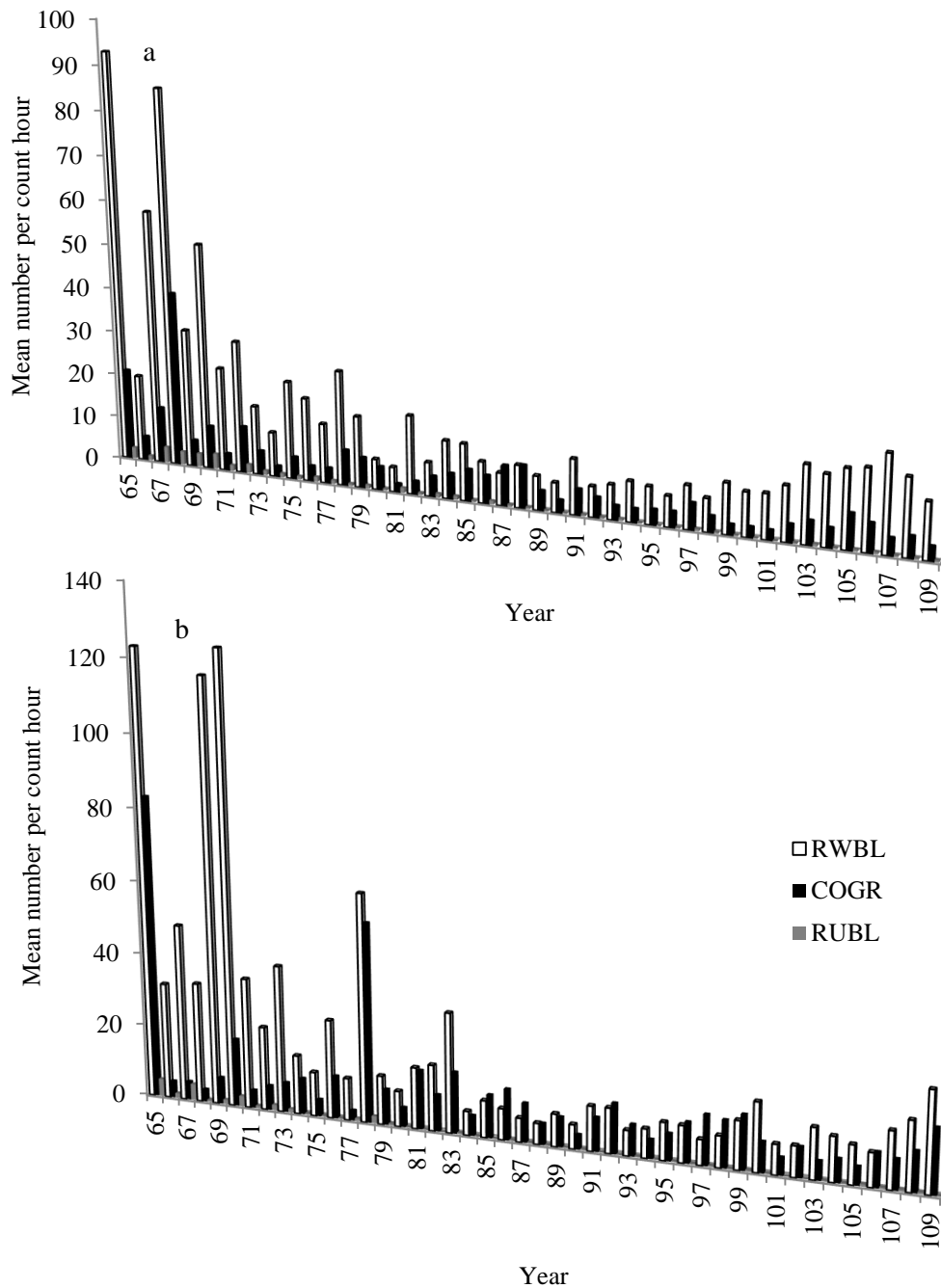
Figure 1.3. Mean number of birds per count hour in Georgia (a) and South Carolina (b) during the

Christmas Bird Count from 1965 (65) to 2009 (109). RWBL = Red-winged Blackbird, COGR =

Common Grackle, and RUBL = Rusty Blackbird.
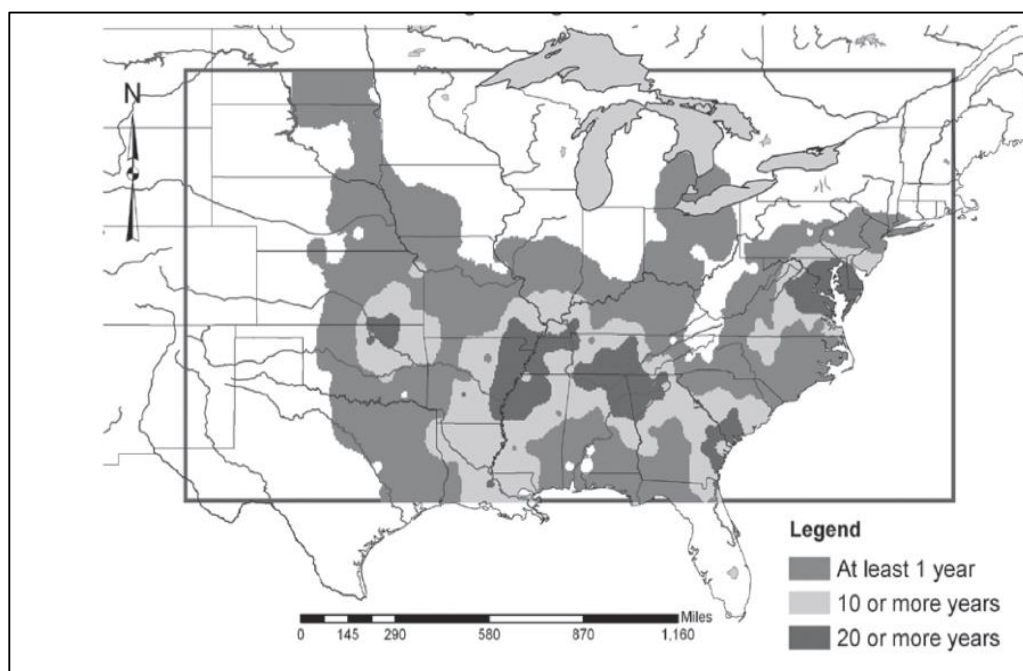
Figure 1.4. Non-breeding distribution of Rusty Blackbird based on spatial filtering of Christmas Bird Counts from 1946-2001. Different shadings reflect portions of the range in which the species was recorded at significantly different rates in at least 1, at least 10, and at least 20 years. Reproduced with permission from Hamel and Ozdenerol (2009).
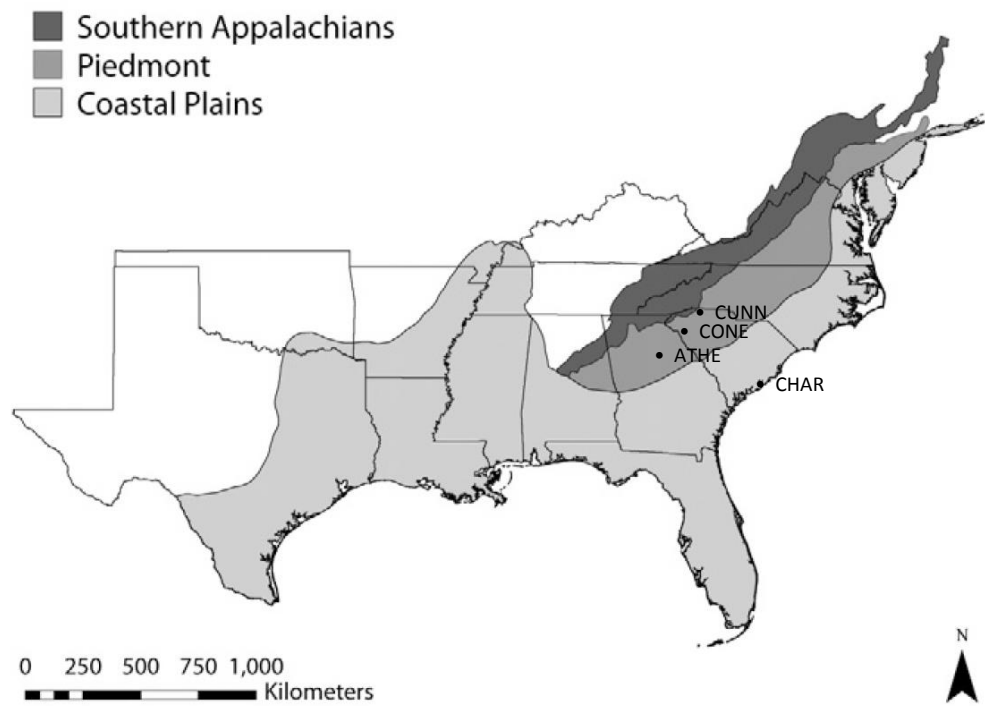
Figure 1.5. Rusty Blackbird study sites overlaid on physiographic regions of the southeastern United States. CUNN = Lake Cunningham SC, CONE = Conestee SC, ATHE = Athens GA, and CHAR = Charleston SC. Map reproduced with permission from Nagy et al. (2011).

CHAPTER 2

INFLUENCE OF WEATHER ON PATCH USE BY RUSTY BLACKBIRD FLOCKS

WINTERING IN SUBURBAN LANDSCAPES[1]

ABSTRACT.–Songbirds wintering in the temperate-zone face unpredictable and sometimes severe weather. Some species have adapted by incorporating high-lipid tree mast into their diet during wintering, either to help them physiologically endure extreme weather events or because during these events, protein-rich invertebrates are not accessible, or both. We studied radio-tagged wintering Rusty Blackbird flocks (*Euphagus carolinus*) that used a matrix of patch types including shallow nature park wetlands, residential lawns, and pecan (*Carya illinoinensis*) groves in suburban areas. Because each patch type was associated with a predominant food type (i.e., tree mast versus invertebrate), we could investigate the influence of weather on winter patch use for foraging. While blackbirds used pecan groves ~30% of the time during a comparatively cold 2011 winter, birds were not observed using pecan groves during a relatively warm 2012 winter. Blackbirds were more likely observed using pecan groves with worsening short-term weather, in wetlands with improving weather and previous rain, and residential lawns with future precipitation. Pecan mast likely helps blackbirds endure times when wetland invertebrates are not easily accessed, and is an important but sporadically used component of a mosaic of habitats that constitute important wintering areas for this rapidly declining species.

Key words: Non-breeding, Pecan, Radiotelemetry, Rusty Blackbird, Suburban, Weather, Wetland invertebrate.

INTRODUCTION

Winter food availability is often cited as the most important factor limiting songbird populations because it affects body condition and ultimately survival (Sherry et al. 2005, Brown and Sherry 2006). In addition to finding enough food resources for surviving the winter, songbirds must also endure sub-optimal weather conditions. Birds that winter in the temperate-zone face unpredictable weather that at times can be severe (Gosler 1996, Pravosudov et al. 1999), even at more southerly latitudes, such as the southeastern United States (Newton 1998). Birds have evolved different strategies for enduring harsh and unpredictable weather such as growing extra body feathers, sunning, roosting together, and incorporating more fat into the diet (Newton 1998). Some species, such as a number of waterfowl species (Fredrickson and Reid 1988, Kaminski et al. 2003), Whooping Crane (*Grus Americana*; Nelson et al. 1996), Alaskan Redpoll (*Acanthus* spp.; White and West 1977), Hermit Thrush (*Catharus guttatus*; Diggs et al. 2011), Red-headed Woodpecker (*Melanerpes erythrocephalus*), and Blue Jay (*Cyanocitta cristata*; Smith and Scarlet 1987), which are mainly insectivorous during breeding or migration but winter in regions with the threat of extreme weather, supplement their invertebrate diet with high-lipid vegetative sources.

Birds experiencing unpredictable food supplies should accumulate fat stores for times when resources are difficult to find (Newton 1998). Tree mast, such as that from oak (*Quercus* spp.) and pecan (*Carya illinoinensis*), is loaded with high-energy lipids compared to many invertebrate sources (Fredrickson and Reid 1988, Kaminski et al. 2003). Pecan trees in particular may be extremely valuable winter forage sources where they occur in the southeastern United States (Santerre 1994). Pecans are higher in

digestible lipids and accessible protein than many other types of tree mast including oak (Fredrickson and Reid 1988). For example, pecans are higher in fat (40.8% dry weight) compared to pin oak (*Q. palustris*; 18.9%) and willow oak (*Q.phellos*; 20.6%) acorns, and contain more protein (8.4%) than the acorns of both pin (6.4%) and willow oak (5.1%; Fredrickson and Reid 1988).

Pecan trees, especially cultivars, are more consistent in crop production year to year than oak trees that typically have highly productive mast events only every two to six years (Clotfelter et al. 2007). Pecan trees drop their fruit gradually from November to February (Worley 2002), typically the coldest months of the year in the southeastern United States, thus providing an energy rich food source when birds are at their greatest need (Newton 1998). In contrast, acorns fall in autumn and once dry, are key food supplies for numerous mammals and birds that may consume or cache them before migrant songbirds arrive on the wintering ground (Clotfelter et al. 2007). Pecan groves and orchards then, particularly those that are abandoned, are potentially high energy food sources for a variety of resident and migrant wintering songbird species (Smith 1986), provided other agents crack and open the hard outer husks.

The Rusty Blackbird (*Euphagus carolinus*) is a migratory species that breeds in boreal and Acadian forests of Canada, Alaska, and New England and winters in the southeastern United States (Greenberg and Droege 1999). The species is estimated to be the fastest declining songbird in North America with a possible 85-95% overall decline continent-wide since at least the 1960s (Greenberg and Matsuoka 2010, Greenberg et al. 2011). Although Rusty Blackbirds are in precipitous decline, there are still an estimated

158,000 to two million individuals (Savignac 2006, Greenberg and Matsuoka 2010) giving us the opportunity to study them during winter.

Historically, Rusty Blackbirds wintered in flocks in bottomland hardwood forests where they foraged on aquatic invertebrates and small-seeded red oak mast in shallow water (Beal 1900, Avery 1995). With the loss of large tracts of traditional bottomland hardwood forests (Pinder et al. 1999), Rusty Blackbird flocks have adapted to suburban landscapes that include a combination of abandoned pecan orchards and groves, residential areas, and shallow nature park wetlands; a landscape mosaic. These habitat patches, seemingly in combination, provide flocks with a mixture of aquatic and terrestrial invertebrates and tree mast.

Invertebrate prey consumed by suburban Rusty Blackbirds includes dragonfly larvae (Odonata), fly larvae (Dipera), small aquatic worms, and large terrestrial worms; Newell Wohner *in prep*.). These invertebrate resources are particularly high in both fat and protein content. For example, small wetland *Tubifex* spp. worms available to Rusty Blackbirds contain ~15-20% fat and ~48% protein dry weight, and terrestrial earthworms (*Lumbricus* spp.) contain ~13-18% fat and ~62% protein (Fredrickson and Reid 1988, Bernard and Allen 1997, Barker et al. 1998). Insect larvae such as that from Odonata are also high in fat averaging 25% with very high levels of protein (average = 58% dry weight; DeFoliart 1991, Ying et al. 2001). While pecans and acorns contain from 20 to 40% fat content, they only have ~5-8% protein (Fredrickson and Reid 1988). The required amount of protein in the diet is not known for most omnivorous songbird species but is estimated at 5.3% for White-crowned Sparrows (*Zonotrichia leucophrys gambelii*; Murphy 1993), 6.9% for White-throated Sparrows (*Zonotrichia albicollis*), and 9.63 for

Hermit Thrush (*Catharus guttatus*; Langlois and McWilliams 2010). Thus, compared to tree mast, fat-laden invertebrates likely have a superior ratio of nutrients for a songbird trying to maintain both lean and lipid mass; that is, based solely on nutrient information. However, birds usually require a diverse diet to obtain all the nutrients they need (Fredrickson and Reid 1988).

Invertebrate productivity in wetlands is governed by short-term water fluctuations and temperature variation (Parsons and Wharton 1978, White 1985, Batema 1987, Fredrickson and Batema 1992, Magee et al. 1999, Batema et al. 2005). Wetland macroinvertebrates available to songbirds are associated with leaf litter that provides habitat and forage for macroinvertebrates and their food (e.g., algae and microbes; Batema et al. 2005). A large body of research exists on leaf-litter inhabiting invertebrate responses to precipitation and water fluctuation in wetlands, due to the importance of invertebrate food resources to waterfowl management (Neckles et al. 1990, Fredrickson and Batema 1992, Wehrle et al. 1995, Magee et al. 1999, Fredrickson and Batema 2005). Aquatic invertebrate prey is less available with colder temperatures, in early morning, and during drought (White 1985, Neckles et al. 1990, Batema et al. 2005, Corcoran et al. 2009). Worms (subclass: Oligochaeta) become more available during precipitation events as they vacate wetlands and other low-lying areas to avoid drowning (Neckles et al. 1990, Corcoran et al. 2009). Insect larvae, such as Odonata and Diptera, experience rapid increases, or pulsing, in response to precipitation events and subsequent receding of water levels (Fredrickson and Batema 1992, Batema et al. 2005).

Therefore, invertebrates available to Rusty Blackbird flocks in the various suburban patch types (i.e., forested wetlands, pecan groves, and residential lawns) are

likely affected by various short-term weather events. Because the patch types can be associated with different food resources (i.e., pecan mast with pecan groves and invertebrates with wetlands), these suburban systems provide an opportunity to determine if patch use and associated food resources are affected by present and short-term past and future weather conditions.

METHODS

Study area.–We studied Rusty Blackbird flocks in two suburban landscape mosaics in Greenville, South Carolina (Lake Conestee [2011] and Lake Cunningham [2012]), and two mosaics in Athens, Georgia (North Athens [2011] and West Athens [2012]; Fig. 2.1). In both Greenville and Athens, observation data were collected within suburban areas in forested wetlands along creeks, in residential lawns surrounding wetlands, abandoned pecan groves, and to a much lesser degree, upland pine forest patches. Bottomland hardwood forests were dominated by native hardwood species such as sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), water oak, red maple (*Acer rubrum*), boxelder (*A. negundo*), river birch (*Betula nigra*), flowering dogwood (*Cornus florida*), and eastern hophornbeam (*Ostrya virginiana*), while upland areas consisted mostly of loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*).

Bird sampling and radiotelemetry.–We used whoosh nets (Skelhorn and Rowe 2009) and mist nets to capture birds in pecan groves from December through February. Blackbirds were lured to nets by concentrating crushed pecans collected from the grove around nets. Each captured blackbird received a unique USGS (USGS BBL Permit # 22665) and color-band combination for identification. Date and time of capture were recorded and dates were later transformed to day of year (Day). Also, time of sunrise in minutes was

subtracted from time of capture in minutes to standardize capture times relative to time from sunrise.

We attached Holohil transmitters (BD2, 1.2 g, duration 45 days) to Rusty Blackbirds during the winters of 2011 and 2012 in order to delineate the locations of Rusty Blackbird flocks. Transmitters were attached via a synsacrum harness with degradable 1-mm jelly cord as per Rappole and Tipton (1991). Transmitter weight with harness varied from 1.8% (for a 70-g bird) to 2.3% (for a 55-g bird) of bird mass.

Location data of radio-marked Rusty Blackbird flocks were collected from January 1 to March 15 and daytime duration was between 4 and 11 hours. We began flock observations at varying times to ensure observations were collected throughout the day. We conducted observations following sunrise and before sunset which was the activity time of Rusty Blackbird flocks during this study. Observers documented flock locations within each landscape mosaic by rotating among frequencies throughout the day with the objective of accumulating one point per blackbird separated by at least 30 minutes or when flocks with tagged blackbirds switched to a new habitat type, whichever came first. Thirty minutes was used as the cut-off point because it usually took this long or longer to get location points of all the birds in their respective flocks.

We tracked blackbirds in flocks with radio-transmitters using hand-held Yagi antennas and Advanced Telemetry Systems radio receivers. Locations were determined either by homing in until flocks were seen or through triangulation. Because flocks could travel large distances between wetlands and residential areas quickly, observers used a vehicle to travel among triangulation points. In this study, Rusty Blackbirds with transmitters that we observed visually *always* co-occurred with other Rusty Blackbirds

within a flock. We always observed at least some proportion of the flock engaged in

foraging while other blackbirds might have been be perched in overhead trees. Thus, we

believed we were justified in assuming that at least part of the flock was participating in

foraging activity in every observation in the dataset.

Because we used the tagged bird to represent a flock, the amount of error

associated with the telemetry process was reduced since the area covered by the flock

was much larger than the area covered by a single blackbird. Because tagged Rusty

Blackbirds were associated with a flock that we *always* observed foraging in the same

patch type, visual locations of flocks with tagged birds were quite accurate. In addition,

patch sizes were large (>150 ha) relative to the area used by the flock (>1 ha). Flock

locations were plotted on a paper map of the site at the time of the observation and were

based on distances and compass bearings from a known position on the map. The

locations were then delineated as wetland (WL), residential (RES), or pecan residential

(PRES). This study plan was approved by the University of Georgia IACUC (AUP#

A2009 1-003).

Statistical analysis.–To avoid autocorrelation due to the fact that multiple birds with

transmitters from the same flock were often found together, we eliminated records where

>1 bird per flock was recorded in the same location on the same date and within 20

minutes of each other (randomly keeping one). Twenty minutes was deemed the amount

of time it would take blackbird flocks to travel between extreme locations in the mosaic.

Thus, the dataset contains only one point ≥20 minutes apart for the entire flock unless

blackbirds in the flock were in distinct patch types. Night roost locations were not

considered in this analysis because selection criteria for foraging sites likely differ from

those for night roost sites. We removed points of capture locations from the day of capture from analyses because flocks may have been lured to the capture area by crushed pecans used to entice birds to the net area. Because we were interested in determining variables associated with pecan use, we only included a subset of the 2011 dataset collected from Lake Conestee and Athens from January because the area directly surrounding pecan trees in Lake Conestee was largely void of pecan nuts after January 31 and blackbirds were not observed foraging there anymore. In 2012, we used data from January and February but excluded March to ensure the analysis included only birds that were actually wintering. Blackbirds captured after February may have been preparing for migration, indicated by departure dates of telemetered birds. We included location data only from patch types that constituted >5% of the total of all observations.

We used multinomial logistic models for 2011 data and binomial logistic models for 2012 data because in 2011, Rusty Blackbirds used three major patch types including wetlands (WL), pecan residential (PRES), or residential lawns (RES) while in 2012, we only observed them using two major patch types (WL and RES). For 2011 data, we conducted multinomial logistic regression using the package "mnet" in program R (R Development Core Team 2012). For 2012 data, we used GLM in program R (R Development Core Team 2012) to run binomial logistic models.

We used an information-theoretic approach to evaluate the relative model fit of logistic regression models for patch type use and combinations of 18 predictor variables (Neter et al. 1990, Burnham and Anderson 2002). For each year, we compared 46 a priori models via AIC_c corrected for small sample bias. We conducted Pearson correlations on all pairs of predictor variables prior to modeling and if variables had $r > 0.45$, they were

not included in the same model because an *r* threshold of 0.45 is generally considered a moderate correlation.

The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002) that range from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. Because the ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham and Anderson 2002), we chose to report a confidence set of models that included only those candidate models with Akaike weights that were within 10% of the largest weight, similar to the general rule-of-thumb (i.e., 1/8 or 12%) suggested by Royall (1997) for evaluating strength of evidence. To choose the best model in analyses that generated several top models, we chose the model with the fewest parameters within $\Delta AIC_c < 2$ of the top model. We chose the top model if the level of support ($w_i > 0.5$) indicated it was far better than other models. We report log odds estimates and 85% confidence intervals of exponentiated log odds ratios from the top model. Confidence intervals that contained zero indicated inconclusive results because we could not determine the nature of the relationship due to imprecision in parameter estimates. To allow for ease of interpretation, we scaled estimates for each predictor variable in the top model. The scalars correspond to what we believe to be ecologically relevant unit changes in predictors (e.g., a 5°C increase in temperature).

The 46 competing models were constructed to discern whether Rusty Blackbirds use patches according to short-term weather and assumed corresponding invertebrate availability. The predictor variables for patch type use included time, temperature, precipitation, and barometric pressure variables (Table 2.1). Weather variables were

constructed from raw hourly data from WeatherUnderground from Athens, Georgia and

Greenville, South Carolina weather stations (The Weather Underground, LLC, 2013).

Aquatic insects have supercooling points typically around -3º to -7°C (Marchand 1996),

thus many of the temperature variables were developed using the number of hours below

-3°C to be relevant to invertebrate availability. We tested for differences in weather

variables among the three months (January 2011, January 2012, February 2012) using a

simple analysis of variance (aov) in program R.

RESULTS

General.–During 2011, we obtained 804 total locations from five birds in Lake Conestee

and 739 from 11 birds from North Athens. During 2012, we obtained 1423 total locations

from eight birds in Lake Cunningham and 261 from five birds in West Athens

(Supplementary material Appendix 1, Table A1). We obtained locations in seven known

patch types in both 2011 and 2012 (Fig. 2.2). After removing autocorrelated observations

and observations from patch types that constituted <5% of the total (i.e., agriculture,

uplands, and pasture), there were 319 records in the 2011 January dataset; WL (170 or

53%), PRES (94 or 29%), and RES (55 or 17%) and 526 records in the 2012 January and

February dataset; WL (276 or 52%) and RES (250 or 48%).

During January 2011, 49% of the locations in the dataset (158) were obtained

from sunrise to 260 min after sunrise (around 1200); the remaining 162 locations (51%)

were collected from 261to 670 min after sunrise (1800), and in 2012; 40% and 60%,

respectively. Most temperature, precipitation, and barometric pressure variables varied

considerably between January 2011 and January-February 2012 (Supplementary material

Appendix 1, Table A2).

We observed no pecan use via radio-telemetry in winter 2012 compared to 2011 even though blackbirds were captured in pecan groves in Athens. The 2011 winter season averaged much colder than winter 2012. Observation temperature was on average colder in January 2011 compared to January (5.9°C) and February 2012 (6.6°C), and the average daily minimum was below freezing in January 2011 (-0.4°C) compared to 3.2 and 3.9°C in January and February 2012, respectively. Also, there was an average of ~4 to 6 hours below -3°C in the two days up to and following observations in January 2011 compared to zero hours in January 2012 and close to zero in February 2012.

Logistic regression for patch use.–The top model for the 2011 multinomial logistic regression was much better (3.2 times; $w_i = 0.76$) than competing models ($w_i \leq 0.24$; Table 2.2). Variables that had the greatest effect on patch use were 2-day future precipitation and barometric pressure change over the previous 24 hrs from the observation time (Table 2.3). Birds were more likely (2.5 and 37 times/2.54cm precipitation) to be observed in pecan groves than in wetlands or residential lawns with every 2.54cm less future precipitation, and more likely (14.5 and 37 times/2.54cm precipitation) to be observed in residential areas with every 2.54cm increase of precipitation in the following two-days from the observation. Rusty Blackbirds were also more likely to use pecan groves for each 2.54cm decrease in barometric pressure in the previous 24 hours and if there was less precipitation in the previous 3 days (Table 2.3). Temperature variables had much smaller effect sizes on patch use. Blackbirds were more likely (1.5 times) to be observed in wetlands than in residential areas and pecan groves with colder hourly temperature, which is the opposite effect we predicted if birds were responding to low invertebrate availability because of cold temperatures. Birds were

more likely (1.1 times) to use pecan groves and residential areas for every hour below -3°C in the previous two days from the observation (Table 2.3).

The top model for the January-February 2012 multinomial logistic regression was much better (43.6 times; $w_i = 0.96$) than competing models ($w_i \leq 0.022$; Table 2.2). Results of the 2012 binomial logistic regression indicate rising barometric pressure in the 24 hrs before the observation, increasing precipitation in the previous 3 days, and increasing hourly temperature, increases the probability of observing Rusty Blackbirds in wetlands versus residential areas (Table 2.3).

The same variables were important in the January 2011 and January-February 2012 analysis. Like 2012, barometric pressure in the previous 24 hrs and precipitation in the previous 3 days were two of the largest effects (Table 2.3). Although the comparison of barometric pressure between probabilities of use of wetlands versus residential areas was not informative in 2011, in 2012 blackbirds were increasingly observed in wetlands over residential areas with increasing barometric pressure in the past 24 hrs. In addition, birds were 1.64 times more likely to be observed in wetlands with each 2.54cm increase in precipitation in the previous 3 days. In contrast to 2012, Rusty Blackbirds were 1.85 times more likely to be observed in wetlands than residential areas with every 5.6°C increase in temperature (Table 2.3).

DISCUSSION

Suburban Rusty Blackbird flocks on the Piedmont Plateau use a matrix of shallow wetlands, residential lawns, and pecan groves for winter foraging sites and use is driven by meteorological events that affect invertebrate abundance and availability. One of the biggest effects on patch use based on results in both years and effect sizes was decreasing

barometric pressure over the previous 24 hrs. It is well known that birds respond to rising

barometric pressure as a cue for departure during migration to take advantage of

favorable flight conditions (Kreithen and Keeton1974, Arkesson and Hedenstrom 2000,

Danhardt and Lindstrom 2001, Bulyuk and Tsvey 2006, Schmaljohann and Naef-Daenzer

2011, Bulyuk 2012). It is therefore not surprising that birds exposed to adverse conditions

during winter would use similar barometric pressure cues as they would for making

decisions during migration to forage optimally in varying winter conditions. This is the

only study we know of that has found correlations of this type, suggesting that songbirds

use barometric pressure to make patch use decisions during wintering.

Blackbirds increased their use of pecan groves with worsening weather in the

previous 24 hrs and increased use of wetlands when weather improved. Increased use of

wetlands is likely due to increased invertebrate availability associated with better short-

term weather. As weather worsens, invertebrates become less available and blackbirds

use pecan groves instead.

In general, precipitation variables played a much more important role in

predicting Rusty Blackbird suburban patch use than temperature variables. Both past and

future precipitation variables occurred in top models more often and had larger effect

sizes than temperature variables. Blackbird flocks increased use of wetlands relative to

pecan groves and residential lawns with more precipitation in the previous 3 days. During

heavy rain events, aquatic invertebrate prey may be less available, but become more

available in the days following wetland flooding as water levels subside (Neckles et al.

1990, Corcoran et al. 2009). Therefore, more precipitation may be associated with

increased availability of invertebrates in wetlands compared to pecan groves and

residential lawns (Neckles et al. 1990, Edwards 2004). American Woodcock (*Scolopax minor*) also uses forested wetlands and upland forests in relation to the availability of their main invertebrate prey, earthworms, likely according to water fluctuations and extreme weather (Vander Haegen et al. 1993, Myatt and Krementz 2007).

During 2011, blackbird flocks were much more likely to be observed in pecan groves (~36 times/2.54cm) with less future precipitation and much more likely to be observed in residential areas with more future precipitation. This finding supports assertions of local residents that the largest flocks use their yards when it was about to rain. In addition, we observed flocks during these events securing large terrestrial non-native earthworms (*Lumbricus* spp.) from residential lawns. Earthworms are more available up to and during precipitation events as they try to avoid inundation or disperse (Neckles et al. 1990, Edwards 2004). In times of drought, when wetland invertebrates and terrestrial earthworms are unavailable, birds may use pecan groves increasingly. Future precipitation, however, was not important in 2012.

In a concurrent diet stable isotope study, we found invertebrates, including large terrestrial earthworms and small aquatic worms as well as Odonata and Diptera larvae, to be the main food incorporated by Rusty Blackbirds (P. Newell Wohner et al. *unpubl. data*). In general, invertebrates are most active with increasing moisture and cease to be active with very low moisture and drought (Edwards 2004). Therefore, dry winters may be particularly hard on wintering blackbirds. Hamel and Ozdenarol (2009) speculated rainfall drives inter-annual variation in Rusty Blackbird distribution within the Mississippi Alluvial Valley.

Temperature variables may have much smaller effects than precipitation and barometric pressure variables because we studied Rusty Blackbirds that primarily winter south of areas with frequent spells of cold weather. Hence, the southerly distribution of the Rusty Blackbird may minimize the impact of temperature on their overwintering ecology (Hamel and Ozdenarol 2009).

The lack of observed pecan use with the warm 2012 winter compared to 30% of observations being made in pecan groves during the cold 2011 winter indicates pecan groves rich in accessible energy may be a valuable and necessary component of the landscape at suburban wintering mosaics only when January and February are cold and invertebrates are less available (Fredrickson and Reid 1988, Patnode and White 1992, Greenberg and Matsuoka 2010).

During 2011, blackbirds were somewhat more likely to be found in pecan groves versus wetlands if there were more hours in the previous two days below -3°C. In contrast to 2011, very few days in January and February 2012 dropped below -3°C and flocks were not exposed to cold weather. Consequently, the temperature variable was not important in 2012. In 2012, blackbirds used wetlands over residential areas with increasing hourly temperature. Invertebrates retreat deeper in mud in cold weather (Fredrickson and Batema 1992) but peak in abundance and are more active (and likely easier to find) in mid- to late-morning hours as temperatures rise (Neckles et al. 1990, Corcoran et al. 2009). The opposite trend in 2011, when birds increasingly used wetlands with colder weather, is a conundrum.

Our results support the idea that wetland flocking species wintering in unpredictable environments make decisions about where to forage based on a complex

interaction of previous, current, and expected weather in the short-term, and availability

of resources. White (2008) believed birds are entirely limited by their food resources and

the abundance and quality of food is dictated by weather. In summary, Rusty Blackbirds

increasingly use residential lawns with increasing future precipitation, pecan groves with

no previous or forecasted precipitation and cold weather, and wetlands after precipitation

events and during warm weather.

CONSERVATION IMPLICATIONS

Although Rusty Blackbirds have previously been considered wetland specialists, they

occur in suburban habitats, sometimes commonly. Researchers of the western population

also discovered wintering Rusty Blackbirds are not as tied to wetlands as previously

thought (Luscier et al. 2010, DeLeon 2012). Suburban landscapes, where the correct

components are available and in close proximity, appear to provide the resources Rusty

Blackbird flocks require for wintering. For instance, the mosaic of various wetlands in

Lake Conestee and the nearby neighborhood pecan source supports consistently large

flocks of Rusty Blackbirds from year to year. Radiotelemetry observations indicate Rusty

Blackbird flocks spend a proportionately similar amount of time in wetland and

residential (including pecan groves) areas. These two patch types constituted over 95% of

the observations in this study.

Pecan groves may be especially important in years when small-seeded red oaks

are not producing much mast. Pecans produce a crop at least every two years while oaks

may produce a good crop only every two to six years (Clotfelter et al. 2007).

Additionally, biomass of nuts in pecan groves is far greater than acorns from oak in forest

and creek habitats (A. Pellegrini and C. Mettke-Hofmann *pers. comm.).* Acorns of many

species of both white and red oak are synchronous over small areas but pecan production seems to be unrelated to oak production, thus providing various sources of tree mast in altering years (Smith and Scarlett 1987). In a study of Western Scrub Jays (*Aphelocoma californica californica*), larger, more stable populations were related to increased abundance and diversity of oak species and larger, more stable populations of *A. c. woodhouseii* were correlated with higher abundance and greater stability of pines and conifers (Koenig et al. 2009). The driver of increased population and stability was due to asynchrony in seed production among different species of trees (Koenig et al. 2009). The suburban Rusty Blackbird system may operate in a similar way with both pecans and acorns contributing to the availability of tree mast.

In addition to pecan groves, residential lawns are an important component of large suburban landscapes. Residential lawns are sources of high-energy terrestrial earthworms (albeit non-native) during rain events or immediately preceding rain events (Edwards 2004). Wetlands support small aquatic worms (families Tubificidae, Lumbriculidae, and Enchytraeidae; Edwards 2004). Since non-native terrestrial worms are considerably larger than the worms normally found in wetlands, it is no wonder that flocks prefer to forage in residential areas when conditions are suitable for acquiring large earthworms.

It is interesting that we did not find a similar effect of increased use of pecan (also non-native in the eastern wintering range) groves during rain events since functionally pecan groves seem similar to residential lawns. However, A. Pellegrini and C. Mettke-Hofmann (*pers. comm.*) found invertebrate availability in pecan groves (0.04 g/mean dry biomass/ $25cm^2$ sample) was much lower than creeks (0.37) and forest (0.4) in both dry and wet habitat. In addition to earthworms, acorns and other invertebrates are also

available in residential areas especially in increased abundance where leaves and tree mast have not been removed by landowners.

To be available for Rusty Blackbirds, acorns need to be broken open by other animals such as white-tailed deer (*Odocoileus virginianus*), and gray squirrels (*Sciurus carolinensis*; Meanley 1972, 1995). Our observations indicated most of the acorn mast blackbirds acquire is from gray squirrels that have cached the nuts and then inefficiently forage on them throughout the winter months.

Since large flocks of Rusty Blackbirds occur in suburban mosaics, and the forecast is for increasing urbanization in the southeastern United States (Pinder et al. 1999), managing Rusty Blackbirds in these habitats may be imperative. Shallow wetlands with small variation in topography that are in close proximity to pecan groves provide blackbirds with mast resources for times when wetland invertebrates are inaccessible or birds need to prepare for inclement weather. Nature parks, state lands, and other public lands therefore could be targeted to protect habitat.

At all four landscape mosaics in this study, most pecan trees were on private lands and older trees were at risk of removal or loss to development. Thus, one major conservation action would be to encourage nature parks and other public landholders to plant pecan trees on public lands to protect the pecan crop. In addition, the pecan crop must have a crushing source since Rusty Blackbirds cannot open the nuts themselves. Strategically-placed trees, such as in the parking lots of nature parks, or on walking trails, would allow pecans to be crushed.

Since precipitation seems to be a major driver of habitat use and invertebrate availability, manipulating water levels, as is done in greentree reservoirs to facilitate

drawing down of water resources, may help prolong the conditions blackbird flocks desire in wetlands. Another possible recommendation is to encourage fallow pastures where earthworms may be accessed in times of precipitation. The important consideration with Rusty Blackbird suburban habitat management is that all habitat components are necessary to ensure consistent use of the mosaic. For example, providing a wetland patch without a pecan grove or orchard in close proximity will not be enough to support large flocks of Rusty Blackbirds.

The presence of predominately non-native earthworms in suburban areas may have consequences for desirability of managing Rusty Blackbird flocks in suburban landscapes. Rusty Blackbird flocks in suburban areas may be exposed to higher densities of, if not exclusive, populations of non-native earthworm taxa while blackbirds in undisturbed landscapes may not. Non-native earthworm species occur in high abundance in extremely disturbed sites such as suburban sites (Hendrix et al. 2006). Disturbed land such as gardens, lawns, and refuse sites are often hypothesized to be ideal for populations of non-native earthworms to prosper and expand (Szlavecz et al. 2006, Szlavecz et al. 2011), however, in a review of many studies of exotic earthworms across the southeast and the world, Hendrix et al. (2006) found high abundances of exotic earthworms occurred only in severely disturbed forest sites, whereas native earthworms occurred in undisturbed to slightly disturbed sites, sometimes in association with exotics. Exotics most often fail to disperse into undisturbed landscapes even decades after introduction (Hendrix et al. 2006).

However, native bird populations such as American Woodcock and American Robin are affected positively by the abundance of non-native earthworm prey in heavily

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disturbed sites (Vander Haegen et al. 1993, Rodriguez 2006, Myatt and Krementz 2007, Cameron and Bayne 2012). Rodriguez (2006) reviewed the facilitative effects of non-native species on native species in 61 studies. In many cases, non-native species tend to facilitate native species (Rodriguez 2006). The facilitative impacts of non-native earthworms may present management dilemmas in conservation and restoration efforts (Rodriguez 2006) because of the negative reputation of exotic species. However, if suburban habitats exclusively contain non-native earthworms, then despite the controversial nature of their increase, they would seem to be a resource that could be managed for wildlife under certain scenarios.

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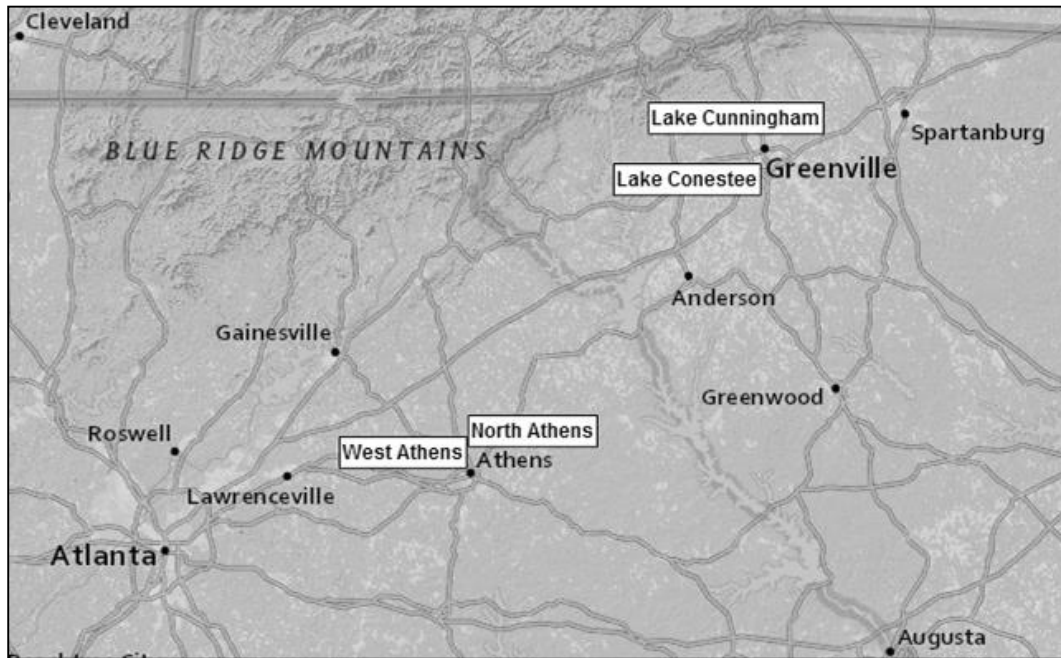
Figure 2.1. Map of Rusty Blackbird study mosaics in Georgia and South Carolina in 2011 (West Athens and Lake Conestee) and 2012 (North Athens and Lake Cunningham).
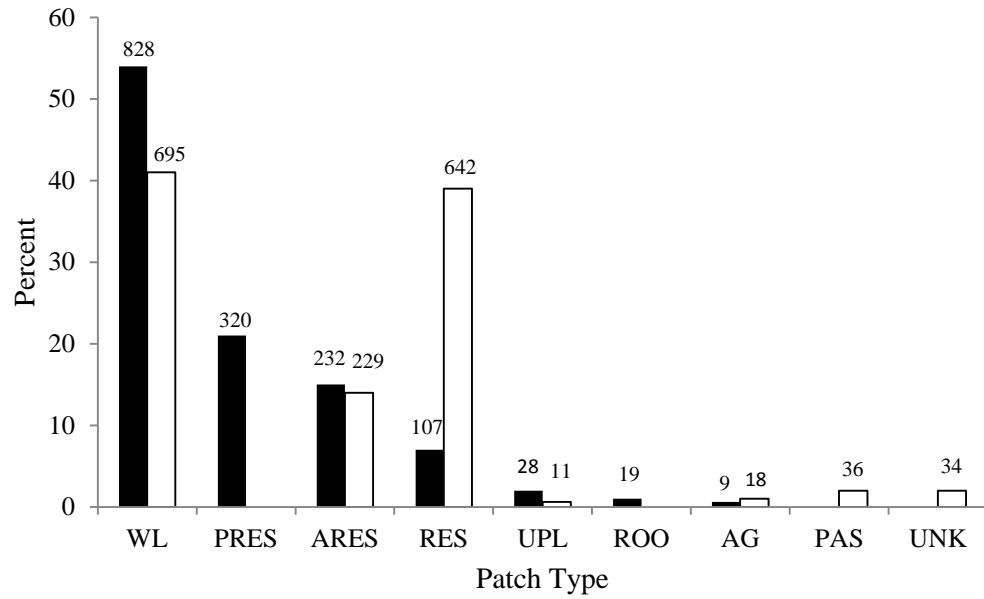
Figure 2.2. Patch types used by Rusty blackbirds in 2011 and 2012 on the Piedmont Plateau with the percent of total observations collected and the number of total observations above bars. WL = wetland, PRES = pecan residential, ARES = acorn residential, RES = residential, UPL = upland, ROO = roost, AG = agriculture, PAS = pasture, and UNK = unknown. Black fill = 2011 and white fill = 2012.

Table 2.1. Current and short term weather variables used in logistic models to determine the relationship between Rusty Blackbird patch use and time, temperature, precipitation, and barometric pressure variables in 2011 and 2012 on the Piedmont Plateau in Georgia and South Carolina. obs = observation.

Variable	Timeframe	Description	Units
Tsunrise	current	Time from sunrise	min
Day	current	Day of year	days
Temphour	current	Temperature during hour of obs	°C
Dailymax	current	Maximum temperature of day of obs	°C
Dailymin	current	Minimum temperature the previous night of obs	°C
Mintempnext	future	Maximum temperature day following obs	°C
Hrsnext2day<-3°C	future	Number hours in 48 hours following obs <-3°C	hrs
Prevdaymax	past	Maximum temp of the previous day to the obs	°C
Hrsprev3day<-3°C	past	Number hours in the previous 72 hrs < -3°C	hrs
Hrsprev2day<-3°C	past	Number hours in the previous 48 hrs < -3°C	hrs
Precipprev3day	past	Precipitation in the previous 72 hrs of obs	mm
Precipnext2day	future	Amount of precipitation in 48 hrs following the obs	mm
Precipnext24hrs	future	Amount of precipitation in 24 hrs following the obs	mm
Preciphour	current	Amount precipitation during hr of obs	mm
Hrsnoprecipprev	past	Number hours of no rain previous to obs	hrs
Barometric5hrs	past	Change in barometric pressure in previous 5 hrs to obs	cm
Barometric12hrs	past	Change in barometric pressure in previous 12 hrs to obs	cm
Barometric24hrs	past	Change in barometric pressure in previous 24 hrs to obs	cm

Table 2.2. Top models for predicting Rusty Blackbird presence in wetlands in 2011 and 2012. k = number of parameters, AIC_c = Akaike information criterion adjusted for small sample sizes, and w_i = weight. **Precipnext2day** = the amount of precipitation in the following two days from the observation, **Barometric24hrs** = change in barometric pressure in the previous 24 hours, **Precipprev3day** = precipitation in the previous three days, **Temphour** = temperature during the hour of the observation, **Hrsprev2day<-3ºC** = the number of hours in the last 3 days below -3°C, **Dailymax** = the maximum temperature of the day of the observation, **Barometric12hrs** = change in barometric pressure in the previous 12 hours, and **Preciphour** = amount of precipitation in the hour of observation. Top models are in bold.

Year	Candidate Models	k	AIC_c	ΔAIC_c	w_i
2011	**Precipnext2day+Barometric24hrs+Precipprev3day+ Temphour+Hrsprev2day<-3ºC**	**6**	**557.56**	**0**	**0.76**
	Precipnext2day+Precipprev3day+Temphour+Hrsprev2day<-3ºC	5	559.90	2.3	0.24
	Precipnext2day+Barometric24hrs+Precipprev3day+ Hrsprev2day<-3ºC+Dailymax	6	568.37	10.8	0.003
2012	**Temphour+Barometric24hrs+Precipprev3day**	**4**	**694.7**	**0**	**0.96**
	Temphour+Barometric24hrs	3	702.2	7.5	0.022
	Temphour+Barometric24hrs+Preciphour	4	702.8	8.1	0.017
	Temphour+Barometric12hrs+Preciphour	4	707.4	12.7	0.002

Table 2.3. Log odds estimate, standard error (SE), and 95% lower (LCI) and upper confidence intervals (UCI) of variables important to Rusty Blackbird probability of use in 2011 (n = 319) and 2012 (n = 526). Included are the biologically relevant unit change and the scaled, back-transformed log-odds ratio. WL = wetland, RES = residential, and PRES = pecan residential. **Precipnext2day** = the amount of precipitation in the following 2 days from the observation, **Barometric24hr**s = change in barometric pressure in previous 24 hours, **Precipprev3day** = precipitation in the previous 3 days, **Temphour** = temperature during the hour of the observation, and **Hrsprev2day<-3ºC** = the number of hours in the last two days below -3°C. n/a means the confidence interval includes zero and the estimate is unreliable. Estimate is read: Rusty Blackbirds are 36.97 times more likely to be observed in pecan residential compared to residential lawn with each 2.54cm increase in precipitation in the following 2 days of the observation. Variables whose confidence intervals do not include zero are in bold.

Year	Variable	Log Odds Estimate	SE	LCI	UCI	Unit Change	Scaled Odds Estimate
2011	WL Intercept	-0.58	0.99	-2.52	1.36	n/a	n/a
	RES Intercept	2.63	1.38	-0.09	5.35	n/a	n/a
	PRES:WL Precipnext2day	**-0.94**	**0.29**	**-1.50**	**-0.37**	**2.54 cm**	**-2.56**
	PRES:RES Precipnext2day	**-3.61**	**1.20**	**-5.97**	**-1.25**	**2.54 cm**	**-36.97**
	WL:RES Precipnext2d	**-2.68**	**1.2**	**-5.02**	**-0.33**	**2.54 cm**	**-14.59**
	PRES:WL Barometric24hrs	**-1.71**	**0.82**	**-3.33**	**-0.10**	**2.54 cm**	**-5.53**
	PRES:RES Barometric24hrs	**-2.39**	**1.11**	**-4.57**	**-0.22**	**2.54 cm**	**-10.91**
	WL:RES Barometric24hrs	-0.68	1	-2.64	1.28	n/a	n/a
	PRES:WL Precipprev3day	**-1.15**	**0.21**	**-1.56**	**-0.74**	**2.54 cm**	**-1.57**
	PRES:RES Precipprev3day	**-1.23**	**0.32**	**-1.86**	**-0.60**	**2.54 cm**	**-1.62**
	WL:RES Precipprev3day	-0.085	0.31	-0.7	0.53	n/a	n/a
	PRES:WL Temphour	0.042	0.019	0.0034	0.081	5.6	1.49
	PRES:RES Temphour	-0.042	0.029	-0.099	0.014	n/a	n/a
	WL:RES Temphour	-0.085	0.026	-0.13	-0.03	5.6	-1.09
	PRES:WL Hrsprev2day<-3ºC	0.08	0.03	0.020	0.14	1	1.08
	PRES:RES Hrsprev2day<-3ºC	-0.087	0.053	-0.19	0.017	n/a	n/a
	WL:RES Hrsprev2day<-3ºC	-0.17	0.05	-0.26	-0.07	1	-1.19
2012	WL Intercept	-3.53	0.67	-4.87	-2.23		
	WL:RES **Barometric24hrs**	**1.92**	**0.44**	**1.075**	**2.79**	**2.54 cm**	**6.82**
	WL:RES Temphour	0.061	0.01	0.039	0.085	5.6	1.85
	WL:RES **Precipprev3day**	**0.50**	**0.16**	**0.18**	**0.82**	**2.54 cm**	**1.64**

APPENDIX

Table A1. Summary of telemetered Rusty Blackbirds from 2011 and 2012 including frequency, sex, date and year captured, site (Lake Cunningham, Lake Conestee, North Athens, or West Athens) whether the bird was in the analysis (N = no and Y = yes), the total number of locations collected, the number of days tracked, and the fate of the bird.

Bird	Sex	Year	Site	In Analysis	Num Locals	Date Banded	Number Days Tracked	Fate
150.629	F	2011	N. Athens	N	135	2/18	11	Migrated
150.050	M	2011	N. Athens	N	10	1/12	2	Disappeared
150.710	F	2011	N. Athens	Y	216	1/12	26	Migrated
150.170	F	2011	N. Athens	N	54	2/7	6	Disappeared
150.190	F	2011	N. Athens	Y	145	1/28	15	Accipiter
150.270	F	2011	Conestee	Y	270	1/22	20	Migrated
150.291	M	2011	N. Athens	N	9	2/7	3	Disappeared
150.368	M	2011	Conestee	Y	200	1/22	14	Migrated
150.389	M	2011	N. Athens	N	2	2/7	2	Disappeared
150.509	M	2011	Conestee	N	3	2/22	1	Disappeared
150.769	M	2011	Conestee	Y	89	1/5	10	Accipiter
150.828	F	2011	N. Athens	Y	142	12/17	24	Transmitter
150.850	M	2011	Conestee	Y	250	1/5	21	Transmitter
150.930	M	2011	N. Athens	Y	14	12/17	3	Disappeared
151.160	F	2011	N. Athens	N	5	2/18	1	Disappeared
151.180	F	2011	N. Athens	N	6	2/18	3	Accipiter
150.719	M	2012	W. Athens	Y	174	2/12	12	Migrated
150.993	M	2012	W. Athens	Y	68	2/12	9	Migrated

151.621	M	2012	W. Athens	N	16	1/31	1	Disappeared
151.889	F	2012	W. Athens	N	3	2/12	1	Disappeared
151.739	F	2012	W. Athens	N	1	2/12	1	Disappeared
150.870	F	2012	Cunningham	Y	889	1/19	34	Migrated
151.800	F	2012	Cunningham	Y	193	1/19	17	Accipiter
151.830	M	2012	Cunningham	Y	322	1/19	30	Migrated
151.920	F	2012	Cunningham	Y	287	1/18	27	Migrated
150.153	M	2012	Cunningham	Y	64	1/19	8	Disappeared
151.770	F	2012	Cunningham	Y	30	1/19	4	Accipiter
151.861	F	2012	Cunningham	Y	186	1/19	19	Migrated
151.950	F	2012	Cunningham	Y	18	1/19	5	Accipiter

Table A2. Summary statistics for temperature, precipitation, and barometric pressure variables used in logistic regression for Rusty blackbird patch use on the Piedmont Plateau during January 2011 and January and February 2012. Includes F statistic and P value for df = 2, 842. A significant P value means there are differences among ≥2 of the monthly comparisons. Temphour = temperature during the hour of observation, Dailymax = maximum temperature of the day of the observation, Dailymin = minimum temperature of the day of the observation, Prevdaymax = maximum temperature of the previous day to the observation, Mintempnext = Maximum temperature the day following the observation, Hrsnext2day<-3ºC = number of hours in the 48 hours following the observation below -3°C, Hrsprev3day<-3ºC = number of hours in the previous 72 hours below -3°C, Hrsprev2day<-3ºC = number of hours in the previous 48 hours below -3°C, Preciphour = amount of precipitation during the hour of the observation, Precipprev3day = precipitation in the previous 3 days, Precipnext2day = amount of precipitation in the 48 hours following the observation, Precipnext24hrs = amount of precipitation in the 24 hours following the observation, Hrsnoprecipprev = number of hours of no rain previous to the observation, and Barometric5hrs, Barometric12hrs, and Barometric24hrs = change in barometric pressure in the previous 5, 12, and 24 hours respectively.

	January 2011	January 2012	February 2012	Fstatistic	Pvalue
Temphour (ºC)	6.29	12.14	12.86	137. 1	<0.001
Dailymax (ºC)	9.3	15.21	16.06	183.9	<0.001
Dailymin (ºC)	-0.38	3.18	3.93	113.5	<0.001
Prevdaymax (ºC)	8.84	14.29	15.75	179.8	<0.001
Mintempnext (ºC)	-1.05	3.64	4.62	184.4	<0.001
Hrsnext2day<-3ºC (hrs)	5.63	0	0.023	119.1	<0.001
Hrsprev3day<-3ºC (hrs)	6.22	0	1.04	69.26	<0.001
Hrsprev2day<-3ºC (hrs)	3.88	0	0.48	52.81	<0.001
Preciphour (cm)	0.018	0.0091	0.013	0.97	0.38

Precipprev3day (cm)	1.55	1.96	0.84	30.14	<0.001
Precipnext2day (cm)	0.51	0.89	0.51	5.9	0.0029
Precipnext24hrs (cm)	0.38	0.64	0.23	8.17	<0.001
Hrsnoprecipprev (hrs)	42.07	36.58	59.47	14.87	<0.001
Barometric5hrs (cm)	-0.046	-0.04	-0.051	0.19	0.827
Barometric12hrs (cm)	-0.041	0.066	0.043	10.43	<0.001
Barometric24hrs (cm)	-0.1	0.036	0.058	7.85	<0.001

CHAPTER 3

EFFECTS OF PRECIPITATION ON WINTER FOOD LIMITATION IN RUSTY

BLACKBIRDS[1]

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ABSTRACT.–Songbirds wintering in temperate-zone regions such as the southeastern United States face the double threat of low food supply and high demand for resources to endure cold weather. According to the adaptive body mass hypothesis, birds must maintain a balance between storing enough resources to endure an unpredictable and harsh environment, and simultaneously be light enough to avoid predation and an increased metabolic rate. The optimum balance should occur at or above a certain threshold where food is not limited; under limitation, birds may not be able to reach an optimum. If birds are operating with food limitation below the threshold, body mass should be related to events associated with increased food availability such as precipitation and temperature, with increased body mass occurring under warmer temperatures and more precipitation. Alternatively, if birds operate above the threshold, body mass should not be positively related to short-term temperature or precipitation. Wetland songbirds are good subjects to study food limitation because they specialize on prey resources, such as wet-soil invertebrates, that have limited availability due to weather conditions. We captured Rusty Blackbirds (*Euphagus carolinus*), a wetland specialist, at sites along the Atlantic Coastal Plain and on the Piedmont Plateau of South Carolina and Georgia during winter 2007, and 2009 to 2012 and estimated scaled total, lean, and lipid body mass. Greater scaled body mass (total and lipid) was related to increased precipitation in the 3 days prior to capture, lower scaled mass (total and lean) was related to increased precipitation in the 24 hrs following capture, and scaled lipid mass was greater in females than males. Total, lean, and lipid scaled mass was greater in blackbirds from the Piedmont Plateau than the Coastal Plain and with increasing day of year through migration. Our results suggest Rusty Blackbirds are not experiencing food

limitation since body mass is unrelated to temperature but they are highly dependent on precipitation for food resources.

INTRODUCTION

Migrant songbirds wintering in the temperate-zone must maintain lean and lipid body mass throughout potentially severe and unpredictable weather to have sufficient reserves for over-winter survival and subsequent migration (Rogers 2005, Schulte-Hostedde et al. 2005, Budki and Kumar 2009). But maintaining mass, let alone increasing mass, can be difficult for temperate-zone wintering songbirds that face the threat of low food supply and a high demand for resources to endure cold weather (Brown and Sherry 2006, Krams et al. 2010). Small songbirds may need to resort to lower quality food choices in the absence of preferred foods, and it is often the case that birds wintering in the temperate-zone must compensate for unpredictable food sources, periods of extreme harsh winter weather, and long cold nights, by storing fat, that can comprise up to 15% of fat-free body mass (Blem 1990, Koivula et al. 1995, Rappole 1995, Newton 1998, Koenig et al. 2008).

Adding fat mass comes with a cost and songbirds typically do not store fat up to their physiologically-determined capacity for two reasons (Brodin 2001). First, songbirds increase their susceptibility to predators by becoming heavier and consequently less agile or by exposing themselves for a longer time to predators while accumulating fat reserves (Newton 1998, Brodin 2001). Second, wintering songbirds may have low fat reserves compared to capacity, due to an increase in basal metabolic rate required to maintain fat (Brodin 2001). Fat storage is thus a trade-off among the risk of starvation versus the risk of predation versus a too-large increase in food demand (metabolism). Several authors have proposed ways that individuals optimize costs and benefits of lipid storage (Caraco 1979, Newton 1998, Krams et al. 2010).

To optimize body mass, temperate-zone birds that experience unpredictable weather should abide by the predictions of the adaptive body mass hypothesis (ABMH) and should have lower fat when no severe weather threat exists and resources are unlimited and/or predictable and higher fat with impending severe weather or unpredictable or limited resources (Rogers 2005, Turcotte and Desrochers 2008). Birds can assess local conditions directly, use short-term predictive cues such as changes in the weather or barometric pressure, or use long-term cues such as photoperiod to change foraging strategies (Buttemer 1985, Cuthill et al. 2000, Neeser and Von Bartheld 2002). Songbirds alter fattening strategies within two to five days of changing weather to adjust between the constant risk of starvation and predation (Rogers et al. 1993, Rogers 1995, Krams et al. 2010).

Regulating fat stores to optimal levels likely occurs only above a certain resource availability threshold and below this threshold birds store as much fat as food availability allows (Danner et al. *in prep.*). If birds adhere to ABMH, components of body mass such as lipid mass should be related to temperature where birds exposed to warmer weather store less fat, reducing predation pressure. Alternatively, if birds are operating under food stressed conditions, body mass may be related to short-term events associated with food availability such as precipitation and temperature, with relatively rapid increases in lean and lipid mass occurring under warmer temperatures and more precipitation.

Songbirds that are dietary specialists provide an opportunity to answer questions about food limitation because these birds are often even more limited by their habitat specialty. Wetland songbirds are highly specialized on limited prey resources, namely, aquatic invertebrates. The availability of wetland invertebrates is subject to short-term

weather conditions with invertebrates becoming more available with warmer temperatures and during or shortly after precipitation events as water levels subside and concentrate resources (Neckles et al. 1990, Corcoran et al. 2009).

The Rusty Blackbird (*Euphagus carolinus*) is a within temperate-zone migrant wetland specialist that winters in flocks in the southeastern United States (Avery 1995, Niven et al. 2004, Sauer et al. 2006) and recently has been found to incorporate a large proportion of terrestrial and aquatic worms from wetlands (*Lumbricus* and *Tubifex* spp.; Chapter 5). The species is estimated to have a possible 85-95% overall decline continent-wide through at least the 1990s (Greenberg and Matsuoka 2010, Greenberg et al. 2011). Although Rusty Blackbirds have experienced a precipitous decline, there are still an estimated 158,000 to 2 million individuals (Savignac 2006, Greenberg and Matsuoka 2010) and can be found in local concentrations of up to a few hundred birds that provide the opportunity to study them during wintering.

Unlike the breeding season, when Rusty blackbirds predominately consume insect larvae, the species accumulates fat in winter months (P. Newell Wohner *pers. obs.*), and incorporates tree mast, including acorns and especially pecan (*Carya illinoinensis*) nuts when they are available, into the winter diet (Greenberg et al. 2011). Pecans are higher in fat content than worms (~41 vs. ~15% dry weight) but contain much less protein (~8 vs. ~50% dry weight) with pecans having higher overall energy (8 vs. 5 kcal/g; Fredrickson and Reid 1988, Bernard and Allen 1997, Barker et al. 1998). However, the incorporation of pecans is more complicated than simple fattening, as blackbirds use pecan groves and wetlands in relation to short-term previous, present, and future weather on the Piedmont Plateau likely according to the availability of invertebrates (Chapter 2).

Little research has been conducted on body mass and fat regulation in temperate-zone passerines and not much research exists regarding causes of variation in lean body mass in general. We captured Rusty Blackbirds during winter 2007, and 2009 to 2012 in two physiographic regions: (1) the Piedmont Plateau where winter lows routinely drop below -3°C and flocks use pecan nuts and (2) the Atlantic Coastal Plain with its warmer winter climate and flocks that do not use pecans. We estimated total, lean, and lipid body mass using Bergstrom and Sherry's (2008) equation, and used these estimates to find relationships with short-term weather variables. The regression equation is based on actual lean and lipid mass, and morphological measurements (i.e., wing, tail, tarsus, bill length and width) of medium-sized songbirds (20-43g), and has high predictive power (r^2 = 98.9% accuracy; Bergstrom and Sherry 2008).

We hypothesized that if Rusty Blackbirds are food limited, we should find a positive relationship between body mass and recent or current precipitation and temperature variables (Fig. 3.1). If birds are at or above the threshold, there should be no relationship between recent or current temperature or precipitation events, and if there is a relationship between body mass variables and temperature or precipitation variables, they should have a positive relationship to short-term *future* weather variables such as the number of cold hours in the future, because this would indicate blackbirds have the resources available to prepare for inclement weather; i.e., to practice adaptive body mass regulation.

METHODS

Study sites.–We captured Rusty Blackbirds in five sites on the Atlantic Coastal Plain of South Carolina and four sites on the Piedmont Plateau in South Carolina and Georgia (Fig. 3.2). In 2007, we captured birds in Coastal Plain sites in South Carolina in Savannah National Wildlife Refuge (NWR), Donnelly Wildlife Management Area (WMA), and Ashepoo Plantation. From 2009 to 2012, we captured birds in Coastal Plain sites in South Carolina in a Charleston residential area (Twelve Oaks) and Magnolia Plantation and Gardens, and on the Piedmont Plateau at Lake Conestee and Lake Cunningham, and two sites in Athens, Georgia (West Athens and North Athens).

Bird capture.–We used mist nets to capture Rusty Blackbirds during February and March 2007 and 2009, and mist nets and whoosh nets (Skelhorn and Rowe 2009) during December to March 2010, 2011, and 2012. Whoosh nets are spring-loaded devices comprised of fine-mesh netting that are launched over ground-foraging birds. Blackbirds were lured to nets by concentrating crushed pecans collected from the grove around nets. Each captured blackbird received a unique USGS and plastic or metal color-band combination (USGS BBL Permit # 22665). We recorded sex, fat (nine scores for furcular fat; Kaiser 1993), wing chord, tail, tarsus length, bill length, width, and depth, mass, date, and time of capture. All dates were later transformed to day of year with January 1 being Day 1. Time of sunrise in minutes was subtracted from time of capture in minutes to standardize capture times to time from sunrise. This study plan was approved by the University of Georgia IACUC (AUP# A2009 1-003).

Statistical analysis.–Size measurements (tail, wing, tarsus, and bill), fat scores, and total

mass were used in a regression equation to calculate lean and lipid mass of each adult

bird captured (Bergstrom and Sherry 2006; Equation 3.1 and 3.2).

Equation 3.1:

$$\text{Lean} = -9 + 0.734\text{LivWt} - 0.835\text{VisFat} - 0.435\text{BL} + 2.08\text{BW} + 2.39\text{BD}$$

$$- 0.0253\text{Wing} + 0.0136\text{Tail}$$

Equation 3.2:

$$\text{Lipid} = 9 + 0.266\text{LivWt} + 0.835\text{VisFat} + 0.435\text{BL} - 2.08\text{BW} - 2.39\text{BD}$$

$$+ 0.0253\text{Wing} - 0.0136\text{Tail}$$

where Lean = lean mass, Lipid = lipid mass, LivWt = field mass of bird, VisFat = fat

score of subcutaneous fat in furculum according to nine scores of Kaiser (1993), BL =

bill length, BW = bill width, BD = bill depth, Wing = wing chord of unflattened wing,

and Tail = tail length. We looked for correlation between scaled lipid mass and furcular

fat scores to support use of estimates of lean and lipid mass for Rusty Blackbird mass

(46.8-70 g) outside the highest mass used to develop the regression (20-43 g).

We used the scaled mass index (Equation 3.3) to standardize all individuals to the

same length value (e.g., wing) and adjust body mass with that which they would have at

their new length value in accordance to the scaling trend between mass and length (Peig

and Green 2009). Recent work has illustrated that this method is better than previous

methods using size-corrected mass from ordinary least squares residuals (Peig and Green

2010).

Equation 3.3:

$$\text{scaled mass index: } \hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i and L_i are body mass and linear body measurement of individual *i* respectively; b_{SMA} is the scaling exponent estimated by the SMA regression of M on L; L_0 is the arithmetic mean for the study population of L; and $\hat{M}_i$ is the predicted body mass for individual *i* when the linear body measure is standardized to L_0. The scaling exponent b_{SMA} can be calculated indirectly by dividing the slope from an OLS regression (b_{OLS}) by the Pearson's correlation coefficient r (LaBarbera 1989). We used the single linear measurement wing chord for the Rusty Blackbird L_0 variable because it had the highest correlation to mass compared to tarsus and tail length (Peig and Green 2009). For the L_0 variable we chose to use the arithmetic mean of wing chord which was 112.28 mm therefore all bird masses were scaled to a bird as if it had a wing chord of 112.28 mm. In all datasets, missing values were replaced by averages for the variable and by sex where appropriate.

Thirteen short-term weather variables were constructed from Weather Underground Inc. for each capture day (Table 3.1). Weather Underground develops historical weather summaries based on information from the National Weather Service and is a free source. We used these variables based on our previous study that found short-term weather variables influence Rusty Blackbird daily foraging decisions during wintering. We used weather data from Savannah, Georgia for the Donnelly WMA, Savannah NWR, and Ashepoo Plantation sites, Charleston, South Carolina for Twelve

Oaks residential area and Magnolia Plantation and Gardens, Athens Georgia for the two

Athens sites, and Greenville, South Carolina for Lake Conestee and Lake Cunningham

sites to develop our short term weather variables.

Birds captured on the Atlantic Coastal Plain were not observed using cultivated

pecans while birds wintering on the Piedmont Plateau had access to cultivated pecans

during certain months and years at certain sites depending on crop production; therefore,

we developed a variable that reflected whether pecans were available to blackbirds or not.

Based on departure times of tagged birds from our telemetry study (Chapter 2),

blackbirds captured in March likely included both birds migrating through study sites

from points south and late-leaving birds that wintered in the study site. We therefore

constructed a variable dividing blackbirds into two categories; wintering (December

through February) and pre-migration-migration (March). A variable was constructed for

each site by year (siteyear) because, due in part to the unpredictability of Rusty Blackbird

winter occurrence, no sites were sampled in every year and most sites were only sampled

in one to two years out of the five years of sampling. In addition, a variable was created

based on whether blackbirds were from the Atlantic Coastal Plain physiographic region

or the Piedmont Plateau (phys).

Total, lean, and lipid scaled body mass were used as the response variable in

linear mixed effects (lme) models in program R using the package nlme (Laird and Ware

1982, R Development Core Team 2012). We included the variables siteyear, phys, and

day as random effects in all models for total and lean mass and sex in all lipid mass

models because we expected differences between sites and years, physiographic region,

sexes, and day of year and wanted to account for that variation but were more interested in determining overall effects of short-term weather variables.

Our process was to first run all single variables against the mass variable and select those variables with the best fit to run together. We also plotted the variables against the best categorical variables to look for possible interactions.

Model selection.–We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative model fit of candidate models for each scaled mass analysis (Neter et al. 1990). Pearson correlations were computed for all pairs of predictor variables prior to modeling. If predictor variables had r >0.45 they were not included in the same model. In cases of correlated variables, we chose to keep the variable that resulted in the highest AIC_c. To assess the fit of each candidate model, we calculated Akaike's Information Criterion with the small-sample bias adjustment (AIC_c; Akaike 1973, Hurvich and Tsai 1989). The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can range from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. Because the ratio of Akaike weights for two candidate models can be used to assess the degree of evidence for one model over another (Burnham and Anderson 2002), we included in the confidence set of models only those candidate models with Akaike weights that were within 10% of the largest weight, which is similar to the general rule-of-thumb (i.e., 1/8 or 12%) suggested by Royall (1997) for evaluating strength of evidence.

To allow for ease of interpretation, we provided model-averaged coefficients for each predictor variable in the top model using the program R package AICcmodavg (Mazerolle 2011). The precision of model-averaged coefficients was assessed by

calculating 85% confidence intervals based on a t-statistic with n-1 degrees of freedom (Arnold 2010). Eighty-five percent confidence intervals are more compatible with AIC methods than 95% CI as explained by Arnold (2010). Confidence intervals that contain zero indicate inconclusive estimates because the nature of the relationships (i.e., whether positive or negative) cannot be determined (Arnold 2010). Goodness-of-fit was assessed for the global model by examining residual and normal probability plots.

RESULTS

General.–We captured and processed 344 Rusty Blackbirds from mid-December through March at varying dates during the five years of study. We removed 34 birds from the datasets because we did not collect enough morphometric or mass data on them to include in the analysis. The dataset included 233 blackbirds from the Piedmont Plateau and 77 from the Atlantic Coastal Plain regions from 2007 (n = 56), 2009 (n = 128), 2010 (n = 30), 2011 (n = 81), and 2012 (n = 15). We captured 166 birds from Lake Conestee from 2009-2011, 10 birds from Lake Cunningham in 2012, 57 birds from two sites in Athens, Georgia from 2011 and 2012, 27 from Ashepoo Plantation in 2007, 17 from Donnelly WMA in 2007, 12 from Savannah NWR from 2007, 10 from Twelve Oaks from 2009-2010, and 11 from Magnolia Gardens Plantation from 2009-2010. Winter fat scores ranged from 0 to 2.5 (median = 1) and pre-migration-migration fat scores ranged from 0 to 3 (median = 1.5). Twenty-two birds during pre-migration-migration had fat scores >2 (25%) compared to two (1%) during wintering.

Ordinal furcular fat scores and scaled lipid mass were moderately correlated (Pearsons r = 0.69). Bill measurements were not recorded for almost half (140 of 310; 45%) the blackbirds in the analysis so we substituted average values for each sex. To

ensure this procedure did not affect model performance, we compared the lean and lipid

mass estimates of average bill measurements and actual bill measurements with

blackbirds for which we did have bill measurements. On average, the lean mass estimates

based on actual bill measurements were only 0.55% (SD = 0.4) different from those

based on the averages of bill measurements by sex, and only 2.8% (SD = 2.31) different

for lipid mass. Therefore, we were comfortable substituting bill size averages by sex for

the 140 blackbirds with no measurements.

Blackbirds from the Piedmont Plateau had higher total, lean, and lipid scaled body

mass than those from the Coastal Plain (Fig. 3.3). Body mass also increased with day of

year (Fig. 3.4), likely due to the inclusion of migratory birds in March.

Total scaled body mass.–The top model explaining scaled total body mass included the

variables precipprev3day and precipnext24hrs (Table 3.2; Figs. 3.5 and 3.6). The top

model (w_i = 0.26) was only 1.08 times more likely than the next best model (w_i = 0.24)

with one fewer variable; precipprev3day. Total scaled body mass was lower with

decreasing precipitation in the 24 hrs after capture, and greater with increased

precipitation in the previous 3 days before capture (Table 3.3). Total scaled mass of

blackbirds was greater in the Piedmont Plateau than in the Coastal Plain and with

increasing day of year (Table 3.3).

Lipid scaled body mass.–The top model for scaled lipid mass included the variable

precipprev3day (Table 3.2). Lipid body mass was greater with increasing precipitation in

the previous 3 days (Table 3.3). Scaled lipid mass was higher on the Piedmont Plateau

where birds had access to pecans and it was colder than in sites on the Coastal Plain,

where pecans were not available. Males had lower lipid mass than females. Like total

body mass, lipid mass was higher on the Piedmont Plateau and with increasing day (Table 3.3).

Lean scaled body mass.–The top model explaining scaled lean body mass included the variable precipnext24hrs (Table 3.2). The top model ($w_i = 0.36$) was 2.4 times more likely than the next best model that included precipprev3day ($w_i = 0.15$). Lean scaled body mass was greater with decreased precipitation in the following 24 hrs from capture (Table 3.3).

DISCUSSION

We sought to determine whether a temperate-wintering songbird is food limited by relating temperature and precipitation to scaled body mass variables. Two opposing theories have been developed to explain the relationship between mass regulation and food limitation; one would be supported by a positive and the other by a negative relationship between mass and decreasing food supply. The two explanations likely operate under different scenarios depending on the type of threat that is most relevant to the songbird. Typically, for example, in Neotropical-wintering songbirds, increased winter body mass, and particularly lipid mass, occurs when resources are unpredictable and limited (Rogers 2005). However, although Neotropical-wintering songbirds may be required to endure periods of resource unavailability, they are not typically exposed to extreme cold weather. Lowering body mass to avoid depredation may be more important than preparation for unpredictable weather events for Neotropical-wintering songbirds (Rogers 2005).

The opposite relationship between body mass and food limitation has been observed in temperate-zone songbirds (i.e., increased body mass with increased food

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availability or predictability; Rogers 2005). Severely cold weather and snowfall in the

temperate zone both limit food supply and increase the demand for resources to endure

cold weather (Rogers 2005, Brown and Sherry 2006, Krams et al. 2010, Danner et al. in

prep.). Therefore, we predicted that greater scaled body mass of Rusty Blackbirds

wintering in the southeastern United States would be linked to greater availability of

resources because unpredictable harsh winter weather necessitates insurance against

starvation (Rogers 2005, Brown and Sherry 2006, Krams et al. 2010, Danner et al. *in*

prep.). Other studies have supported this prediction for the temperate-zone (Brittingham

and Temple 1988, Rogers 2005, Danner et al. *in prep.*). Based on these findings, we

further predicted that if blackbirds are operating above a certain threshold of resource

availability, where resources are not limited, scaled body mass variables should be

unrelated to short-term precipitation and temperature variables. In addition, if blackbirds

are operating above the threshold and if body mass variables *are* related to temperature or

precipitation variables, they should only have a positive relationship to *future* weather

variables such as the amount of precipitation or cold days in the future because this

indicates blackbirds have the resources available to prepare for inclement weather, i.e., to

practice adaptive body mass regulation.

   If birds are operating below the critical threshold, we expect birds to gain lean and

lipid mass when resources become more available (i.e., with more precipitation) or when

birds are operating under less stressful short-term temperature conditions and do not

require as many resources for thermal regulation (i.e., warmer short-term weather). We

would expect birds to lose lean mass with colder more extreme temperatures because

birds cannot accumulate enough lipid stores to endure short-term severe weather and must metabolize lean mass.

Temperature variables indicate lack of resource limitation.–Temperature variables were unrelated to both lean and lipid mass, supporting the assertion that blackbirds are not resource limited. These results agree with our radiotelemetry study (Chapter 2), which also indicated temperature variables are not important to foraging habitat selection. Under low temperatures, many invertebrates, and especially worms, become less active, making them more difficult to find, so temperature should be related to body mass if birds are food limited (Krams et al. 2010, Danner et al. *in prep.*). This relationship was not detected in our study in contrast to other studies on wintering temperate songbirds. Fat stores of Swamp Sparrows (*Melospiza georgiana*) without supplemental food (and that are presumably resource limited), increased with increased minimum temperature averaged over the previous five to six days, suggesting that birds with low food availability lost fat when temperatures were low and they deposited fat when temperatures warmed (Danner et al. *in prep.*). Experimentally food-supplemented sparrows without resource limitation maintained steady fat stores despite fluctuations in temperature, presumably because they were able to replenish their fat stores constantly (Danner et al. *in prep.*). These results indicate blackbirds are not operating under the resource limitation threshold because they are neither gaining nor losing weight according to temperature variables. Blackbirds are able to find enough wetland invertebrates and tree mast to endure cold weather and maintain their weight through cold periods.

Future precipitation decreases lean mass.–Resource availability and mass regulation in Rusty Blackbirds are driven by precipitation events which can be sporadic and unpredictable. We predicted a positive relationship between body mass and precipitation 24 hrs after capture to verify resources are not limiting; however, we found the opposite relationship. In a separate radiotelemetry study, daily patch use by suburban Rusty Blackbirds was driven by short-term future precipitation (Chapter 2). Rusty Blackbirds were 2.6 to 3.6 times more likely to be observed using residential lawns than wetlands or pecan groves (respectively) with short-term future precipitation events >1 cm. The increased use of residential lawns with future rain is likely due to the increase in availability of relatively large terrestrial non-native earthworms in residential areas preceding precipitation events as earthworms move to escape potential inundation or disperse (Neckles et al. 1990, Corcoran et al. 2009). In our study, lean mass actually decreased with impending precipitation events, although occasions with precipitation events ≥1 cm were rare (n=15 or 5%). Blackbird flocks seem to be attracted to residential areas, likely because of the availability of large earthworms, but they lose lean mass in these events. It is unknown what percentage of these events would be required to negatively affect the flock. The frequency of large precipitation events seems inconsequential, but the probability of residential lawn use being 3.6 times greater than wetlands suggests there is a strong tendency for blackbirds to use residential lawns preceding big precipitation events rather than wetlands that may provide a better food resource for the flock. These precipitation events that occur infrequently could be disproportionately important for maintaining lean mass.

Previous precipitation increases lipid mass.–In the present study, increased lipid mass was best explained by increased rain in the previous three days before capture. In our radiotelemetry study of patch use, we found that Rusty Blackbirds were much more likely to use wetlands than residential lawns and pecan groves with increased precipitation in the previous three days (Chapter 2). Increased use of wetlands with previous precipitation is likely due to the increased availability of invertebrates in wetlands as water levels subside and concentrate prey. The finding that blackbirds increase lipid mass with increased previous precipitation is interesting because we predicted that increased lipid mass would be associated with pecan use because pecans contain a greater proportion of fat than worms (~41 vs. ~15% dry weight). Our finding that blackbirds are more likely to occur in wetlands and residential areas with more precipitation in the previous three days and gain lipid mass there, and worms are the main resource in wetlands, indicates lipid mass is primarily gained through invertebrate-eating as opposed to pecan-eating. Our patch use and body mass studies, taken together, support our hypothesis that pecan groves are most likely used for times when worms are not available because birds actually accumulate lipid mass from habitats with greater invertebrate availability as opposed to pecan groves (Mettke-Hofmann and Pellegrini *unpubl. data*).

Although invertebrates are known for their high protein content, they are typically not thought of as fat-rich, but the primary food of Rusty Blackbird flocks has a comparatively high fat content. For example, small wetland *Tubifex* spp. worms available to Rusty Blackbirds contain ~15-20% fat and ~48% protein dry weight, and terrestrial earthworms (*Lumbricus* spp.) typically found in residential lawns contain ~13-18% fat and ~62% protein (Fredrickson and Reid 1988, Bernard and Allen 1997, Barker et al.

1998). Insect larvae such as that from Odonata are also high in fat averaging 25% with very high levels of protein as well (average = 58% dry weight; DeFoliart 1991, Ying et al. 2001). Thus, based solely on nutrient information, compared with tree mast, worms have a superior ratio of nutrients for a bird trying to maintain both lean and lipid mass. Tree mast may only be used when invertebrate resources are less available due to weather conditions.

Females maintain higher fat than males.–Assuming more fat is better for wintering temperate-zone songbirds relying on an unpredictable resource associated with precipitation events, our finding that subordinate females in our sites stored more lipid mass than did males is opposite what we predicted - we expected males to outcompete females for preferred resources. Male and female Alpine Chough (*Pyrrhocorax graculus*), a flocking temperate corvid, had the same foraging efficiency when competition was low, but when competition was high, females were less efficient than males, and had less access to food (Delestrade 1999). Dominant Great Tits (*Parus major*) responded to the rising risk of starvation under low temperatures by gaining mass while subordinate individuals decreased body weight and fat score under extremely low temperatures (Krams et al. 2010). That females had greater lipid mass than males suggests at least that there is a lack of competition for food between the sexes. Stable isotope diet data from Chapter 5 indicate the proportion of invertebrates and mast incorporated in the diet is similar between females and males.

Alternatively, our assumption that fatter is better could be erroneous and birds are operating in a food-limited system with less fat indicating better conditions for males. Under this hypothesis, males have more access to food than females. Dominant White-

breasted Nuthatches (*Sitta carolinensis*) and Hermit Thrushes (*Catharus guttatus*) carried

lower fat reserves than subordinates, supporting the prediction that the more predictable

food supply, presumably available to socially dominant animals, enables them to

maintain lower fat reserves (Clark and Ekman 1995, Pravosudov et al. 1999).

Climatic region.–Under our original assumption that more fat is better where resources

are more unpredictable, blackbirds could be in similar condition in both climatic regions

but adaptively managing mass. On the Piedmont Plateau, the climate is on average colder

than the Coastal Plain (e.g., Greenville SC January low is 0°C, high is 10°C whereas

Charleston SC January low is 3°C high of 16°C; Weather Underground). Blackbirds on

the Piedmont Plateau were fatter than blackbirds from the Coastal Plain as was expected

of birds in the colder climate of the Piedmont that need to store more fat for more

unpredictable resources. Higher fat in colder climate indicates a lack of resource

limitation since blackbirds are capable of storing more fat.

Short-term strategy.–Our results indicate mass maintenance strategies of blackbirds

change relatively quickly, within 2-3 days, reflecting an adaptive role of winter mass

regulation that is sensitive to precipitation. Other songbirds wintering in temperate areas

such as Great Tits (*Parus major*) and chickadees (*Poecile* spp.) also change fattening

strategies quickly (Krams et al. 2010). To our knowledge, this is the first study to identify

precipitation as a critical variable in mass regulation, a logical finding because we studied

a wetland specialist that relies on the availability of an invertebrate resource dependent

on precipitation events.

Day of year.–Rusty Blackbirds increased total, lean, and lipid mass with increasing day

of year. Rusty Blackbirds begin preparing for migration in late February and early March,

and many blackbirds captured in March were likely migrating blackbirds from points south. Late winter and early spring also marks the emergence of various invertebrates (Batema et al. 2005). Blackbirds are likely gaining mass in March as they prepare for migration. This is supported by the larger average fat scores during pre-migration than during wintering.

CONSERVATION IMPLICATIONS

This study and our previous patch-use study (Chapter 2) combined indicate that precipitation is the main determinant of Rusty Blackbird foraging decisions and body mass on the wintering ground, likely because precipitation affects the availability of invertebrate resources. Because of the unpredictable nature of wetland resources due to their dependence on precipitation events (Batema et al. 2005, Fredrickson and Batema 1992), Rusty Blackbirds seem to have adapted to mast-eating in times of invertebrate unavailability.

The fact that Rusty Blackbirds lose lean mass with short-term future precipitation indicates residential lawns are either less valuable foraging patches or blackbirds are just making due until after precipitation events when invertebrates are more available in wetlands. A potential concern is that this native bird species is foraging on a resource that is non-native. Other dramatically declining within-temperate zone migrants, that winter in the Southeastern United States, such as the American Woodcock (*Scolopax minor*), Red-winged Blackbird (*Agelaius phoeniceus*), and Common Grackle (*Quiscalus quiscula*; Blackwell and Dolbeer 2001, USGS 2011) also use non-native earthworms as a major food source in winter.

The implications of the importance of precipitation to invertebrate food availability for conservation of the Rusty Blackbird lead to water manipulation as a management option. There is a large body of research available on the effects of water level fluctuations on invertebrate abundance due to the importance of invertebrate resources to wintering waterfowl (Neckles et al. 1990, Fredrickson and Batema 1992, Wehrle et al. 1995, Magee et al. 1999, Batema et al. 2005). The International Rusty Blackbird Working Group (IRBWG) has highlighted research involving water manipulation in wetlands as an important next step to the conservation of Rusty Blackbird wintering habitat.

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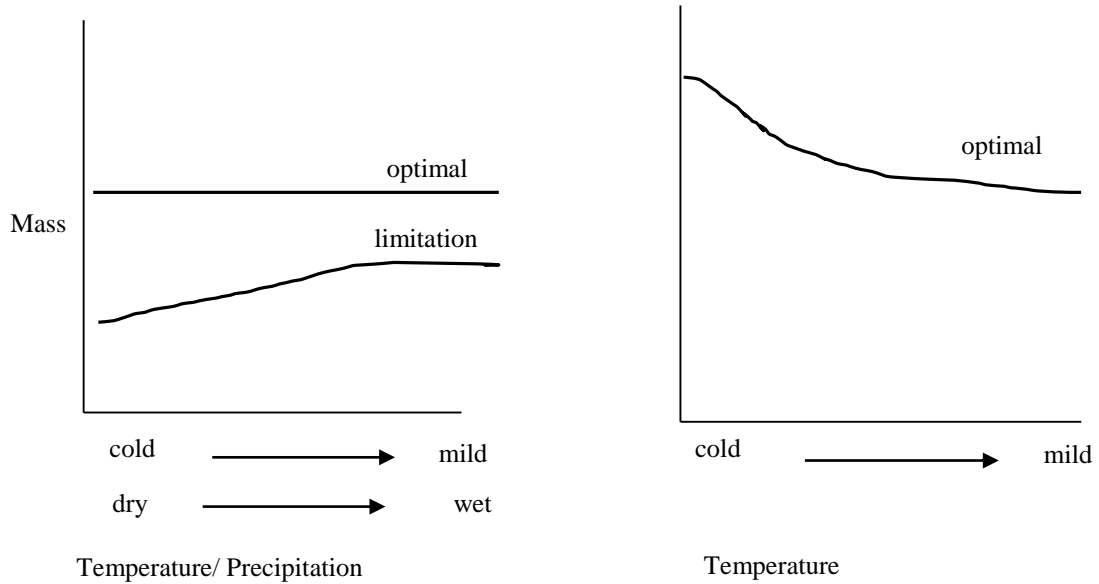   Odonata species and their nutritive value. Forest Research 14(4):421-424.

Figure 3.1. Relationship of expected bird mass to temperature and precipitation variables under a) resource limitation and b) optimal conditions. With food limitation body mass increases with increased temperature and precipitation because more resources become available for deficit. Under no resource limitation, body mass is not related to short-term increases in temperature and precipitation because birds maintain optimal body mass.
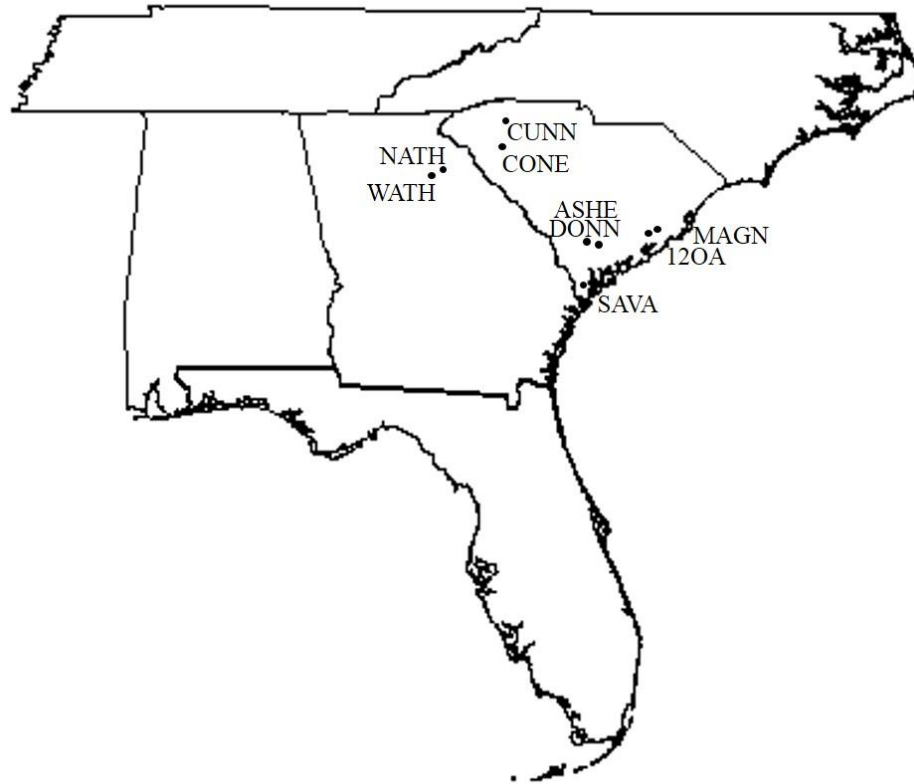
Figure 3.2. Map of southeastern United States showing approximate locations of Rusty Blackbird study sites: 12OA is Twelve Oaks residential area, MAGN is Magnolia Plantation and Gardens, ASHE is Ashepoo Plantation, DONN is Donnelly WMA, SAVA is Savannah NWR, WATH is West Athens, NATH is North Athens, CONE is Lake Conestee, and CUNN is Lake Cunningham.
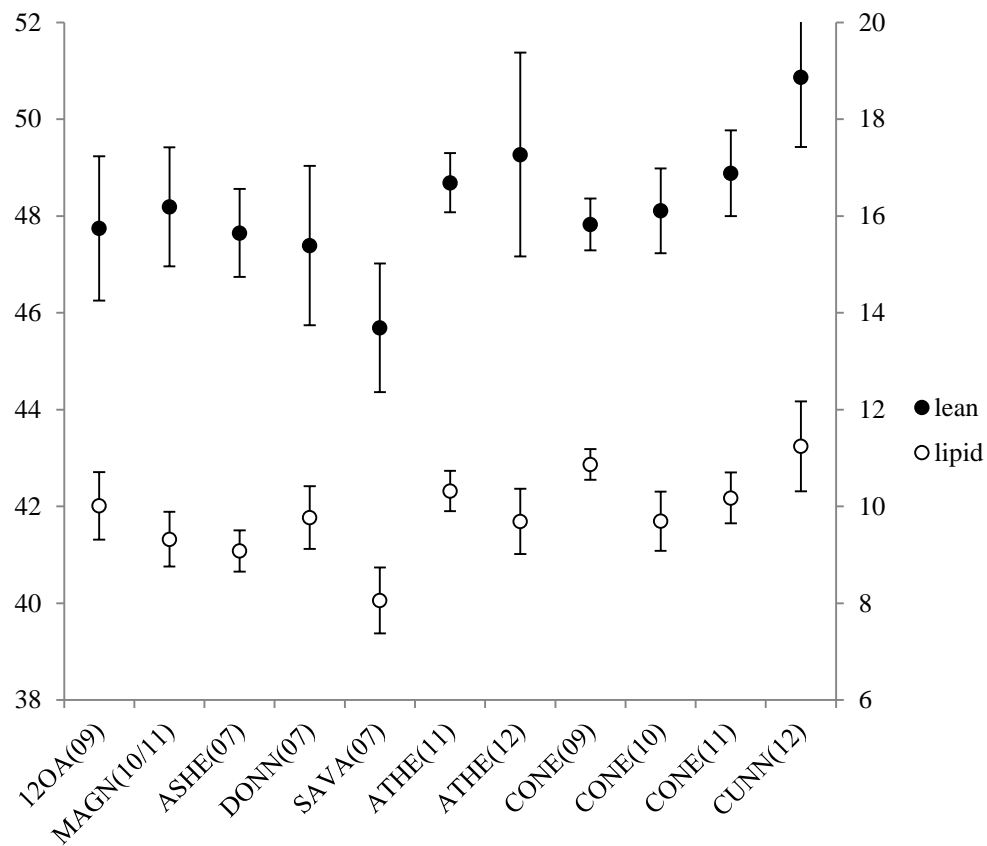
Figure 3.3. Mean and standard deviation of lean (closed circles) and lipid (open circles) scaled body mass by the variable siteyear. 12OA is Twelve Oaks residential area, MAGN is Magnolia Plantation and Gardens, ASHE is Ashepoo Plantation, DONN is Donnelly WMA, SAVA is Savannah NWR, ATHE is two sites in Athens GA (West Athens and North Athens), CONE is Lake Conestee, and CUNN is Lake Cunningham. Left y-axis is lean scaled mass and right axis is lipid scaled mass.
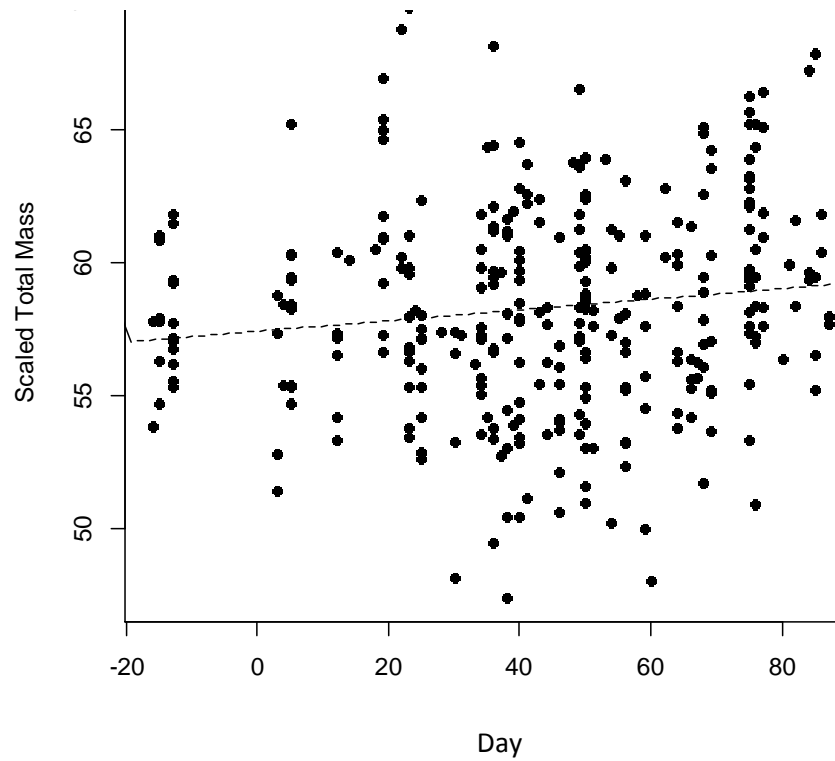
Figure 3.4. Day of year of capture (Day) by Rusty Blackbird scaled total body mass in the

Piedmont Plateau and Coastal Plain in 2007 and 2009-2012. Negative x-axis numbers indicate

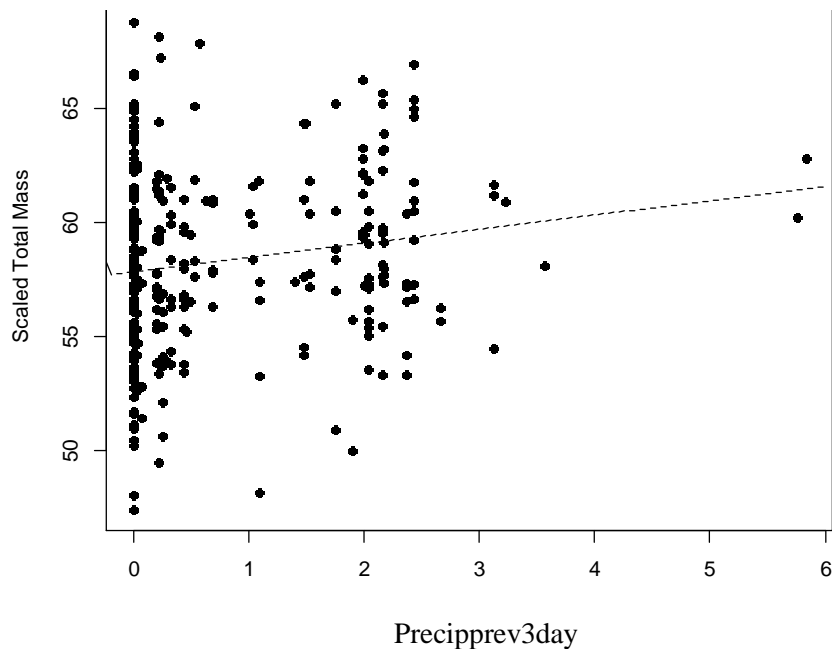days in December.

Figure 3.5. Precipitation in the previous three days (Precipprev3day) from capture by Rusty

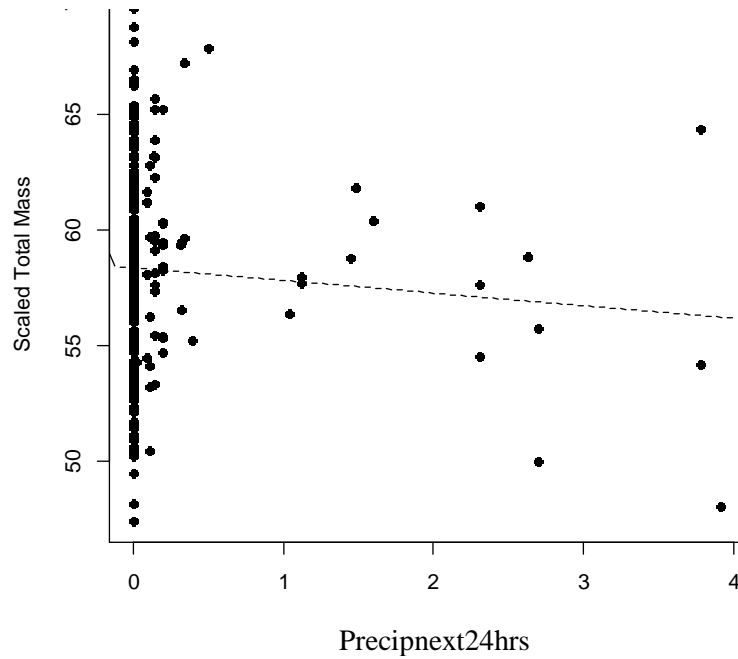Blackbird scaled total body mass in the Piedmont Plateau and Coastal Plain in 2007 and 2009-

2012.

Figure 3.6. Precipitation in the following 24 hours (Precipnext24hrs) from capture by Rusty

Blackbird scaled total body mass in the Piedmont Plateau and Coastal Plain in 2007 and 2009-

2012.

Table 3.1. Temperature, precipitation, and barometric pressure variables used in models to determine the relationship between weather and Rusty Blackbird total, lean, and lipid scaled body mass in 2007, and 2009 to 2012 on the Piedmont Plateau and Gulf Coastal Plain in Georgia and South Carolina.

Variable	Description	Units
Tsun	Time from sunrise	minutes
Day	Day of year	days
Temphour	Temperature during hour of capture	°C
Dailymax	Maximum temperature of day of capture	°C
Dailymin	Minimum temperature the previous night of capture	°C
Prevdaymax	Maximum temperature of the previous day to capture	°C
Hrsnext2day<-3°C	Number hours in 48 hours following capture <-3°C	hrs
Hrsprev3day<-3°C	Number hours in the previous 72 hrs below -3°C	hrs
Hrsprev2day<-3°C	Number hours in the previous 48 hrs below -3°C	hrs
Precipprev3day	Precipitation in the previous 72 hrs of capture	mm
Precipnext2day	Amount of precipitation in 48 hrs following capture	mm
Precipnext24hrs	Amount of precipitation 24 hrs following capture	mm
Barometric24hrs	Change in barometric pressure in previous 24 hrs to capture	cm
Precipmonth	Amount of precipitation the month of capture	cm
Tempmonth	Average temperature the month of capture	°C
Sex	Male or female	

Table 3.2. Model selection results of top models for Rusty Blackbird scaled total, lean, and lipid body mass in two physiographic regions (**Phys**); the Coastal Plain (CP; n = 77) and Piedmont Plateau (PP; n = 233); **Day** = day of year, **Precipnext24hrs** = the amount of precipitation in the following 24 hours from capture, **Precipprev3day** = precipitation in the previous three days from capture, **Tempmonth = a**verage temperature the month of capture, **Temphour** = temperature during hour of capture, and **Dailymin** = minimum temperature the previous night of capture. Models presented include the best-supported model (lowest AIC_c value) and candidate models with w_i within 10% of the top model w_i or w_i >0.03. k = number of parameters, AIC_c = Akaike information criterion adjusted for small sample sizes, and w_i = weight. Top models are highlighted.

Analysis	Candidate Models	k	AICc	ΔAICc	w_i
Total Mass	Phys+Day+Precipprev3day+Precipnext24hrs	7	1714.11	0	0.26
	Phys+Day+Precipnext24hrs	6	1714.23	0.12	0.24
	Phys+Day+Precipnext24hrs+Sex	7	1715.57	1.46	0.12
	Null	5	1716.65	2.55	0.07
	Phys+Day+Sex	6	1717.66	3.55	0.04
	Phys+Day+Precipprev3day	6	1717.68	3.57	0.04
	Phys+Day+Precipprev3day+Tempmonth+ Precipnext24hrs	8	1718.07	3.96	0.04
Lipid Mass	Phys+Day+Sex+Precipprev3day	7	1127.99	0	0.22
	Phys+Day+Sex+Temphour+Precipprev3day	8	1128.01	0.03	0.22
	Phys+Day+Sex+Tempmonth	7	1128.61	0.63	0.16
	Phys+Day+Sex+Temphour	7	1128.67	0.68	0.16
	Phys+Day+Sex+Tempmonth+Precipprev3day	8	1130.04	2.06	0.08
	Phys+Day+Sex+Precipprev3day	8	1130.07	2.08	0.08
	Phys+Day+Sex+Dailymin	7	1131.97	3.98	0.03

Lean Mass	Phys+Day+Precipnext24hrs	6	1502.25	0	0.36
	Phys+Day+Precipnext24hrs+Precipprev3day	7	1504.08	1.83	0.15
	Phys+Day	5	1504.12	1.88	0.14
	Phys+Day+Precipnext24hrs+Sex	7	1504.83	2.58	0.1
	Phys+Day+Precipnext24hrs+Tempmonth	7	1506.53	4.29	0.04
	Phys+Day+Precipnext24hrs+Sex+Precipprev3day	8	1506.7	4.45	0.04
	Phys+Day+Sex	6	1506.72	4.48	0.04
	Phys+Day+Precipprev3day	6	1506.83	4.58	0.04
	Phys+Day+Precipfor24h+Sex+Precipprev3day	8	1506.7	4.45	0.04

Table 3.3. Estimate, standard error (SE), and 85% lower (LCI) and upper confidence intervals (UCI) of variables important to Rusty Blackbird scaled total, lean, and lipid mass index in two physiographic regions (Phys); the Coastal Plain (CP; n = 77) and Piedmont Plateau (PP; n = 233); Day = day of year, Precipnext24hrs = the amount of precipitation in the following 24 hours from capture, and Precipprev3day = precipitation in the previous three days from capture.

	Variable	Estimate	SE	LCI	UCI
Total Mass	Intercept	55.12	0.94	53.76	56.47
	Phys(PP)	2.72	0.97	1.32	4.12
	Day	0.03	0.01	0.02	0.05
	Precipnext24hrs	-0.91	0.41	-1.5	-0.31
	Precipprev3day	0.42	0.23	0.09	0.75
Lipid Mass	Intercept	8.59	0.52	7.84	9.34
	Phys(PP)	1.49	0.38	0.95	2.03
	Day	0.01	0.01	0	0.02
	Sex(M)	-0.94	0.17	-1.19	-0.7
	Precipprev3day	0.19	0.09	0.06	0.33
Lean Mass	Intercept	46.77	0.66	45.83	47.72
	Phys(PP)	1.47	0.69	0.47	2.46
	Day	0.02	0.01	0.01	0.03
	Precipnext24hrs	-0.64	0.29	-1.05	-0.22

CHAPTER 4

CARBON AND NITROGEN DISCRIMINATION FACTORS FOR PLASMA, RED

BLOOD CELLS, AND CLAW TIPS OF WINTERING RUSTY BLACKBIRDS[1]

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[1]P. Newell Wohner, R. Cooper, and R. Greenberg. To be submitted to *The Condor*.

ABSTRACT.–A diet isotopic discrimination factor represents the difference between an isotopic signature of a consumer tissue and the consumer diet. Using assumed discrimination factors in isotopic bird diet models can present major bias in estimates of dietary proportions, but the true discrimination factor is difficult to determine without a captive study. Many variables can affect the true value of the discrimination factor such as isotopic routing of carbon, protein quantity and quality, and perhaps even the value of isotopic signatures themselves. However, it is often not feasible, either through limited funding or time, to conduct a captive study, especially on rare or threatened species. This is the case with the Rusty Blackbird (*Euphagus carolinus*) which has experienced an 85-95% population decline over the past 60+ years and is difficult to study because of poor detectability. In the absence of a captive study, we evaluated discrimination factors for carbon and nitrogen (Δ^{13}C and Δ^{15}N) for red blood cells (RBC), plasma, and claw tips from a large dataset of wintering Rusty Blackbirds (n = 275) captured in four sites over four years in Georgia and South Carolina. We first determined RBC discrimination factors using SIAR by systematically modeling diet proportions with potential combinations of Δ^{13}C and Δ^{15}N within the known range for songbirds to find the best solutions compatible with food source availability information by site and year. We then determined Δ^{13}C and Δ^{15}N values of plasma and claw tips by back-adjusting signatures to plot over RBC values over the same time frame. Since plasma represents diet over ~3 days and RBC over the past three weeks to a month, and blackbirds exhibit site-fidelity, we reasoned that plasma values of individuals should overlay RBC values for the same time-frame during which plasma was sampled in the same site. We used similar logic to determine discrimination factors for claw tips. The resulting RBC Δ^{13}C and Δ^{15}N were

0.75‰ and 3.25‰ respectively, plasma Δ^{13}C and Δ^{15}N were 0.25‰ and 4.05‰

respectively, and claw tips were 3‰ and 4.5‰. This methodology resulted in

discrimination factors that were expected based on patterns emerging in the literature.

Key words: Rusty Blackbird, Discrimination factor, Plasma, Red blood cells (RBC),

Claw tips, SIAR, Carbon, Nitrogen, Diet

INTRODUCTION

Recently, stable isotope mixing models have increasingly been developed, evaluated, and

used to estimate proportions of potential food items in bird diets (Bearhop et al. 2003,

Caut et al. 2009, 2010, Martínez del Rio et al. 2009, Sabat et al. 2013). The technique is a

less biased and obtrusive method of evaluating bird diets when birds cannot be observed

easily or sacrificed to determine gut contents (Phillips 2001). Mixing models are used to

estimate the proportion of food sources consumed by an animal by comparing the

isotopic signature of diet items to that of consumer tissues such as blood plasma, red

blood cells (RBC), and claw material (Bearhop et al. 2003, Podlesak et al. 2005, Inger

and Bearhop 2008). In passerines, blood plasma, RBC, and claw tip stable isotope

signatures indicate diet composition for varying time scales, with plasma indicating the

past ~24 hours to 3 days and RBC ~10 days to a month. Claw tips represent a time scale

of a month excluding the month immediately preceding capture because it takes

approximately one month for keratin to reach the claw tip (Bearhop et al. 2003, Podlesak

et al. 2005).

Previous studies indicate animal tissues are enriched relative to diet for both

carbon and nitrogen stable isotope signatures (δ^{13}C and δ^{15}N respectively) and especially

for birds with diets consisting of a high percentage of animals (Pearson et al. 2003). This

enrichment must be accounted for by adding the discrimination factor specific to each

consumer tissue (Phillips 2001). It is often assumed the δ^{15}N value of a consumer is

enriched by 3.4‰ and that δ^{13}C has little or no enrichment (0.4‰; Post 2002). Recently;

however, controversy has developed as to whether one discrimination factor, frequently

an overall average, should be assumed for all bird species and even the same species on

varying diets (Caut et al. 2009, 2010, Sabat et al. 2013). Quality and quantity of protein

varies by plant or animal origin (Boyd and Goodyear 1971), and has been found to be

linearly related to discrimination factors in omnivores (Caut et al. 2009, 2010). Caut et al.

(2010) suggest using a regression equation to account for this variation; however, others

have disputed the relationship, saying it is a statistical artifact (Auerswald et al. 2010,

Sabat et al. 2013) or an unaccounted-for biological effect (Perga and Grey 2012).

In addition, carbon routing affects discrimination factors when carbon from

proteinaceous sources is routed preferentially to proteinaceous tissue and carbon from

carbohydrate diet sources is preferentially routed to carbon stores or metabolized quickly

(Kelly and Martínez del Rio 2010). Therefore, it is unlikely the average discrimination

factor is applicable to all, or even most bird species, and all tissues when there is such

discrepancy between the quantity and quality of protein in bird diets and how carbon may

be routed (Caut et al. 2009). Also, small differences in discrimination factors can greatly

affect dietary proportion output from mixing models (Bond and Diamond 2011). For

example, a difference of $\Delta^{15}N = 2.1‰$ and $\Delta^{13}C = 3‰$ resulted in a median projection of

11% versus 91% krill in Common Tern (*Sterna hirundo*) diet (Bond and Diamond 2011).

Thus, choosing accurate discrimination factors is important for developing reliable

dietary profiles (Bond and Diamond 2011).

The Rusty Blackbird (*Euphagus carolinus*) winters in the southeastern United

States and has experienced an 85-95% overall decline continent-wide over the past 60

years or more with accelerated rates of decline since the early 1970s (Greenberg and

Droege 1999, Niven et al. 2004, Sauer et al. 2005, Greenberg and Matsuoka 2010,

Greenberg et al. 2011). The species was declared a focal species of conservation concern

of the USFWS and considered vulnerable to extinction according to the IUCN Red List (U.S. Fish and Wildlife Service 2008, IUCN 2010). The decline is likely occurring because of habitat loss on the wintering grounds (Greenberg et al. 2011).

Rusty Blackbirds are gregarious during the non-breeding season, occurring in flocks that are found in landscapes consisting of patches of bottomland hardwood forests, moist soil impoundments, pecan (*Carya illoensis*) orchards or groves, and residential areas (Greenberg and Matsuoka 2010). During wintering, Rusty Blackbirds are omnivorous and consume wetland invertebrates and a variety of tree mast such as pecan nuts and small-sized red oak acorns such as those from willow oak (*Quercus phellos*) and water oak (*Q. nigra*; Greenberg et al. 2011). To aid in conservation of the Rusty Blackbird, and ensure the birds can meet their wintering requirements, it is important to determine what aspects of their diet are most important for overwintering (Greenberg et al. 2011). Because dietary choices made by Rusty Blackbirds are difficult to observe while foraging, we conducted a stable isotope diet study. However, the true value of discrimination factors for Rusty Blackbird tissues is unknown. Output from diet isotopic mixing models are highly sensitive to small variation in discrimination factors (Bond and Diamond 2011) and because we were unable to conduct a captive study, we were required to use estimations. Recognizing that the value of the discrimination factors we choose greatly affects output, we estimated both $\Delta^{13}C$ and $\Delta^{15}N$ using two methods to increase the probability of selecting accurate discrimination factors: 1) We searched the literature for point estimates of discrimination factors of passerines in similar foraging guilds, and 2) we estimated discrimination factors by systematically comparing potential combinations of $\Delta^{13}C$ and $\Delta^{15}N$ output from SIAR mixing models and ruling out

unfeasible combinations. Our objectives were to develop reliable estimates of carbon and nitrogen discrimination factors for plasma, RBC, and claw tips to use in diet stable isotope mixing models for Rusty Blackbirds.

METHODS

Study site.–From 2009 to 2012, we captured Rusty Blackbirds in two sites on the Atlantic Coastal Plain of South Carolina and four sites on the Piedmont Plateau in South Carolina and Georgia (Fig. 4.1). The Coastal Plain sites (CHAR) in South Carolina included a Charleston residential area and Magnolia Plantation and Gardens. The Piedmont Plateau sites included Lake Conestee (CONE) and Lake Cunningham (CUNN), and two sites in Athens, Georgia (ATHE). The CONE and ATHE sites included suburban residential areas, wooded wetlands and pecan groves while the CUNN and CHAR sites included wooded wetlands and residential areas.

Bird capture.–We used whoosh nets and mist nets to capture individuals from flocks of wintering Rusty Blackbirds from 16 December to 20 March that extensively used residential areas for foraging. It was rare (n = 6) that individuals were recaptured, thus, the dataset is composed of >98% unique individuals. Each captured blackbird received a USGS band (USGS BBL Permit # 22665) and we recorded date, time of capture, and time the blood sample was extracted. For stable isotope analyses, we clipped 1-2 mm of two claws and drew two capillary tubes (200 µl total) of blood via brachial veinipuncture. This amount accounted for approximately 5% of total blood volume, which is below the AOU recommended 10-20% blood volume (Hoysak and Weatherhead 1991). Blood samples were placed on ice in a small cooler and centrifuged within four hours of collection with a sprout mini-centrifuge at $\geq$ 6000 RPMs for $\geq$10 $\leq$20 minutes. After

centrifuging, plasma was drawn off red blood cells with a 100-uL Hamilton syringe, placed in new centrifuge tubes and both RBC clots and plasma were frozen until processing. Claws were also stored frozen in small centrifuge tubes.

Invertebrate and tree mast collections.—At each known foraging site, potential invertebrate prey items were collected, frozen whole, and later identified to order and family using Merritt and Cummins (1994). Tree mast including pecans and pre-opened small-seeded red oak acorns were collected from each site as well. Rusty Blackbirds avoided unopened acorns, likely because of an inability to open the tough husk. Red oak acorns were predominately pre-opened by inefficiently foraging squirrels that preferentially cache red oak acorns and consume them throughout the winter (Smallwood et al. 2001). Because opened acorns had different isotopic signatures than unopened acorns, we only included isotopic signatures from pre-opened acorn specimens for this analysis. Samples of specimens were freeze-dried and analyzed for δ^{13}C and δ^{15}N via mass spectrometry.

Laboratory methods.—We prepared bird tissue and diet (source) samples for isotopic analysis at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Laboratory (SI) and the Analytical Chemistry Laboratory of the University of Georgia (UGA). Lipid was not removed from RBC and plasma because there is generally a low proportion of lipid in blood (Bearhop et al. 2000, 2002, Podlesak and McWilliams 2006). RBC and plasma from 100-μL blood samples were freeze-dried >24 hours and used for stable isotopic analysis of δ^{13}C and δ^{15}N. For each bird, RBC sample was weighed from 0.6 to 0.9 mg, plasma sample from 0.4 to 0.8 mg, and whole claw tip from 0.6 and 0.9 mg

into 5 x 9 mm tin cups. Animal and tree mast specimens were weighed from 2.5 to 3.5 mg to increase consistency of the sample.

Samples were analysed for $\delta^{13}C$ and $\delta^{15}N$ via combustion in a Costech 4010 Elemental Analyzer coupled to a Thermo Delta V Advantage Mass Spectrometer via a Conflo IV interface at the SI.

Stable isotope signature.–Stable isotope signatures in this paper are expressed according to the formula:

$$\delta = ((R\text{sample}/R\text{standard}) - 1) \times 1000$$

where δ is the isotopic ratio of the sample relative to the international standard (Kelly 2000). Rsample and Rstandard are the fractions of heavy to light isotopes in the sample and standard, respectively (Kelly 2000). One is subtracted from the Rsample/Rstandard fraction which results in samples with a lower ratio of heavy isotopes than the standard having a negative value, and those with higher ratios of heavy isotopes than the standard having a positive value (Kelly 2000). This number is multiplied by 1000 so the δ notation is in units of parts per thousand (‰). One standard was run for every five unknowns. $R_{standard}$ vales are based on Vienna PeeDee Belemite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Discrimination factors: literature.–We reviewed the literature and extrapolated and compiled $\Delta^{13}C$ and $\Delta^{15}N$ values for omnivorous songbirds eating similar quantities of protein as Rusty Blackbirds as indicated by nitrogen concentration where possible. In our search, we selected documented discrimination factor points that were within the $\delta^{15}N$ and $\delta^{13}C$ signature value range we found in our isotopic data for Rusty Blackbirds in order to increase relevancy of the discrimination factor to Rusty Blackbird.

Discrimination factors: mixing models.–We used mixing models in SIAR (Parnell et al. 2010), a package that runs in Program R (R development core team 2012), to estimate Rusty Blackbird dietary proportions with varying combinations of Δ^{13}C and Δ^{15}N for RBC at intervals of 0.5 from 0 to 6 for both carbon and nitrogen, i.e., 0, 0.5, 1, 1.5, 2, 2.5‰ and so on. SIAR employs Bayesian analysis to provide marginal posterior distributions for dietary proportion parameters from data on consumer and source stable isotopes and other dietary parameters (Hopkins et al. 2012) using Markov Chain Monte Carlo (MCMC) sampling (Parnell et al. 2010). SIAR takes varying source concentrations into account, an approach important for omnivorous consumers like the Rusty Blackbird (Phillips and Koch 2002, Hobson and Bairlein 2003). The Bayesian paradigm allows for uncertainty in all the parameters, including sources, concentrations, and discrimination factors. While SIAR allows for a Dirichlet prior on p_k, we used non-informative priors because we were trying to determine discrimination factors and did not want to influence the posterior distributions (Hopkins and Ferguson 2012).

The model is formulated as follows where data comprise N measurements on J isotopes with K sources (Parnell et al. 2010):

$$X_{ij} = \frac{\sum_{k=1}^{K} p_k q_{jk}(Sjk + cjk)}{\sum_{k=1}^{K} p_k q_{jk}} + \varepsilon_{ij}$$

where

$S_{jk} \sim N\ (\mu_{jk},\ \omega_{jk}^2)$

$c_{jk} \sim N\ (\lambda_{jk},\ \tau_{jk}^2)$

$\varepsilon_{ij} \sim N\,(0,\,\sigma_j^2)$

X_{ij} = observed isotope value j of the consumer i.

S_{jk} = source value k on isotope j, normally distributed with mean μ_{jk} and variance ω_{jk}^2.

c_{jk} = discrimination factor for isotope j on source k, normally distributed with λ_{jk} and variance τ_{jk}^2.

p_k = dietary proportion of source k, estimated by model.

q_{jk} = concentration of isotope j in source k.

ε_{ij} = residual error, describing additional inter-observation variance not described by the model, σ_j^2 estimated by model.

We ran several group models in SIAR according to site and capture date. Birds were first divided into the four sites – CONE, CUNN, ATHE, and CHAR – because source carbon and nitrogen signatures varied considerably between sites and we wanted to ensure we matched source signatures to consumer signatures. We then grouped birds by capture date to estimate group diet to increase the probability we were estimating the diet of birds that were consuming similar items. This approach resulted in 23 capture date groups over the four years as follows: CONE (12), CUNN (1), ATHE (6), and CHAR (4).

Because mixing models cannot accommodate many different food sources (Parnell et al. 2010) and we collected many different invertebrate species per site, we divided sources into five groups. Groups included the most common invertebrate available; worms (*Oligochaeta*) including both large terrestrial earthworms and small aquatic worms, invertebrates in trophic position 3‰, 6‰, and 9‰ based on their isotopic $\delta^{15}N$ signatures, pre-opened acorns, and pecans. Trophic position 3‰ included Diptera

and Odonata larvae, spiders (Araneae), and slugs Onchidiacea and Soleolifera, trophic position 6‰ included minnows (Cyprinidae) and Isopoda, and trophic position 9‰ included minnows, crayfish (Astacidea), Amphipoda, and snails. For each group, we used only source signatures from the corresponding site but used averages and standard errors combined for all capture years because there was not much variation in signatures in mast among years, and invertebrates were grouped based on trophic position (δ^{15}N).

Selection of discrimination factor.–For each pair of potential discrimination factors, we created a decision table to help us decide whether mixing model output on dietary proportions was feasible or not depending on whether it resulted in realistic results across all sites in all years for each capture date. For instance, a model that concluded Rusty Blackbirds ate a larger proportion of pecans in March 2009 than in early February 2009 would be deemed unfeasible because the pecan source was no longer available.

We then back-adjusted plasma and claw tip signatures to overlap RBC signatures using the logic that if plasma signatures estimate diet over the previous three days, then plasma signatures should fall within the range of RBC values for the same time frame within the same sites. In Yellow-vented Bulbuls (*Pycnonotus xanthopygos*), a medium-sized bird (36.5 ± 0.6g) with a high protein content similar to Rusty Blackbirds, plasma indicated diet within the previous five days and RBC from the previous 21 days (Tsahar et al. 2008). In Yellow-rumped Warblers (*Setophaga coronate*) plasma represented diet over the past three days and RBC from one month (Podlesak et al. 2005). Therefore, plasma generally represents a much shorter time-frame. We also used a subset of claw tip signatures to back-adjust claw tips to overlay RBC values over the appropriate time frame for two sites: CONE and CHAR.

RESULTS

Discrimination factors from the literature.–There were few data available from the

literature on songbird discrimination factors for plasma and red blood cells and even

fewer for claw tips (Table 4.1). The average value for plasma $\Delta^{13}C$ is close to zero and

plasma $\Delta^{15}N$ is 2.85 (Caut et al 2009). The range of $\Delta^{13}C$ for plasma was -0.2 to 0.6 and

2.6 to 3.24‰ for $\Delta^{15}N$. RBC $\Delta^{13}C$ was 1.4 ± 0.3 and $\Delta^{15}N$ was 3.24‰ (Table 4.1).

Discrimination factors for collagen tissues (e.g., feathers), which have been found to be

similar to claws (Bearhop et al. 2003), were much higher than blood tissue with $\Delta^{13}C$

from 1.8 to 2.7‰ and $\Delta^{15}N$ from 2.4 to 4‰. In general, claw tip $\Delta^{13}C$ and $\Delta^{15}N$ > RBC>

plasma.

Discrimination factors based on Rusty Blackbird capture data.–Rusty Blackbird $\delta^{15}N$

and $\delta^{13}C$ signature values were within the range recorded for other songbird species

(Tables 4.1 and 4.2). Among all sites in all years, uncorrected plasma, RBC, and claw

tips had similar $\delta^{13}C$ and $\delta^{15}N$ signatures and fell within the range of 5.5-10‰ for $\delta^{15}N$

and -29.6 to -18.2‰ for $\delta^{13}C$ indicating little overall variation in signatures between

tissues, especially for $\delta^{15}N$ (Table 4.2). Furthermore, dietary endpoints (C: N ratio) had

very little variation, especially within tissue type, indicating discrimination factors do not

need to vary based on C: N ratio to account for protein quality for Rusty Blackbird winter

diets (Kelly and Martinez del Rio 2010; Table 4.2).

Sensitivity analysis.–Estimates from SIAR of dietary proportions based on RBC were

moderately sensitive to the range of $\Delta^{13}C$ and $\Delta^{15}N$ discrimination combinations (Table

4.3). The most feasible combinations of discrimination factors were 2 to 4‰ for $\Delta^{15}N$ and

0.5 to 2‰ for $\Delta^{13}C$ (Table 4.4). Within the range of feasible combinations, the estimate

of dietary proportions from mixing models for trophic position 9‰ was the least sensitive and was the most sensitive for worms. The average difference in mixing model estimated proportions ranged from 0.06% for trophic position 9‰ to 0.19% for worms (Table 4.3). The range of discrimination factors resulted in more sensitivity in source proportions in March groupings while the model output was less sensitive for December groupings (Fig 4.2). For instance, a range of 2 to 4‰ for $\Delta^{15}N$ and 0.5 to 2‰ for $\Delta^{13}C$ resulted in an average 2% difference in estimation of proportion of worms and an average 5 to 6% difference in acorns and pecans in December 2010 in ATHE (Fig. 4.2a). We found much more sensitivity in March 2009 in CONE, where there was a 52% variation in proportion of worms and a 59% and 7% difference in acorns and pecans respectively (Fig. 4.2b).

Feasible solutions.–The feasible solutions for RBC based on the decision table included $\Delta^{13}C$ of 0.5 or 1‰ and $\Delta^{15}N$ of 3 or 3.5‰ (Table 4.4). We chose to take a middle value resulting in $\Delta^{13}C$ of 0.75‰ and $\Delta^{15}N$ of 3.25‰. These values are similar to the values for RBC we found in the literature (Table 4.1). We then back-adjusted plasma signatures +0.7‰ from RBC for $\delta^{15}N$ and -0.5‰ for $\delta^{13}C$ (Fig. 4.3). This resulted in plasma $\Delta^{13}C$ = 0.25‰ and $\Delta^{15}N$ = 4.05‰. For $\delta^{15}N$ in claw tips, we adjusted another 1.25‰ and 2.25‰ for $\delta^{13}C$ resulting in $\Delta^{13}C$ = 3‰ and $\Delta^{15}N$ = 4.5‰ (Fig 4.4).

DISCUSSION

Comparison with literature.–In general, our discrimination factors for claw tips, RBC, and plasma were not different than expected based on the literature for other passerine species. Our claw tip $\Delta^{13}C$ and $\Delta^{15}N$ discrimination factors (3 and 4.5‰) were just outside the upper end of the range of previously published discrimination factors for collagen ($\Delta^{13}C$ = 1.76-2.7‰ and $\Delta^{15}N$ = 2.37-4‰), making our discrimination factors

plausible; we could not find discrimination factors for claw tips from the literature. Our claw tip discrimination factors were much higher than for RBC which also agrees with patterns in the literature based on keratin based tissues. Our RBC Δ^{13}C and Δ^{15}N discrimination factors (0.75 and 3.25‰ respectively) are also very similar to the reported values in the literature for RBC (1.43±0.3 and 3.24 respectively). Plasma Δ^{13}C (0.25‰) was lower than RBC Δ^{13}C and similarly low compared with values reported in the literature (-0.2-0.6‰). Our plasma Δ^{15}N estimate of 4.05‰ was out of the range previously reported for songbirds. Interestingly, percent nitrogen values for plasma are consistently lower than for both RBC and claw tips indicating nitrogen may be routed disproportionately to the various tissues. Rusty Blackbirds consume a high protein diet with a nitrogen content of ~10% (Tsahar et al. 2008). Dietary nitrogen may be preferentially routed to the more proteinaceous tissue such as RBC, leaving plasma less enriched than RBC (Podlesak et al. 2005). Podlesak and McWilliams (2006) have concern that the insect portion of an omnivorous diet might be overrepresented if the δ^{15}N values for the insect protein and fruit protein are quite different (in their study; 7.3‰). However, in our Rusty Blackbird study, the δ^{15}N values for tree mast items (~2.5‰) were similar to values from invertebrate items (~4‰) indicating that the animal portion of the Rusty Blackbird diet is not overrepresented. This interpretation is supported by the sometimes very high values of tree mast estimated by mixing models in the January diets. Also, recent research has shown that isotopic signatures of carbon and nitrogen get assimilated into proteinaceous tissues such as RBC and plasma at similar rates and are therefore considered coupled and effectively denote C and N from diet

(Podlesak and McWilliams 2006). Because we back-adjusted plasma values to overlay RBC, we have hopefully accounted for this discrepancy.

An alternative explanation for the higher concentration of nitrogen in Rusty Blackbird plasma than RBC could be that birds were actually consuming items with more nitrogen in the previous three days before capture (indicated by plasma) compared with their overall diet in the past month (indicated by RBC). This effect could be possible if diets changed over time. Blackbirds were more easily attracted to whoosh and mist nets with colder weather and we did not capture birds on days with precipitation; thus capture days could possibly represent a different diet than what would be expected overall by RBC values.

RBC sensitivity analysis.–Because we had a large dataset (n = 275 birds), we were able to evaluate model output from varying combinations of discrimination factors via a decision table. This method worked well to rule out unfeasible combinations of discrimination factors that would have resulted in nonsensical output. We also had four sites, which aided us in reproducing our results and decisions. Our RBC models seem to be more sensitive proceeding from December to March, possibly because there are more sources of food available as temperature and precipitation increase in the spring.

Our RBC results are consistent with the literature and thus we have confidence that our discrimination factors are accurate for Rusty Blackbird RBC. However, in addition to a literature review we conducted a sensitivity analysis adding confidence in our estimates. Our sensitivity analysis indicates that for a broad range of discrimination factor combinations (i.e., $\Delta^{13}C = 0.5\text{-}2‰$ and $\Delta^{15}N = 2\text{-}4‰$), we do not get very different answers within most capture groups. Therefore, even if we chose incorrect discrimination

factors (<2‰) for plasma and claw tips, we would arrive at similar conclusions for

dietary proportions. In addition, if we had just used the average values for RBC as do

other researchers, we would have arrived at similar answers. Our methodology of first

finding RBC discrimination factors and then overlaying plasma and claw tips will

hopefully allow us to estimate short, medium, and long term diet choices throughout the

winter.

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Figure 4.1. Rusty Blackbird capture sites in South Carolina and Georgia from 2009 to 2012.

ATHE = Athens, CUNN = Lake Cunningham, CONE = Lake Conestee, and CHAR = Charelston.

2a. ATHE Dec 2010
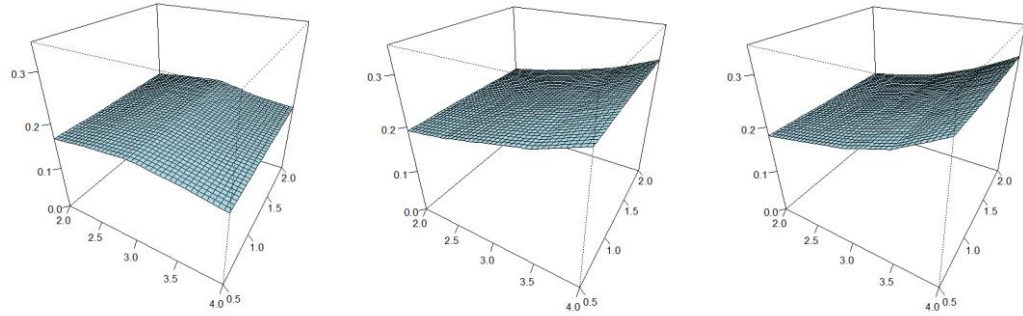
2b. CONE Mar 2009
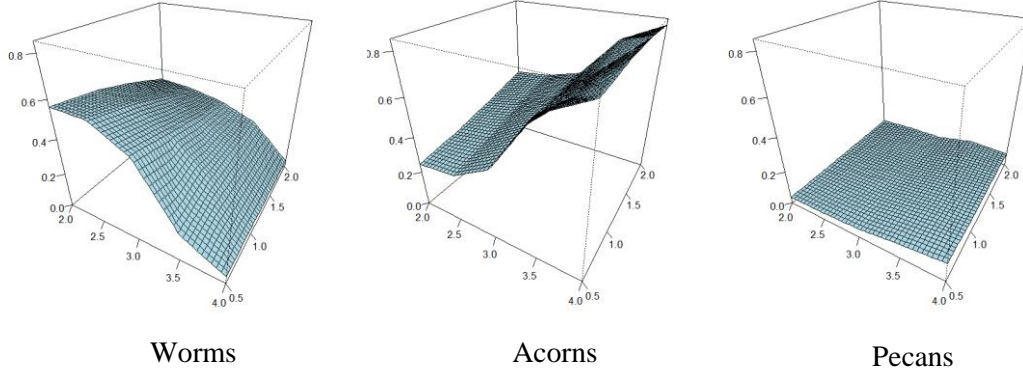
Worms   Acorns   Pecans

Figure 4.2. Variation in estimates of proportion of source items in the diet of Rusty Blackbirds in 2 of 23 capture groups. 2a) variation in worms, acorns, and pecans in Athens GA from birds captured on December 17 2010. 2b) variation in Conestee SC from birds captured on March 16-18 2009. The x-axis is $\Delta^{15}N$, the y-axis is $\Delta^{13}C$, and the vertical z-axis is proportion.
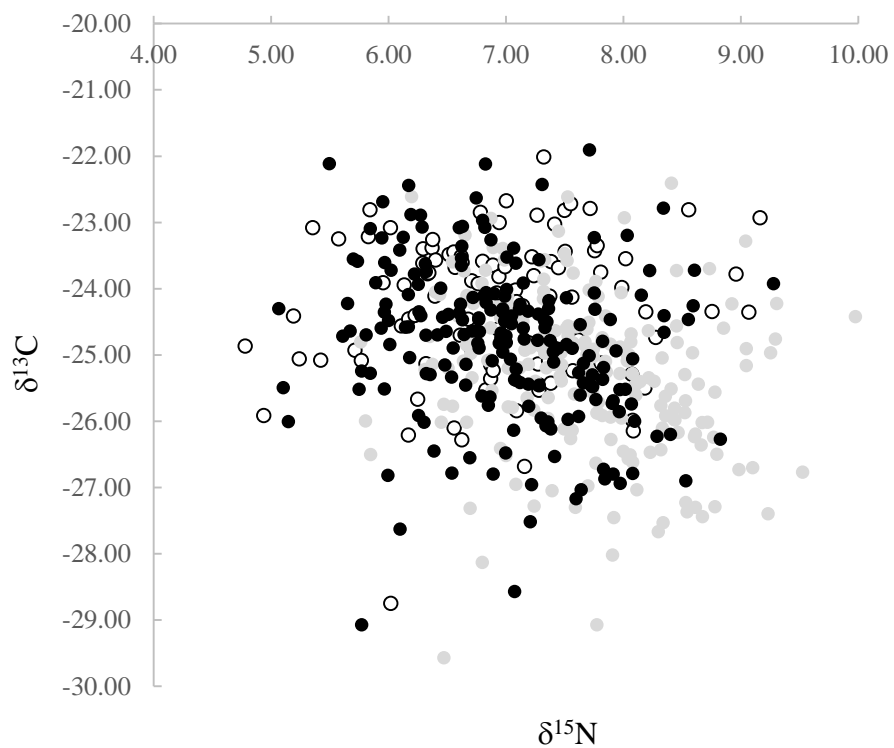
Figure 4.3. Rusty Blackbird back-adjusted δ^{13}C and δ^{15}N for plasma plotted on RBC for all four

sites (Athens, Charelston, Lake Conestee, and Lake Cunningham in all years from 2009 to 2012.

Unclosed circles are unadjusted RBC signatures, grey circles are unadjusted plasma signatures,

and black circles are plasma signatures adjusted by -0.25 for δ^{13}C and +0.7 for δ^{15}N to overlay

RBC values.

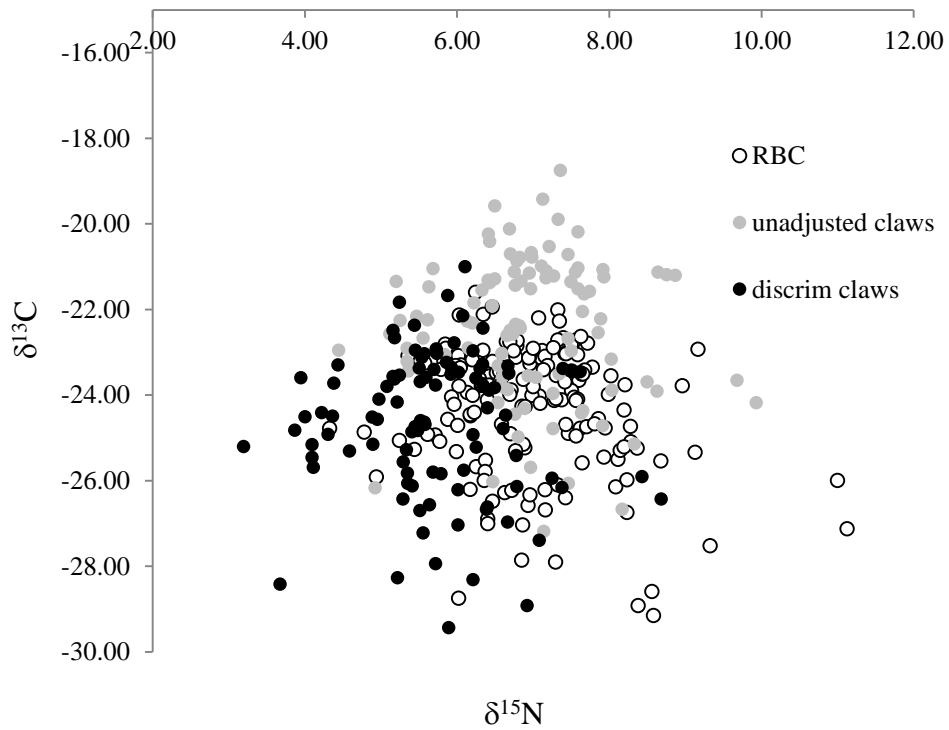Figure 4.4. Rusty Blackbird back-adjusted $\delta^{13}C$ and $\delta^{15}N$ for claw tips plotted on RBC for two

sites (CHAR, CONE) in two years (2009 and 2010) in which claw tips were collected.

Unclosed circles are unadjusted RBC signatures, grey circles are unadjusted claw tips and

black circles are claw tip signatures adjusted by -2.25 for $\delta^{13}C$ and -1.25 for $\delta^{15}N$ to

overlay RBC values.

TABLES

Table 4.1. Point values from the literature for discrimination factors (Δ^{13}C and Δ^{15}N) of various tissues from passerines with similar δ^{13}C and δ^{15}N values as Rusty Blackbird data. Other Icteridae are bolded. Rusty Blackbird δ^{13}C fell within the range of -29.6 to -18.2‰ and the range of δ^{15}N was 4.9 to10‰ for all tissues.

Species	Family	Diet	Tissue	Δ^{13}C‰	Δ^{15}N‰	δ^{13}C	δ^{15}N	Reference
52 species	various	various	average	**1.2±0.18**	**2.9±0.16**	~(-30 to-19)	~3-15	Caut et al. 2009
<25 species	various	various	**plasma**	**-0.08±0.38**	**2.82±0.14**	~(-30 to-19)	~3-15	Caut et al. 2009
Dendroica coronata	Parulidae	49-97% insect	**plasma**	**-0.2-0.6**	**2.6-3**	-24.9-(-27.9)	6.07-6.17	Pearson et al. 2003
Dendroica coronata	Parulidae	insectivore	plasma	0.1±0.2	n/a	-24.6±1.2	n/a	Podlesak and McWilliams 2005
Pycnonotus xanthopygos	Pycnonotidae	omnivore	plasma + RBC	n/a	3.24	n/a	7.8-8.3	Tsahar et al. 2008
Dendroica coronata	Parulidae	insectivore	RBC	1.4±0.3	n/a	-21.5±2.6	n/a	Podlesak and McWilliams 2005
<23 species	various	various	whole blood	-0.199Δ^{13}C-3.99x	2.25±0.2	~(-30 to-19)	~3-15	Caut et al. 2009
Dendroica coronata	Parulidae	49-97% insect	whole blood	1.5-2.2	1.8-2.7	-24.9-(-27.9)	6.07-6.17	Pearson et al. 2003
Sylvia Borin	Parulidae	control	whole blood	1.7	2.4	-25.8	6.5	Hobson and Bairlein 2003
Habia fuscicauda	Cardinalidae	omnivore	whole blood	2.2±0.1	2.6±0.2	-21.7±0.8	3.6±0.1	Herrera and Reyna 2007
19 species	various	various	collagen	1.76±0.64	2.37±0.47	~(-30 to-19)	~3-15	Caut et al. 2009
Sylvia Borin	Parulidae	control	feather	2.7	4	-25.8	6.5	Hobson and Bairlein 2003
5 omnivorous species	various	omnivore	muscle and liver	1-4.5	0.5-4.5	-24 to -23	4-10	Sabat et al. 2013
Curaeus curaeus	**Icteridae**	**omnivore**	**muscle and liver**	**1.7-4.0**	**2.5-3.8**	-23.22±0.96	4.7±0.75	**Sabat et al. 2013**
Sturnella loyca	**Icteridae**	**omnivore**	**muscle and liver**	**1.6-4.5**	**0.5-4.5**	-23.64±1.31	6.3±2.13	**Sabat et al. 2013**

Table 4.2. Summary of range of uncorrected signatures (δ^{13}C and δ^{15}N) and concentrations (%C and %N) and mean of C: N ratio for Rusty Blackbirds at four sites on the wintering ground from 2009 to 2012. CONE = Conestee SC, CUNN = Lake Cunningham SC, CHAR = Charleston SC, and ATHE = Athens GA.

Site	Tissue	n	δ^{13}C	δ^{15}N	%C	%N	C: N ratio
CONE	plasma	151	-29.6-(-22.4)	5.8-10	35.5-56.8	6-11.5	4.9±0.65
CUNN	plasma	4	-23.7-(-23.1)	5.9-6.6	46.6-48.6	12.6-13.8	3.6±0.12
CHAR	plasma	18	-28.6-(-24.3)	5.5-7.6	36.7-44.9	8.2-10	4.5±0.28
ATHE	plasma	55	-27.7-(-23.3)	6.6-9.3	41.1-48.5	8.1-10.6	4.8±0.35.
CONE	RBC	147	-29.2-(-19.2)	5.2-9.3	41.4-51.3	13-15.8	3.3±0. 01
CUNN	RBC	9	-24.2-(-22.2)	5.3-6.7	46.1-50.1	13.1-15.9	3.3±0.08
CHAR	RBC	22	-27.9-(-22.7)	5.4-7.3	40.3-51	14-15.5	3.2±0.16
ATHE	RBC	56	-27.4-(-18.9)	5.1-9.1	45.4-52.2	13.1-15.7	3.3±0.07
CONE	claw	120	-27.2-(-18.2)	4.9-9.9	35-50.4	10.6-15.1	3.3±0.12
CUNN	claw	n/a	n/a	n/a	n/a	n/a	n/a
CHAR	claw	21	-26.2-(-21.1)	5.8-8.3	40.2-48.4	12.1-14.6	3.3±0.06
ATHE	claw	n/a	n/a	n/a	n/a	n/a	n/a

Table 4.3. Maximum difference in estimated proportion of food groups consumed by Rusty Blackbirds projected by SIAR using a $\Delta^{13}C$ range of 0.5 to 2‰ and a $\Delta^{15}N$ range of 2 to 4‰. ATHE = Athens GA, CHAR = Charleston SC, CUNN = Lake Cunningham SC and CONE = Lake Conestee SC.

Group	Worm	Acorn	Pecan	Troph3	Troph6	Troph9
ATHE Dec17 2010	0.02	0.05	0.06	0.07	n/a	0.19
ATHE Jan 12 2011	0.12	0.13	0.21	0.16	n/a	0.09
ATHE Feb 7 2011	0.04	0.03	0.04	0.02	n/a	0.06
ATHE Feb17 2011	0.21	0.12	0.03	0.04	n/a	0.11
ATHE Mar 2011	0.27	0.17	0.20	0.11	n/a	0.12
ATHE Feb12 2012	0.03	0.06	0.07	0.04	n/a	0.13
CHAR 12OA Feb/Mar 2009	0.18	0.10	n/a	0.19	0.09	0.03
CHAR MAGN Feb 2009	0.09	0.05	n/a	0.04	0.09	0.07
CHAR 12OA Feb 2010	0.06	0.03	n/a	0.05	0.05	0.03
CHAR MAGN Feb 2010	0.13	0.09	n/a	0.07	0.16	0.08
CUNN Jan 19 2012	0.17	0.22	n/a	0.03	n/a	0.02
CONE Feb 5 2009	0.28	0.31	0.19	0.15	n/a	0.09
CONE Feb 6/7 2009	0.20	0.14	0.26	0.18	n/a	0.03
CONE Feb 9/10 2009	0.43	0.37	0.19	0.13	n/a	0.03
CONE Feb 23-25 2009	0.29	0.38	0.07	0.08	n/a	0.08
CONE Feb 28 2009	0.11	0.06	0.09	0.04	n/a	0.02
CONE Mar 3-10 2009	0.39	0.39	0.19	0.14	n/a	0.04
CONE Mar 16-18 2009	0.52	0.59	0.07	0.1	n/a	0.07
CONE Dec9/10 2009	0.04	0.04	0.06	0.07	n/a	0.04
CONE Jan 3-4 2010	0.09	0.11	0.15	0.14	n/a	0.04
CONE Mar 5-10 2010	0.26	0.18	0.19	0.1	n/a	0.02
CONE Dec 19 2010	0.12	0.21	0.2	0.21	n/a	0.05

CONE Jan 10 2011	0.27	0.38	0.11	0.14	n/a	0.05
Average	0.19	0.18	0.13	0.10	0.10	0.06
SD	0.13	0.15	0.07	0.06	0.06	0.04

Table 4.4. Decision table for determining feasible solutions for $\Delta^{13}C$ and $\Delta^{15}N$ among four sites. To be considered a possibility, the discrimination factor had to be feasible across all four sites. Solutions that are feasible across all sites are highlighted. ATHE = Athens GA, CHAR = Charleston SC, CUNN = Lake Cunningham SC and CONE = Lake Conestee SC. ✓ = feasible solution, X = unfeasible solution, and - = not tested because of unfeasible solution in another category.

$\Delta^{15}N$	ATHE		CUNN		CONE		CHAR	
	$\Delta^{13}C=0.5$	$\Delta^{13}C=1$	$\Delta^{13}C=0.5$	$\Delta^{13}C=1$	$\Delta^{13}C=0.5$	$\Delta^{13}C=1$	$\Delta^{13}C=0.5$	$\Delta^{13}C=1$
0	X	X	-	-	X	X	-	-
0.5	X	X	-	-	X	X	-	-
1	X	X	-	-	X	X	-	-
1.5	X	X	-	-	X	X	-	-
2	X	X	✓	✓	✓	✓	X	X
2.5	X	X	✓	✓	✓	✓	X	X
3	✓	✓	✓	✓	✓	✓	✓	✓
3.5	✓	✓	✓	✓	✓	✓	✓	✓
4	X	X	✓	✓	X	X	✓	✓
4.5	X	X	✓	✓	X	X	✓	✓
5	X	X	✓	✓	X	X	X	X
5.5	X	X	-	-	X	X	X	X
6	X	X	-	-	X	X	X	X

CHAPTER 5

DIET OF WINTERING RUSTY BLACKBIRDS IN SOUTH CAROLINA AND

GEORGIA[1]

ABSTRACT.–We studied Rusty Blackbirds (*Euphagus carolinus*) that use suburban

landscapes to meet dietary requirements on the Piedmont Plateau and Atlantic Coastal

Plain. We estimated the proportion of pecan, acorn, worm, and other invertebrates from

trophic positions $\delta^{15}N = 3‰$, $6‰$, and $9‰$ incorporated into individual Rusty Blackbird

diets. We captured blackbirds from six flocks in Athens, Georgia, and Conestee, Lake

Cunningham, and Charleston, South Carolina from 2009 to 2012. Aquatic and terrestrial

non-native worms constituted the largest proportion of incorporated food items in the diet

of suburban Rusty Blackbirds (39% ± 2.9; mean ± SD by site and year) on the Piedmont

Plateau while invertebrates other than worms constituted 27% ± 12.9. In contrast, worms

constituted a much lower proportion (19% ± 1.2) of incorporated food items on the

Coastal Plain and invertebrates other than worms comprised the majority of the diet (62%

± 3.3). Rusty Blackbirds incorporate more tree mast into the diet on the Piedmont Plateau

(34% ± 11.2) than the Coastal Plain (19% ± 2.7). This is the first study to document

significant worm-use by Rusty Blackbirds. Managing Rusty Blackbird populations in

suburban landscapes in the bird's eastern range may be complex because the diet there

consists of non-native components (i.e., pecan [*Carya illinoenensis*] and non-native

terrestrial earthworms [*Lumbricus* spp.). Increased incorporation of worms in the diet 1-3

days before capture was related to increasing daily maximum temperature and increasing

precipitation in the following 48 hours after capture. Incorporation of mast in the

previous 1-3 days from capture increased with the number of hours in the following 48

hours from sampling that fell below -3°C. We found support that mast, including crushed

pecan and pre-opened red oak acorn, is an important dietary component for blackbirds

wintering in colder climates, and is likely incorporated to prepare for extreme weather.

INTRODUCTION

The Rusty Blackbird (*Euphagus carolinus*) winters in the southeastern United States and breeds in boreal and Acadian forests of New England, Canada and Alaska, and is reported to be the fastest declining songbird in North America (Greenberg et al. 2011). The species has experienced an estimated 85-95% overall decline continent-wide with accelerated rates of population decline since the 1960s (Greenberg and Droege 1999, Niven et al. 2004, Sauer et al. 2005). Because of this decline, it was declared a focal species of conservation concern by the USFWS (USFWS 2008) and considered vulnerable to extinction according to the IUCN Red List (IUCN 2010). Although Rusty Blackbirds have declined precipitously, a few million may still persist and it may not be too late to take conservation measures to stop and reverse further decline (Greenberg and Matsuoka 2010).

The reason for the decline remains unclear but it is increasingly thought the decline is related to loss and/or modification of winter wetland habitat (Greenberg and Matsuoka 2010, Greenberg et al. 2011). Winter wetland habitat systems have been disappearing and were converted to other land uses rapidly compared with breeding ground habitats (Greenberg and Matsuoka 2010, Greenberg et al. 2011). High quality winter habitat and associated food supply may be required to maintain remaining flocks of this species.

Rusty Blackbird flocks have recently been found using landscapes that include patches of bottomland hardwood forests, waterfowl impoundments, pecan orchards, and suburban residential lawns. These patches, in combination, provide aquatic invertebrates, worms (*Lumbricus* spp.), and pre-opened tree mast such as small-size red oak acorns from willow oak (*Quercus phellos*) and water oak (*Q. nigra*), and pecan nuts (*Carya*

illinoenensis; P. Newell Wohner *pers. obs*). Tree mast is relatively high in high-energy lipids compared with many invertebrate sources and is included in the diet in winter (Smith and Scarlett 1987, Fredrickson and Reid 1988).

Although we know many bird species incorporate mast in their winter diet, it is unknown if they do so to help them physiologically endure extreme weather events such as temperatures below freezing, or because invertebrates are not accessible during these times, or both (Blem1990, Nelson et al. 1996). Thus, short-term weather events may affect the availability of invertebrates and be a driving factor in Rusty Blackbird use of mast as a substitute when invertebrates are not available. Alternatively, or additionally, birds may use mast to stock up fat stores to physiologically endure long, cold nights during severe weather events. Determining the proximate reason behind mast-use could benefit conservation efforts for omnivorous wintering songbirds by providing insight into whether it would be better to provide more high energy lipid resources for increasing fat stores, or by increasing invertebrate resources during times when invertebrate availability is low.

There are few documents available on the actual diet of wintering Rusty Blackbirds, and none on diet in the eastern population. The one previous study that analyzed diet was conducted more than a century ago and does not include sufficient information on the winter diet in the eastern population (Beal 1900). From Beal's (1900) analysis of 132 stomachs of Rusty Blackbirds throughout the year (only 10 total from December, January, and February combined), from Rusty Blackbirds collected over a century ago, we know the blackbirds predominately ate aquatic invertebrates such as spiders, snails, crawfish, worms, and larvae, and also consumed vertebrate prey items

such as small fish during winter. No one invertebrate order was reported to be dominant with small proportions of a variety of invertebrates represented (Beal 1900). Beal (1900) reported grain, seed, and a small amount of tree mast in the stomachs of Rusty Blackbirds during non-breeding and laments the lack of information from January and February, likely the most limiting months during winter for these blackbirds (Chapters 2 and 3).

In summary, then, virtually no diet studies have been conducted on the eastern population of this dramatically declining species. We therefore aimed to determine the current winter diet and the relationship of diet to short-term weather conditions for suburban Rusty Blackbirds to provide conservation recommendations.

In the southeastern United States, the most evident land use change has been the conversion from agricultural to urban and suburban lands (Hamel et al. 2009, Nagy et al. 2011). Rusty Blackbirds have seemingly adapted to suburban areas, and because the area of suburban landscapes is currently increasing on both the Piedmont Plateau and Atlantic Coastal Plain, and is projected to increase into the foreseeable future (Wear 2001, Koneff and Royle 2004, Nagy et al. 2011), we studied the blackbirds in suburban areas. Our specific objectives were to: 1) determine the proportion of tree mast and invertebrate sources in the short and medium-term winter diet of Rusty Blackbirds through stable isotope mixing models, 2) determine the relationship between short-term weather events and diet, 3) determine the reason for incorporation of mast in the diet, i.e., for enduring extreme winter weather, or to tide birds over when invertebrates are not available during extreme weather, and 4) provide recommendations for improving habitat for wintering suburban Rusty Blackbirds.

METHODS

Study site.–From 2009 to 2012, we captured Rusty Blackbirds in two sites on the Atlantic Coastal Plain of South Carolina and four sites on the Piedmont Plateau in South Carolina and Georgia (Fig. 5.1). The Coastal Plain sites (CHAR) in South Carolina included a Charleston residential area and Magnolia Plantation and Gardens. The Piedmont Plateau included Lake Conestee (CONE) and Lake Cunningham (CUNN), and two sites in Athens, Georgia (ATHE). The CONE and ATHE sites included suburban residential areas, wooded wetlands and pecan groves while the CUNN and CHAR sites included wooded wetlands and residential areas.

Bird capture.–We used whoosh nets (Skelhorn and Rowe 2009) and mist nets to capture individuals from flocks of wintering Rusty Blackbirds from 16 December to 20 March that extensively used residential areas for foraging. Whoosh nets are spring-loaded devices comprised of fine-mesh netting that are launched over ground-foraging birds. Blackbirds were lured to nets by concentrating crushed pecans collected from the grove around nets. It was rare (n=6) that individuals were recaptured, thus, the dataset is composed of >98% unique individuals.

Each captured blackbird received a USGS band (USGS BBL Permit # 22665) and we recorded date, time of capture, and time the blood sample was extracted. To estimate diet via stable isotope analysis, we drew two capillary tubes (200 µl total) of blood via brachial veinipuncture which accounted for approximately 5% of total blood volume. This volume is below the AOU recommended 10-20% blood volume (Hoysak and Weatherhead 1991). Blood samples were placed on ice in a small cooler and centrifuged within four hours of collection with a sprout mini-centrifuge at $\geq$ 6000 RPMs for $\geq$10 $\leq$20

minutes to separate plasma from red blood cells (RBC). Plasma was used to elucidate short-term diet and RBC to estimate mid-term diet. After centrifuging, plasma was drawn off red blood cells with a 100-uL Hamilton syringe, placed in new centrifuge tubes and both RBC clots and plasma were frozen until processing.

Invertebrate and tree mast collections.–At each known foraging site, potential invertebrate prey items were collected, frozen whole, and later identified to order and family using Merritt and Cummins (1994). Mast, including pecans and pre-opened small-seeded red oak acorns, was collected from each site. Rusty Blackbirds avoided unopened acorns, likely because of an inability to open the tough husk. Red oak acorns were predominately pre-opened by inefficiently foraging squirrels that preferentially cache red oak acorns and consume them throughout the winter (Smallwood et al. 2001). Because opened acorns had different isotopic signatures than unopened acorns, we only included isotopic signatures from pre-opened acorn specimens for this analysis. We collected potential diet sources at the time we observed birds foraging based on telemetry locations (Chapter 2).

Laboratory methods.–We prepared plasma, RBC, and diet (source) samples for isotopic analysis at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Laboratory (SI) and the Analytical Chemistry Laboratory of the University of Georgia (UGA). Lipid was not removed from plasma and RBC because there is generally a low proportion of lipid in blood (Bearhop et al. 2002, Podlesak and McWilliams 2006). Plasma and RBC from 100-μL blood sample, and samples of diet source specimens, were freeze-dried >24 hours and used for stable isotopic analysis of $\delta^{13}C$ and $\delta^{15}N$. For each bird, RBC sample was weighed from 0.6 to 0.9 mg and plasma sample from 0.4 to 0.8

mg. Animal and tree mast specimens were weighed from 2.5 to 3.5 mg to increase consistency of the sample. Samples were then analysed for $\delta^{13}C$ and $\delta^{15}N$ via combustion in a Costech 4010 Elemental Analyzer coupled to a Thermo Delta V Advantage Mass Spectrometer via a Conflo IV interface at the SI.

Stable isotope signature.–Stable isotope signatures in this paper are expressed according to the formula:

$$\delta = ((R\text{sample}/R\text{standard}) - 1) \times 1000$$

where δ is the isotopic ratio of the sample relative to the international standard (Kelly 2000). Rsample and Rstandard are the fractions of heavy to light isotopes in the sample and standard, respectively (Kelly 2000). One is subtracted from the Rsample/Rstandard fraction which results in samples with a lower ratio of heavy isotopes than the standard having a negative value and those with higher ratios of heavy isotopes than the standard having a positive value (Kelly 2000). This number is then multiplied by 1000 so the δ notation is in units of parts per thousand (‰). One standard was run for every five unknowns. $R_{standard}$ vales are based onVienna PeeDee Belemite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$.

Mixing models.–We used mixing models in SIAR (Parnell et al. 2010), a package that runs in Program R (R development core team 2012), to generate posterior distributions for Rusty Blackbird dietary proportions of five source groups (Parnell et al. 2010) as indicated by plasma (diet over previous 1-3 days) and red blood cells (diet over previous 3-4 weeks). SIAR employs Bayesian analysis to provide marginal posterior distributions for dietary proportion parameters from data on consumer and source stable isotopes and other dietary parameters (Hopkins et al. 2012) using Markov Chain Monte Carlo

(MCMC) sampling (Parnell et al. 2010). SIAR takes varying source concentrations into account, an approach important for omnivorous consumers like the Rusty Blackbird (Phillips and Koch 2002, Hobson and Bairlein 2003). The Bayesian paradigm allows for uncertainty in all the parameters, including sources, concentrations, and discrimination factors. While SIAR allows for a Dirichlet prior on p_k, we used non-informative priors because we had a large enough dataset from which to base inference, and previous data on diet parameters for Rusty Blackbirds do not exist (Hopkins and Ferguson 2012).

The model is formulated as follows where data comprise N measurements on J isotopes with K sources (Parnell et al. 2010):

$$X_{ij} = \frac{\sum_{k=1}^{K} p_k q_{jk} (Sjk + cjk)}{\sum_{k=1}^{K} p_k q_{jk}} + \varepsilon_{ij}$$

where

$S_{jk} \sim N\ (\mu_{jk},\ \omega_{jk}^2)$

$c_{jk} \sim N\ (\lambda_{jk},\ \tau_{jk}^2)$

$\varepsilon_{ij} \sim N\ (0,\ \sigma_j^2)$

X_{ij} = observed isotope value j of the consumer i.

S_{jk} = source value k on isotope j, normally distributed with mean μ_{jk} and variance ω_{jk}^2.

c_{jk} = discrimination factor for isotope j on source k, normally distributed with λ_{jk} and variance τ_{jk}^2.

p_k = dietary proportion of source k, estimated by model.

q_{jk} = concentration of isotope j in source k.

ε_{ij} = residual error, describing additional inter-observation variance not described by the model, σ_j^2 estimated by model.

We used individual models (siarsolo) to calculate proportions of food groups incorporated in the diet for each Rusty Blackbird. We chose to estimate individual diet as opposed to group diet to relate individual diet proportions to short-term weather variables for each blackbird (Table 5.1). Stable isotope signatures of carbon and nitrogen (δ^{13}C and δ^{15}N) and the variance of potential diet items from six groups collected from wintering sites were included in mixing models as source values; however, only five groups were ever included in a model at a time because of source availability at each site. Groups included: (1) worms (*Oligochaeta*) including both large terrestrial earthworms and small aquatic worms, (2) aquatic invertebrates in trophic position δ^{15}N = 3‰ (Troph3), (3) aquatic invertebrates in trophic position δ^{15}N = 6‰ (Troph6), (4) aquatic invertebrates in trophic position δ^{15}N = 9 (Troph9) (5) pre-opened red oak acorns, and (6) pecans.

Trophic levels were based on nitrogen signature (δ^{15}N). Troph3 included Diptera and Odonata larvae, spiders (Araneae), and slugs (Onchidiacea and Soleolifera). Troph6 included minnows (Cyprinidae) and Isopoda, and Troph9 included minnows, crayfish (Astacidea), Amphipoda, and snails (Stylommatophora). For each capture group, we used source signatures from the corresponding site but used averages and standard errors combined for all capture years within a site because there was not much variation in signatures in mast among years. We used discrimination factors specific for plasma and RBC that were developed in Chapter 4; i.e., plasma Δ^{13}C and Δ^{15}N were 0.25‰ and 4.05‰ respectively and RBC Δ^{13}C and Δ^{15}N were 0.75‰ and 3.25‰ respectively.

Once we obtained diet group proportion values from SIAR, we further grouped dietary groups into three groups: 1) proportion of mast (pecan and acorn; Mast), 2) proportion of worms (terrestrial and aquatic; Worms), and 3) proportion of invertebrates other than worms (Troph3‰, 6‰, and 9‰; Troph).

Weather variables.–Eleven short-term weather variables, including temperature, precipitation, and barometric pressure, were constructed from raw hourly data from the free source, WeatherUnderground, from local weather stations (Table 5.1; The Weather Underground, LLC, 2013) for each capture date and time. Weather Underground develops historical weather summaries based on information from the National Weather Service. Aquatic insects have supercooling points typically around -3º to -7°C (Marchand 1996), thus temperature variables were developed using the number of hours below -3°C to be relevant to invertebrate availability. We used these variables based on our previous study that found short-term weather variables influence Rusty Blackbird daily foraging decisions during wintering. We used weather data from Charleston, South Carolina for Twelve Oaks residential area and Magnolia Plantation and Gardens, Athens Georgia for the two Athens sites, and Greenville, South Carolina for Lake Conestee and Lake Cunningham sites to develop our short term weather variables. We also developed two variables for monthly precipitation and temperature (Table 5.1).

Mast incorporation.–We developed predictions to differentiate two hypotheses for the reason Rusty Blackbirds incorporate tree mast into their diet (Fig. 5.2). Briefly our logic is that Rusty Blackbirds either incorporate mast because of the present or oncoming threat of low availability of invertebrates due to severe weather or to prepare for or endure severe weather (Fig. 5.2). The short-term weather variable that would have to be

related to increased proportion of tree mast in the diet in order to support the severe weather hypothesis is future cold weather, because at the time of sampling, blackbirds still should have been incorporating invertebrates, since they would still be available prior to cold weather. Under the invertebrate availability hypothesis, blackbirds should still incorporate invertebrates when available. If future cold weather is not important for mast incorporation, tree mast proportion should be unrelated to future cold weather.

Model selection.–We conducted three analyses using generalized linear models (GLM) in Program R (R development Core Team 2012) to determine short-term weather variables (Table 5.1) related to short-term proportions of source groups incorporated into the diet. The three short-term response variables were the log of the median value of the posterior distribution of source group proportions (e.g., Worm, Mast, Troph) from mixing model output by SIAR. We log-transformed the Day variable because we found a non-linear relationship with diet proportion variables. The Day variable began at Day 1 for blackbirds captured on 16 December and ended on Day 93 or 18 March. We also log-transformed the proportion variables because they were proportion data (Sokal and Rohlf 1995).

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative plausibility of candidate models for each of the three GLM analyses (Neter et al. 1990, Burnham and Anderson 2002). We conducted Pearson correlations on all pairs of predictor variables prior to modeling and if variables had $r > 0.45$, they were not included in the same model. An r threshold of 0.45 is generally considered a moderate correlation. In cases of correlated variables, we chose to keep the variable that resulted in the highest AIC_c.

To assess the fit of each candidate model, we calculated Akaike's Information

Criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and

Tsai 1989). The relative fit of each candidate model was assessed by calculating Akaike

weights (Burnham and Anderson 2002) which can range from 0 to 1, with the best-fitting

candidate model having the greatest Akaike weight. The ratio of Akaike weights for two

candidate models can be used to assess the degree of evidence for one model over

another (Burnham and Anderson 2002). We reported a confidence set of models that

included models with Akaike weights within 10% of the model with the largest weight,

which is similar to the general rule-of-thumb (i.e., 1/8 or 12%) suggested by Royall

(1997) for evaluating strength of evidence. If many models were within 10% of the

model with the top w_i, we reported models within $w_i > 0.03$. We also report the null

model in each analysis.

To allow for ease of interpretation, we provide model-averaged coefficients for

each predictor variable in the top model using the program R package AICcmodavg

(Mazerolle 2011). To choose the best model in analyses that generated several top

models, we chose the model with the fewest parameters within $\Delta AIC_c < 2$ of the top

model. We chose the top model if the level of support ($w_i > 0.5$) indicated it was far better

than other models. The precision of model-averaged coefficients was assessed by

calculating 85% confidence intervals based on a t-statistic with n-1 degrees of freedom

(Arnold 2010). Eighty-five percent confidence intervals are more compatible with AIC

methods than 95% CI as explained by Arnold (2010). Confidence intervals that contain

zero indicate inconclusive estimates because the nature of the relationships (i.e., whether

positive or negative) cannot be determined (Arnold 2010). Goodness-of-fit was assessed for the global model by examining residual and normal probability plots.

RESULTS

General.–We generated proportional diet posterior distributions from 275 Rusty Blackbirds captured in ATHE in 2011 (n = 54) and 2012 (n = 5), CONE in 2009 (n = 118), 2010 (n = 27), and 2011 (n = 33), CHAR in 2009 (n = 14) and 2010 (n = 9), and CUNN in 2012 (n = 10). Rusty Blackbirds generally consumed more invertebrates than mast; however, mast constituted a large proportion of the incorporated diet as indicated by both short and long term diet in both regions (Fig. 5.3). Terrestrial and aquatic worms constitute the largest proportion of incorporated food items in the diet of suburban Rusty Blackbirds (39% ± 2.9; mean ± SD by site and year) on the Piedmont Plateau while invertebrates other than worms constitute 27% ± 12.9. In contrast, worms constitute a much lower proportion (19% ± 1.2) of incorporated food items on the Coastal Plain and invertebrates other than worms comprise the majority of the diet (62% ± 3.3). Blackbirds incorporate more tree mast into the diet on the Piedmont Plateau (34.5% ± 11.2) than the Coastal Plain (19% ± 2.7).

On average, short-term incorporation did not differ from incorporation during the previous month from sampling (Fig. 5.3); however, birds incorporated slightly more amounts of worms and invertebrates in the longer term and slightly more amounts of tree mast in the short-term, especially on the Piedmont Plateau (Fig. 5.3).

Blackbirds captured in January and February generally consumed a higher proportion of tree mast than in December and March in both the short-term (Fig. 5.4) and during the previous month (Fig. 5.5). The proportion of Worm, Troph, and Mast follow a

non-linear trend with day of year in the two sites on the Piedmont Plateau for which we had enough data to plot with Day (Fig. 5.6).

Short-term weather analysis.–All temperature variables were correlated at r >0.49, while none of the precipitation variables were correlated, and barometric variables were correlated with precipitation variables. Therefore, we did not include temperature and barometric variables in the same models. Both SITE and Day were the most important variables in all analyses, therefore, we included these two variables in all models to account for variation in the data other than current and short-term weather variables.

The top model for short-term proportion of mast incorporated in Rusty Blackbird diet included the number of hours in the following 48 hours from capture that were below -3°C (Hrsnext2day<-3) and indicated birds consumed more tree mast when more hours would be cold in the immediate future (Tables 5.2 and 5.3, Fig. 5.7). The top models for proportion of mast included variables related to temperature and the worst models included precipitation variables (Table 5.2).

Proportion of worms incorporated into the short-term diet was positively related to the daily maximum temperature (Dailymax) and the amount of precipitation in the following 2 days after sampling (Precipnext2day; Tables 5.2 and 5.3).

The best model for proportion of invertebrates other than worms (Troph) in the short-term diet was the null model that only included Day and SITE. Birds consumed a lower proportion of Troph in CONE versus ATHE and there likely is no relationship between Day and Troph since the Day estimate included zero (Table 5.3).

DISCUSSION

Worm-use. –This is the first study that documents significant worm-use by Rusty Blackbirds. We found Rusty Blackbirds consuming both large terrestrial non-native earthworms from residential areas and wetlands and small aquatic worms from nearby forested wetlands in suburban landscapes. Worms constituted 39% of the incorporated diet on the Piedmont Plateau and 19% at Coastal Plain sites. This variation was likely related to the difference in availability of worms among the sites that could be due to climatic, water quality, or site differences.

The large proportion of worms incorporated into the diet of Rusty Blackbirds is not unexpected given both Rusty Blackbird and earthworm ecology. We are increasingly discovering that this blackbird is an opportunistic forager and largely forages based on prey availability. Although the species may be an opportunist, it is within the limiting context of foraging by flipping leaf litter in shallow water around the margins of predominately forested wetlands (Avery 1995). Non-native *Lumbricus* spp. earthworms, the predominate earthworm in suburban landscapes in the southeast (Szlavecz et al. 2006), are leaf litter feeders and are active from fall to late spring when there is abundant leaf litter (James and Hendrix 2004); this also is the timing of Rusty Blackbird wintering in the southeast. Earthworms are active at temperatures above 0°C and if the soil is moist, *Lumbricus* spp. will be abundant (K. Szlavecz *pers. comm*.).

Weather and worms. –Precipitation facilitates movement on the earth surface for earthworm dispersal and mating; during precipitation events, earthworms come to the surface, when it is dry they recede (James and Hendrix 2004). In addition, worms are more active with increasing temperature (Batema et al. 2005). Therefore, it is not

surprising we found a large proportion of worms incorporated in the diet of suburban Rusty Blackbirds, especially related to precipitation events and daily temperature maximum.

Consequences of worm management.–All four suburban study sites on the Piedmont Plateau had human components that retained fallen leaves on their lawns overwinter. This human-influenced feature provides a food source for earthworms in suburban communities and habitat with abundant food for Rusty Blackbirds and other bird species. Managing Rusty Blackbirds in suburban landscapes may be complex because the diet in the eastern population consists of this non-native earthworm component. Non-native species have traditionally been associated with negative consequences for native species; however, non-native earthworms have been found to have positive effects on native songbirds (Loss et al. 2012). In addition, high abundances of exotic earthworms occur only in severely disturbed forest sites, whereas native earthworms occur in undisturbed to slightly disturbed sites, sometimes in association with exotics (Hendrix et al. 2006). Native earthworm species tend to outcompete non-native earthworms in undisturbed landscapes even decades after introduction of non-natives (Hendrix et al. 2006). Non-native earthworms have a positive influence on American Robin (*Turdus migratorius*; Cameron and Bayne 2012) and American Woodcock (*Scolopax major*) in heavily disturbed sites (Vander Haegen et al. 1993, Myatt and Krementz 2007), where non-native earthworms primarily occur (Hendrix et al. 2006). Suburban landscapes may, therefore, offer sources of high-energy earthworms to a variety of wintering birds (James and Hendrix 2004, Szlavecz et al. 2006, Szlavecz et al. 2011). Higher availability of large nutrient-rich non-native earthworms in leaf litter may be the reason Rusty Blackbirds

have been able to adapt so successfully to anthropogenic habitats. Therefore, increasing the abundance of earthworms in suburban areas may be a multi-species benefit without risking detrimental effects of non-native worms dispersal to outlying undisturbed forested areas.

Wetland invertebrate-use. –The invertebrate group in this study, excluding worms, consisted mostly of Diptera and Odonata larvae, spiders, and slugs in both the Piedmont and Coastal Plain sites. Diptera and Odonata larvae grow and develop in wetlands during winter, and disperse in spring or summer (Batema et al. 2005). Invertebrates other than worms composed 62% of the diet of Rusty Blackbirds on the Coastal Plain while invertebrates other than worms constituted a much lower proportion (27%) incorporated in Piedmont Plateau diets. Invertebrate biomass and density in wetlands is related to fluctuations in temperature and precipitation, with lower abundance during cold, dry periods (Batema et al. 2005). Short-lived peaks occur when temperatures increase during winter and spring peak results in very high density (Batema et al. 2005). Cold winters result in lower invertebrate density than mild years (Batema et al. 2005). Because winters are on average much warmer on the Coastal Plain than the Piedmont, Rusty Blackbirds may have more access to wetland invertebrates there. Short-term weather variables did not explain the proportion of invertebrates other than worms in the diet.

Wetland invertebrate management. –Water manipulation is cited as the single most important element in enhancing invertebrate production in wetlands (Fredrickson and Batema 1992). Rusty Blackbirds could therefore benefit from frequent short-term water manipulations such as partial drawdowns, especially during times of hardship such as drought and following periods of cold weather. Water manipulations that emulate

naturally fluctuating water regimes in wetlands provide the most diverse habitat for wildlife (Fredrickson and Batema 1992). For multi-species management, consistent flooding during the entire season as is done in poorly managed waterfowl impoundments and green-tree reservoirs, should be discouraged (Fredrickson and Batema 1992).

Mast-use.–Rusty Blackbirds in both physiographic areas consumed a large proportion of mast, with both acorns and pecans well represented in diets (19-34%). In sites where pecans were not available (i.e., the Coastal Plain), blackbirds consumed more acorns. The pecan groves in our study sites were abandoned and had a source for crushing pecans such as vehicles and other animals. As with the pecan resource that must first be crushed before it can become available to Rusty Blackbirds, blackbirds were also particular about the acorns they consumed in the suburban sites we studied. Rusty Blackbirds only consumed red-oak acorns that were first broken open by gray squirrels (*Sciurus carolinensis*). We frequently found blackbirds foraging in residential areas where gray squirrels inefficiently foraged in the trees above. However, on numerous occasions, blackbirds would not eat recently opened acorns we cut open for bait. This is an important management implication because it suggests Rusty Blackbirds are dependent on other animals for winter success to crack open both red oak acorns and pecans.

Red oak acorns have a much higher tannin content than white-oak acorns, making them difficult to digest for many species including gray squirrels, Blue Jays (*Cyanocitta cristata*), and woodpeckers (Smallwood et al. 2001). Caching red oak acorns allows for tannins to be leached from them resulting in a nut that is more edible and digestible for many species (Smallwood et al. 2001). It is thought this is why squirrels preferentially cache red oak and immediately consume white oak acorns (Smallwood et al. 2001).

Mast and extreme weather.–We found increased mast incorporated in the diet with future short-term colder temperatures (i.e., number hours in following 2 days from capture <-3°C), suggesting blackbirds use mast to prepare for severe weather as opposed to responding to resource limitation. This relationship provides support that management of tree mast should be prioritized along with invertebrate management to maintain, conserve, or improve landscapes for Rusty Blackbirds and potentially other species. Because tree mast is important to Rusty Blackbirds, and potentially other species, for preparing for extreme weather events, it is important to provide sources of mast for Rusty Blackbirds, now and for the future.

Mast management.–In all of the sites we studied, water oak was a major component of trees in residential areas in addition to wetlands and uplands immediately surrounding wetlands. Red oak silviculture has advanced in recent years, and provides opportunities for Rusty Blackbird management (Hamel et al. 2009). Forest management decisions that promote small-seeded red oak species such as water and willow oak would enhance habitat quality for Rusty Blackbirds. In addition, leaf litter from oaks provides a desirable substrate for invertebrates (Fredrickson and Batema 1992). Favoring red oak species would provide multiple benefits for multiple species by providing tree mast and high quality leaf litter substrate.

Abandoned pecan groves in our study sites included mature trees in residential areas, fallow orchards, and small abandoned farms. The groves were very small, constituting as few as 40 mature, mast-producing trees. At all four landscape mosaics on the Piedmont Plateau, pecan trees were predominately on private lands and older trees were at risk of removal or loss to development.

Nature parks, state lands, and other public lands could be targeted to protect

current Rusty Blackbird hotspots by introducing a younger rotation of pecan trees.

Current Rusty Blackbird hotspots without a pecan component could be supplemented

with new pecan trees. Strategically-placed trees, such as in the parking lots of nature

parks, or on walking trails, would allow pecans to be crushed. As pecans are non-native

in the range of the eastern population of Rusty Blackbird, e.g., Georgia and South

Carolina (Santerre 1994, Worley 2002), this may pose problems for management in sites

that target native species. However, since Rusty Blackbird primarily used pecans in

upland areas fairly far from wetlands, pecan management may not be problematic.

Short versus medium term diet.−Short and medium term diets were similar in this study,

indicating birds are consuming a similar resource base over the course of the winter.

However, the fact that dietary proportions were related to short-term weather variables

indicates birds are adjusting their diets on a day to day basis according to temperature and

precipitation and availability of resources. This diet study corroborates our previous

radio-telemetry and body mass studies (Chapters 1 and 2) that indicated future

precipitation and current temperature, and subsequent availability of invertebrates, likely

drive foraging choices in Rusty Blackbirds.

Peter Doherty, Magnolia Plantation and Gardens, Conestee Foundation, Sandy Creek Nature Center, Greer Fire Department, Lake Cunningham County Park, and numerous private landowners and volunteers.

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Figure 5.1. Rusty Blackbird capture sites in South Carolina and Georgia from 2009 to 2012.

ATHE = Athens GA, CUNN = Lake Cunningham SC, CONE = Lake Conestee SC, and CHAR =
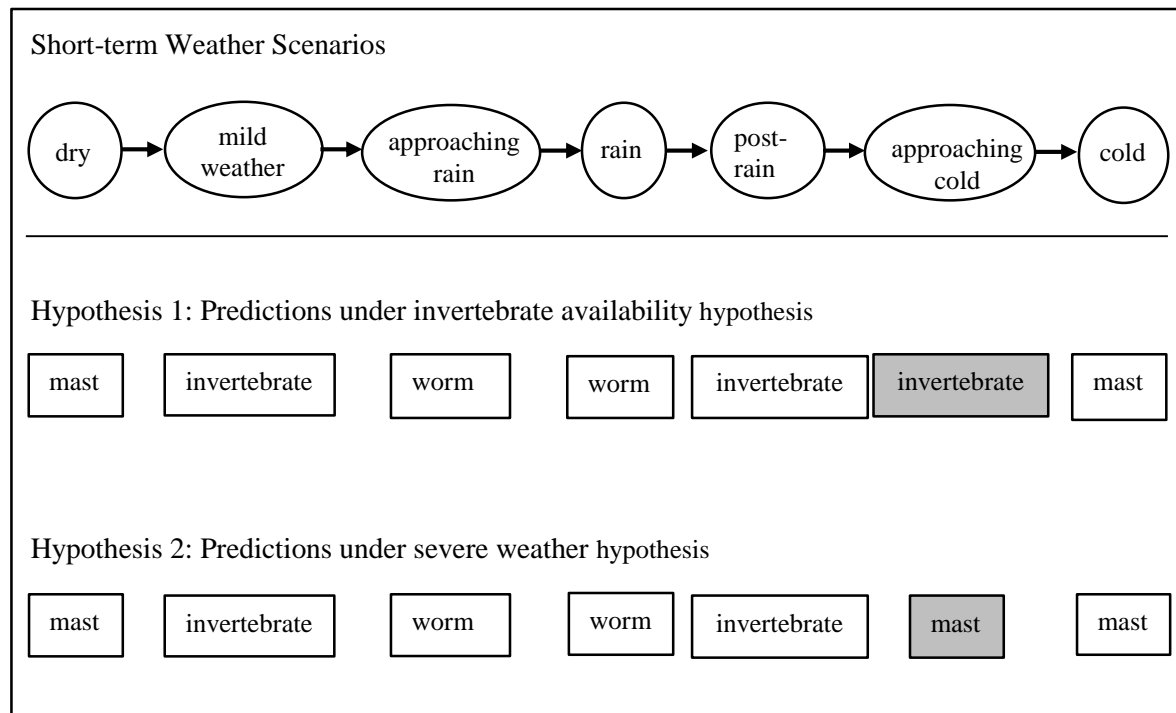
Charleston SC.

Figure 5.2. Predictions for predominate food source type (Mast, Worms, and other invertebrates [Troph]) predicted to be incorporated under prevailing short-term weather conditions into winter diet of Rusty Blackbirds in 2009 to 2012. The two hypotheses explaining whether blackbirds incorporate mast into diet because of low invertebrate availability (Hypothesis 1) or to prepare for extreme weather (Hypothesis 2) can only be differentiated with approaching cold weather. If the relationship between proportion of mast incorporated and approaching cold weather variable is positive, then Hypothesis 1 is supported. If there is no relationship, Hypothesis 2 is supported.
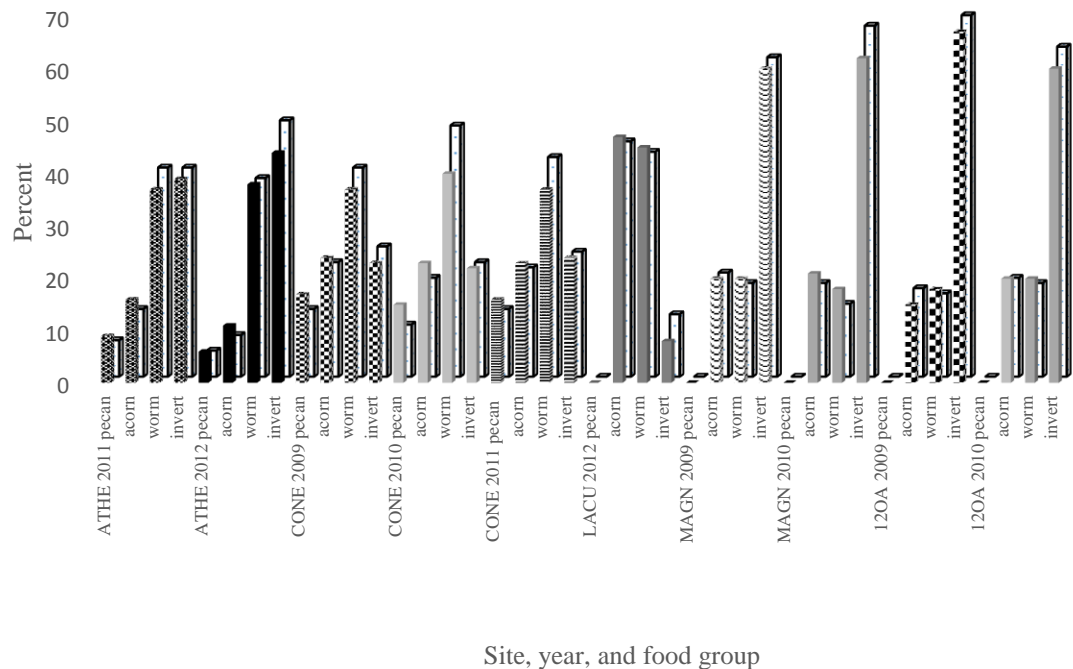
Figure 5.3. Average percent pecan, acorn, worm, and invertebrates from trophic level $\delta^{15}N$ 3‰, 6‰, and 9‰ (invert) in the short term diet (patterned bars) and medium-term diet (white bars) by site and year. ATHE = Athens, GA, CONE = Conestee, SC, LACU = Lake Cunningham, SC, MAGN = Magnolia Plantation, SC, and 12OA = Twelve Oaks residential Area, SC. Short-term diet is indicated from plasma and medium-term from RBC.
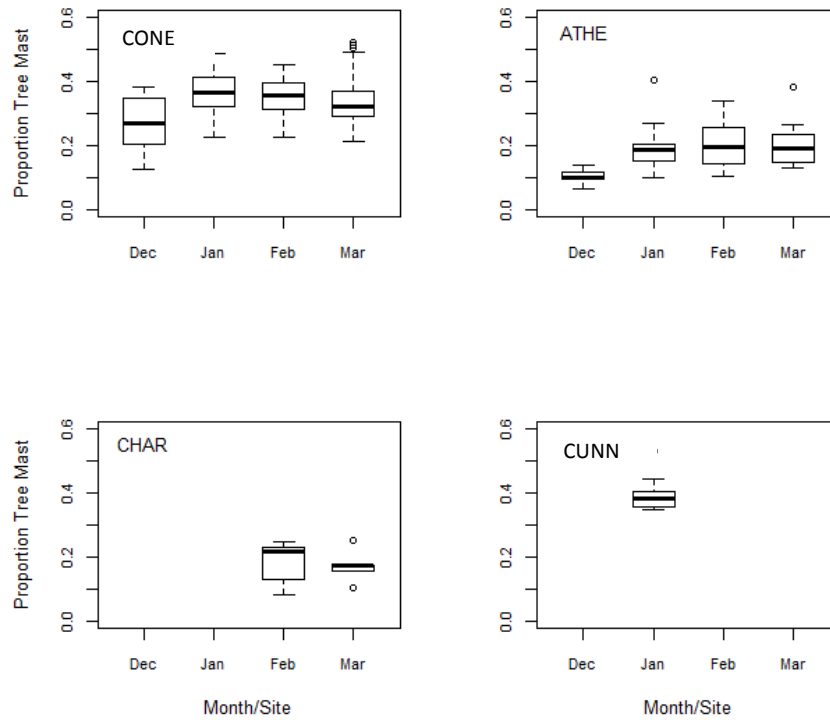
Figure 5.4. Box and whisker plot showing the variation in proportion of mast (acorn and pecan) estimated through plasma to be in the short-term diet in the previous 1 - 3 days of Rusty Blackbirds in four sites: CONE = Conestee, SC, ATHE = Athens, GA, CHAR = Charleston, SC, and CUNN = Lake Cunningham, SC.

Figure 5.5. Box and whisker plot showing the variation in proportion of tree mast (acorn and pecan) estimated through RBC to be in the diet in the previous month of Rusty Blackbirds in four sites; CONE = Conestee, SC, ATHE = Athens, GA, CHAR = Charleston, SC, and CUNN = Lake Cunningham, SC.
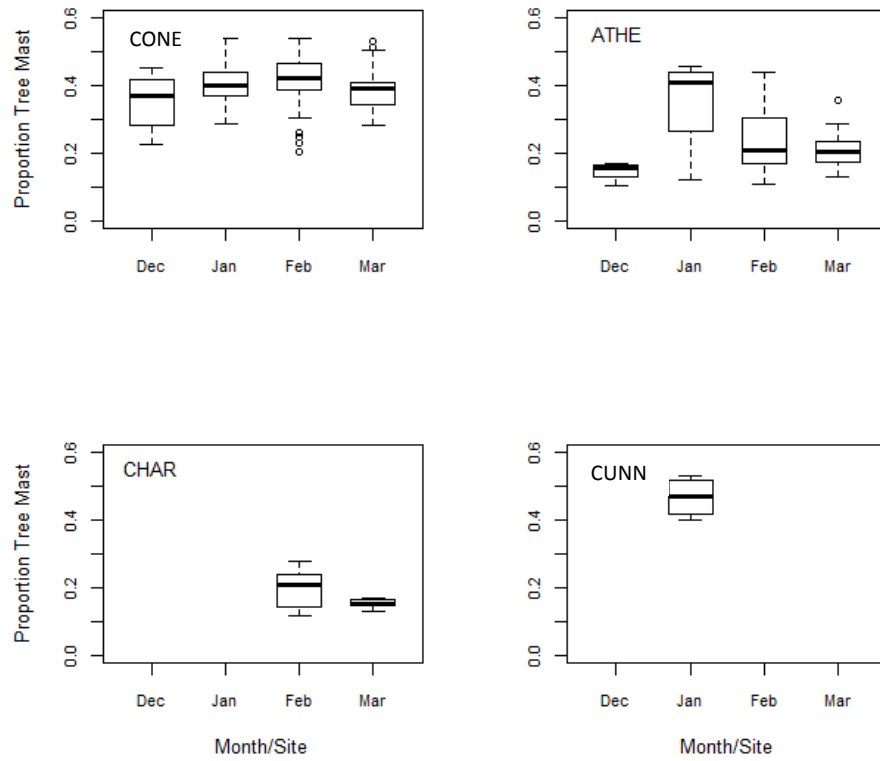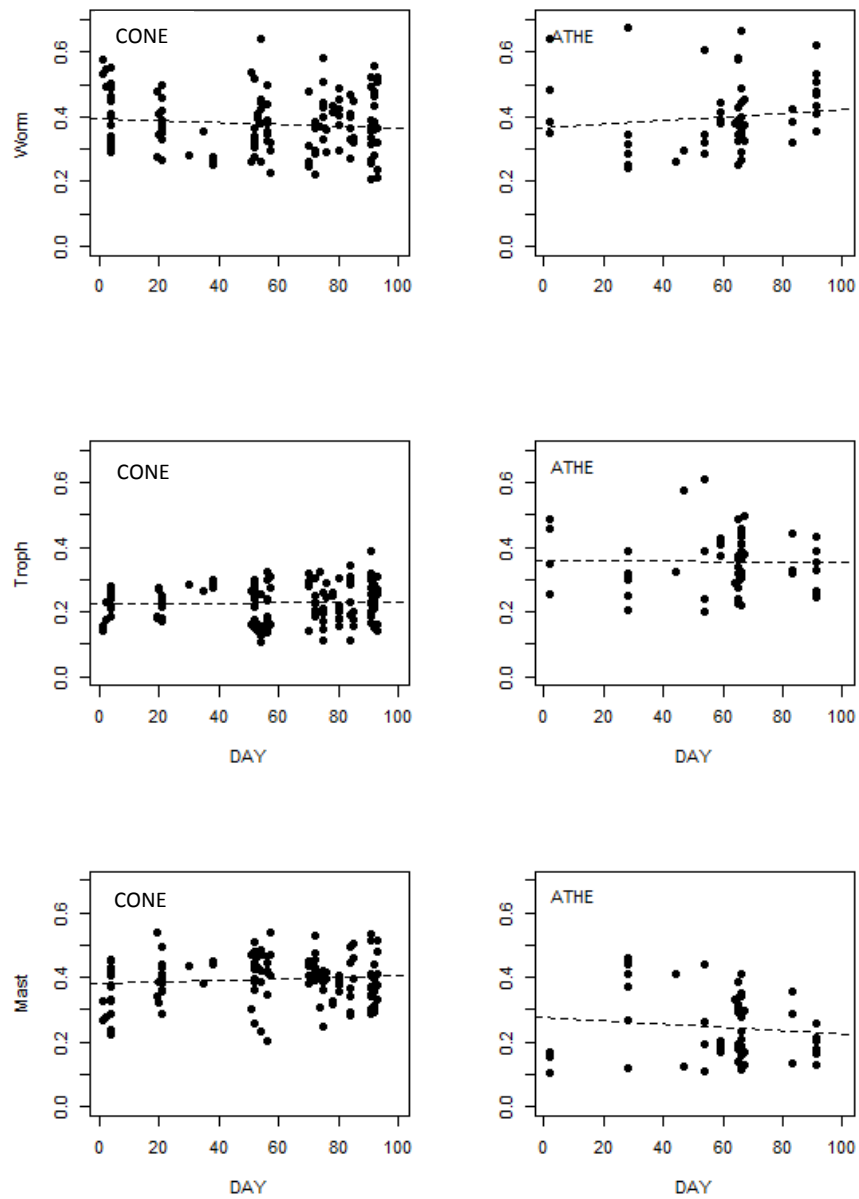
Figure 5.6. Proportion of Worm, Troph, and Mast in the individual diets of Rusty Blackbirds from December 16 to March 18 in Conestee, SC (CONE 2009-2011) and Athens, GA (ATHE 2011).

Figure 5.7. Proportion of tree mast incorporated in the diet by Rusty Blackbirds in the previous 1-3 days by the number of hours below -3°C in the following 48 hours from capture. Solid upper red line is plotted through data points from Athens, GA (2011) and the dashed lower black line is plotted through points from Conestee, SC (2009-2011).

Table 5.1. Variables used in GLM models to determine the relationship between short-term weather and proportion of food items incorporated in the short-term diet of Rusty Bla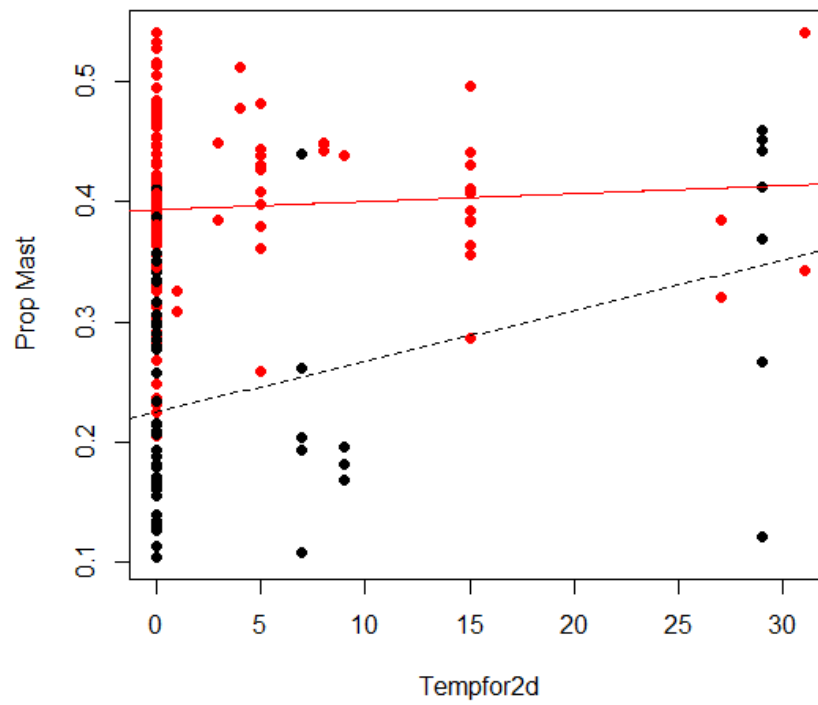ckbirds, from 2009 to 2012 in Georgia and South Carolina. Short-term temperature, precipitation, and barometric pressure, and day of year, and sex are included.

Variable	Description	Units
Dailymax	Maximum temperature of day of capture	°C
Dailymin	Minimum temperature the previous night of capture	°C
Prevdaymax	Maximum temperature of the previous day to capture	°C
Hrsnext2day<-3°C	Number hours in 48 hrs following capture <-3°C	hrs
Hrsprev3day<-3°C	Number hours in the previous 72 hrs <-3C	hrs
Hrsprev2day<-3°C	Number hours in the previous 48 hrs <-3C	hrs
Precipprev3day	Precipitation accumulation in 72 hrs before capture	mm
Precipnext2day	Precipitation accumulation in 48 hrs following capture	mm
Precipnext24hrs	Precipitation accumulation in 24 hrs following capture	mm
Barometric24hrs	Change in barometric pressure in 24 hrs before capture	cm
Barometric12hrs	Change in barometric pressure in 12 hrs before capture	cm
Precipmonth	Precipitation accumulation the month of capture	cm
Tempmonth	Average temperature the month of capture	°C
Sex	Male or female	
Day	Day of year	day

Table 5.2. Top models for Rusty Blackbird short-term diet proportions of Mast, Worms, and Troph (trophic positions $\delta^{15}N$ = 3‰, 6‰, and 9‰) in four sites (**SITE**) in Georgia and South Carolina. **Hrsnext2day<-3°C** = number of hours below -3°C in the following 48 hrs from capture, **Day** = day of year, **Barometric12hrs =** change in barometric pressure in previous 12 hrs from capture (cm), **Precipnext2day** = amount of precipitation in the following 48 hrs from capture (mm), **Precipprev3day** = precipitation in the previous 72 hrs before capture (mm), **Dailymax** = the maximum temperature (°C) the day and previous night of capture, **Dailymin** = minimum temperature the previous night of capture (°C), **Prevdaymax** = the previous day maximum temperature (°C), **Precipnext24hrs** = precipitation (mm) in the following 24 hrs from capture, and **Hrsprev3day<-3°C** = number hours in the previous 72 hrs <-3C. Models presented include the best-supported model (lowest AIC$_c$ value) and candidate models with w^i within 10% of the top model w^i or w^i >0.03. k = number of parameters, AIC$_c$ = Akaike information criterion adjusted for small sample sizes, and w^i = weight. Best model is highlighted.

Analysis	Candidate Models	k	AIC$_c$	ΔAIC$_c$	w^i
Proportion Mast	Hrsnext2day<-3°C+Day+SITE	7	51.91	0	0.25
	Hrsnext2day<-3°C+Sex+Day+SITE	8	52.86	0.95	0.15
	Hrsnext2day<-3°C+Barometric12hrs+Day+SITE	8	53.2	1.29	0.13
	Hrsnext2day<-3°C+Precipnext2day+Day+SITE	8	53.26	1.36	0.12
	Hrsnext2day<-3°C+Precipprev3day+Day+SITE	8	53.6	1.69	0.11
	Hrsnext2day<-3°C+Barometric12hrs+Sex+Day+SITE	9	54.14	2.23	0.08
	Hrsnext2day<-3°C+Precipprev3day+Sex+Day+SITE	9	54.72	2.81	0.06
	Null (Day+SITE)	6	61.15	9.24	0
Proportion Worms	Precipnext2day+Dailymax+Day+SITE	8	3.14	0	0.21
	Precipnext2day+Hrsnext2day<-3°C+Day+SITE	8	4.12	0.98	0.13
	Precipnext2day+Dailymin+Day+SITE	8	4.13	0.99	0.13
	Dailymax+Precipprev3day+Day+SITE	8	4.46	1.32	0.11

	Dailymax+Precipnext2day+Sex+Day+SITE	9	5.11	1.98	0.08
	Dailymax+Precipprev3day+Sex+Day+SITE	9	6.35	3.21	0.04
	Null (Day+SITE)	6	10.71	7.58	0
Proportion Troph	Precipnext24hrs+Day+SITE	7	31.54	0	0.14
	Precipnext2day+Day+SITE	7	32.29	0.76	0.1
	Null (Day+SITE)	6	32.76	1.22	0.08
	Dailymax+Precipnext2day+Day+SITE	8	33.16	1.62	0.06
	Hrsprev3day<-3°C+Day+SITE	7	33.18	1.64	0.06
	Prevdaymax+Day+SITE	7	33.54	2	0.05
	Dailymax+Day+SITE	7	33.88	2.34	0.04
	Hrsnext2day<-3°C +Precipnext2day+Day+SITE	8	34.15	2.61	0.04

Table 5.3. Model-averaged estimate, standard error (SE), and 85% lower (LCI) and upper confidence intervals (UCI) of variables important to Rusty Blackbird short-term diet in the Coastal Plain and Piedmont Plateau; **Day** = day of year, **Hrsnext2day<-3°C** is the number of hours in the following 48 hours from capture below -3°C, **Dailymax** is the daily maximum temperature in °C, and P**recipnext2day** = precipitation in the following 48 hours from capture. Estimates with confidence intervals that include zero are not included. **SITE** estimates are compared to ATHE (Athens, GA). CONE = Lake Conestee, SC, CHAR = Charleston, SC, and CUNN = Lake Cunningham, SC.

Analysis	Variable	Estimate	SE	LCI	UCI
Proportion Mast	Intercept	-1.73	0.09	-1.85	-1.6
	SITE(CONE)	0.57	0.04	0.51	0.63
	SITE (CHAR)	-0.21	0.07	-0.37	-0.11
	SITE (CUNN)	0.78	0.14	0.57	0.98
	log(Day)	0.05	0.02	0.03	0.08
	Hrsnext2day<-3°C	0.01	0	0.01	0.01
Proportion Worm	Intercept	-0.83	0.08	-0.94	-0.71
	SITE (CHAR)	-0.77	0.07	-0.86	-0.67
	log(Day)	-0.05	0.02	-0.08	-0.02
	Dailymax	0.01	0	0	0.01
	Precipnext2day	0.02	0.01	0.01	0.03
Proportion Troph	Intercept	-1.06	0.08	-1.17	-0.95
	SITE(CONE)	-0.45	0.04	-0.51	-0.39
	SITE (CHAR)	0.58	0.07	0.49	0.68
	SITE (CUNN)	-1.52	0.13	-1.71	-1.33

CHAPTER 6

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

I found wintering Rusty Blackbird flocks (*Euphagus carolinus*) on the Piedmont Plateau

and Atlantic Coastal Plain used varying patch types within suburban landscapes to meet

dietary requirements (Chapters 2, 3, and 5). Suburban blackbird flocks visited a matrix of

abandoned pecan (*Carya illinoinensis*) groves, forested wetlands, and residential areas at

various times throughout the day. The common theme throughout this dissertation is that

short-term weather variables are very important in shaping the way Rusty Blackbirds use

different patches in suburban landscapes during wintering. This species winters in the

unpredictable environment of the temperate zone, both in terms of temperature and

precipitation (Rogers 2005, Schulte-Hostedde et al. 2005, Budki and Kumar 2009). I

found support that Rusty Blackbirds incorporate tree mast into their winter diet largely to

compensate for periods of invertebrate shortages, but also to prepare for extreme winter

weather. The use of various patches in the landscape is predominately associated with

precipitation that affects the availability of invertebrates.

Patch-use in the landscape.–The Rusty Blackbird has been described as nomadic

(Mettke-Hofmann et al. 2008, Hamel and Ozdenerol 2009, Greenberg and Matsuoka

2010, DeLeon 2012) but my findings indicate this species just uses habitats within the

landscape at a relatively large scale. The telemetry study indicates Rusty Blackbirds

exhibit site fidelity throughout the winter in terms of the suburban landscape, but may

visit many different patch types throughout the day to acquire resources. Radiotelemetry

observations indicate Rusty Blackbird flocks spend a proportionately similar amount of

time in wetland and residential (including pecan groves) areas. This is an important consideration for the design of future studies. For although Rusty Blackbirds likely require wetlands in the suburban landscape, they are not wetland obligate species, and use the landscape at a much bigger scale than a wetland or group of wetlands.

Suburban landscapes, where the correct components are available (i.e., residential lawns, pecan groves, and wetlands), and in close proximity to each other, appear to provide the resources Rusty Blackbird flocks require for wintering. Since large flocks of Rusty Blackbirds occur in suburban mosaics, and there is no sign that traditional bottomland hardwood wetland habitat conversion will cease (Pinder and Funsch 1999, Nagy et al. 2009), managing Rusty Blackbirds in these landscape mosaics may be imperative. The important consideration for Rusty Blackbird suburban habitat management is that all habitat components are necessary to ensure consistent use of the mosaic. For example, providing a wetland patch without a pecan grove or orchard in close proximity will not be enough to support large flocks of Rusty Blackbirds. Shallow wetlands with small variation in topography should be <2km from pecan groves.

Residential lawns: worm component.–Residential lawns are sources of large, high-energy, non-native terrestrial earthworms (*Lumbricus* spp.), that constitute a large part of the invertebrates consumed by Rusty Blackbirds in suburban landscapes. There is overwhelming evidence Rusty Blackbirds forage increasingly on residential lawns with impending precipitation to take advantage of terrestrial non-native earthworms. Proportion of worms increase in the diet with future precipitation (Chapter 5) and blackbird flocks increasingly use residential areas with increasing future precipitation

(Chapter 2). Non-native earthworms are thus very important to manage through retention of leaf litter in suburban areas (James and Hendrix 2004).

Residential lawns: acorn component.–A common factor in all the residential areas I studied was large grassy areas were covered with leaf litter throughout the winter because residents refrained from using leaf blowers and rakes. Leaf litter in these neighborhoods was predominately from oak species (*Quercus* spp.). Blackbirds foraged extensively on acorns when the pecan source was no longer available. Although acorn mast is generally consumed by other animals rapidly in forested areas (Smallwood 2001, Smith and Scarlett 1987), in suburban areas, I found abundant acorn mast throughout the winter. To be used by Rusty Blackbirds, acorns must be pre-leached of tannins and broken open. I found gray squirrels (*Sciurus carolinensis*) and human vehicular traffic were important acorn mast facilitators for Rusty Blackbirds. Gray squirrels inefficiently forage on cached red-oak acorns throughout the winter providing opened acorns to other ground-foraging species. Based on my observations, other animals such as white-tailed deer (*Odocoileus virginianus*), Common Grackles (*Quiscalus quiscula*), and Blue Jays likely also serve the same function in residential areas.

Abandoned pecan groves.–Pecan groves provide blackbirds with mast resources for times when wetland invertebrates are inaccessible during inclement weather and to prepare for extreme weather. Abandoned pecan groves in our study sites included mature trees in residential areas, fallow orchards, and small abandoned farms. The groves can be very small, constituting as few as 40 mature, mast producing trees as in sites on the Piedmont Plateau. At all four landscape mosaics on the Piedmont Plateau, most pecan trees were on private lands and were at risk of removal or loss to development.

Nature parks, state lands, and other public lands could be targeted to protect current Rusty Blackbird hotspots by introducing a younger rotation of pecan trees. Current Rusty Blackbird hotspots without a pecan component could be supplemented with pecan trees. Strategically-placed trees, such as in the parking lots of nature parks, or on walking trails, would allow pecans to be crushed. As pecans are non-native in the range of the eastern population of Rusty Blackbird, e.g., Georgia and South Carolina (Santerre 1994, Worley 2002), this may pose problems for management in areas that target native species. However, since Rusty Blackbird primarily used pecans in upland areas fairly far from wetlands, this may not be problematic.

Wetlands: invertebrate component.–I report for the first time that a large proportion of Rusty Blackbird diet consists of terrestrial and aquatic worms, especially on the Piedmont Plateau. Wetlands support both small aquatic worms and the larger terrestrial non-native earthworms, in addition to other invertebrates such as Odonata and Diptera larvae. Blackbirds were more associated with wetlands after precipitation events likely because declining water levels are associated with increased availability of invertebrates (Fredrickson and Batema 1992, Batema et al. 2005). Since precipitation seems to be a major driver of Rusty Blackbird habitat use and invertebrate availability, manipulating water levels, as is done in well-managed Greentree reservoirs to facilitate drawing down of water resources, may help prolong the conditions blackbirds desire in wetlands (Fredrickson and Batema 1992, Batema et al. 2005). It is important to model water regulation after natural water fluctuations throughout the season to maximize the benefit to invertebrates and Rusty Blackbirds (Fredrickson and Batema 1992, Batema et al. 2005).

Wetlands: oak component.–In addition to invertebrates, acorn availability is important to manage in wetlands for Rusty Blackbirds, especially in the colder climates of the Piedmont Plateau. Blackbird consumption of tree mast occurs when invertebrates are unavailable due to cold weather. To be available for Rusty Blackbirds, the tough husks of acorns need to be opened by other animals such as gray squirrels, white-tailed deer, Common Grackles, and Blue Jays that also inhabitat forested wetlands in suburban areas. Water oak (*Quercus nigra*) was the primary red oak tree in our wetland sites. Providing an oak component in wetlands provides both acorn mast and preferred leaf litter for invertebrates.

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