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Sexual Dimorphism, Diet, and Body Condition  
of Rusty Blackbirds Wintering in Virginia

Andrew John McGann

York, PA

Bachelor of Science, Biology, Villanova University, 2007

A Thesis presented to the Graduate Faculty  
of the College of William and Mary in Candidacy for the Degree of  
Master of Science

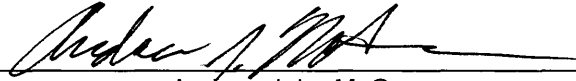
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## APPROVAL PAGE

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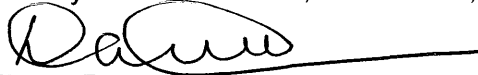
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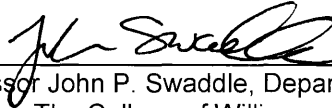
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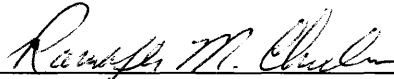
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## COMPLIANCE PAGE

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## ABSTRACT PAGE

The Rusty Blackbird (*Euphagus carolinus*) has suffered one of the most precipitous population declines of any songbird species in North America. For the period 1968-1998, the population declined by an estimated 88%. The species also exhibits a sexual size dimorphism, with males being approximately 15% larger than females by mass. Some other bird species that exhibit sexual size dimorphisms have been shown to exhibit niche segregation, whereby males and females exploit different diets, or forage in different areas. However, the ecological implications of the sexual size dimorphism in Rusty Blackbirds have gone unstudied. In order to develop a meaningful recovery plan for the species, more information on the species' winter diet and the potential fitness implications of different diets is crucial. I set out to further define the sexual size dimorphism in Rusty Blackbirds, and to test whether males and females consume different diets during the winter, by analyzing the stable isotope ratios of carbon and nitrogen in their blood. I detected no differences between the diets of male and female Rusty Blackbirds wintering in the vicinity of Williamsburg, Virginia. This indicates that management guidelines would not require separate recommendations for male and female segments of the wintering population. In spite of the lack of differences between the diets of the sexually dimorphic male and female Rusty Blackbirds, I hypothesized that diet varied on an individual basis relating to body size and/or bill size. To evaluate this, I quantified the putative contributions of bill size and body size to individual birds' trophic level. Bill size and body size both had extremely weak correlations with trophic level. Next, I hypothesized that individual variation in diet (trophic level and carbon source) correlated with body condition (a proxy for relative health). I found that individual birds that derived more energy from lower in the food web were also in better body condition, on average. Rusty Blackbirds are omnivorous in the winter, and previous natural history accounts, based on visual observations and the gut contents of a small number of dissected birds, have emphasized the role of small acorns in the diet. This study suggests that there is a relationship between body condition and the proportion of vegetative material in the diet. Future evaluations of winter habitat quality should specifically examine the importance of tree mast crops to the overwintering success of Rusty Blackbirds. Finally, methyl mercury toxicity is one of the suggested potential causes of the decline of the Rusty Blackbird population. For consumers in a food web, mercury concentrations can increase over time and with increasing trophic position. I examined the correlation between the diet of Rusty Blackbirds and the mercury concentration in their bloodstream. As expected the mercury levels corresponded with trophic level. However, concentrations were low when compared to populations of songbirds in areas with point sources of mercury pollution. This study suggests that future examinations of Rusty Blackbird winter habitat quality should test whether overwinter survivorship and fitness indicators are related to body condition and diet. Given the ostensibly high rates of reproductive success recently observed by others on the breeding grounds, research efforts should remain focused on the wintering grounds.

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## Introduction

The Rusty Blackbird (*Euphagus carolinus*) is a member of the avian family Icteridae that was once common in North America, but this species' population has declined by approximately 90% during the last four decades (Greenberg and Droege 1999, Greenberg and Matsuoka 2010). The Rusty Blackbird is an omnivorous, wetland-dependent and migratory songbird that breeds across the boreal forests of Canada and Alaska and winters exclusively in the southeastern United States (Avery 1995). The species has been widely regarded as common, but qualitative analysis of historical ornithological literature suggests a slow, chronic decline preceding the recent, acute decline (Greenberg and Droege 1999). The current decline prompted the formation, in 2005, of a group of concerned scientists and conservationists, called the International Rusty Blackbird Working Group (IRBWG) (Greenberg and Matsuoka 2010), to facilitate directed research and coordinate recovery efforts.

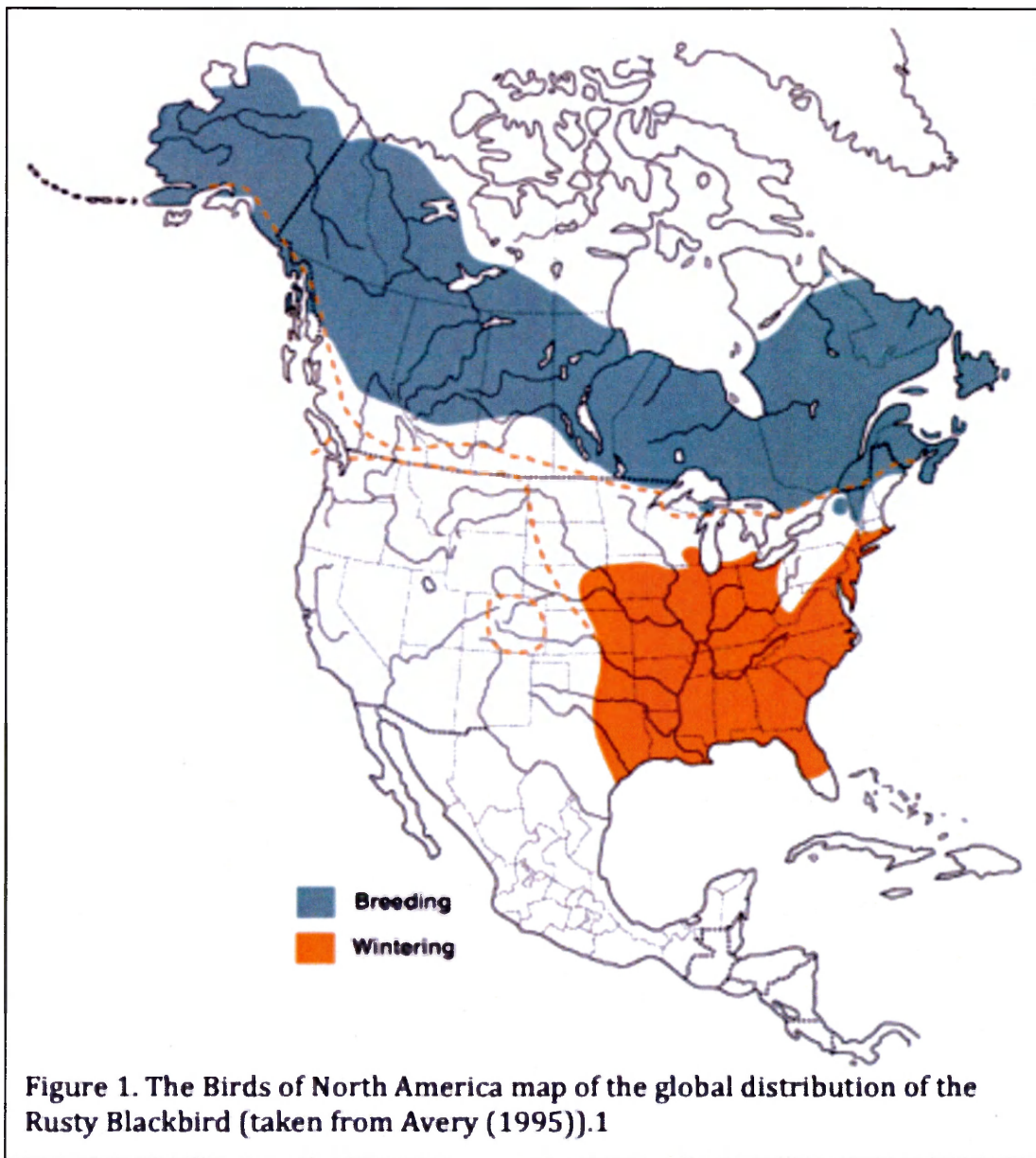
The Rusty Blackbird is an unusual member of its large taxonomic family, with only one other North American species exhibiting population declines recently, the Tricolored Blackbird (*Agelaius tricolor*) (Shuford and Gardali 2008). The avian family Icteridae also includes all of the other New World blackbirds, grackles, cowbirds, meadowlarks, and orioles (Avery 1995). The Rusty Blackbird

is one of two species in its genus, the other being the Brewer's Blackbird (*Euphagus cyanocephalus*), which is abundant and widespread in western North America, including in habitats heavily impacted by humans. The genus *Euphagus* may be more closely related to the grackles (*Quiscalus* spp.) than to the more similarly-sized *Agelaius* blackbirds, such as Red-winged Blackbird (*Agelaius phoeniceus*), with which they can sometimes be found (Lanyon 1994, Lanyon and Olmland 1999). The Icteridae are restricted to the New World, and most of the species in the family are distributed in the tropics (Jaramillo 2009).

The Rusty Blackbird has been studied very little until recently, and in fact its dramatic population decline remains the most well known aspect of its ecology (Greenberg et al. 2011). Much information is needed in order to direct an effort to stem the population loss through a recovery plan. Research and monitoring are needed in the following three critical areas: (1) basic ecology and natural history; (2) the effects of putative causes of decline; and (3) the most efficacious survey techniques and monitoring program (Greenberg and Droege 1999, Greenberg and Matsuoka 2010, Greenberg et al. 2011).

## ***Natural History of Rusty Blackbirds***

The Rusty Blackbird breeds across the vast boreal forests of Canada, barely extending into the northeastern United States, from the Atlantic provinces of Canada westward through most of Alaska (Fig. 1, image from Avery (1995)). The species entirely vacates its breeding range and migrates to the southeastern United States for the winter (Avery 1995). Although both the breeding and wintering ranges, respectively, are illustrated as contiguous areas on the cited map (Fig. 1), there is evidence of two separate concentrations of winter distribution: the lower Mississippi alluvial valley, and the southeastern coastal plain (Hamel and Ozdenerol 2008). The Appalachian Mountains separate the two wintering regions. Furthermore, a recent population connectivity analysis, for which the study described here contributed samples, used stable isotopes of carbon and hydrogen in feathers to link wintering Rusty Blackbirds from east and west of the Appalachian mountains, to corresponding eastern and western portions of the breeding range, respectively (Hobson et al. 2010). Rusty Blackbirds wintering in the lower Mississippi alluvial valley possessed isotope ratios that indicated origins from Alaska to central Canada during the breeding season, while Rusty Blackbirds wintering in the southeastern Atlantic coastal plain possessed stable isotope ratios that reflected origins in eastern Canada, principally Ontario and Quebec (Hobson et al. 2010).



On the wintering grounds, Rusty Blackbirds typically occur in flocks (Avery 1995). They forage both in single-species and mixed flocks with other blackbirds and American Robins (*Turdus migratorius*). Rusty Blackbirds forage in two ways, but the most commonly observed mode is walking on the ground. They also exhibit arboreal

foraging on pine seeds, fruits, and nuts in the canopy. Like other flocking species of blackbirds, groups will fly significant distances to reach multiple foraging sites during the course of a day (Avery 1995, Yasukawa and Searcy 1995). As night approaches, flocks settle into communal roosts, where they sleep for the night, typically in low vegetation such as regenerating clearcuts or marshy habitats (Avery 1995).

Undergraduate student Jacob Armiger conducted the preliminary observations and netting/banding of Rusty Blackbirds foraging on the campus of the College of William and Mary in March and April of 2008. He observed that the sex ratio of these foraging flocks was heavily male-biased. If there is not a sex ratio bias from the capturing technique, such a biased sex ratio could be the result of a sex-ratio bias in the overall population, or it could indicate that males and females segregate either by habitat or latitude during the non-breeding season, as has been observed in Red-winged Blackbirds (*Agelaius phoeniceus*) (Yasukawa and Searcy 1995).

Segregation by latitude is a pattern called differential migration, where different age and/or sex classes of a population segregate across the wintering range due to different average southward migration distances. In the review by Cristol et al. (1999), one of the three hypotheses to explain differential migration is that competition for food and other wintering resources drives the less dominant

individuals in the population farther than the more dominant individuals. Another hypothesis is the body-size hypothesis, where the physically smaller-bodied segments of the population are less able to survive periods of fasting during difficult weather conditions and thus migrate to more temperate latitudes than the physically larger-bodied segments of the population. The last hypothesis is the arrival-time hypothesis, where a segment of the population migrates a shorter distance so they can arrive sooner on the breeding grounds after spring migration. Red-winged Blackbirds are known to migrate at different times, in single-species flocks, with males moving earlier in spring and later in fall (Yasukawa and Searcy 1995).

In a continent-wide analysis of recoveries of marked birds, Dolbeer (1982) found that Red-winged Blackbirds and Common Grackles exhibited patterns of differential migration by age and sex classes, with females migrating longer distances and wintering farther south than males. Additionally, for both Red-winged Blackbirds and Common Grackles, young of the year (birds migrating for the first time after having hatched the previous summer) migrated longer distances and wintered farther south than adult birds. These continental patterns of differential migration by sex and age class were not found in the Brown-headed Cowbird (*Molothrus ater*). The European Starling (*Sturnus vulgaris*) exhibited a continent-wide pattern of differential migration by age class, but not by sex. The European Starling is not a

member of the Icteridae, yet it shares many behavioral similarities with the blackbirds and often joins large flocks and roosts with them.

Recoveries of marked birds on a region-by-region basis indicated geographic variation in the patterns of differential migration (Dolbeer 1982). Red-winged Blackbirds exhibited significant differences in migration distance for both sex classes and age classes across all the sampled regions of eastern North America. In contrast, Common Grackles exhibited significant differences in the migration distances of sex and age classes only in the Midwest (although when the regions were aggregated, the continent-wide differences were statistically significant). European Starlings exhibited significant patterns of differential migration by age class, but not by sex, in the Great Lakes and the Midwest regions. Again, the overall continent-wide pattern was significant when the regions were aggregated. Due to the restrictions of sample size and the coarse-grained nature of bird banding data, analyses like those by Dolbeer (1982) do not necessarily get to the heart of differential migration, and whether some birds (e.g. males, females, juveniles, adults) from a particular breeding location will migrate farther than others on average. However, differential migration is clearly a pattern exhibited by some members of the Icteridae.

There is no published information on wintering distributions of each sex of Rusty Blackbird. Because of the initial observations of the



disproportionately low number of females in the campus flocks, I attempted to replicate the methods employed by Dolbeer (1982) and others (Jenkins and Cristol 2002) to determine if this species exhibits differential migration like some other blackbirds. However, the paucity of bird-banding records for Rusty Blackbirds precluded any robust analysis of this nature. In the fall of 2008, I queried all records of Rusty Blackbirds in the U.S. Geological Survey's Bird Banding Laboratory (Patuxent, MD) database. I excluded all records outside of the narrow overwintering period from January 15 to March 15, in order to filter out breeding and migrating birds. I separated records into the Atlantic, Mississippi, and Central flyways, longitudinally. The Central flyway was dropped from the analysis because it lacked a credible sample size (total n=28). The remaining records were collated by degree of latitude, for each flyway, and the number of males, female, and unknown sex records were tallied for each degree of latitude. The final sex ratio scores were expressed as the percent of the known-sex birds that were male (Table 1). The expected pattern (a decreasing proportion of males to females with decreasing latitude) was not supported by the data in the Atlantic flyway, however, a much higher percentage of the known-sex birds were female at 32° in the Central flyway, with a relatively large sample of known-sex birds (n=150). However, my analysis based on sex-ratio data provided by

the BBL did not provide strong evidence for a pattern of differential migration by sex.

**Table 1.** Differential migration analysis: BBL records by latitude and flyway

| Atlantic Flyway    | Latitude | # ♂ | # ♀ | # unk | Total | % ♂  |
|--------------------|----------|-----|-----|-------|-------|------|
|                    | 40°      | 108 | 7   | 6     | 121   | 0.94 |
|                    | 39°      | 33  | 8   | 95    | 136   | 0.80 |
|                    | 38°      | 6   | 3   | 3     | 12    | 0.67 |
|                    | 37°      | 2   | 1   | 5     | 8     | 0.67 |
|                    | 36°      | 0   | 0   | 0     | 0     | NA   |
|                    | 35°      | 14  | 3   | 8     | 25    | 0.82 |
|                    | 34°      | 28  | 5   | 1     | 34    | 0.85 |
|                    | 33°      | 0   | 0   | 0     | 0     | NA   |
| 32°                | 67       | 24  | 3   | 94    | 0.74  |      |
| Mississippi Flyway | Latitude | # ♂ | # ♀ | # unk | Total | % ♂  |
|                    | 40°      | 25  | 19  | 23    | 67    | 0.57 |
|                    | 39°      | 12  | 5   | 2     | 19    | 0.71 |
|                    | 38°      | 3   | 0   | 17    | 20    | 1.00 |
|                    | 37°      | 2   | 0   | 1     | 3     | 1.00 |
|                    | 36°      | 45  | 33  | 81    | 159   | 0.58 |
|                    | 35°      | 47  | 12  | 87    | 146   | 0.80 |
|                    | 34°      | 5   | 7   | 0     | 12    | 0.42 |
|                    | 33°      | 80  | 60  | 7     | 147   | 0.57 |
| 32°                | 48       | 102 | 345 | 495   | 0.32  |      |

In the field study described here, the sex ratio was likewise measured by the number of captures via mist net, and was heavily male-biased in each year of the study (Table 2). The study described here lies on the northern end of the Rusty Blackbird wintering range, where the sex ratio would be expected to be more male-biased if the species exhibits differential migration by sex. This is because all three

hypotheses for differential migration predict females migrating farther south in most songbird species (Cristol et al 1999). Anecdotal reports reflecting both banding records and casual visual observations of blackbird flocks in the areas where mist-netting was taking place, by other Rusty Blackbird researchers from Georgia and South Carolina, seemed to support the idea that the sex ratio was more female-biased farther south. However, there are no published accounts of the wintering distribution of age or sex classes of Rusty Blackbirds.

**Table 2.** Sex ratio of Rusty Blackbirds captured in 2008, 2009, 2010.

| <b>Season</b> | <b>Male</b> | <b>Female</b> | <b>Unknown</b> | <b>Total</b> | <b>% Male</b> |
|---------------|-------------|---------------|----------------|--------------|---------------|
| 2007-08       | 25          | 15            | 1              | 41           | 63%           |
| 2008-09       | 48          | 20            | 0              | 68           | 71%           |
| 2009-10       | 27          | 12            | 0              | 39           | 69%           |
| Total         | 100         | 47            | 1              | 148          | 68%           |

While there is no clear evidence that Rusty Blackbirds have latitudinal segregation in winter through differential migration, the informal reports of sex-ratio biases at northern and southern extremes of the wintering range suggest that this possibility should be tested with additional data from future standardized surveys. There is another potential explanation for the sex-bias observed on campus, and that is habitat segregation by sex. Perhaps females are using some other habitat, such as agricultural fields, while males prefer forested wetlands like those found on campus. Rusty Blackbirds are opportunistic in their food habits. They eat plant and animal matter

year-round, though Avery (1995) suggests that plant matter is relatively more prevalent in winter and animal prey is relatively more prevalent during the warmer months. The microhabitat where foraging takes place is primarily on the ground, especially along streams or the borders of ponds or wetlands. Rusty Blackbirds forage in shallowly submerged areas, where their feet will be wet, but their feathers remain dry. Like other members of the Icteridae, Rusty Blackbirds have an unusual muscle arrangement around their jaws that allows them to probe their closed bill into soft sediment and expand it, a behavior known as “gaping” (Beecher 1951). However, when compared to the other blackbirds studied by Beecher (1951), Rusty Blackbirds have the thinnest bills, which that author asserted makes them the most adept at catching insects, and the least adept at processing hard seeds and nuts. In the winter, foraging may also occur in upland fields and agricultural feedlots. Within the breeding range in Canada and Alaska, some birds also forage at landfills with gulls (*Larus* spp.), especially during the post-breeding dispersal phase, following the conclusion of breeding activities in late summer into early autumn (Avery 1995).

In winter, Rusty Blackbirds utilize swamps, wooded wetlands, cypress lagoons, the margins of ponds and streams, and open fields adjacent to wetlands (Avery 1995). In the breeding season, Rusty Blackbirds nest around wet openings in the boreal forest such as fens,

alder and willow bogs, muskegs, beaver ponds, and lakeshores (Avery 1995). In migration, birds sometimes forage in uplands like agricultural fields, but they also forage in wetland habitats like those described above. The Rusty Blackbird is associated with wetlands year-round (e.g. Avery 1995, Hamel et al. 2008, Powell et al. 2010a, 2010b, Greenberg et al. 2011).

### ***Sexual Size Dimorphism and Niche Differentiation***

Rusty Blackbirds exhibit sexual dimorphism by both size and plumage color (Avery 1995). Males average approximately 16.5% larger than females by mass. Mean male mass is 64.3g (range = 45.9–80.4g, n = 91) and mean female mass is 55.2g (range = 47.0–76.5g, n = 105) (Dunning 1984), included in Avery (1995). The sexes are distinguishable by plumage, with males being generally blacker and females being generally browner or grayer.

Sexual size dimorphism generally results from different size optima between the sexes, which arise by natural selection and/or sexual selection (Price 1984). However, sexual size dimorphism by itself does not necessarily translate to intersexual niche differentiation (Stein et al. 2008). On top of a size dimorphism, intersexual competition for food can drive niche differentiation by disruptive selection for differences in bill morphology (Price 1984, Stein et al.

2008). Rusty Blackbirds exhibit a sexual size dimorphism, but there are no definitive studies that have analyzed bill size. Meanley (1967) assessed bill size and detected a dimorphism (male avg. = 19.6mm, range 18.5 – 21.5mm; female avg. = 18.2mm, range 17.5 – 19.0mm), but his sample size was extremely small (n = 7 males, 3 females), and thus it is impossible to draw any conclusions.

One way of detecting intersexual niche differentiation is by quantifying differential foraging behavior, including habitat use. Many species that forage on tree trunks exhibit sexual microhabitat segregation. For example, Eurasian Treecreepers (*Certhia familiaris*) divide their territories spatially during the breeding season, with males foraging on the lower parts of the tree trunks and females foraging on upper parts of the tree trunks (Aho et al. 1997). Willow Tits (*Parus montanus*) exhibit horizontal tree-habitat segregation, with adults foraging more than juveniles on interior parts of trees (Alabau 1999). Crested Shrike-Tits (*Falcunculus frontatus*) in Australia divide foraging resources with females spending more time on leaves and petioles and males spending more time on dead branches and large coiled ribbons of peeling bark (Noske 2003). In bats, two recently-identified cryptic species of *Pipistrellus* (*P. pygmaeus* and *P. pipistrellus*) exhibit habitat segregation with the former foraging over water and along riparian corridors, and the latter foraging along isolated tree-lines and upland woodland edges (Nicholls and Racey 2006). Western Sandpipers

(*Calidris mauri*) are a sexually dimorphic species that has been shown to exhibit niche differentiation via divergent bill lengths (Stein et al. 2008). That species also exhibits a pattern of differential migration, but specifically testing whether differential migration indeed represent a kind of large-scale geographical intersexual niche differentiation within a species is difficult (Stein et al. 2008).

A relatively new method for describing niche differentiation by diet is the analysis of the ratios of the so-called stable (as opposed to radioactive) isotopes of elements, primarily carbon and nitrogen. Because the heavy isotope of nitrogen is enriched in consumers in a food chain, relative to the protein in their diet, which comes from organisms lower in the food web, the ratio of the heavy isotope to the typical isotope reflects the trophic position of the species (Post 2002). The ratio of carbon isotopes does not change as energy and mass move up through a food web, and thus, it reflects the provenance of the carbon in the food web, indicating whether it was fixed from the atmosphere by the C3 and / or C4 photosynthesis pathways (Post 2002). Different body tissues integrate the chemical signatures of the diet over different lengths of time, with blood being one of the most responsive indices (Mizutani et al. 1992; Bearhop et al. 2002; Olive et al. 2003; Carleton and del Rio 2005; Tsahar et al. 2008). Stable isotope ratios have been used to identify sexual differences in diets within species (Przybylo 1995; Przybylo and Merila 2000; Forero et al. 2005;

Awkerman et al. 2007). Stable isotope ratio analysis can also be used to estimate the timing of shifts in diet (Bearhop et al. 2002; Phillips and Eldridge 2006; Perez et al. 2008). Because relatively little is known about even basic aspects of the Rusty Blackbird's ecology, stable isotope analysis of carbon and nitrogen could reveal new information about diets during winter. I used it as a test of the hypothesis that males and females are eating at different positions in the food chain (e.g. acorns versus insects) and/or sit atop food chains with different initial carbon sources (e.g. wetland plants versus oak trees). If males and females have niche differentiation, and thus are utilizing different food resources, we would have a better ability to understand the drastic decline in this species and would have reasons for predicting the importance of differential environmental pressures. Future management recommendations could potentially cater to each sex specifically.

### ***What is known about the Decline***

The two empirical measures of the recent acute decline of the Rusty Blackbird are the Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC) surveys. The BBS is comprised of annually repeated, randomly placed point-count surveys in routes along roadsides in North America. Three-minute counts of all birds are conducted during the breeding season at half-mile intervals along a route (Greenberg and



Droege 1999, Greenberg and Matsuoka 2010, Greenberg et al. 2011). Unfortunately, although there are roughly 3,000 BBS survey routes across North America, the coverage of the Rusty Blackbird's breeding range is poor. Only 83 BBS routes have detected Rusty Blackbirds to the extent that they could be utilized in the trend analyses by Greenberg and Droege (1999). BBS data for the period 1966-1996 showed a decline of 92.8% ( $p \leq 0.1$ , 95% CI = -99.7, +38.8) (Greenberg and Droege 1999). That rate equates to an average yearly rate of 12.5%, but it should be noted that because most of the breeding range of this species is roadless, these results are not representative of the whole population. While the large range in confidence interval around the trend estimate leaves room for the possibility that the Rusty Blackbird population is in fact increasing, data from the more extensive Christmas Bird Count survey corroborates the population decline.

Christmas Bird Counts are area-search surveys of fixed 15-mile diameter circles, conducted by volunteers over the three-week Christmas and New Year holiday periods. The surveys are non-randomly distributed, and conducted by an unregulated mix of amateur birdwatchers and professional biologists (Greenberg and Droege 1999). However, what the CBCs lack in sampling regime rigor, they make up in sample size and effort, with coverage across the entire Rusty Blackbird wintering range. In the analysis by Greenberg and Droege (1999), Rusty Blackbirds were reported in 1201 CBC surveys.

CBC data for the period 1958-1988 showed a decline of 89.6% ( $p \leq 0.01$ , 95% CI = -98.8, -55.1) (Greenberg and Droege 1999, Greenberg et al. 2011).

Lacking quantitative data prior to the development of the two aforementioned monitoring schemes, Greenberg and Droege (1999) conducted a qualitative analysis of historical trends in Rusty Blackbird abundance. Published accounts of regional avifauna and annotated checklists containing historical information on Rusty Blackbird relative abundance were analyzed by assigning the following ordinal rankings to standard adjectives used to describe abundance: 1) uncommon; 2) fairly or locally common; 3) common; and 4) very common/abundant. The account publication data ranged from 1877 to 1997, and were broken up into four time periods for analysis (<1920, 1920-1950, 1950-1980, >1980). All combinations of comparisons between time periods indicated declines in status. Furthermore, Greenberg and Droege (1999) detected an increasing rate of decline over time.

### ***Proposed Causes of Decline***

#### **Breeding Grounds**

Globally, one of the biggest threats to bird populations everywhere is habitat loss, either through direct conversion to other land use, or through degradation of specific resources within a habitat (Wells 2011). While many natural disturbance patterns alter habitats

and landscapes, such as fire, windstorms, floods, and volcanic eruptions, these forces have been ever-present over the timeframe in which Rusty Blackbirds have been evolving. The timeframe of the species' decline, both the long-term decline and the more recent precipitous crash, suggests that anthropogenic causes should be investigated first. The species is now absent in a number of areas of the Canadian boreal forest where it was formerly known as a common breeder (Greenberg et al. 2011). This includes northern Alberta and Saskatchewan, the Northwest Territories, and northern Ontario (Machtans et al. 2007, Greenberg et al. 2011). The BBS routes, which primarily sample the southern extreme of the Rusty Blackbird breeding population, have suggested that the sharpest rates of decline lie within the eastern and central portion of the boreal zone, although the rates of decline have been quite variable, and the BBS program is not particularly efficacious in monitoring Rusty Blackbirds.

Certain industrial activities, such as peat production, logging, natural gas and oil extraction, and the construction of water reservoirs account for direct losses of boreal wetlands, as well as increased fragmentation of the remaining forests (Greenberg and Matsuoka 2010, Greenberg et al. 2011, Wells 2011). Additionally, these anthropogenic actions can alter the hydrology of an area. Furthermore, anthropogenic climate change is implicated in large-scale changes to the boreal zone. The areal extent of wetlands is contracting, and changes to the water

chemistry are altering the structure of the invertebrate communities (Schindler 1988, 1998). Global warming may be altering natural fire regimes as well, although the result may be less frequent fires in some areas, and more frequent fires in other areas (e.g. Flannigan et al. 1998, Bergeron et al. 2004). It is not clear whether Rusty Blackbirds would benefit or be hurt by either increased or decreased wildfire frequencies around their nesting areas, but the changes to the fire regime may be reflecting broad ecosystem changes that have other direct impacts on the Rusty Blackbird lifecycle. Other species that nest with Rusty Blackbirds in boreal wetlands are also showing alarming rates of decline. Lesser Yellowlegs (*Tringa flavipes*), Solitary Sandpipers (*T. solitaria*), Horned Grebe (*Podiceps auritus*), Lesser Scaup (*Athya affinis*), White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*), are known to be exhibiting declines from both BBS data and waterfowl surveys (Austin et al. 2000, North American Waterfowl Management Plan 2004, US Fish and Wildlife Service 2004).

In the southeastern extreme of the Rusty Blackbird breeding range, Powell et al. (2010c) found that Rusty Blackbird nests placed in regenerating clear-cuts suffered higher rates of predation than nests in unaltered wetlands. Rusty Blackbirds appeared to have an equal preference for the short, dense spruces and firs of upland sites regenerating after logging, which ostensibly resemble the stunted spruces and firs of wetland habitats. However, Rusty Blackbirds

nesting in the logged uplands suffered higher rates of nest failure, with significantly higher rates of depredation than nests located in unaltered wetlands. Thus, Powell et al. (2010c) found that the Rusty Blackbirds nesting in Maine were subject to an “ecological trap”, as birds did not prefer (as measured by inter-year rates of return) the more productive nesting sites (Powell et al. 2010b) also observed some Rusty Blackbirds in Maine nesting solitarily, while others were clustered in “loose colonies.” The home ranges of adult Rusty Blackbirds were large during the nesting season, as the adults gathered food from multiple disconnected wetlands (Powell et al. 2010a); the home ranges of adult Rusty Blackbirds nesting in the loose colonies were even larger than those nesting solitarily (Powell et al. 2010b). In comparison, other species of Icterids that have been studied have shown smaller home ranges in the nesting phase of their lifecycle. However, Powell observed relatively high levels of nest success, estimating that 61% (n=40) of all observed nests fledge young. Nests in unaltered wetland habitats were especially successful, with 71% of nests fledging young, as compared to only 33% of nests (n=30) located in regenerating upland clearcuts. Even so, the overall nest success rate did not appear to be so chronically low as to hinder population growth.

A similarly high level of productivity was found by Matsuoka et al. (2010b), for Rusty Blackbirds nesting in Alaska. Rusty Blackbirds

nesting in spruce exhibited high rates of nest success (79% of nests fledging young), and nests placed in deciduous vegetation were somewhat less successful (52% of nests fledging young). The pattern of spruce versus deciduous nesting sites varied geographically in Alaska, with willows (*Salix* spp.) dominating the vegetation near water in interior Alaska, where they were used most frequently for nest sites. Overall, nest success rates in Alaska averaged 56%, and were similar to rates observed by Powell et al. (2010c) in New England, and were notably higher than those found in studies of other North American blackbirds (30-39%). Matsuoka et al. (2010a) suggest that survival rates of adults or juveniles might be more limiting to population growth.

### **Wintering Grounds**

Habitat loss and degradation are also potential causes of the decline on the Rusty Blackbirds' wintering grounds in the southeastern United States. Most of the habitat loss for this species has been due to conversion of the bottomland hardwood forests to agricultural land uses, with about 80% of the historic total being converted since European colonization of the U.S. (Hefner and Brown 1984, Hefner et al. 1994). More recently, bottomland hardwood forest communities have been converted to pine plantations and urban areas. Over time, the loss of bottomland hardwoods has progressed from drier to wetter sites, such that more recent habitat losses might have been increasingly

detrimental to Rusty Blackbird populations (Greenberg et al. 2011). Habitat fragmentation is a correlate of the conversion of the bottomland hardwoods forests to other land uses. When patches of bottomland hardwood forest shrink, there is an attendant increase in the percentage of the remaining forests that are subject to edge effects (Wells 2011). Such changes might be exposing Rusty Blackbirds to increased predation from *Accipiter* hawks, like Cooper's Hawk (Greenberg et al. 2011).

One of the problems of working with Rusty Blackbirds, in both the breeding season and the winter is simply detecting their presence. Especially in the wintertime, they are not especially vocal, and they may be overlooked deep in wooded swamps difficult of access. In order to study the species, they must first be located. To begin the process of defining putative Rusty Blackbird habitat across the winter range, Lusnier et al. (2010) first established a wintertime survey protocol for modeling occupancy with presence/absence surveys. On the breeding grounds, (Matsuoka et al. 2010a) developed survey methods for estimating the abundance of Rusty Blackbirds in nesting areas on Department of Defense properties in Alaska. Rusty Blackbirds are most detectable near their nests, and early in the breeding season when males sing the most and conspicuously follow females (Matsuoka et al. 2010a).

One potential implication of habitat loss and/or degradation, might be that Rusty Blackbirds are forced to forage more in open habitats, which may subject them to direct competition with other blackbird species such as Common Grackles and Red-winged Blackbirds. It might also be the case that the smaller, and potentially socially-subordinate female Rusty Blackbirds would suffer more from increased interspecific competition (Greenberg et al. 2011).

Another potential threat is the environmental toxicant methyl mercury (Driscoll et al. 2007). Rusty Blackbirds might be particularly at risk of mercury toxicity given their affinity for wetlands and highly predaceous diet. Wildlife ingests mercury through their diet, and the impacts of mercury on wildlife populations have been documented in food webs in a number of ecosystems (e.g. Spalding et al. 2000, Evers et al. 2005, Rimmer et al. 2005, Shriver et al. 2006, Custer et al. 2006, Jackson et al. 2011a, 2011b, Cristol et al. 2011). Furthermore, a dosing study (Heinz et al. 2008) under laboratory conditions has indicated that the embryos of a another blackbird species, the Common Grackle (*Quiscalus quiscula*), might be among the more sensitive avian species to mercury toxicity. Current aviary studies are beginning to elucidate potential mechanisms for sublethal physiological and behavioral effects of mercury toxicity in songbirds (Lemelin 2011, D. Cristol, personal communication). In food webs, the mercury content of some invertebrate animal prey is composed of high proportions of the toxic



bioavailable form, methyl mercury (Brasso and Cristol 2008, Cristol et al. 2008). Consequently, mercury can accumulate in the bodies of animals over their lifetime (bioaccumulation) and concentrations can increase with increasing position in the food chain (biomagnification). Thus a species' mercury exposure risk depends on that species' diet and foraging ecology. One of the objectives of this thesis was to measure the level of mercury in the blood (and hence the recent diet) of Rusty Blackbirds wintering on the William & Mary campus to evaluate whether this trace metal might be posing a threat to overwinter survival in this species. The question of differential mercury concentrations by sex may be especially pertinent for understanding survival and reproductive success, given that females can transfer their mercury burdens to their offspring during the egg formation process. Mercury has effects on reproductive output and survival in other songbird species (e.g. Brasso and Cristol 2008, Jackson et al. 2011a), and thus could have implications for population-level effects in the Rusty Blackbird.

Disease is another potential cause of the decline. The role of disease in regulating wildlife populations has recently received increased attention and study, with the emergence and spread of novel diseases such as West Nile Virus (Marra et al. 2004, Ladeau et al. 2008). Occasionally, small numbers of Rusty Blackbirds roost with extremely large groups of Red-winged Blackbirds, Common Grackles, Brown-

headed Cowbirds, and European Starlings, in numbers that can exceed a million birds. These large roosting groups might be centers of disease transmission, and there may be some yet-unknown disease dynamics factoring into the Rusty Blackbird decline (Greenberg et al. 2011).

Rusty Blackbirds studied in the lower Mississippi alluvial valley exhibited an unexpectedly high prevalence of hematozoan blood parasites (primarily *Leucocytozoon*, *Plasmodium*, or *Trypanosoma* spp), with 49% of individuals demonstrating infections in blood smears (Barnard et al. 2010). With insect vectors mostly dormant in the winter, and the host birds free of the known stressors of courtship and reproductive cycles, most studies of songbirds wintering at temperate latitudes have found very low prevalence of hematozoan parasites. Barnard et al. (2010) suggest that such an unprecedented case of parasite prevalence during the winter might be indicative of stressed hosts undergoing a “nonseasonal relapse”, where the parasites that are typically sequestered in various host organ systems re-infect the hosts’ bloodstream, as they typically do at the onset of the breeding season.

In addition to being a concern for human public health, massive wintertime flocks of multiple blackbird species can also be a nuisance to agriculture. Consequently, the USDA issues permits to kill birds in these roosts with applications of the surfactant chemical PA-14. This chemical reduces the surface tension of water, and decreases the water repellency of birds’ feathers. Properly applied, it is sprayed over a

group of nocturnally roosting birds a few hours before wet precipitation is expected, or alternatively it is applied with supplemental water canons or deployed with water via a ground-based sprinkler system. Upon soaking, the birds eventually die of hypothermia/exposure. Rusty Blackbirds composed < 1% of kills, when species composition was estimated from PA-14 deployment at 43 roosts (Dolbeer 1995). When that roost composition percentage was multiplied by the total number of blackbirds killed in all 83 applications of PA-14 between 1974 and 1992 (the estimated total number of birds killed was 38,181,325), Dolbeer (1995) estimated that 117,625 Rusty Blackbirds were killed. The impact of the mortality was assumed by Avery (1995) not be a significant contributor to the declining Rusty Blackbirds population. However, Greenberg and Matsuoka (2010) added that the impact of such mortality events is cumulative. Recent efforts by the IRBWG have successfully removed the Rusty Blackbird from the list of species for which the USDA can issue these lethal permits.

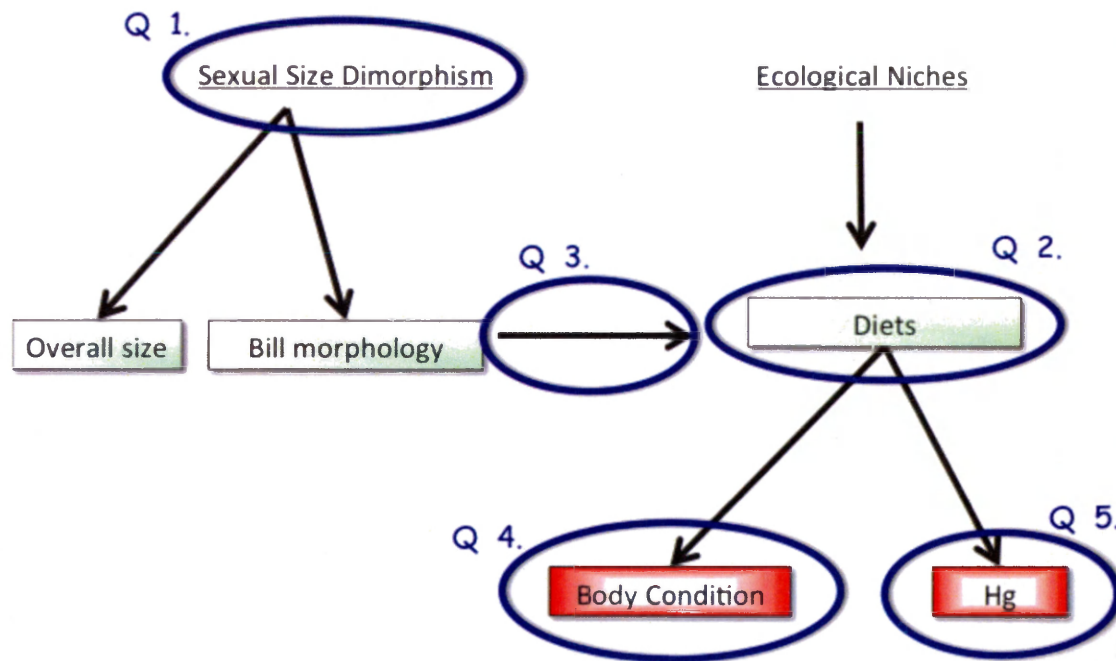
### ***Rationale and Significance***

The Rusty Blackbird working group compiled a list of potential threats to the species, or barriers to population recovery (Greenberg

and Matsuoka 2010, Greenberg et al. 2011). Future study and testing of those threats requires a better understanding of the species basic winter ecology. Little is know about the diet of the Rusty Blackbird (Beecher 1951, Avery 1995, Meanley 1995). The little information that has been published has been limited to narrative accounts of the species, which have been summarized in avifaunal compilations, most recently Avery (1995), and Greenberg and Matsuoka (2010). Among the many unstudied features of the Rusty Blackbird's natural history relating to its foraging ecology are the implications of its sexual size dimorphism. Male Rusty Blackbirds are approximately 15% larger than females by mass (Avery 1995). Some bird species with sexual dimorphism have been shown to exhibit differential diets by sex. The main objective of my project was to investigate the role of sexual dimorphism in the trophic ecology of Rusty Blackbirds by capturing and measuring Rusty Blackbirds wintering in the Williamsburg, Virginia area. Sexual size dimorphism was assessed through morphological measurements in the field. Niche differentiation was assessed by sampling blood and feathers for the analysis of carbon and nitrogen stable isotope ratios. Body condition was assessed as size-corrected mass, and used as a proxy for the health of a given individual, to be correlated with its diet. Lastly, because mercury intake is closely correlated with trophic level, individual Rusty Blackbirds' mercury levels were measured directly in two tissues.

I asked the following the following specific research questions (Fig. 2): (1) How dimorphic are male and female Rusty Blackbirds? (2) Do male and female Rusty Blackbirds exhibit diets of differing trophic level and carbon source? (3) On an individual level, what are the correlations between bill/body size and trophic level? (4) How does the dietary composition (assessed through carbon and nitrogen stable isotope ratios) of individual birds correlate with their body condition (a proxy for relative health)? (5) How do the measured mercury levels in both feathers and blood correlate with the trophic level of individual Rusty Blackbirds?

# Theoretical model



**Figure 2.** A model describing this study's five questions.

This study contributes to the IRBWG's stated long-term goal of synthesizing demographic data gathered at multiple breeding and wintering sites, which, when combined with connectivity information from others studies, will form a foundation for population models. The results of this study will contribute to the relatively slim body of knowledge of Rusty Blackbird trophic ecology. The results of this proposed study will be explicitly communicated to the IRBWG, and the information will be compared to a similar study being conducted

in Georgia and South Carolina (P. Newell, personal communication). The IRBWG seeks to convert emerging information about diet and habitat quality into management guidelines for landowners. The mercury data have already been published as part of a continent-wide analysis (Edmonds et al. 2010).

## **METHODS**

Rusty Blackbirds primarily use wet forested bottomlands and the adjacent uplands as foraging habitat in winter. This study took place on the campus of the College of William and Mary in Williamsburg, Virginia, because of the unusually accessible flocks of Rusty Blackbirds that regularly forage on campus. Rusty Blackbirds were not always present in the areas where they were observed foraging on campus, and there was a possibility that they were spending significant amounts of time not on the college campus. Additional sites were sought, however no other sites were located where Rusty Blackbirds could be found reliably. These efforts included radio telemetry tracking of four individuals captured on campus, in the hopes that it would lead to the discovery of additional foraging areas, but no individual birds could be tracked to off-campus foraging sites. Additionally, it was hoped that Rusty Blackbirds foraging on campus could be sampled with mist netting as they approached their nocturnal roost site for the evening, given that they typically roost on or near the ground (Avery 1995). The nocturnal roost site was located during the 2009 field season; however, it proved untenable for mist netting.

One of the primary challenges faced in this study was capturing enough Rusty Blackbirds. This was due not only to the scarcity of the

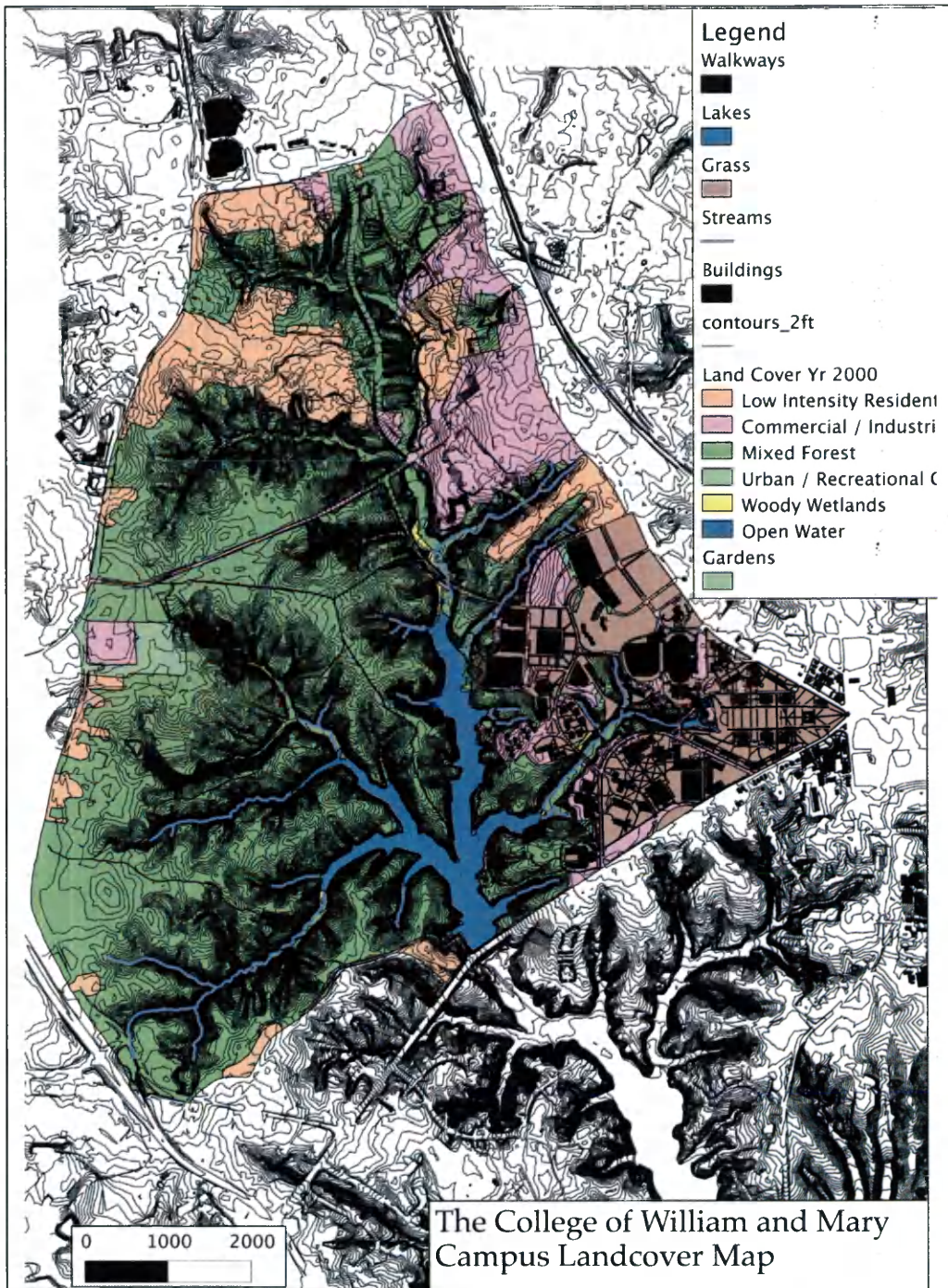


species, but their seemingly wary nature. Rusty Blackbirds typically flew into the mist nets and were captured when a group foraging on the ground was flushed into the treetops by a predator or other perceived threat. Often, a flock of Rusty Blackbirds would show up at the mist netting site, only to remain in the treetops, and not fly down to the ground to forage. Indeed, the foraging activities of the observed flocks of Rusty Blackbirds were frequently disrupted by the hunting activities of Cooper's Hawks (*Accipiter cooperi*), which seemed to be especially adept at hunting the Rusty Blackbirds. A Cooper's Hawk depredated two of the Rusty Blackbirds fitted with radio transmitters.

### ***Study Site***

The College of William and Mary campus is situated in the City of Williamsburg, in the coastal plain of the Commonwealth of Virginia (Fig. 2). The campus is a relatively large area of forested and sparsely impacted habitat surrounded by a much larger urban area. Roughly 202 hectares (500 acres) of the 485-hectare (1200 acre) campus is composed of maturing second-growth woodland known as the "College Woods." Additionally, the prominent, 16-hectare Lake Matoaka was constructed between 1700 and 1750 by damming the headwaters of College Creek. The lake is shallow, with an average depth of 2m, and is composed of multiple arms. Five small streams feed the lake, and each is lined with bottomland hardwood tree

communities. The USGS National Land-Cover Dataset (NLCD) classifies these areas as Woody Wetlands, in contrast to the Mixed Forest of the uplands. The forested floodplain wetlands, where the mouths of these five streams transition into the upper reaches of the lake's arms are the areas where Rusty Blackbirds were first observed foraging, and mist nets were later erected. Additionally, mist nets were positioned in the more recently man-made stormwater management impoundments that were created within these narrow natural floodplains, in order to regulate the stormwater runoff from the developed and largely impervious upland portions of campus. These impoundments were created without the removal of the mature trees growing in the narrow floodplain, and they comprise the primary field sites for the research presented in this thesis. The developed portions of the campus are classified by the NLCD program as Commercial / Industrial / Transportation land uses, as well as Urban / Recreational Grasses. The adjacent properties surrounding the College are classified as Low Intensity Residential (Fig. 3).



**Figure 3.** Landcover and contour map of the field site at the College of William and Mary in Williamsburg, Virginia. Landcover classification from the USGS National Land-Cover Dataset. Green is Mixed Forest. Bright Green is Woody Wetlands. Pink is developed Commercial/Industrial/Transportation. Yellow is Low Intensity Residential. Building footprints and paved sidewalks are black.

### ***Sampling with Mist Nets***

Rusty Blackbirds were captured using 2-7 mist nets 12m long and 2m high. Mist net mesh size was 60mm in the 2008-09 season, but replaced with 36mm mesh for the 2009-10 season, to reduce the amount of time spent detangling and extracting smaller, nonfocal bird species from the 60mm mesh mist nets.

### ***Timing of field work***

Rusty Blackbirds were captured from March 1<sup>st</sup> to April 16<sup>th</sup>, 2008; February 2<sup>nd</sup> to April 3<sup>rd</sup>, 2009; and January 8<sup>th</sup> to February 19<sup>th</sup>, 2010. The Rusty Blackbird is known to have a protracted autumn migration, and the annual Christmas Bird Count survey that takes place over the three-week holiday period typically counts the species before it settles into its more stable overwintering distribution (Hamel et al. 2008). Rusty Blackbirds were sighted on the William and Mary campus prior to the start of fieldwork; however, the early groups were irregular and unpredictable in their appearance on campus and were thought to be migrants continuing on to their overwintering destinations. Likewise, the tail end of the winter fieldwork may have been influenced by northbound migrants passing through and intermingling with the flock of marked individuals overwintering in Williamsburg. Separating these unmarked Rusty Blackbirds from the unmarked individuals in the locally overwintering population was

essentially impossible because not all residents were marked.

However, at least some marked and radiotagged individuals were present on campus or in the vicinity until the end of the fieldwork period.

### ***Field Protocol***

Captured Rusty Blackbirds were fitted with size “2” serially-numbered metal alloy bands from the U.S. Geological Survey Bird Banding Laboratory (Patuxent, MD). Additionally, Rusty Blackbirds were fitted with a unique combination of colored plastic leg bands (L & M Bird Leg Bands, Inc., San Bernadino, CA; “Lovebird” size), to allow for the visual recognition of individuals without the need to recapture with mist nets.

### ***Collecting Morphometric Data***

Captured birds were weighed and measured. Specific measurements taken were wing chord, tail length, tarsus length, bill length from the anterior of the nares to bill tip (“culmen”), bill length from the base of cranial feathering to the tip of the bill (“exposed culmen”), bill width and bill depth at the anterior of the nares, following techniques described in the North American Bird Banders’ Study Guide (Council 2001) (Fig. 4).

Of the two measurements of bill length that were collected in the field, the culmen measurement was preferred over the exposed culmen measurement. This was due to the subjectivity of determining the precise location of the “base” of the bill, given the nature of feathering at that location. For the analyses included in this thesis, the culmen measurement was used for bill length. In the analysis of the comparative roles of bill size and body size as correlates of diet in individual Rusty Blackbirds, it was desirable to reduce the number of bill morphology variables for modeling purposes. To that end, the raw bill measurements were combined into a variable called bill volume, which was derived using the geometric formula for a three-dimensional wedge shape,  $\text{bill volume} = \frac{1}{2} * \text{culmen} * \text{width} * \text{depth}$  (i.e.  $\text{volume} = \frac{1}{2} * \text{length} * \text{width} * \text{height}$ ). A second approach was evaluated as well, where the three raw bill measurements were reduced to their principle components using Program R (R Development Core Team 2009). The principle components analysis (PCA) reduced the three bill dimensions to two principle components (PC1, PC2), which accounted for 91% of the cumulative variance with those two uncorrelated vectors (Table 3). PC1 loaded strongly negative for the culmen measurement, and PC2 loaded strongly positive for the bill width and bill depth measurements (Table 4). The first two principle components were later evaluated against bill volume and the

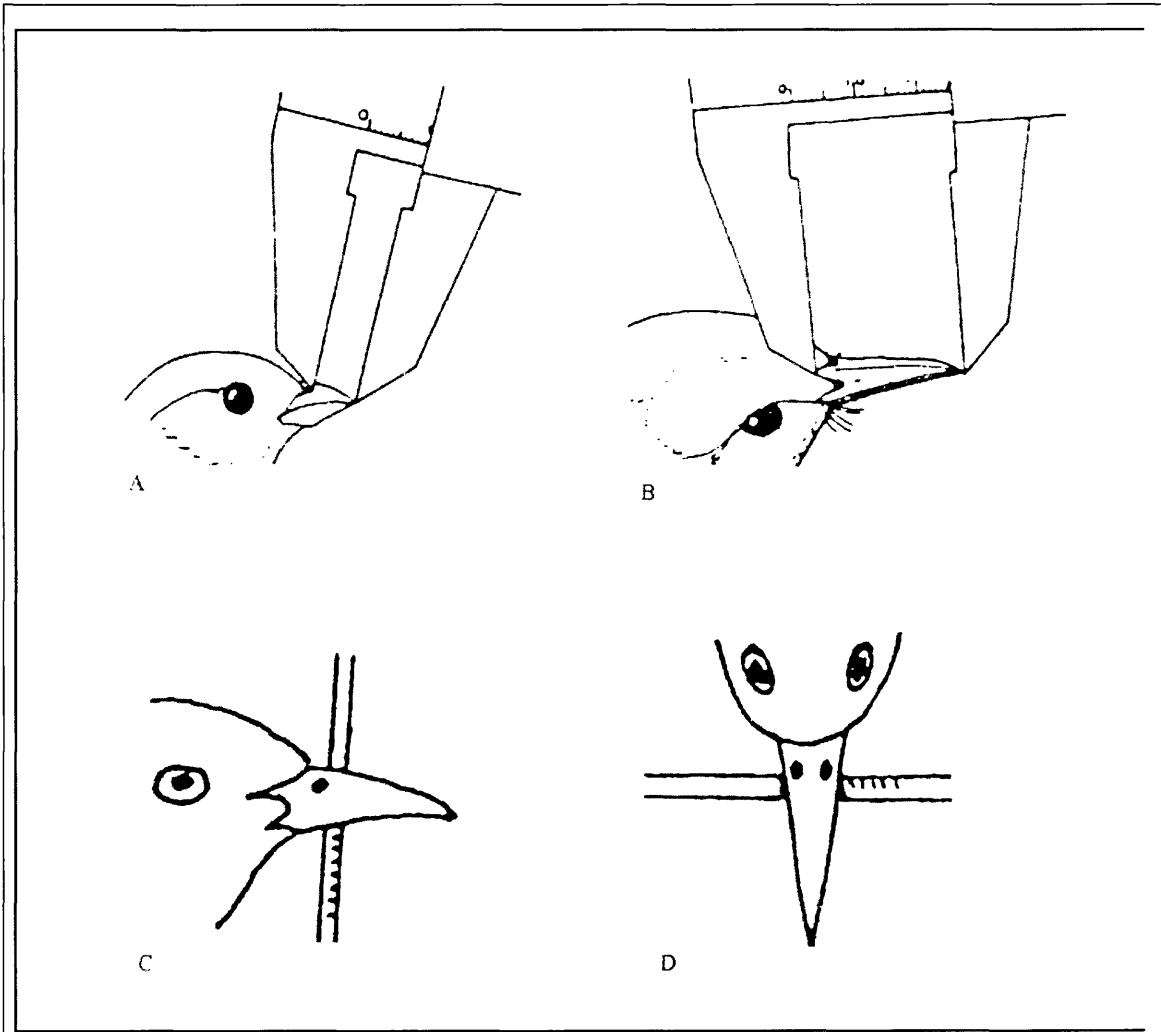
raw bill measurements, to see which schematic of bill size correlated most closely with variation in trophic level.

**Table 3.** Importance of the principle components of bill size measurements

|                        | <b>PC1</b> | <b>PC2</b> | <b>PC3</b> |
|------------------------|------------|------------|------------|
| Standard deviation     | 0.81       | 0.41       | 0.28       |
| Proportion of Variance | 0.73       | 0.19       | 0.09       |
| Cumulative Proportion  | 0.73       | 0.91       | 1.0000     |
| Eigenvalue             | 0.66       | 0.17       | 0.08       |

**Table 4.** Loadings of the principle components of bill size measurements

|        | <b>PC1</b> | <b>PC2</b> | <b>PC3</b> |
|--------|------------|------------|------------|
| Culmen | -0.96      | -0.29      | 0.04       |
| Width  | -0.24      | 0.69       | -0.68      |
| Depth  | -0.17      | 0.66       | 0.73       |



**Figure 4.** Bill measurements from Figure 23 of the North American Bird Banders' Manual. (A) Measuring the culmen, which is a measure of bill length from the anterior of the nares to the tip of the bill. (B) Total exposed culmen, which is a measure of bill length from the base of cranial feathering to the tip of the bill. (C) Bill depth measured vertically in cross-section at the anterior of the nares. (D) Bill width measured horizontally in cross-section at the anterior of the nares.

### ***Collecting Feather Samples***

For the 2008-09 winter season, feathers were collected in accordance with the WG's Winter Working Scheme (2007). Under this



protocol, both of the innermost primary feathers (“P1” feathers), which are the first flight feathers to be replaced in typical annual prebasic molt [insert citation??], were cut with scissors and collected for geographic stable isotope analysis and for mercury analysis, the results of which have already been published (Hobson et al. 2010, Edmonds et al. 2010). Additionally, 5-7 body contour feathers were plucked from the breast and back, as prescribed in the IRBWG Winter Working Scheme. Finally, the two outermost rectrices (tail feathers) were pulled and included in stable isotope and mercury analyses. Individual Rusty Blackbirds that were fitted with radio transmitters were not subjected to the primary feather sampling, on the rationale that we did not want to further hinder their flight abilities beyond harnessing them with the transmitters.

For the 2009-10 winter season, we revised our protocol to collect only the tissues that we needed for our own analyses and to decrease processing time in the field. Thus, in the 2009-10 season, we only collected the two outermost rectrices for mercury and stable isotope analysis.

### ***Blood Samples for Stable Isotope Analysis***

Small blood samples (<70  $\mu$ L) were collected via heparinized and non-heparinized micro-capillary tubes, following venipuncture of the brachial ulnar vein. Venipuncture was conducted using 26 G sterile

needles. Microcapillary tubes were capped and stored in clean Vacu-tainers. Blood and feather samples were stored at  $-80^{\circ}\text{C}$  within 2 hours of collection.

Blood samples were freeze-dried with a Labconco freeze-dryer at the Keck Lab at the College of William and Mary, and homogenized as they were weighed and packed into tins before shipping to California for stable isotope analysis.

### ***Stable Isotope Analysis at UC Davis***

Blood samples were analyzed by the University of California, Davis Stable Isotope Facility. Blood samples were analyzed for  $^{13}\text{C}$  and  $^{15}\text{N}$  isotope ratios using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were combusted at  $1020^{\circ}\text{C}$  in a reactor packed with chromium oxide and silvered cobaltous/cobaltic oxide. Following combustion, oxides were removed in a reduction reactor (reduced copper at  $650^{\circ}\text{C}$ ) and the helium carrier flowed through a water trap (magnesium perchlorate) and an optional  $\text{CO}_2$  trap (for N-only analyses). Nitrogen and  $\text{CO}_2$  were separated on a Carbosieve GC column ( $65^{\circ}\text{C}$ ,  $65\text{ mL/min}$ ) before entering the IRMS.

During analysis, samples were interspersed with several replicates of at least two different laboratory standards. These laboratory standards, which were selected to be compositionally

similar to the samples being analyzed, have been previously calibrated against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, IAEA-CH7, and NBS-22).

The samples' preliminary isotope ratios were measured relative to reference gasses analyzed with each sample. These preliminary values were finalized with a correction factor that adjusted the values for the entire batch based on the known values of the included laboratory standards. The final delta values were expressed relative to international standards PDB (PeeDee Belemnite) for carbon and air for nitrogen.

### ***Mercury Analysis of Blood and Feathers***

Total mercury concentrations were quantified in blood and feathers via gold-amalgamation atomic absorption spectroscopy with a Milestone DMA-80 direct mercury analyzer. Blood samples were thawed and expressed from capillary tubes into combustion boats, and weighed to the nearest 0.1 mg. Feathers were weighed to the nearest 0.1 mg and placed directly in a combustion boat. Total mercury was determined by EPA method 7473 (United States Environmental Protection Agency 1998). Internal quality control included initial and continuing verification of calibration, blanks, sample replication, and certified reference materials (DOLT-3, DOLT-4, and /or DORM-3, National Research Council of Canada, Ottawa, Canada) every 10 to 15

samples. The relative percent difference (RPD) for duplicate samples was  $4\pm 2\%$  SD (n=17) for blood and  $16\pm 20\%$  SD (n=44) for feathers. Mean recovery of certified reference materials was 95% for each batch analyzed with an overall mean recovery of  $102\pm 3\%$  SD (n=220).

Edmonds et al. (2010) additionally analyzed a subsample of five blood and five feathers from 10 individuals for methyl-mercury at Acadia University to confirm that total mercury in these tissues was representative of methyl-mercury, as demonstrated in previous studies (Evers et al. 2005, Rimmer et al. 2005, Wada et al. 2009). Each sample was weighed to the nearest 0.1 mg, digested in 10 mL of 25% KOH/MeOH, shaken for 1 hr, and placed in a dry bath for 2 hr at 95 °C. A sample aliquot (20 µL) was transferred to a reaction bubbler and analyzed for MeHg through ethylation and purge-and-trap gas chromatography prior to detection by atomic fluorescence spectrometry (Brooks Rand Model III) by EPA method 1630 (U S Environmental Protection Agency 2001). Quality assurance included analytical sample replication (RPD blood  $2\pm 1\%$ ; RPD feathers  $0.1\pm 0.05\%$ ), international standards, method blanks, and certified reference material (DOLT-4, mean recovery  $98\pm 4\%$  SD, n 3).

## ***Statistical Analyses***

All calculations, graphs, and statistical analyses were conducted in Program R (R Development Core Team 2009). Tests of equal mean values between males and females for the various morphological measurements were made using Welch two-sample t-tests, because it does not assume equal sample size and equal variance. I hypothesized that diet was correlated with morphology on an individual basis, however, I sought to additionally discern the simplest equation that best explained that relationship. The trophic levels of individual Rusty Blackbirds might be best described as a function of bill size, body size, sex, or combinations of those variables. Therefore, I took an Information-Theoretic (Burnam and Anderson 2002) approach to select the best equation and quantify the relative importance of sex, bill size and body size to the diets of individual Rusty Blackbirds. I used the same approach to select the best equation to describe the relationship between individual diets and body condition, and quantify whether body condition was best described as a function of carbon source ( $\delta^{13}\text{C}$ ), trophic level ( $\delta^{15}\text{N}$ ), or the combination of those variables. Program R was also used to calculate the model selection criteria and parameter estimates when modeling the role of bill size and body size in trophic level, and modeling the role of carbon and nitrogen stable isotope ratios in body condition.

## RESULTS

### *Sampling regimes*

Rusty Blackbirds were sampled during three winters (Table 2). In the winter of 2007-08, undergraduate student Jacob Armiger conducted observations of the Rusty Blackbirds and first brought attention to the fact that these birds were foraging on the William and Mary campus. In March and April of 2008, he succeeded in capturing and banding 41 Rusty Blackbirds. I began my project in the winter of 2008-09, and first succeeded in capturing Rusty Blackbirds in February 2009. The following field season, in 2009-10, Rusty Blackbirds were first captured in January, however they were less frequently observed on the campus in the latter half of the 2009-10 field season, and none were captured after February 19. In all three seasons, Rusty Blackbirds were only captured after January 1<sup>st</sup>, thus simplifying the field season terminology to 2008, 2009, and 2010. The full sampling and measurement protocol was implemented in 2009, and 68 Rusty Blackbirds were sampled with mist nets & measured (Table 2). Of those, 19 were females and 47 were males. In 2010, only 39 Rusty Blackbirds were captured & measured. Of those, 11 were female and 28 were male. The bias in the sex ratio of birds captured was consistent with visual observations of flocks in the field, both foraging on campus

and during a few instances when flock were observed staging in treetops before flying down to a tidal marsh to roost for the night.

### ***Sexual Size Dimorphism***

Male Rusty Blackbirds sampled and measured in this study were larger than females, on average, for all of the morphological features measured (Table 5). Sample sizes, listed below, varied somewhat because certain measurements could not be taken on particular individuals. All birds included in this analysis were measured by the author.

**Table 5.** Sexual size dimorphism of Rusty Blackbirds wintering in coastal Virginia

| Measurement     | Male      |    | Female    |    | Welch Two Sample t test |       |         |
|-----------------|-----------|----|-----------|----|-------------------------|-------|---------|
|                 | $\bar{x}$ | n  | $\bar{x}$ | n  | t                       | DF    | p       |
| Mass (g)        | 63.67     | 68 | 55.79     | 24 | 7.24                    | 35.21 | <0.0001 |
| Wing (mm)       | 112.82    | 69 | 104.49    | 24 | 14.52                   | 50.85 | <0.0001 |
| Tail (mm)       | 86.97     | 69 | 80.32     | 24 | 6.91                    | 47.12 | <0.0001 |
| Tarsus (mm)     | 30.82     | 69 | 29.41     | 23 | 5.14                    | 36.22 | <0.0001 |
| Culmen (mm)     | 14.88     | 69 | 13.94     | 24 | 7.11                    | 60.33 | <0.0001 |
| Bill Width (mm) | 4.99      | 69 | 4.63      | 24 | 4.47                    | 45.77 | <0.0001 |
| Bill Depth (mm) | 6.25      | 69 | 5.95      | 24 | 4.00                    | 45.96 | 0.0002  |
| Bill PC1        | -0.267    | 69 | 0.769     | 24 | -7.92                   | 62.93 | <0.0001 |
| Bill PC2        | 0.0461    | 69 | -0.133    | 24 | 1.92                    | 42.82 | 0.0609  |

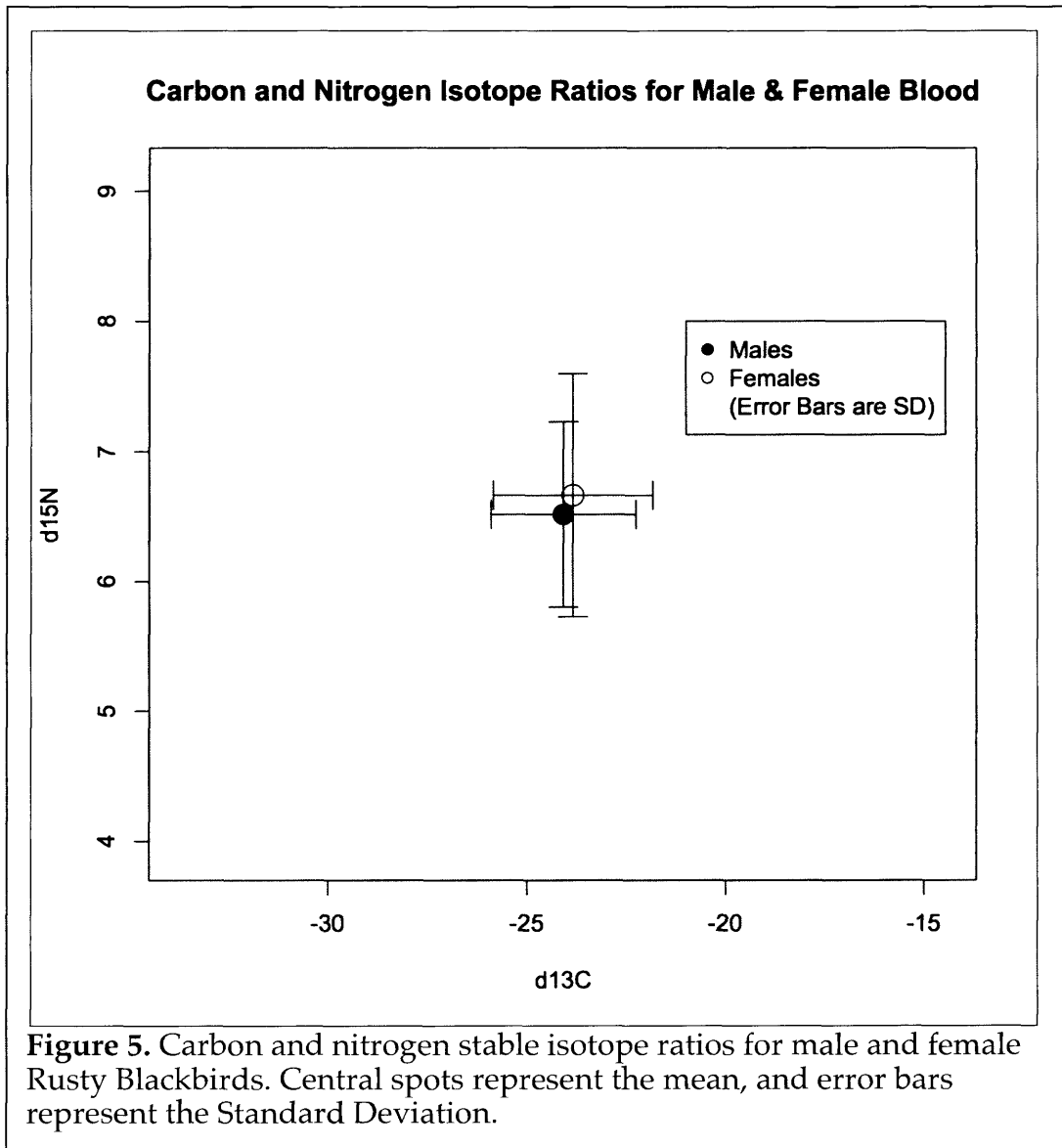
These results are similar to (Dunning 1984). Whereas Dunning calculated males to be 16.5% larger than females by mass, in my sample males were 14.1% larger than females by mass. However, it should be noted that I had a notably smaller sample size, especially for females.

### ***Differential Diets by Sex***

As quantified by analysis of stable isotopes of nitrogen and carbon, the composition of the blood of male and female Rusty Blackbird did not differ statistically (carbon: Welch two sample t-test,  $t = -0.54$ ,  $df = 43.5$ ,  $p = 0.59$ ; nitrogen:  $t = -0.74$ ,  $df = 38.3$ ,  $p = 0.46$ .) (Fig.



5). I cannot reject the null hypothesis that male and female Rusty Blackbird exhibit similar diets in terms of trophic level and carbon sources.



### ***Correlates of Individual Variation in Trophic Level***

I also examined whether dietary differences between individuals, as estimated by stable isotope ratios, were correlated with body size and bill size. In order to quantify the putative contributions of body size and bill size to variation in diet, a series of candidate models were proposed, and evaluated with Akaike's Information Criterion, corrected for small sample size (AIC<sub>c</sub>). This procedure allowed me to assess the relative importance of the proposed independent variables in correlation to variation in trophic level (as quantified by the nitrogen stable isotope ratio).

However, first I wanted to select the most informative index for estimating bill size as it related to trophic level. In the field protocol, four measurements of the bill were collected (Fig. 3). Of the two measurements of length, culmen was selected for use in analyses and exposed culmen was ignored, due to the subjective nature of judging where the start of feathering is located when taking the exposed culmen measurement in the field. That left three primary measurements, corresponding to the length, width, and depth dimensions of the bill. For modeling exercises designed to compare the relative importance of bill size and body size as correlates of trophic level, it was desirable to reduce bill size down to a single variable. However, it was not desirable to lose relevant information

about the correlation between trophic level and bill size. Thus, in order to select the optimal bill measurement schematic that is most informative about implications for trophic level, I conducted a model selection exercise using Akaike's Information Criterion (corrected for small sample size) to determine which form of variable reduction best explained  $\delta^{15}\text{N}$  (Table 6).

**Table 6.** Model selection: bill measurement schematic

| Model   | K | AIC <sub>c</sub> | $\Delta\text{AIC}$ | w <sub>i</sub> |
|---|---|------------------|--------------------|----------------|
| $\delta^{15}\text{N} = \text{sex} + \text{L} + \text{W} + \text{D}$ | 6 | 226.75           | 2.34               | 0.188          |
| $\delta^{15}\text{N} = \text{sex} + \text{PC1} + \text{PC2}$        | 5 | 226.56           | 2.16               | 0.206          |
| $\delta^{15}\text{N} = \text{sex} + \text{bill volume}$             | 4 | 224.41           | 0                  | 0.606          |
| Total   |   |                  |                    | 1.0            |

According to the AIC<sub>c</sub> model selection process, the best bill measurement schematic turned out to be simply bill volume. Even though the delta AIC values were somewhat small in magnitude, suggesting that the bill volume equation was perhaps not unequivocally the best model, it had the added advantage of easy interpretation, as compared to the PC scores. Thus, bill volume was utilized for the next modeling exercise, which was designed to compare the relative importance of bill size and body size as correlates of trophic level (Table 7.). I hypothesized that bill size and body size might be correlated with diet, specifically the relative importance of plant seeds (i.e. acorns) versus animal prey, with individual Rusty Blackbirds of larger body size and/or bill size having diets lower in

the food web. In order to find the best equation describing the influence of individual morphology on diet, a set of *a priori* models were proposed. I evaluated whether trophic level ( $\delta^{15}\text{N}$ ) was best explained as a function of a.) bill volume, b.) body size index (which was the first principle component of all body size measurements, including mass), c.) bill volume + body size index, d.) sex + bill volume + body size index, and e.) sex + bill volume + body size index + bill volume\*body size index.

**Table 7.** Model selection: morphological correlates of trophic level

| Model   | K | AIC <sub>c</sub> | $\Delta\text{AIC}$ | $w_i$ |
|---|---|------------------|--------------------|-------|
| $\delta^{15}\text{N}$ = bill volume   | 3 | 222.75           | 3.28               | 0.095 |
| $\delta^{15}\text{N}$ = body size index   | 3 | 219.46           | 0                  | 0.489 |
| $\delta^{15}\text{N}$ = body size index + bill volume                                     | 4 | 221.62           | 2.15               | 0.167 |
| $\delta^{15}\text{N}$ = sex + bill volume + body size index                               | 5 | 223.69           | 4.22               | 0.059 |
| $\delta^{15}\text{N}$ = sex + bill volume + body size index + bill volume*body size index | 6 | 221.36           | 1.89               | 0.190 |
| Total   |   |                  |                    | 1.0   |

Selecting the best-performing model or set of models using Akaike's information criterion (corrected for small sample size) turned out to be difficult in the case of correlates of trophic level, because the best performing model was the one that included only the body size variable. However, the next best-performing model was the full model, followed by body size + bill volume. The inconsistent variable composition of the models with the greatest support was difficult to

explain and thus all candidate models were combined, in proportion to their explanatory power, to create the composite model (Box 1).

The multi-model parameter estimates were derived from the set of all candidate models, in proportion to their weighted inference values ( $w_i$ ) (Table 8).

**Box 1. Composite Model: Morphological Correlates of Trophic Level**  
 $\delta^{15}\text{N} = 6.65 + (-0.0001)\text{Bill Volume} + (0.029)\text{BSI} + (-0.094)\text{Sex} + (-0.00016)\text{Bill Volume}*\text{BSI} + \text{error}$

**Table 8.** Multi-model parameter estimates: morphological correlates of trophic level

| Parameter             | Estimate               | SE                    | 90% CI Upper          | 90% CI Lower           |
|-----------------------|------------------------|-----------------------|-----------------------|------------------------|
| Intercept             | 6.652                  | 0.410                 | 7.32                  | 5.98                   |
| Bill Vol              | $-1.01 \times 10^{-4}$ | $2.15 \times 10^{-3}$ | $3.42 \times 10^{-3}$ | $-3.62 \times 10^{-3}$ |
| Body Size Index (BSI) | 0.029                  | -0.036                | 0.088                 | -0.030                 |
| Sex                   | -0.094                 | 0.1010                | 0.071                 | -0.260                 |
| Bill Vol*BSI          | $-1.59 \times 10^{-4}$ | $1.06 \times 10^{-4}$ | $1.52 \times 10^{-5}$ | $-3.33 \times 10^{-4}$ |

The estimates of all of the explanatory parameters (bill volume, body size, sex, and the interaction term (bill volume\* body size) were low in magnitude, and with the exception of sex, when their error values were considered, they intercepted zero. This indicates the weakness of bill size and body size as correlates of trophic level. Of the

explanatory variables evaluated in this exercise, sex was most strongly correlated with trophic level.

### ***Correlates of Individual Variation in Body Condition***

Despite a lack of evidence for dietary differences between the sexes, I hypothesized that body condition (a measure of size-corrected mass) might vary on an individual basis, correlating with diet. In order to quantify the relative importance of trophic level (as estimated by  $\delta^{15}\text{N}$ ) and carbon source correlating to variation in body condition, a series of candidate models were proposed *a priori*, and then evaluated with Akaike's Information Criterion (corrected for small sample size) (Table 9).

**Table 9.** Model selection: dietary correlates of body condition index

| Model   | K | AIC <sub>c</sub> | $\Delta_{\text{AIC}}$ | w <sub>i</sub> |
|---|---|------------------|-----------------------|----------------|
| BCI = $\delta^{13}\text{C}$   | 3 | 540.04           | 5.78                  | 0.04           |
| BCI = $\delta^{15}\text{N}$   | 3 | 534.26           | 0                     | 0.65           |
| BCI = $\delta^{13}\text{C} + \delta^{15}\text{N}$   | 4 | 536.27           | 2.01                  | 0.24           |
| BCI = $\delta^{13}\text{C} + \delta^{15}\text{N} + \delta^{13}\text{C} * \delta^{15}\text{N}$ | 5 | 538.51           | 4.25                  | 0.08           |
| Total   |   |                  |                       | 1.0            |

Next, the two best-performing models, accounting for 89% of the weighted inference (w<sub>i</sub>) were combined into a composite model (Box 2) and the model-averaged parameter estimates were calculated, to quantify the relative contributions of the nitrogen and carbon stable

isotope ratios as they related to individual variation in body condition (Table 10). Compared with the carbon stable isotope ratio, the nitrogen stable isotope ratio of the diet was more related to the body condition of individual birds (about 8 times greater in magnitude than carbon). Furthermore, when the error estimates were considered, the nitrogen stable isotope ratio did not intercept zero, and thus holds the most explanatory connection to body condition. Also, the negative direction of the parameter estimate indicates that on average, individual birds that ate more at a lower trophic level also exhibited better body condition.

**Box 2. Composite Model: Dietary Correlates of Body Condition Index**

$$\text{BCI} = 5.146 + (-0.168) \delta^{13}\text{C} + (-1.401) \delta^{15}\text{N} + \text{error}$$

**Table 10.** Multi-model parameter estimates: dietary correlates of body condition

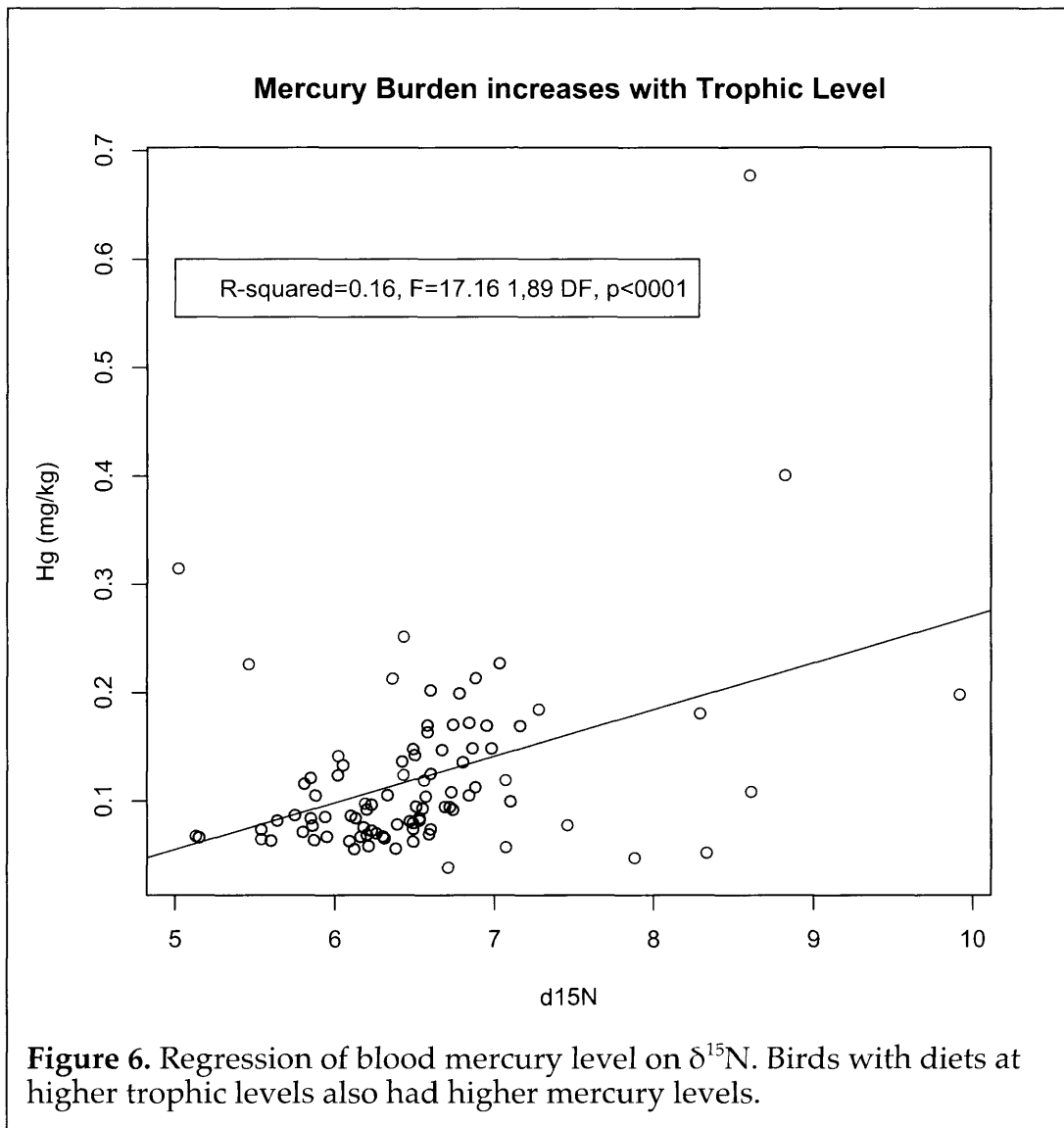
| Parameter             | Estimate | SE    | 90% CI Upper | 90% CI Lower |
|-----------------------|----------|-------|--------------|--------------|
| Intercept             | 5.146    | 6.939 | 16.526       | -6.233       |
| $\delta^{13}\text{C}$ | -0.168   | 0.154 | 0.084        | -0.420       |
| $\delta^{15}\text{N}$ | -1.401   | 0.636 | -0.358       | -2.444       |

***Mercury was Correlated with Trophic Level***

I hypothesized that Rusty Blackbirds foraging at higher trophic levels would also have higher burdens of mercury in their bodies. Measurements of total mercury in whole blood (mg/kg, which is

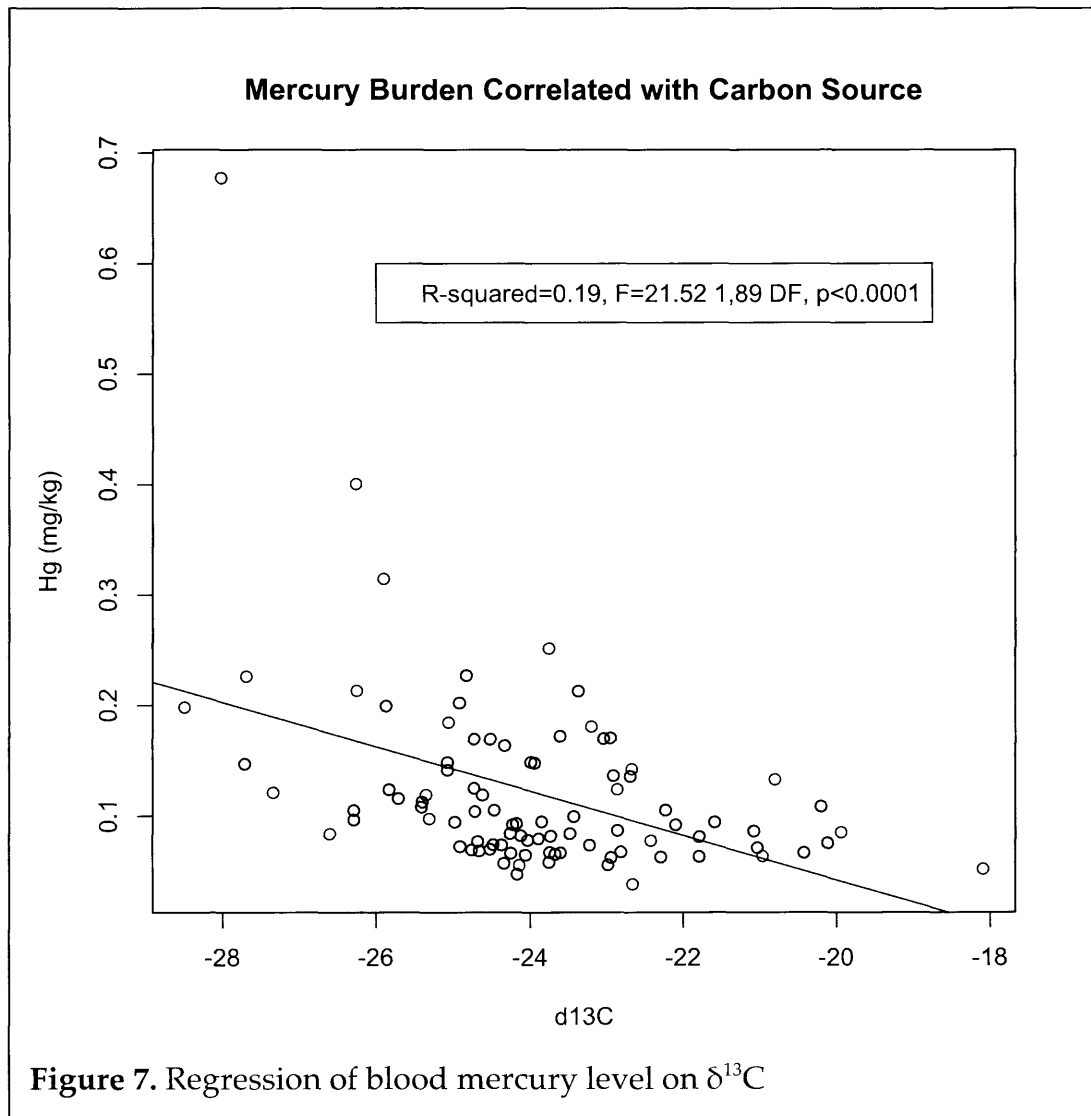
equivalent to parts per million, ppm) was regressed (for males and females combined) on  $\delta^{15}\text{N}$  (Fig. 6). Mercury levels were significantly correlated with trophic level of individual Rusty Blackbirds ( $R^2=0.16$ ,  $F(1, 89) = 17.2$ ,  $p<0.0001$ ). Given that birds ingest mercury through their prey items, and that mercury bioaccumulates and biomagnifies at higher trophic levels, it is expected that for birds foraging together in the same area, individuals foraging at a higher trophic level (higher  $\delta^{15}\text{N}$ ) would have relatively higher levels of mercury.





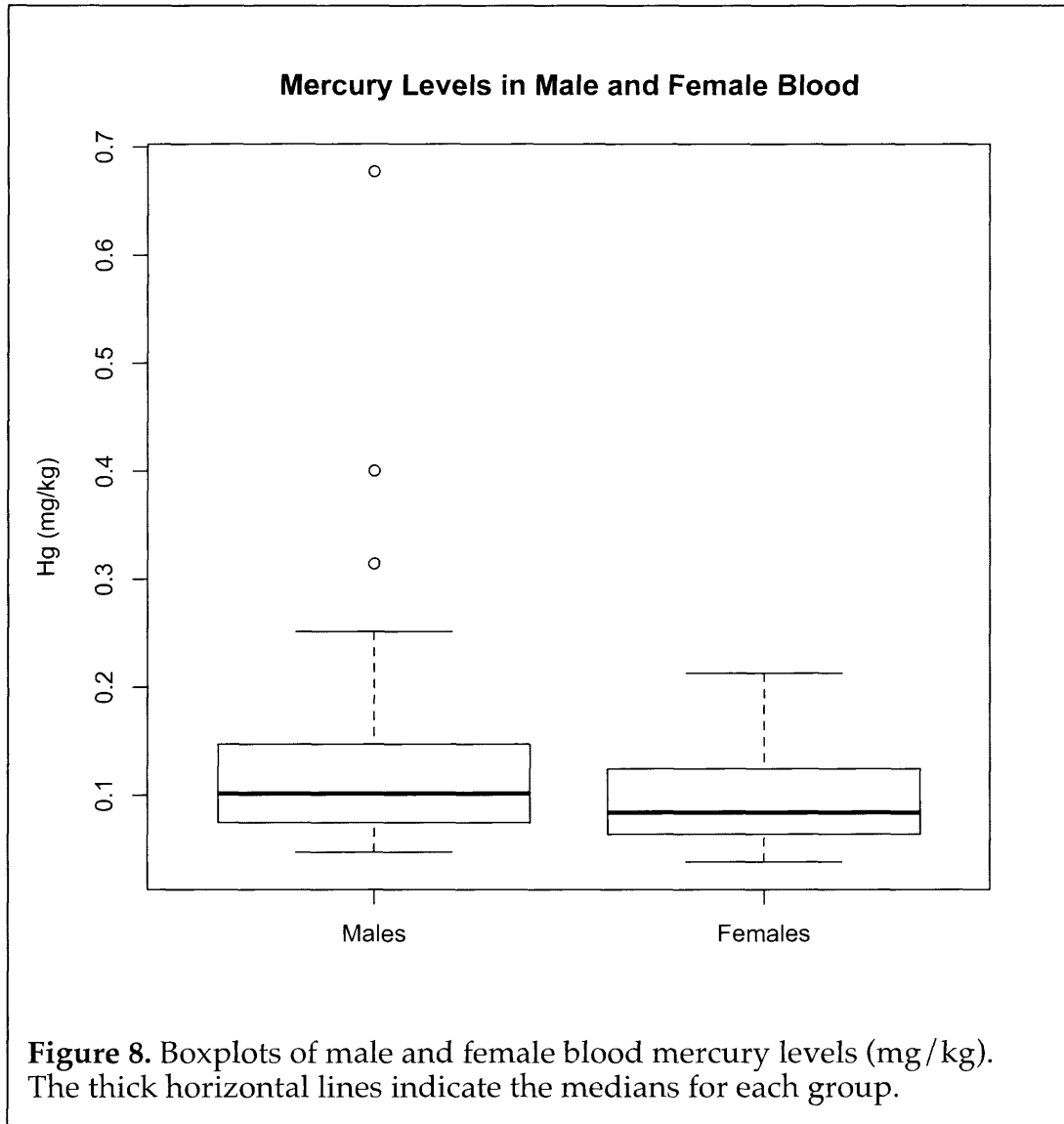
Unexpectedly, there was an even stronger relationship between an individual bird's carbon source in their diet (as measured by  $\delta^{13}\text{C}$ ), and their mercury level (Fig. 7) ( $R^2=0.19$ ,  $F(1, 89) = 21.5$ ,  $p<0.0001$ ). This relationship is harder to interpret, given that I did not measure the carbon stable isotope ratios at the base of the likely alternative food

webs for this species, such as aquatic plants and tree mast. This result deserves further investigation.



As expected, given the similarity of diets for males and females, as quantified by the stable isotope ratios of carbon and nitrogen, there was only a slight difference in the mercury concentration of blood in

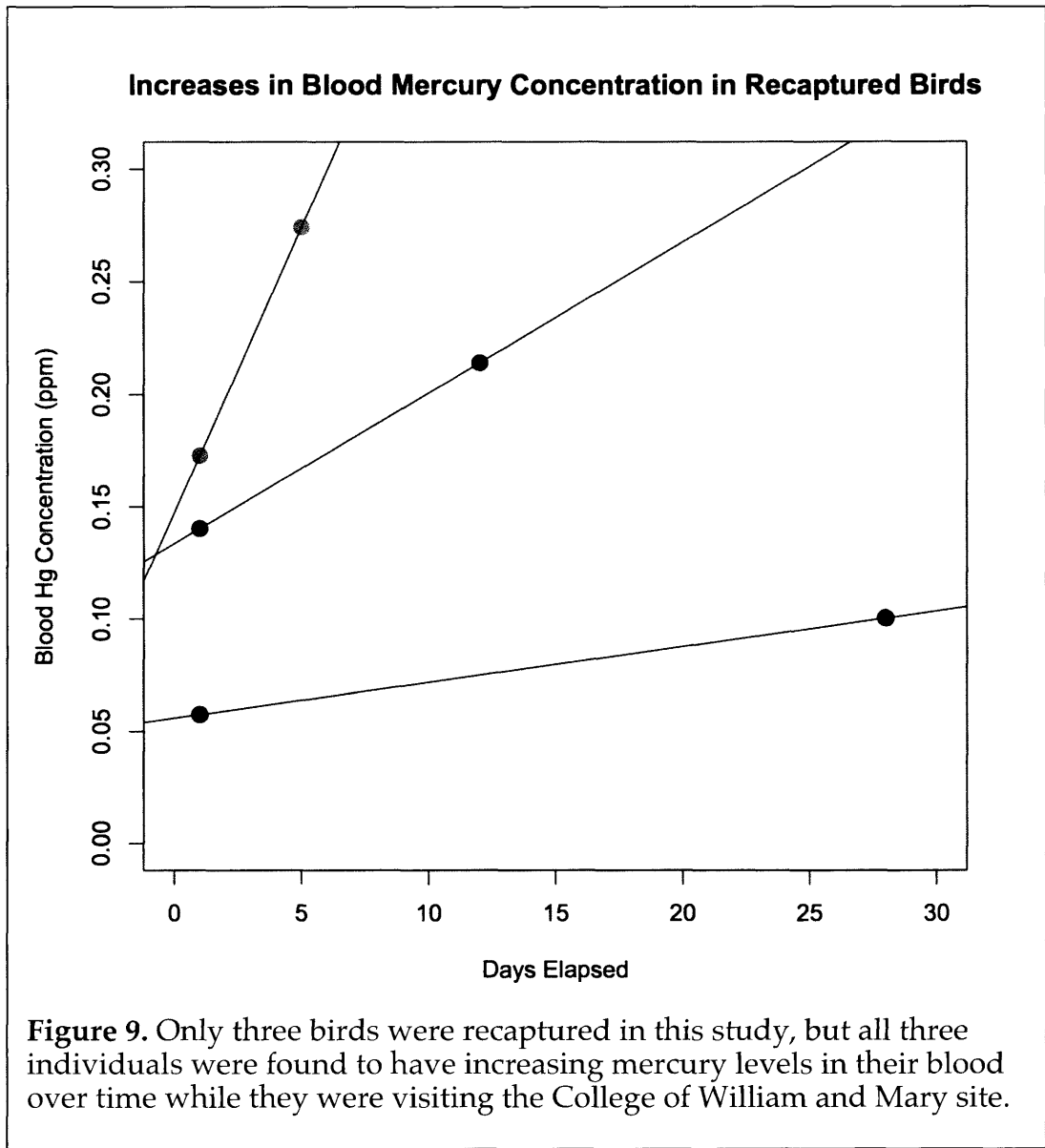
males and females, with males having slightly higher mercury values (Fig. 8.) (Welch two sample t-test,  $t(70) = 1.76$ ,  $p = 0.082$ ).



The mercury results from this study were contributed to a collaborative study organized through the IRBWG, and our sample (n=80) represented a significant portion of the Rusty Blackbirds sampled in the winter in the Southeastern Coastal Plain of the United

States (n=209), and 16% of the total sample size for that study (Edmonds et al. 2010), which described regional and seasonal patterns in mercury exposure in Rusty Blackbirds across the continent.

Finally, it should be noted that there were only three occasions in the entire study when individual Rusty Blackbirds were recaptured and a second blood sample was collected. This allowed for the quantification of change in diet over time while the birds were utilizing this site. Though this is an extremely small and anecdotal sample (n=3), it is worth noting that the mercury levels were increasing for all three Rusty Blackbirds, at different rates, as shown by the slopes of the lines connecting the individual samples over elapsed time (Fig. 9).



## **Discussion**

This study addressed five research questions. The first was whether male and female Rusty Blackbirds exhibit sexual size dimorphism based on mass, wing chord, tail length, tarsus length, culmen, bill width, bill depth. This has been previously reported based on a large sample of body masses (Dunning 1984) and a small sample of beak sizes (Meanley 1967). The second was whether males and females eat different diets when wintering at the same location, predicated on the expectation that differences in body size and bill size might lead to trophic segregation. My third question was whether, regardless of sexual dimorphism, individuals with different sizes of bills and bodies ate different diets. If so, the fourth question, whether diet and body condition were related, would have been particularly relevant. Finally, I asked whether mercury, which accumulates more in birds higher in the food web, differed between the sexes or was associated with diet. This final question was part of a continent-wide collaborative study (Edmonds et al 2010), the results of which are not repeated here.

### ***Sample sizes***

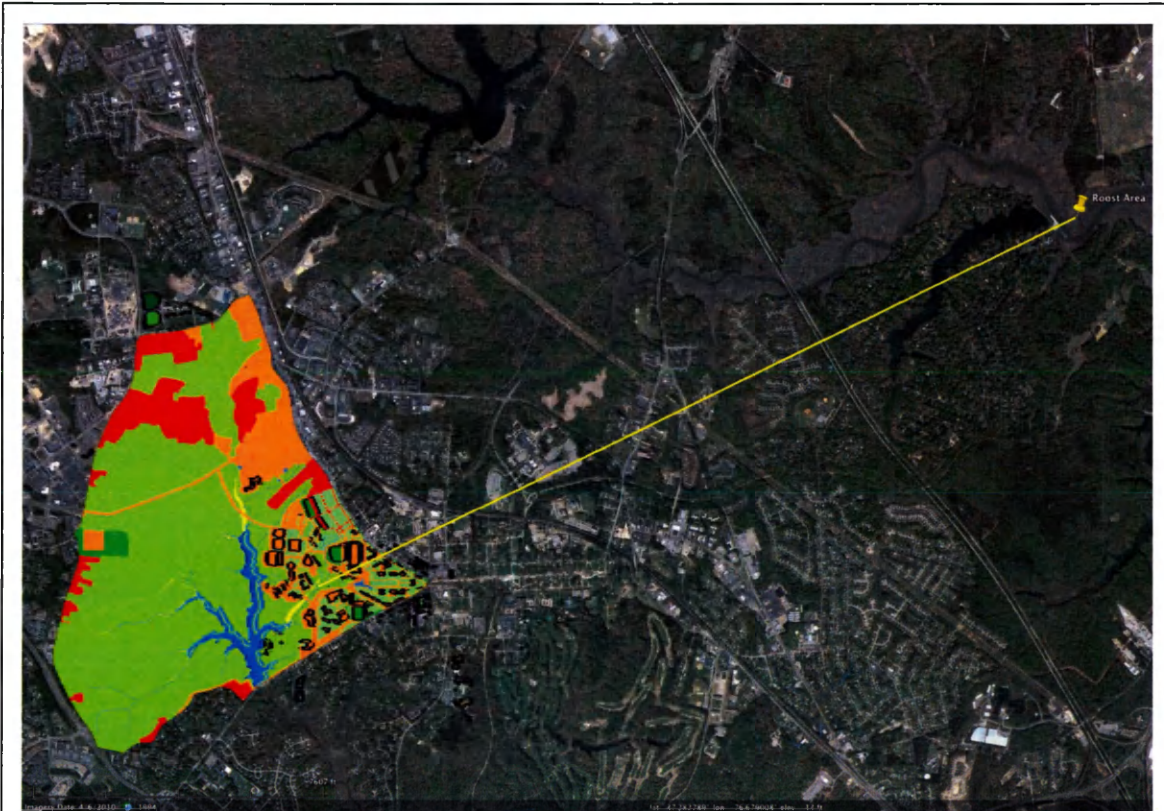
This study demonstrated one of the challenges of working with a rare and declining species: large sample sizes are difficult to acquire.

This obvious fact is worth mentioning, as it is one of the primary struggles that all studies of rare species face. Two recent studies on Rusty Blackbirds, have devoted significant effort to develop methodologies for simply detecting the presence or absence of the species (Luscier et al. 2010, Matsuoka et al. 2010a). Furthermore, another challenge to this study was the difficulty faced in capturing the Rusty Blackbirds that could be located. Blackbird flocks wander and change size dynamically; they can be overwhelmingly abundant at one place for a brief moment before flying away to parts unknown. Mist-netting, in contrast, is a static endeavor. The nets in this study were set up where the Rusty Blackbirds were most frequently observed to be foraging, but it was difficult to predict the best occasions to open the nets for trapping, because the blackbirds were only present on the site intermittently and unpredictably. To combat that issue, the area was regularly baited with cracked corn, and the nets were left closed, in efforts to get the flock habituated to feeding in this exact location on a more frequent basis. This study was originally supposed to incorporate multiple flocks at different locations, however, even with frequent searches by car and the use of radio transmitters to track a few individual Rusty Blackbirds, no other off-campus foraging locations were found.

In an effort to increase and improve the sampling of the Rusty Blackbird flock, I located their nocturnal roost by following radio-

tracked birds that departed from campus each evening to the unknown roost. The idea was to set up nets at the roost during the day to capture large numbers of birds as they settled in for the evening. Other species that form flocks, such as American Robins, Common Grackles, and Red-winged Blackbirds, roost together for the night in very large groups. Colonial Williamsburg has an area of dense bamboo stands where thousands of American Robins, Common Grackles, Red-winged Blackbirds, Brown-headed Cowbirds, and European Starlings roost for the night. It was suspected that the Rusty Blackbird flock might also use this roost. However, through the use of tracking with radio transmitters, I located the roost in 2009 in the tidal marsh along Queen's Creek, across from the Queen's Lake Marina. (Fig. 10). This site was approximately 6.7 km from the William and Mary campus.





**Figure 10.** Straight-line path (yellow line) from foraging area of campus (colored area) to the roost site in 2009 (yellow marker).

The Queen's Creek site proved to be untenable for mist-net sampling efforts, for three reasons. First, the property is part of Camp Peary, a US Naval Reservation. The military heavily restricts access. Second, the muddy substrate of that particular tidal marsh was extremely soft, and nearly impossible to walk across. Field work would have not only been difficult, but probably dangerous. Third, by observing the Rusty Blackbirds settling down into the marsh on numerous nights, it was noted that they utilized different sections of the marsh from night to night, and thus it would have been very

difficult to predict where productive net placements should have been located.

### ***Sexual Size Dimorphisms***

I expected to find that male Rusty Blackbirds were roughly 15% larger than females by mass, with a similar dimorphism for the other various measurements. While the sexual size dimorphism was quantified by Dunning (1984) at 16.5% by mass, the sample in this study produced a difference of 14.2%. This minor difference may have been due to the fact that I had a much smaller sample of females (n=24) than Dunning (n=105). Comparisons of mean and range to all published sources are included below (Table 11). Indeed, there are probably also geographical differences in size between the population in this study and that of the other sources below, with the notable exception of the Meanley (1967) study, which was located in the Great Dismal Swamp, also on the Coastal Plain of Virginia. However, as previously noted, Meanley's (1967) sample size was extremely small (n=7 males, 3 females), so differences between his means and mine might well be expected.

**Table 11.** Comparison of linear measurements (mm) and mass (g) of this study to published sources.

|            | Sex | Source             | $\bar{x}$ (range)     | n   | $\Delta\%$ |
|------------|-----|--------------------|-----------------------|-----|------------|
| MASS       | ♂   | Dunning (1984)     | 64.3 g (45.9 – 80.4)  | 91  |            |
|            |     | Meanley (1967)     | 69.2 g (63.9 – 80.2)  | 8   |            |
|            |     | McGann (2011)      | 63.7 g (53.5 – 71.5)  | 68  |            |
|            | ♀   | Dunning (1984)     | 55.2 g (47.0 – 76.5)  | 105 |            |
|            |     | Meanley (1967)     | 54.6 g (52.8 – 57.7)  | 3   |            |
|            |     | McGann (2011)      | 55.8 g (46.5 – 65.0)  | 24  |            |
| WING CHORD | ♂   | Meanley (1967)     | 118.0 (115.5 – 123.5) | 7   |            |
|            |     | Godfrey (1986)     | 114.6 (110.5 – 117.4) | NA  |            |
|            |     | Pyle et al. (1987) | NA (111.0 – 123.0)    | 100 |            |
|            |     | McGann (2011)      | 112.8 (106.5 – 119.0) | 69  |            |
|            | ♀   | Meanley (1967)     | 110.0 (106.0 – 113.0) | 3   |            |
|            |     | Godfrey (1986)     | 107.3 (103.1 – 112.4) | NA  |            |
|            |     | Pyle et al. (1987) | NA (101.0 – 113.0)    | 100 |            |
|            |     | McGann (2011)      | 104.5 (99.0 – 108.0)  | 24  |            |
| TAIL       | ♂   | Meanley (1967)     | 93.1 (88.0 – 99.0)    | 7   |            |
|            |     | Godfrey (1986)     | 88.9 (83.0 – 91.0)    | NA  |            |
|            |     | McGann (2011)      | 87.0 (76.0 – 104.0)   | 69  |            |
|            | ♀   | Meanley (1967)     | 87.7 (83.0 – 91.0)    | 3   |            |
|            |     | McGann (2011)      | 80.3 (74.0 – 93.5)    | 24  |            |
| TAR-SUS    | ♂   | Godfrey (1986)     | 31.4 (29.5 – 33.0)    | NA  |            |
|            |     | McGann (2011)      | 30.8 (27.9 – 33.6)    | 69  |            |
|            | ♀   | McGann (2011)      | 29.4 (27.1 – 31.9)    | 23  |            |
| BILL       | ♂   | Meanley (1967)     | 19.6 (18.5 – 21.5)    | 7   |            |
|            |     | McGann (2011)      | 19.6 (18.0 – 22.0)    | 69  |            |
|            | ♀   | Meanley (1967)     | 18.2 (17.5 – 19.0)    | 3   |            |
|            |     | McGann (2011)      | 18.0 (16.3 – 19.2)    | 24  |            |

For the respective linear morphometric measurements of body size recorded in this study, males were larger than females on average by the following percentages: wing chord: 7.9% (compared to 7.3% for Meanley (1967) and 6.8% for Godfrey (1986)); tail length: 8.3%

(compared to 6.2% for Meanley (1967); tarsus length: 4.8% (no other published sources for comparison). For the following linear measurements of the bill dimensions, males were larger than females on average by the following percentages: culmen: 6.7%, width: 7.73%, depth: 5.11%. The only other published source by which to compare bill morphology is Meanley (1967), which reports only the exposed culmen (measured from base of the bill) measurement. The exposed culmen measurement of males in my study was 8.9% larger than females (as compared to 7.7% for Meanley (1967)).

While the means of the various morphological measurements were compared for males and females with t-tests in the Results section, the frequency distributions of the relative differences in the magnitude of the sexual size dimorphisms can be visually compared with simple boxplots (Fig. 11, 12). Fig. 11 illustrates the frequency with which males and females overlap in size for each of the each of the body size measurements. Fig. 12 illustrates the frequency with which males and females overlap in size for each of the bill size measurements. In this way, the sexual size dimorphisms of the male and female segments of the local population can be visualized.

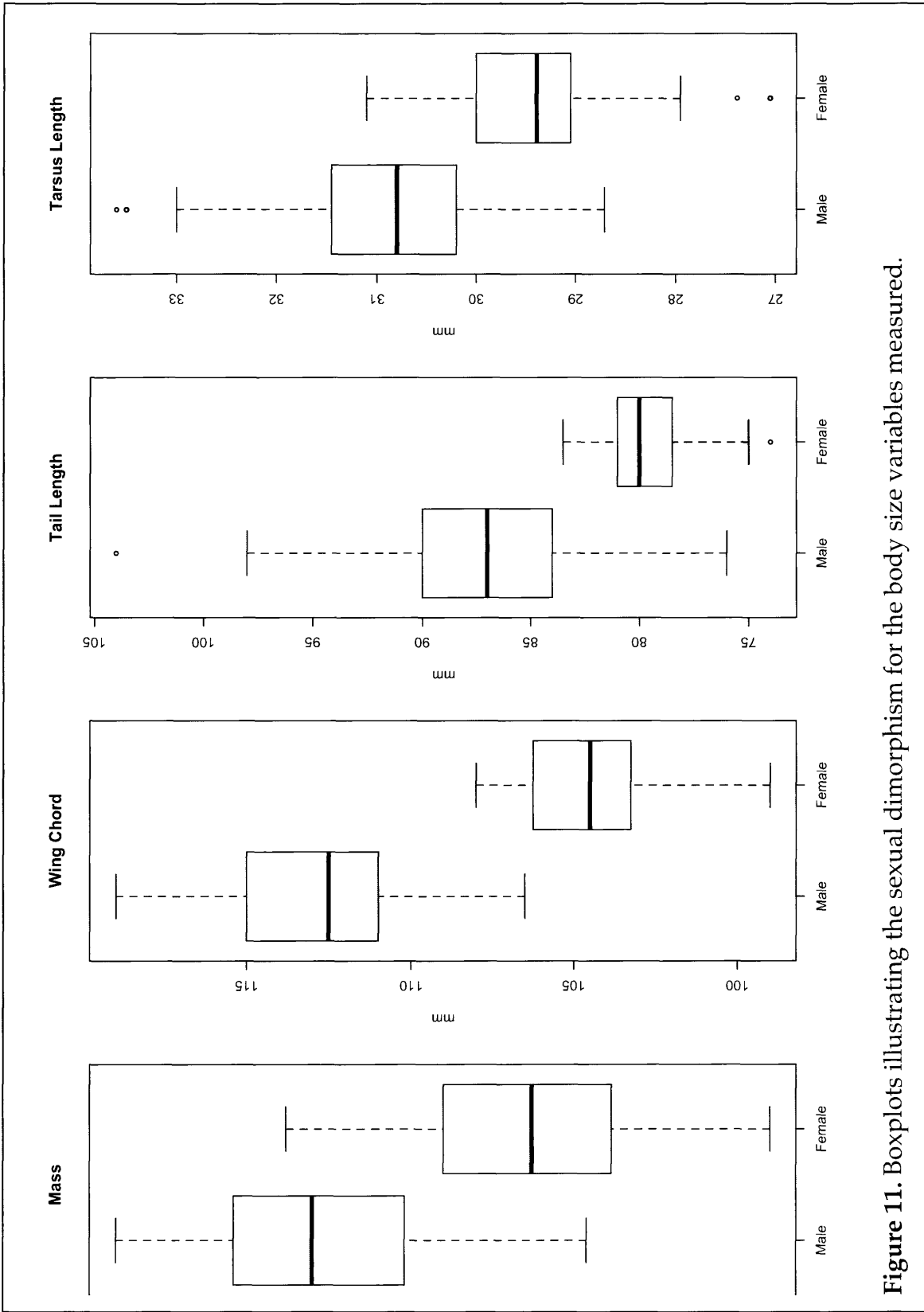
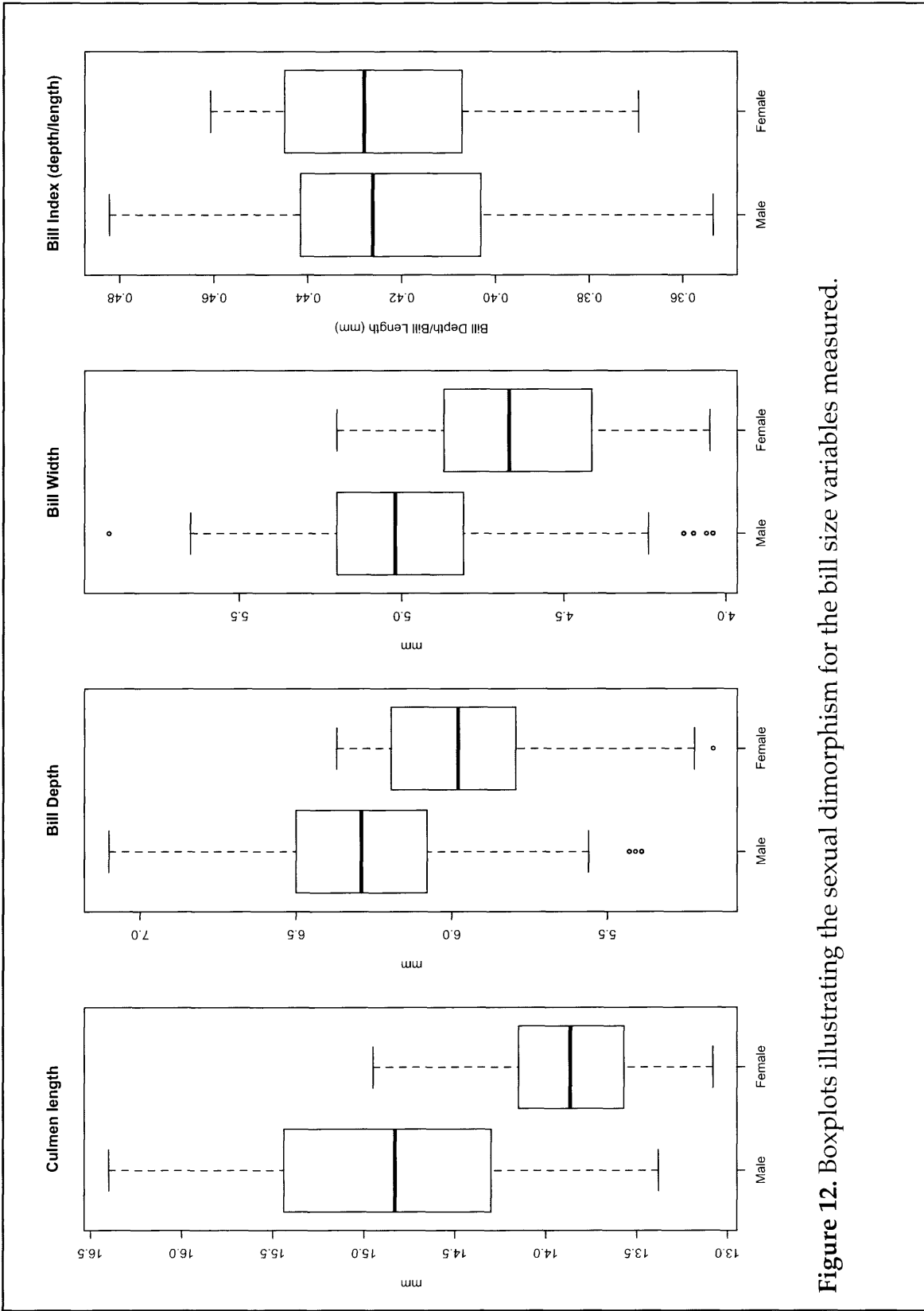


Figure 11. Boxplots illustrating the sexual dimorphism for the body size variables measured.



**Figure 12.** Boxplots illustrating the sexual dimorphism for the bill size variables measured.

Of the body size measurements recorded, wing chord was the most dimorphic. This information could be useful in developing a discriminant function to be used by researchers to verify sex in cases where identification by plumage pattern might be difficult. When Rusty Blackbirds are in fresh plumage during their southbound fall migration, having recently completed their annual molt in late summer, the margins of the birds' feathers are rust-colored. This is the basis for their name, and both sexes exhibit this chromatic plumage pattern. Over the course of the winter, the rusty feather edges are worn down, and the plumage pattern changes, to reflect the underlying base color to a larger degree. The base color of males is black and females are a dull grayish brown. This base color is the best plumage feature for identifying male and female Rusty Blackbirds. However, in fresh fall plumage, both males and females can be strikingly rusty colored, and the brightness of the pattern distracts many bird-watchers from the base color. This is the also the time when Rusty Blackbirds are perhaps most likely to be encountered by inexperienced banders operating migration-surveillance banding stations, who probably have a lesser amount of experience working with the species.

Furthermore, sexual difference in wingtip shape might have fruitful implications for future studies of differential migration in the

species. Within species, longer-distance migrating segments of the population often exhibit pointier wingtips, but not necessarily longer wings than sedentary or shorter-distance migrating populations (Mulvihill and Chandler 1991). However, simple wing chord measurements are not appropriate measures of the shape of the wingtips, but rather more descriptive and accurate measures such as pointedness and convexity should be compared (Lockwood et al. 1998). Long-distance migrants exhibit pointier and more convex wingtips than shorter-distance migrants. For the entire population of Rusty Blackbirds, if they exhibit a pattern of differential migration, I would predict that the females would have relatively pointier and more convex wingtips, and higher aspect-ratio wings than males. However, the sexual size dimorphism complicates such an analysis, and thus any studies would have to control for bodysize, such as with a size-constrained components analysis method (Lockwood et al. 1998). Furthermore, such a proposed study would have to representatively sample Rusty Blackbirds along a north-south transects of the entire wintering ranges within both the Atlantic and Mississippi flyways.

Thus, I confirmed that Rusty Blackbirds wintering in Virginia do exhibit sexual size dimorphism, as previously reported for Virginia and elsewhere, with males being larger for all traits measured. This has



implications for understanding cold-weather tolerance, differential migration, and competition for resources in this species.

### ***Differential Diets by Sex***

I hypothesized that the larger male Rusty Blackbirds would differ in diet from the female as a result of their larger body and bills. In particular, a larger bill would allow exploitation of acorns and other large seeds, while their larger body size would give them an advantage in competition for preferred foods. I predicted that males would have lower ratios of stable isotopes of nitrogen, due to greater reliance on easily acquired tree seeds, and lower reliance on insects, which are higher in the food chain. I expected that males and females would have different carbon stable isotope signatures, either because the males were better at exploiting the corn that was set out for bait, or because females relied more heavily on the aquatic food web. This study was not set up to test the hypothetical mechanisms behind a potential differential diet between the sexes of Rusty Blackbirds. However, I set out to first evaluate whether there was evidence for dietary differences between the sexes as a result of size dimorphism. There was only weak evidence for average differences between the sexes in the signatures of carbon or nitrogen stable isotopes, when looking at the components of the averaged model. The signatures are

virtually superimposed on one another. To put this result into perspective, the difference in  $\delta^{15}\text{N}$  that results in a shift of one trophic level is approximately 3 parts-per-thousand units, whereas male and female Rusty Blackbirds differed by 0.18 units. Interpreting differences in carbon signature is more difficult in the absence of information on dietary items, but suffice it to say that the two sexes appear to be eating very similar diets.

This study area lies on the northern end of the wintering range of the Rusty Blackbirds, and the sex ratio of the locally observed Rusty Blackbird population was heavily male biased. Just as (Stein et al. 2008) proposed that competition between the sexes of the dimorphic Western Sandpipers would increase as the sex ratio approaches 1:1, I predict that Rusty Blackbirds would experienced increased competition for food resources as their sex ratio approaches 1:1. However, it is not known if the Rusty Blackbird exhibits a latitudinal gradient in sex ratio, like the Western Sandpipers studied by (Stein et al. 2008), or if the Rusty Blackbirds are alternatively or additionally segregating into separate flocks by sex and foraging in different areas, or at different times. The duration of my field work conducted at the College of William and Mary site led me to believe that the latter scenario was not occurring, at least around this college campus site. The vast majority of the time in which groups of Rusty Blackbirds were observed on the campus, in all years of the study, the groups

were numerically dominated by males. I cannot rule out that there were undetected flocks of females around the vicinity of the study area, but it seems unlikely that they would have gone completely undetected in my repeated explorations of other potential habitat. However, that question was not evaluated with empirical data.

Male and female Rusty Blackbirds may exhibit forms of niche segregation that were not addressed by the analysis of stable isotope ratios. While the sexes were consuming chemically similar diets, they may have been appropriating the dietary items in from different micro-habitats, or in separate areas, or at separate times. Indeed many other forms of niche segregation have quantified time-budgets and spatial relationships to particular environmental resources (e.g. Moysey 1997). These other types of niche differentiation may serve each sex in reducing the amount of aggressive interactions around food items (a reduction in competition) while still providing chemically indistinguishable diets. Trophic segregation is only one specific subset of niche segregation.

### ***Individual Morphological Correlates of Diet***

I expected to find that both body size and bill size were correlated with diet. The null model in this exercise was that neither body size nor bill size correlated strongly with diet. This was evaluated by performing ordinary least squares (OLS) regressions of

$\delta^{15}\text{N}$  on both body size and bill size. Unexpectedly, I cannot rule out the null hypothesis, as OLS regressions demonstrated that trophic level, as indicated by  $\delta^{15}\text{N}$ , was not strongly correlated with the Body Size Index ( $R^2=0.0097$ ,  $F=0.88$  1,89 DF,  $p=0.35$ ), or Bill Volume ( $R^2=0.0045$ ,  $F=0.45$  1,91 DF,  $p=0.53$ ). However, I was still able to complete the model selection and parameter estimate exercises, and evaluate whether bill size or body size variables were more correlated with trophic level. Even though the result was statistically insignificant, the modeling exercise allowed me to conclude that body size was 8x more correlated with trophic level than bill size. If anything, this indicates the functional insignificance of bill volume in the observed trophic statuses of individual Rusty Blackbirds. Indeed, bill size might be a poor proxy for its functional abilities to process seeds or capture prey. Musculature and lever-arm ratios may play a role equally or more important than bill volume when it comes to procuring and/or processing food items in blackbirds. It is interesting to note in Fig. 11, that in spite of sexual dimorphism in bill measurements, the bill index (ratio of depth to length) was no different between males and females. Perhaps the bill shape character has more direct implications for food processing—and the sexes do not differ in bill shape as indicated by bill index (Fig. 12)—so perhaps the sexes are equally capable of handling these food items?

### ***Influence of Diet on Body Condition***

I was not sure in which direction trophic or carbon source differences in diet (as assessed by stable isotope ratios) would correlate with better or worse body condition, because Rusty Blackbirds are omnivorous in winter, and the question of access to food is not necessarily related to differences in the stable isotope ratios of nitrogen and carbon. However, this study lays the groundwork for a more strongly evaluative study of diet *quality* in Rusty Blackbirds. More likely, body condition is related to the quantity and quality of dietary items consumed. That being said, I was able to model whether individual Rusty Blackbirds foraging at higher or lower average positions in the food chain, or foraging in food chains of differing carbon source were exhibiting differential body conditions. What I found was that the nitrogen stable isotope ratio was about eight times more correlative with body condition than the carbon stable isotope ratio. Rusty Blackbirds consuming a diet that was lower in trophic level, on average, had a better body condition.

Unknown in Rusty Blackbirds is the influence of social dominance on access to food. Blackbirds forage in flocks, and in many flocking species of birds, subordinates have less-reliable access to food, and increased risk of starvation. Typically, species increase their fat reserves in accordance to risk of starvation, and thus more socially-dominant individuals will have lower body fat scores than

subordinates (Pravosudov et al. 1999). It might be true that the larger male Rusty Blackbirds are more dominant over females when foraging side-by-side on the ground. Or not. To evaluate the role of social dominance in future studies of Rusty Blackbird body condition, body fat might be interpreted as a proxy for access-to-food, given that in Black-capped Chickadees (*Poecile atricapillus*), more dominant individuals are both heavier for their size (better body condition) and have lower body fat scores (Pravosudov and Lucas 2000). However, studying social interactions to evaluate dominance rank is difficult enough in relatively small, sedentary, and stable flocks of Chickadees. Translating the same behavioral-interaction monitoring techniques to large, mobile, dynamic blackbird flocks would be extremely difficult. It is also important to remember that correlation is not causation, and in a range of species body condition and dominance are complexly related to each other. However, it might be feasible to generalize whether the larger or smaller sex is more socially dominant.

### ***Mercury Burden***

I expected that female Rusty Blackbirds would exhibit higher mercury burdens than males, on average, if they were foraging at a higher trophic level. However, there was no difference in the diets of males and females, so therefore I expected their mercury burdens to be similar. This was in fact the case, and there was only a small

observable difference in the mercury concentration in the blood of male and female Rusty Blackbirds, with males having slightly higher values on average ( $t = 1.76$ ,  $df = 70$ ,  $p\text{-value} = 0.082$ ).

In the respective regressions of mercury burdens on the nitrogen and carbon stable isotope ratios of individual birds, it was expected that mercury would be significantly related to trophic level, because methyl mercury bioaccumulates and biomagnifies up food webs. The functional link between nitrogen stable isotope ratio and mercury concentration is well described in the literature, and that pattern was observed in this study. The functional link between carbon stable isotope ratios and the mercury concentration of Rusty Blackbirds in this study is a mystery. Speculating that the food web in the area of this study is based mostly on plants photosynthesizing with the C3 pathway, such as oaks (i.e. tree leaves and detritus serve as a major putative carbon source in the terrestrial and aquatic food webs), it was expected that the carbon isotope ratios for the blackbirds sampled in this study would be very similar—whether the birds were foraging on insect constituents of food webs founded on detrital oak leaves, or whether the blackbirds were consuming vegetative matter such as acorns. Nothing is known about the variation in mercury among dietary items of different carbon isotope ratios in this ecosystem. One recognized source of carbon derived from the C4 photosynthesis pathway in this study, was the cracked corn I provided

as bait around the netting site. Importantly, the Rusty Blackbirds were observed feeding on the cracked corn, but they spent the majority of their day away from the site, so it was assumed that the corn was only a small (however, potentially significant) constituent of their diet. Speculating, it might be the case that Rusty Blackbirds that were eating more corn were doing so as a 'last resort', and they were not having great success foraging on acorns and other plant seeds. If true, these particular birds may have been foraging at a higher trophic level as well, and subjected to higher levels of dietary mercury. The results of the body condition modeling suggest that individuals that were foraging at lower trophic levels also had better body condition, but that result was not robust and deserves further study.

Finally, it should be noted that the anecdotal number of recaptures (n=3) in this study all indicated increasing levels of mercury concentration while the birds were present during the study (Fig. 8). This is an unexpected result, as the area is not known as an area of especially high levels of this ubiquitous trace metal. Furthermore, given that Rusty Blackbirds typically undergo a prealternate molt on their wintering grounds, the mercury level in the bloodstream could be reasonably expected to decline during the overwintering timeframe of this study, as feather growth occurs (Brasso and Cristol 2008). However, recent dietary mercury exposure alone may not account for the increasing mercury concentrations observed in the blood of



overwintering Rusty Blackbirds. A controlled dosing study of molting Great Skuas (*Catharacta skua*) found that mercury levels in the blood outside of the molting period reflected extended dietary intake, and a similar sustained rise in blood mercury levels was observed during molt periods (Bearhop and Ruxton 2000). I did not observe whether the Rusty Blackbirds sampled in this study were molting or not, and in fact the discovery of a prealternate molt in Rusty Blackbirds occurred while this study was taking place (Mettke-Hofmann et al. 2010). Future winter ecology studies of Rusty Blackbird should monitor molt, given that it is an energetically expensive endeavor, and the plumage quality may reflect the quality of the overwintering resources, with potential downstream implications relating to mate choice and reproductive success on the breeding grounds.

### ***Conclusions and Implications for Rusty Blackbird Conservation***

One of the biggest limitations to this study is that it dealt with only one site and ostensibly one group of Rusty Blackbirds, over the course of only two winters. The conclusions of this thesis may only pertain to the single group of Rusty Blackbirds foraging on the campus of the College of William and Mary. However, this research is contributing directly to the International Rusty Blackbird Working Group, and the findings herein will be joining those of other

researchers working in South Carolina, Georgia, and the lower Mississippi alluvial valley. Indeed, no other studies of Rusty Blackbird winter trophic ecology were conducted on the northern end of their winter range. Through the working group, the results of all studies in all locations will be combined into management guidelines as quickly and efficiently as possible. The best time to conserve a species is while it is still relatively common, and there is no time to waste with the Rusty Blackbird.

The nesting success rates found by (Powell et al. 2010c, Matsuoka et al. 2010b, Powell et al. 2010b) seem to indicate that the population is not suffering from limitations during the nesting phase of its lifecycle. Those authors point to juvenile survival, or low annual adult survival, as more likely candidates for what's driving the declining population. Furthermore, the results of (Barnard et al. 2010) might indicate that Rusty Blackbirds are facing challenges on their wintering grounds above and beyond those faced by the other more common species of Icterid. More work is needed on all components of the Rusty Blackbird's lifecycle, but the overwintering phase should be emphasized. Additionally, the migratory phase of this species should not be overlooked, especially given the protracted periods of migration in late autumn into early winter. Deuterium isotope studies have made the most broad-scale generalizations about Rusty Blackbird movement across the North American landscape. Simple radio-telemetry efforts

have attempted to assess landscape-scale movements and patterns of habitat use, but efforts have been limited by the seemingly large home ranges of wintering Rusty Blackbirds, as well as the larger-scale movements within the breeding season. Perhaps definitive answers to the questions of overwinter survival and regional-scale population movements and habitat use will only come through the development of more powerful tracking technology. The use of light-sensing geolocator tags, which have recently been successfully employed (Stutchbury et al. 2009) on the similarly-sized Purple Martin (*Progne subis*) and Wood Thrush (*Hylocichla mustelina*), would be unworkable with Rusty Blackbirds given their abysmally low rates of recapture.

Studies of Rusty Blackbird winter foraging ecology should continue, with increased usage of some of the methods used to evaluate the quality of stopover habitat of migrant songbirds. Studies of stress hormones, body condition, and the recently-discovered prealternate molt should be used to evaluate the health of Rusty Blackbirds utilizing various habitat types. One advantage of conducting such studies on the northern extreme of the wintering range might be that the ecology more closely resembles the stopover ecology during the especially protracted migratory phases of the lifecycle. Studying Rusty Blackbirds during their migratory phase is an even more difficult scenario, as evidenced by the inability of efforts

described in this thesis to capture Rusty Blackbirds on the campus of the College of William and Mary prior to the New Year.

One of the advantages of working on the northern extreme of the wintering range is that conditions may be more representative of the stopover ecology of the species during its protracted migratory phases of its lifecycle. The techniques of studies of stopover habitat quality should be used to evaluate the habitats used by Rusty Blackbirds during the winter.

Future studies should additionally take an experimental approach not employed in my correlational, descriptive approach. One example would be experimentally raising and lowering water levels in bottomland hardwood forests, such as the Great Dismal Swamp National Wildlife Refuge, in efforts to improve and adaptively-manage the property for Rusty Blackbirds. Indeed, there is a very important role for the National Wildlife Refuge system to play in the protection and management of extensive bottomland hardwood forests for Rusty Blackbirds. Managers should manipulate water levels to promote areas of shallow flooding, with temporal periodicity that would promote patchy distributions of exposed wet substrate. Furthermore, mast-crop trees should be protected, especially those with smaller acorn sizes, such as Willow Oak. Lastly, the provision of supplemental food should be experimentally studied, with the ultimate measure of success being the size and health of the local Rusty Blackbird population.

Supplemental feeding may well have yet-unknown costs, such as by increasing competition with other blackbird species. The role of other blackbird species in competition with Rusty Blackbirds is a significant question that deserves study.

In my study of Rusty Blackbirds, I found that male and female Rusty Blackbirds, while sexually dimorphic, do not seem to be targeting different food resources during the overwinter phase of their lifecycle. The future recovery plan for Rusty Blackbirds will not have to concern itself on potentially different nutritional requirements for the dimorphic males and females. Secondly, the International Rusty Blackbird Working Group will have to figure out a framework among all research conducted on the wintering grounds, so we can evaluate with certainty whether the species exhibits patterns of differential migration. Conditions may vary on a latitudinal gradient, with different implications for the foraging ecology of male and female Rusty Blackbirds as the sex ratio varies and/or approaches parity. My study suggests that Rusty Blackbirds deriving more of their nutrition from vegetative matter during the overwintering period are in better body condition than Rusty Blackbirds deriving more of their nutrition from animal prey. This result calls attention to the significance of tree mast crops for the overwintering success of Rusty Blackbirds. More research is needed on the specifics of their winter dietary requirements, and the role of nutrition in overwinter survival, body

condition, and prealternate molt. My results suggest that the mercury levels of overwintering Rusty Blackbirds are not obviously and catastrophically high, but the nonlethal effects of mercury toxicity are largely unknown, and there no information available about the thresholds for detrimental effects in Rusty Blackbirds. Rusty Blackbirds may be especially sensitive to mercury toxicity, and given the relative severity of the decline of the more eastern Rusty Blackbirds, and the increased levels of mercury in some of the eastern population, mercury deserves further study. Future studies should determine the sources of mercury in the diet, and specifically how they vary in carbon stable isotope ratios.

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