

Migration Ecology of a Declining Songbird, the Rusty Blackbird (*Euphagus carolinus*)

Thesis

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By

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## Abstract

Each spring and fall, hundreds of species of North American birds migrate thousands of kilometers between breeding and wintering grounds. Most of the migratory period is not spent in flight, but rather at stopover sites where birds rest and refuel. This is a vulnerable time for migrants, since they are often in an unfamiliar landscape, balancing the necessities of rapidly refueling with increased risk of predation and competition for resources with other migrants. Many migrant songbirds are in steep decline, and understanding the movement behavior and habitat use of these birds on stopover is crucial to developing effective conservation action.

One of the most rapidly declining songbirds in North America is the Rusty Blackbird (*Euphagus carolinus*), which has experienced population declines of more than 85% over the last 50 years. Some possible causes of this decline have recently been identified on the breeding and wintering grounds, but very little is known about their behavior and habitat requirements during migration. We attempted to fill this knowledge gap by studying the species during spring and fall migration at a high-traffic stopover site in northern Ohio, on the southwest shore of Lake Erie. We utilized an automated telemetry array in the western Lake Erie basin and across Ontario to track landscape-scale movements of radio-tagged individuals during and after stopover events. Specifically, we wanted to know how long individuals spent at the study site, since stopover duration is one way to determine how reliant a population is on particular stopover sites.

We found that stopover duration of Rusty Blackbirds at our site was unusually long for a songbird, at an average of ~25 days during both fall and spring migrations. During the spring, nearly all captured birds (98%) were molting body feathers, which may partly explain the long stopover in that season. Furthermore, many individuals made landscape-scale (10-35km) movements during their stopover event. Taken together, these behaviors describe a migration strategy that closely resembles shorebird migration strategies, where birds congregate to forage for several weeks at a few key staging areas. This indicates that high-quality stopover habitat may be critically important to Rusty Blackbird populations. We also found that departure decisions were largely determined by favorable tailwind conditions, and birds made nocturnal migratory flights that exceeded 400km. This is the first time nocturnal migration has been described in this species, which could expose a large portion of the population to risk of collision with offshore wind turbines being installed in Lake Erie.

In addition to our study of movement behavior, we investigated Rusty Blackbird fine-scale habitat preferences on stopover. We tracked radio-tagged individuals by hand to locate foraging flocks, and compared habitat characteristics at foraging locations versus random locations. Rusty Blackbirds selected microhabitat with shallow water and leaf litter, often avoiding grass, forbs, and herbaceous shrub cover. Outside of forest patches, they preferred areas closer to habitat edges and with some canopy cover, as well as areas with a mixture of different habitat types. Our description of Rusty Blackbird stopover habitat use and behavior will help inform conservation and management practices across the species' migratory range.

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## **Chapter 1: Automated Telemetry Reveals Staging Behavior in a Declining Migratory Songbird, the Rusty Blackbird (*Euphagus carolinus*)**

### **Introduction**

Each spring and fall, hundreds of species of North American birds migrate thousands of kilometers between their breeding grounds and wintering grounds. For many species, these migrations are completed as quickly as energetically possible (Alerstam et al. 2003), and their annual cycle is essentially two stationary periods punctuated by two periods of rapid movement. Those periods of rapid movement, in turn, are punctuated by stopover events, where most birds stop to refuel for several days before continuing on their migration (Newton 2008). For these species, the location of these stopover events is largely stochastic (Catry et al. 2004), and they are not considered distinct features of their annual cycle. Many birds follow this migratory pattern, but there are numerous examples of species for which stopover locations are not stochastic. Instead, specific locations are repeatedly used and can function as more than refueling sites (Cantos and Telleria 1994, Leu and Thompson 2002, Harrington et al. 2010).

One measure of the reliance of a population on particular stopover locations is the length of time individuals utilize a site (Pledger et al. 2009). Long stopover durations could be driven by a number of factors, such as availability of a specialized resource or rate of energy acquisition. For instance, Red Knots (*Calidris canutus rufa*) specialize on

energy-rich horseshoe crab eggs (*Limulus polyphemus*) during spring stopover, resulting in 12-14 days at specific stopover sites around Delaware Bay, USA (Gillings et al. 2009). Other species complete important life history events during stopover (e.g. molt; Leu and Thompson 2002), requiring extended stays at sites beyond what is required for refueling. These strategies represent “staging” (i.e. long stopover at particular, traditionally utilized high-quality sites) in contrast to “stopover” (i.e. short stays at stochastic, variably utilized low to moderate quality sites; Warnock 2010). For species that exhibit a staging migratory strategy, where stopover fulfills multiple functions and specific sites are used repeatedly, habitat conservation is essential (Sheehy et al. 2011).

Stopover duration can vary among individuals within a population due to intrinsic factors. Most obvious is energy stores, as birds arriving with lower fat content must remain on stopover longer to build up energy reserves for continuing migration (Deppe et al. 2015, Lupi et al. 2016). In addition, pre- versus post-breeding migrations are expected to vary due to the time constraints of breeding resulting in shorter spring stopovers (e.g. Morris et al. 1994). Furthermore, age or sex may influence duration due to asymmetric selective pressures on arrival phenology at breeding areas (Izhaki and Maitav 1998, Morbey and Ydenberg 2001, Morris and Glasgow 2001) and differing levels of experience in old versus young birds (Newton 2008, McKinnon et al. 2016).

Extrinsic environmental factors may also influence stopover dynamics. For instance, departure timing is strongly correlated to favorable wind conditions in a number of species (Mitchell et al. 2015, Dossman et al. 2016). Rainfall may drive food availability, and therefore refueling rates, influencing stopover duration and survival

(Halupka et al. 2017). Geography can also be a factor, as migrants will congregate and remain longer at sites that are adjacent to large barriers to migration (Alerstam and Lindstrom 1990).

Many migratory songbird populations are in steep decline, and identifying the causes of these declines is one of the most pressing concerns in modern ornithology (Robbins et al. 1989, Martin et al. 2007). When examined relative to other annual cycle stages, the highest mortality in migrant species takes place during migration (e.g. Sillett and Holmes 2002, Klaassen et al. 2014). However, migration is also one of the least understood stages of a bird's annual cycle, largely due to the difficulties of studying individuals during a period of large-scale movement (Marra et al. 2015). The Rusty Blackbird (*Euphagus carolinus*) is a once-common species that has experienced 85-95% declines over the last 50 years (Niven et al. 2004), and shows qualitative evidence of declines dating to the 19th century (Greenberg and Droege 1999). The last decade has seen a number of studies attempting to identify causes of the decline on the breeding grounds (e.g. Matsuoka et al. 2010, Powell et al. 2010) and the wintering grounds (e.g. Lusnier et al. 2010, Mettke-Hofmann et al. 2015). Some possible causes have been identified, including climate change (McClure et al. 2012), habitat loss on the wintering grounds (Greenberg et al. 2011), and methyl-mercury contamination (Edmonds et al. 2010), but the decline of this widespread species remains largely enigmatic (Greenberg and Matsuoka 2010).

One significant gap in knowledge is the stopover ecology and behavior of Rusty Blackbirds. From the scant literature available, we know that spring migrants form large

congregations in some areas, but remain diffuse across most of their migratory range (Rusty Blackbird Spring Migration Blitz; Evans et al. in prep). However, we have no information on how individuals utilize stopover sites, and whether there are specific stopover sites that play an important role in their annual cycle. To fill this gap, we conducted a study at a high-traffic Rusty Blackbird stopover site to determine how individuals utilize stopover sites and to elucidate challenges they may experience during migration and stopover. During the non-breeding period, Rusty Blackbirds are a flocking species strongly associated with forested wetland habitat (Luscier et al. 2010). Thus, it is possible that stopover site selection is not stochastic; rather, birds may aggregate in traditional high-quality habitat sites, particularly since large expanses of forested wetland have been drained and felled for agricultural development (Dahl and Johnson 1991).

Our overarching goal was to describe Rusty Blackbird stopover ecology, and specifically determine whether use of high-traffic stopover sites represents a “staging” strategy in this species. To determine whether Rusty Blackbirds exhibit a “staging” or “stopover” strategy, we consider long stopover durations, high site fidelity between seasons, long migratory flights post-departure, and large-scale spatial use of the site to be evidence of “staging”; whereas short stopover durations, low site fidelity, short migratory flights, and restricted spatial use of the site to be evidence of “stopover” behavior. We utilized a large automated telemetry array to track these behaviors in both spring and fall. We also gathered information on intrinsic factors that may influence stopover and movement behaviors (age, sex, body condition, and molt); and extrinsic factors (wind, temperature, and precipitation conditions) at the stopover site. We sought to determine

stopover duration for comparison to other species, and to determine where Rusty Blackbirds sit within the spectrum of migratory strategies (Alerstam 2011). We predicted that stopover duration would be 1) longer in fall than in spring, as birds do not experience pressure to breed during fall migratory movements, and 2) longer for birds in poor body condition and with higher molt scores. In addition to stopover duration, we investigated arrival and departure dynamics. As males are under greater pressure to return to the breeding grounds to establish territories (Morbey and Ydenberg 2001), we predicted that 3) males would arrive sooner than females in the spring, but expected no such relationship in the fall. Since inexperienced juvenile passerines often remain longer on the breeding grounds before venturing south (Markovets et al. 2008, Jakubas and Wojczulanis-Jakubas 2010), we predicted 4) younger birds would arrive later than older birds in the fall. Lastly, we expected that 5) most migratory departures would occur diurnally (Avery 2013), and that among extrinsic environmental variables, migratory departure would be 6) best predicted by wind conditions, with increasing tailwinds predicting departure (Dossman et al. 2016). In addition to these predictions, we describe other poorly known behaviors for Rusty Blackbirds such as flight speed, movement behavior during stopover, and site fidelity between seasons. Our results will fill a large gap in our knowledge of the full annual cycle of this species, which is critical to understanding their ecology and the causes of population declines.

## **Methods**

### **Study Site**

We captured Rusty Blackbirds over the course of four migration seasons from Fall 2015 to Spring 2017, at a high-traffic stopover site in northern Ohio. Our selection of the site was based on data from the Rusty Blackbird Spring Migration Blitz (Evans et al. in prep), a citizen science-based effort (developed by the International Rusty Blackbird Working Group and implemented using eBird checklists) to closely monitor spring migration across the species' range from 2014 to 2016. The Blitz identified Ottawa National Wildlife Refuge and Magee Marsh State Wildlife Area (41.608° N, 83.208° W), on the southwest shore of Lake Erie, as receiving among the highest number of migrant Rusty Blackbirds in North America. This site consists of a managed complex of wetlands approximately 28 km<sup>2</sup> in size, containing a substantial amount of suitable habitat (e.g. wet forest/shrublands; Avery 2013) for the species in a region dominated by agricultural development.

### **Capture Methods**

We captured birds passively (i.e. without playback or baiting) using mist nets by targeting reliable Rusty Blackbird foraging areas. All capture sites were located within 3km of each other. We banded birds with uniquely numbered U.S. Geological Survey aluminum bands and plastic color bands for individual field identification. We determined age and sex using feather and eye characteristics (Pyle 1998; Mettke-

Hofmann et al. 2010). We measured mass ( $\pm 0.1$ g), wing chord ( $\pm 0.5$ mm), tail length ( $\pm 0.5$ mm), tarsus length ( $\pm 0.1$ mm), fat score (scale of 0-7; Desante et al. 2008), and breast muscle (scale of 0-3; Cooper et al. 2015) in each individual. We examined each bird for flight feather and body molt; for birds captured in the spring, we recorded body molt using a variation of the Greenwood et al. (1983) method of combined contour molt index (hereafter CCMI). In brief, we estimated the percentage of molting feathers for a given patch of body feathers, and then summed all patch percentages and divided by the total number of patches to produce an overall CCMI score on a scale of 0 to 100 (Wright et al. in review). Molt was rare in the fall, so we did not employ this detailed method for fall-captured birds.

### **Automated Radio Telemetry**

We deployed 2.1g coded nanotags (model NTQB-6-1; Lotek Wireless, Inc., Newmarket, Ontario) on a subset of all captured birds each season, using the leg-loop harness method of attachment (Rappole and Tipton 1991). These tags broadcast on the same frequency (166.380 MHz, pulse rate 6.1 – 10.1 seconds), but have unique digitally coded signatures to allow for individual identification. Battery life of tags is approximately 9 – 12 months depending on the pulse rate, allowing for repeat detections should individuals return to the site during subsequent migrations. All field methods were approved by the Institutional Animal Care and Use Committee of The Ohio State University (protocol# 201500000028).

We used an automated telemetry tower array to track movements of tagged birds (Figure 1.1; Dossman et al. 2016). For ease of describing large-scale movements of birds, we divide the array into “local” and “regional” arrays. The “local” array consisted of 4 towers surrounding the main study site where we conducted bird capture (Ottawa NWR/Magee Marsh WA). These towers were in close proximity to one another, providing full coverage of the study site. The “regional” array consisted of seven additional towers spread out over 75 km to the west and east of the study site, along the southwestern shore of Lake Erie. We also monitored a tower 55 km to the north, on the northern shore of Lake Erie at Detroit River International Wildlife Refuge (not considered in the “regional” array). In addition to our local and regional arrays, we used data collected from the Motus Wildlife Tracking System array (Taylor et al. 2017) in Ontario, Canada and Indiana and Michigan, U.S.A. Motus is a collaborative network of automated telemetry operators, which coordinates data sharing among researchers. The towers outside the local array allowed us to monitor large-scale movements and confirm departure events. The deployment of Motus towers at the time of data collection can be found at [www.motus.org/data/receivers](http://www.motus.org/data/receivers).

The towers in the local and regional arrays each consisted of two to four 9-element yagi antennas mounted 9m above ground, connected to a Lotek Wireless receiver (model SRX 600, 800, or DL). Under ideal conditions (birds flying above trees, no obstructions between tag and tower) the detection range could reach >15 km (Taylor et al. 2011, Mitchell et al. 2015); under normal foraging and roosting conditions (birds on ground in forest or marsh) detection range was < 500m (Wright, unpublished data). We



oriented antennas such that they acted as roughly east-west or north-south “fences” to detect any birds flying by within the detection range. The receivers were scanning continuously throughout the study period, cycling through each connected antenna every 10 seconds. For every tag detection, receivers recorded the tag ID, time and antenna of detection, and signal strength.

### **Movement and Departure Categorization**

There was great variability in movements of tagged birds, so in order to identify migratory departures and relocations it was necessary to categorize the types of tower detections that occurred. For this categorization, we define stopover relocations as movements within the greater stopover landscape (Taylor et al. 2011), in the form of detections in the regional array as opposed to the local array. Further, since Rusty Blackbirds forage during the day and roost at night, we categorize diurnal and nocturnal detections separately. Lastly, we distinguish between “local” birds (tagged present season) and “returned” birds (tagged previous season).

#### *Diurnal detections:*

1. **To/from roost:** By far the most common detection, when birds group together in the tops of trees before going to ground to roost in evening, or after coming off roost in early morning.

2. **Foraging breaks:** Birds were rarely detected while actively foraging since they forage on the ground, but occasional detections occur throughout the day when they fly up to treetops for periods of time.
3. **Sporadic:** When birds left the local array, they might be missing for days and would be detected at seemingly random intervals in the regional array. This meant they were somewhere in the area but at a distance from the towers and only occasionally coming within detection range. We considered these types of detections evidence of stopover relocation.
4. **Diurnal migratory flyby:** If a “returned” bird was detected for only a few minutes at one or more towers, this was considered a migratory flyby. At a single tower, a regional flyby of a “local bird” is often indistinguishable from a “sporadic” detection, so we only define migratory flybys for “returned” birds (i.e. when a bird appears to be flying through the region on a migratory flight in a season subsequent to initial tagging).
5. **Diurnal departure:** Similar to a migratory flyby, but for local birds. If we detected a local bird flying by multiple towers in an appropriate migratory direction and never detected it again, this was considered a probable migratory departure.
6. **Absence:** The absence of any detections from the local array for greater than 2 days, followed by the return of detections, indicated the bird was not utilizing the study site and was considered a probable temporary stopover relocation.

*Nocturnal detections:*

1. **On roost:** If a bird was roosting very close to a tower it could be detected for either a portion of or the entire night. In this case it was always detected the following morning leaving the roost.
2. **Disturbed from roost:** Birds were occasionally detected briefly during the night, probably due to some disturbance on the roost. In this case, we always detected the birds the following morning at the same tower leaving the roost.
3. **Nocturnal migratory flyby:** This is the same type of detection as the diurnal migratory flyby, only occurring at night.
4. **Nocturnal departure:** After going down to roost, birds would be detected at one or more towers at some point several hours later. The factor distinguishing these detections from “disturbed” detections is that these birds were not detected the following morning, nor were they ever detected again in the regional array. We considered these probable migratory departures.

Nocturnal flights never resulted in subsequent diurnal detections elsewhere in the regional array, nor did “absences” ever begin or end at night; therefore, nocturnal flights never resulted in known stopover relocations. With the types of tower detections now

defined, we present our criteria for determining when birds made migratory departures, stopover relocations, or unknown movements (Table 1.1).

*Confirmed departure:* A bird made a “diurnal departure” or a “nocturnal departure”, and was detected at a distant tower in the Motus array the same day/night. Due to the geographical coverage of the Motus array (i.e. few towers south of the study area), very few fall departures resulted in “confirmed departures.”

*Probable departure:* A “diurnal” or “nocturnal departure”, not subsequently followed by Motus array detections. Both probable and confirmed departures were included in stopover and departure analyses.

*Confirmed relocation:* Birds were detected by diurnal categories 1-3 (most often “sporadic”), in the regional array after having left the local array.

*Probable relocation:* “Absence” from the array for over 2 days, followed by subsequent detections in either the local or regional array.

*Unknown movement:* When the final detections of birds were indistinguishable from diurnal detection categories 1-3, we were unable to categorize the apparent end of stopover as a true departure or a stopover relocation.

*Migratory flyby:* Either diurnal or nocturnal “migratory flyby” of returning bird (see above).

## Statistical Analysis

*Preparation of variables* – In order to avoid biasing our results, we excluded birds with unknown departures from stopover duration and departure behavior analyses. Furthermore, as there are different evolutionary and ecological factors driving fall and spring migration (Alerstam et al. 2003), we analyzed the two seasons separately. Intrinsic explanatory variables included day of capture, sex, age, fat score, body condition, and molt score (spring only, as we did not detect molt in fall). We quantified body condition as scaled mass index to correct mass for body size, with wing chord as our measure of structural body size (Peig and Green 2009). Capture day (or arrival day for returning birds) was correlated with sex in the spring, so we mean-centered Julian day of capture/arrival by sex to remove this collinearity (= standardized Julian day, hereafter SJD). For ease of interpreting coefficients, we also scaled and centered other continuous variables (body condition and molt score) to a mean of zero and standard deviation of one. To test for year effects in spring, we included year and all two-way interactions with year in model evaluation. Our first fall season did not have a large enough sample size ( $n=5$ ) to test for year effects in fall analysis. Additional two-way interaction terms were tested as appropriate, including age, sex, and body condition interactions with capture day and molt score. Returned birds (spring  $n=2$ , fall  $n=2$ ) were not captured again upon return, so we had several missing values for body condition, fat score, and spring molt score. In order to avoid removing relevant data from analyses, these few missing values were generated by multiple imputation by Gibbs sampling (package ‘mice’ for Program

R; Van Buuren & Groothuis-Oudshoorn 2011), which maintained the distribution of values for each variable.

*Stopover duration* – For statistical analyses, we calculated minimum stopover duration (date/time of capture/arrival until migratory departure) rounded to the nearest whole number of days. We used generalized linear regression models in a Bayesian framework to perform analyses, using the “brms” package (Bürkner 2017) in Program R (v 3.4.1; R Core Development Team 2017). As there was evidence of overdispersion in our dataset (dispersion = 6.7; function ‘dispersiontest’ in package “AER” for Program R; Kleiber and Zeileis 2008), we used a negative binomial error distribution with a log link function with flat priors (default for ‘brm’ function) for our models. Model evaluation was performed using leave-one-out (LOO) cross-validation, beginning with a global model and sequentially removing covariates based on 95% credible intervals overlapping zero to find the best-fitting model for each season. We assessed convergence and fit of our final models using the potential scale reduction factor ( $\hat{R}$ ; Brooks and Gelman 1998), effective sample sizes, and visual inspection of posterior predictive diagnostic plots. Models were run on four Markov Chain Monte Carlo (MCMC) chains of 2000 iterations each (burn-in = 1000, thin = 1).

*Departure behavior* – To examine the effects of weather and other covariates on the probability of departure, we employed extended Cox Proportional Hazards (CPH) models (detailed in Dossman et al. 2016). The primary advantage of using CPH models in this system is that it allows us to model the effects of time-dependent variables such as weather on the probability of migratory departure. Whereas the response variable is

typically risk of death occurring over a given time period, here CPH models are used to model “risk” of departure (Dossman et al. 2016). We performed CPH analyses using the “survival” (Therneau 2015) and “survminer” (Kassambara and Kosinski 2017) packages for Program R.

Meteorological data for the duration of each season were obtained from the Toledo Express Airport (Toledo, OH; <http://cdo.ncdc.noaa.gov/>; 48 km W of the study area), where a number of weather variables are recorded multiple times per hour. We tested the effect of temperature (°C), visibility (0-10 miles), cloud cover (four categories, from clear to overcast), precipitation (inches), and tailwind (see below) on the probability of departure, as well as endogenous variables such as age, sex, fat content, and body condition. Weather conditions at departure (except precipitation) were taken as the average of conditions over the hour previous to departure (Dossman et al. 2016). To test whether overall dryness of habitat had an influence on departure, precipitation was calculated as the cumulative precipitation over the 10 days prior to departure. As temperature is strongly correlated to time in these seasons and thus violates the proportional hazard assumption, we tested whether sudden changes in temperature predicted departure, using change in temperature from the previous day as our variable. For days where departure events did not occur, weather conditions (except precipitation) were taken as the average of conditions for the median hour of departure for all birds that season (2300 for each season). Tailwind component was calculated following Safi et al. (2013), using the formula:

$$[1] \text{ tailwind} = V_w * \cos(\beta)$$

Where  $V_w$  is wind speed and  $\beta$  is the difference between the bird's track direction and the wind direction. Increasing positive values represent greater tailwind, while increasing negative values represent increasing headwind.

We used likelihood ratio tests to select the best-fitting model for each season, beginning with all interaction terms tested in the stopover duration analysis, then iteratively removing them. In addition, we tested interactions between weather variables and year in our spring models. In the interest of parsimony, non-significant predictors ( $p > 0.05$ ; 95% confidence intervals overlapped zero) were sequentially removed from the global model. The relevant hazard ratios (exponentiation of the coefficients, hereafter HRs) of covariates are reported, such that HRs greater than 1 indicate greater probability of departure and shorter stopover durations, while HRs less than 1 indicate lower probability of departure and longer stopover durations. As our study site is located at a potential spring migratory barrier (the southern shore of Lake Erie; Dossman et al. 2016), we also classified known departure routes as being either around the lake (to the west) or across the lake (to the north and northeast).

*Arrivals, flight speed, and site fidelity* – To aid in our understanding of Rusty Blackbird migratory strategies, we summarize several other observed migratory movement behaviors. We used non-parametric Kruskal-Wallis tests to determine whether stopover arrival timing differs between age and sex classes, using capture day for all individuals and arrival or flyover day for all returning individuals. Minimum distance traveled in a single migratory flight and corresponding flight speed was calculated for all birds with confirmed departures or multiple detections on a returning flight. Distance



traveled was measured as the great-circle-distance between the two furthest automated telemetry towers where birds were detected (package “geosphere” for Program R; Hijmans 2016). To calculate flight speed (not accounting for wind conditions), we divided distance traveled by the time between departure from one tower and detection at the last tower. We used simple linear regression to determine if flight speed or distance was related to tailwind conditions on departure. Lastly, between-season stopover site fidelity (Table 2) was calculated as the proportion of birds known to survive the intervening stationary period (i.e. detected in the Motus array on the following migration) that stopped over at our study site for  $> 1$  day versus those that did not stop at the site.

## **Results**

In fall, we deployed nanotags on 5 and 34 birds (2015 and 2016, respectively). We deployed tags on 30 and 22 birds in spring (2016 and 2017, respectively). In fall, we tracked 19 after-hatch-year (AHY; 11 females, 8 males) and 20 hatch-year birds (HY; 6 females, 14 males). In spring, we tracked 38 after-second-year (ASY; 14 females, 24 males) and 14 second-year (SY; 8 females, 6 males) birds. Including returned birds in Fall 2016 and Spring 2017 (Table 1.2), we obtained confirmed or probable departures for 22 birds in the fall and 39 birds in the spring (Table 1.1). The mean minimum stopover duration for tagged birds with known (confirmed or probable) departures was 30.0 days in the fall and 28.9 days in the spring (Fig 1.2). Nearly all fall departures (95%) and 82% of spring departures occurred at night. The median hour of nocturnal departure in all

seasons was 2300, while the median hour of diurnal departure was 0700. Of 39 known spring departure flights, 28 (72%) went across Lake Erie, while the remainder went around the lake.

*Stopover duration* – The final model for fall stopover duration included only capture/arrival day as a predictor of stopover length (Appendix A). This model explained 29% of the variation in stopover length, with later capture/arrival dates resulting in shorter stopovers (Bayesian  $R^2 = 0.29$ ;  $\beta = -0.03$ , 95% credible interval of posterior distribution  $\{-0.04, -0.01\}$ , effective sample size  $> 2000$ ,  $\hat{R} = 1$ ). For the spring season, our final model included capture/arrival day (SJD), the interaction between sex and year (sex X year), and the interaction between body condition and molt score (condition X CCMI) (Appendix A). This model explained 63% of the variation in stopover length (Bayesian  $R^2 = 0.63$ , all effective sample sizes  $> 1500$ , all  $\hat{R} = 1$ ). Stopovers were shorter for later capture/arrival dates ( $\beta_{SJD} = -0.02$ ,  $\{-0.03, -0.01\}$ ) and males had longer stopovers than females in 2016, but shorter stopovers in 2017 (Figure 2;  $\beta_{int} = -0.46$ ,  $\{-0.87, -0.05\}$ ;  $\beta_{sex} = 0.18$ ,  $\{-0.08, 0.44\}$ ;  $\beta_{year} = 0.02$ ,  $\{-0.31, 0.36\}$ ). Higher molt scores (CCMI) resulted in longer stopovers when birds were in relatively poor condition, but this effect was absent from birds in better condition ( $\beta_{int} = -0.15$ ,  $\{-0.27, -0.03\}$ ;  $\beta_{ccmi} = 0.14$ ,  $\{0.03, 0.25\}$ ;  $\beta_{condition} = 0.14$ ,  $\{0.04, 0.23\}$ ) (Figure 1.3). Although stopover length tended to differ between the sexes in spring, in univariate analyses these differences were not significant (Spring 2016: Kruskal-Wallis test:  $\chi^2 = 2.15$ ,  $df = 1$ ,  $P = 0.14$ ; Spring 2017: Kruskal-Wallis test:  $\chi^2 = 3.05$ ,  $df = 1$ ,  $P = 0.08$ ).

*Departure behavior* – Our final Cox Proportional Hazard (CPH) model predicting probability of departure in the fall included only tailwind as a relevant variable (Figure 1.4, Table 1.3). Increasing tailwind was strongly associated with increased daily probability of departure (Hazard Ratio ( $HR_{\text{tailwind}}$ ) = 1.51, 95% CI {1.25, 1.83}, Figure 1.5), with birds being nearly 12 times more likely to depart when experiencing a tailwind of 6 mph. No other covariates predicted fall probability of departure (all 95% confidence intervals of HRs overlapping 1). Our final spring model included capture/arrival day (SJD), body condition, tailwind, and the interaction between sex and year (sex X year) (Figure 1.4, Table 1.3). Later capture days, increasing tailwind, and lower body condition were associated with higher probability of departure ( $HR_{\text{SJD}} = 1.07$ , {1.03, 1.11};  $HR_{\text{tailwind}} = 1.14$ , {1.06, 1.24};  $HR_{\text{condition}} = 0.85$ , {0.77, 0.95}). The effect of tailwind was weaker than in the fall, with birds being just over twice as likely to depart under tailwinds of 6 mph (Figure 1.5). Furthermore, the interaction between sex and year influenced probability of departure, such that males were less likely to depart on a given day than females in 2016 but more likely to depart in 2017 ( $HR_{\text{int}} = 3.5$ , {1.55, 7.9};  $HR_{\text{sexM}} = 0.02$ , {0.002, 0.21};  $HR_{\text{year2017}} = 0.48$ , {0.26, 0.89}).

*Stopover relocations* – Of 49 total fall stopovers, 35 birds (71%) made confirmed or probable stopover relocations; of 58 total spring stopovers, 19 birds (33%) made confirmed or probable relocations (Table 1.1). Stopover relocations ranged from 10 km to 35 km from the local array, often in directions against the predominant migratory direction (north in spring, south in fall). In the spring, males were much more likely to relocate (58% of males relocated) than females (15%; Fisher's exact test = 0.003,  $P <$

0.01), and the mean capture day (SJD) of birds that relocated was significantly earlier than birds that did not relocate (Kruskal-Wallis test:  $\chi^2 = 11$ ,  $df = 1$ ,  $P = 0.0009$ ).

*Arrivals* – Julian day of capture/arrival did not significantly differ between ages (Kruskal-Wallis test:  $\chi^2 = 0.38$ ,  $df = 1$ ,  $P = 0.5$ ) or sexes (Kruskal-Wallis test:  $\chi^2 = 0.002$ ,  $df = 1$ ,  $P = 0.9$ ) in the fall. In the spring, Julian day of capture/arrival did not differ among ages (Kruskal-Wallis test:  $\chi^2 = 0.01$ ,  $df = 1$ ,  $P = 0.9$ ), but males (mean capture day  $\pm$  SE =  $86.9 \pm 2.5$  days) arrived significantly earlier than females (mean  $\pm$  SE =  $100 \pm 2.1$  days; Kruskal-Wallis test:  $\chi^2 = 12.7$ ,  $df = 1$ ,  $P < 0.001$ ).

*Flight speed and distance* – We calculated flight speed and minimum distance traveled for 27 true migratory movements (not relocations). Known minimum distances traveled in a single overnight or daytime flight ranged from 38 km to 425 km (the latter flight completed at 62 km/h), with a median distance of 257 km. Overland flight speeds (not accounting for wind conditions) ranged from 8 km/h to 88 km/h (the latter flight a distance of 356 km), with a median flight speed of 49 km/h. Tailwind did not explain flight speed or distance traveled ( $p > 0.1$ ), but flight speeds were greater for birds that traveled longer minimum distances ( $\beta = 2.67$ ,  $R^2 = 0.22$ ,  $P = 0.01$ ).

*Site fidelity* – Between-season site fidelity was 29% for Fall 2016 and 36% for Spring 2017 (Table 1.2). We also calculated migratory route fidelity, incorporating birds that flew over the site but did not stop (Table 1.2), which was 71% for Fall 2016 and 43% for Spring 2017. Outside of our regional array, the Motus array detected five additional stopover events  $>1$  day in Ontario, which ranged in duration from 3 days to 11 days. One of these birds made an apparent stopover relocation, spending 9 days at a site before

relocating 58 km to the south (against the migratory direction in the spring) and stopping for an additional 11 days. Since the Motus array does not provide full coverage of the migratory landscape, other undetected stopovers and relocations may have occurred.

## **Discussion**

Our results clearly indicate that Rusty Blackbirds in our region are not among those passerines that undertake rapid migrations punctuated only by short refueling stopovers. Individuals may have made refueling stops before or after stopping in our high use study site, but overall the behavior we observed is more consistent with the “staging” behavior of groups such as shorebirds (Warnock 2010). In fact, we found that on average, Rusty Blackbirds spent 5-times longer on stopover than other songbirds at the same site (Dossman et al. 2016). Further, this long duration may be due to an interaction with prealternate molt in spring, drawing another parallel with staging migratory systems (Lourenço and Piersma 2015, Wright et al. in review). The high percentage of birds migrating at night overturns the previously held assumption that Rusty Blackbirds are diurnal migrants (Avery 2013), and the proportion of birds crossing Lake Erie (~50 km) suggests that it is not a significant barrier to migration for this species (Gesicki et al. 2016). Collectively, our study highlights several incorrect assumptions about migration and the importance of specific stopover locations, as well as the potential exposure to conservation challenges in this species of concern.

The patterns and behaviors described in our study are much more closely aligned with shorebird migration strategies than any documented passerine strategy. Rusty Blackbirds share several important life history characteristics with shorebirds as well: they are a highly social flocking species, often found in company with other similar flocking species, and are habitat specialists that rely heavily on a particular type of wetland (shallow flooded areas with leaf litter, DeLeon 2012). Furthermore, whereas their migratory distance is shorter than many shorebirds, they differ from their close relatives (e.g. Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscula*), Brewer's Blackbird (*Euphagus cyanocephalus*)) in being an obligate migrant that breeds in the northern boreal zone. As such, it is perhaps more appropriate to draw on shorebird stopover terminology in order to describe the function of our study site. While there is some debate on the best way to classify shorebird stopover sites, one widely accepted method differentiates between staging areas and stopover areas (Warnock 2010, Ma et al. 2013). Staging areas are high-quality sites where large groups of birds congregate to refuel before long migratory flights, stopover durations are relatively long, and individuals return year after year. Stopover areas, in contrast, are usually lower quality sites where birds happen to end up after a migratory flight, and are only used for short periods of time to refuel before moving on to a better staging area (Warnock 2010). Based on patterns of stopover duration, migratory flights, site fidelity, and space use of our tagged Rusty Blackbirds, we conclude that they exhibit a variant of the staging migratory strategy.

## **Stopover Duration**

Rusty Blackbirds utilize southwestern Lake Erie for variable, but generally lengthy bouts of stopover (25.5 days on average). Contrary to our expectations, stopover duration did not differ between fall and spring, but average minimum stopover duration was much longer than most reported stopovers of passerines (~1-12 days; e.g. Aborn and Moore 1997, Yong and Moore 1997, Catry et al. 2004, Tietz and Johnson 2007, Rush et al. 2014, Liu and Swanson 2015). In both the fall and spring, a significant predictor of stopover length was the capture/arrival day, with birds captured earlier remaining longer than birds captured later. Given the overall long stopovers and tendency for birds to move in flocks, this result probably indicates that birds captured later in the season had already been at the site for a substantial period of time before capture. Thus, if anything, we are likely underestimating stopover length for birds captured later in the season. However, another possibility is that there were more time constraints on birds arriving later, which necessitated shorter stopovers for those birds.

These lengthy stopovers appear to run counter to the expectation that migrant songbirds should minimize the amount of time spent migrating, by maximizing fuel deposition at stopover sites (Alerstam et al. 2003). Stopover length is usually dependent on the energetic condition of the individual (Goymann et al. 2010), as birds with heavily depleted energy reserves must stop longer to recoup those losses. Expected flight distance is also a determinant of stopover length, and there are examples of shorebirds making exceptionally long stopovers to accumulate >50% of their body mass in fat stores when they have an exceptionally long flight ahead of them (Warnock 2010). It is

possible that Rusty Blackbirds at our site are expecting to rapidly complete the migration to breeding/wintering grounds after departure, and use the high quality habitat to accumulate large fat reserves. Whereas the distances of tagged individuals' subsequent migratory flights were not comparable to long-distance shorebird movements (thousands of km; e.g. Gill et al. 2009, Alves et al. 2016), the recorded Rusty Blackbird flights of >400km are substantially longer than most passerine migratory flights (150-270km; Wikelski et al. 2003, Stutchbury et al. 2009). Yet, while these distances are substantial, it seems unlikely that Rusty Blackbirds require lengthy stopovers for refueling alone, as comparable shorebird stopovers are generally related to energetic needs of crossing major marine boundaries in non-stop flights (Gill et al. 2009, Warnock 2010, Alves et al. 2016).

One possible reason for lengthy stopovers in spring is molt. We found that nearly all captured birds in spring (98%) were undergoing a partial prealternate molt of contour feathers, often quite extensively around the head (Wright et al. in review). The need to molt and refuel could conflict energetically necessitating a longer stopover in spring. Our finding that poor conditioned birds in heavy molt had longer stopovers supports this. Body molt is an energetically costly activity due to reduced effectiveness of thermal insulation (Piersma et al. 1995) and increased metabolic rates associated with replacing feathers (Lindström et al. 1993). Several shorebird species undergo prealternate or presupplemental molt at staging areas, including Great Knots (Battley et al. 2006, Peng et al. 2015), Black-tailed Godwits (Lourenço and Piersma 2015), and Bar-tailed Godwits (Piersma and Jukema 1993). In the fall, some passerines undergo their prebasic molt at stopover sites in the Mexican monsoon region (Leu and Thompson 2002, Pyle et al.



2009), although this molt includes flight feather replacement and is likely not, energetically, directly comparable to Rusty Blackbird prealternate molt. Nevertheless, the presence of prealternate molt on stopover, previously undocumented for a passerine (Wright et al. in review), very likely plays a role in the unusual strategy (for a songbird) of having a long stopover on spring migration.

Though they are of similar length, long stopovers by Rusty Blackbirds in the fall and spring probably have different evolutionary and ecological drivers (Nilsson et al. 2013), and the lack of a difference in seasons could have to do with molt. There was no molt occurring in the fall, thus birds did not have to complete two potentially conflicting physiological tasks, as in spring. Further, since there is no breeding-associated selective pressure on early fall arrival, it is unlikely that there is as much selection on refueling rate in fall. Fall migrants typically have longer stopover durations and slower flights than spring migrants (Nilsson et al. 2013). In addition, fall migration is less stressful on birds, as they have lower levels of testosterone and corticosterone than during spring (O'Reilly and Wingfield 1995). Tøttrup et al. (2012) found that Red-backed Shrikes also make exceptionally long stopovers during fall migration (average 53 days), and suggested that this serves as a third residence period when birds exploit favorable foraging conditions following late summer rains. Likewise, Rusty Blackbirds may be exploiting the high dogwood (*Cornus* sp.) berry abundance at our site in early autumn (68% of autumn foraging observations occurred in dogwood stands; Wright unpublished data). Additionally, there is some evidence that the long fall stopover period is common across the species' migratory range. In a study utilizing light-level geolocators (Johnson et al.

2012), all three individuals tagged in Alaska, U.S.A. made approximately one-month long stopovers on fall migration in Iowa and the Dakotas. As Johnson et al. (2012) suggest and our study corroborates, this month-long stopover may in fact be a distinct stationary period of the annual cycle when birds take advantage of abundant early autumn resources before continuing to their wintering grounds.

### **Arrival Behavior**

In many species, spring arrival timing is dependent on sex, with males departing wintering grounds and arriving at stopover sites earlier than females (known as “protandry”; e.g. Stewart et al. 2002, Markovets et al. 2008, Seewagen et al. 2013, McKinnon et al. 2016). As expected, Rusty Blackbirds exhibited protandry in the spring, and sex did not influence arrival timing in the fall. However, contrary to our predictions, age did not influence arrivals in the fall as it has in other songbird and shorebird species (Markovets et al. 2008, Henningsson and Karlsson 2009, Jakubas and Wojczulanis-Jakubas 2010). Perhaps this is due to the social behavior of Rusty Blackbirds, as there is evidence that they form mixed-age flocks in late summer before migrating (Avery 2013). This may allow inexperienced juveniles to learn migratory routes from adults (Henningsson and Karlsson 2009).

### **Departure Behavior**

Our departure behavior results expectedly echoed stopover duration, but the strong effect of tailwind outweighed some of the other variables that were significant in

the duration analysis. In particular, the overwhelming effect of tailwind made it the only significant predictor of departure probability in the fall, and it was a strong predictor of departure in the spring as well. This result is consistent with other migration studies that show favorable wind conditions as being of primary importance in a bird's decision to depart (Kranstauber et al. 2015, Mitchell et al. 2015, Dossman et al. 2016). The difference in tailwind effect between the fall and spring could indicate that fall migrants are content to wait for especially favorable wind conditions, not experiencing any significant internal pressure to depart; whereas spring migrants are more likely to depart under less ideal wind conditions as they are experiencing internal breeding pressure to depart (O'Reilly and Wingfield 1995).

The significant interaction between sex and year for both stopover duration and departure analyses was unexpected. Other studies have found variable effects of sex on stopover duration. Male common yellowthroats and yellow-rumped warblers exhibited higher refueling rates than females during spring migration (Seewagen et al. 2013), but snow buntings did not exhibit any strong differences in stopover duration between sexes (McKinnon et al. 2016). Whereas male Rusty Blackbirds tended to remain longer than females in Spring 2016 and shorter than females in 2017, these differences were not significant in univariate analyses ( $p > 0.1$ ), so perhaps this interaction only provides evidence that sex is not a regular predictor of stopover duration or departure behavior in Rusty Blackbirds. However, our sampling effort between the two seasons likely contributed to this year interaction. Tag deployment in Spring 2016 occurred from mid-March to late April, whereas in Spring 2017 tag deployment was completed by early

April. Since more females were captured later in the season, we may have underestimated stopover duration for females in 2016.

### **Stopover Relocations**

The prevalence of relocations within the greater stopover landscape indicates Rusty Blackbird individuals are not limited to a tightly bound home range during stopover. Social species typically move around stopover sites on a scale of 2 – 10 km (Butler et al. 2002, Obernuefemann et al. 2013) as resource information is shared in flocks, but Rusty Blackbirds were relocating to sites 20-35 km away from the capture area. Prior knowledge of the stopover landscape does not explain these relocations, as older birds were no more likely to make these movements than younger birds. Resource availability and competition could explain these relocations in the spring, as most relocations occurred early in the season when density of aquatic invertebrates is lower (MacKenzie et al. 2004, MacKenzie and Kaster 2004). This is consistent with the result that males were more likely to relocate than females since they arrived at the site earlier in the season. Similarly, Mills et al. (2011) found that landscape-scale stopover relocations in *Catharus* thrushes were most likely to occur early in the stopover period (~30% of total minimum stopover time). In contrast to our findings, however, thrushes made these movements nocturnally, while our relocations occurred during daylight, and the authors suggested this was to avoid predation risk while exploring the landscape. It is possible that Rusty Blackbirds are able to mitigate this risk by flocking, and gain the benefit of exploring the landscape for foraging habitat in full daylight. The distance of

relocations could be related to the fragmented nature of the landscape, since there are large expanses of farmland between wetland habitats. As other studies have noted (e.g. Mills et al. 2011, Taylor et al. 2011), this highlights the need to expand the scale at which stopover behavior is quantified beyond a single site.

### **Site Fidelity**

Site fidelity is another important consideration when determining the use and function of a stopover site (Warnock 2010). Between-season stopover site fidelity is low for most passerines, with estimates ranging from 0.3% return rates for Tennessee Warblers (Winker et al. 1991, Vogt et al. 2012) to 5.4% for Sedge Warblers (Catry et al. 2004). However, habitat specialists may exhibit moderate to high stopover site fidelity in some areas (up to 54% in Eurasian reed warbler (*Acrocephalus scirpaceus*); Cantos and Telleria 1994, Yohannes et al. 2007, discussed in Catry et al. 2004). Shorebirds generally exhibit high site fidelity to stopover locations between seasons (Harrington et al. 1988), with return rates of >60% at some sites (Gudmundsson and Lindström 1992, Catry et al. 2004, Buchanan et al. 2012). In this context, we observed moderate fidelity to our study site between seasons, with approximately one-third of the birds known to survive the intervening stationary period returning to the site for a stopover event in the following migration (Table 1.2). A number of other individuals migrated past the site without stopping, and in Fall 2016, more returning birds flew over than stopped for more than a day. This latter point could suggest that birds are faithful to migratory routes, and that the location of stopover events is somewhat stochastic based on where birds are at the

end of a migratory flight. However, given that our site is located on the south shore of Lake Erie, it is possible that southbound Rusty Blackbirds (in the fall) have adequate staging areas on the north side of the lake and need not stop at our site after crossing.

## **Conclusions**

Our findings demonstrate the necessity of examining individual behaviors of migrants at multiple spatial scales. Without such studies, our understanding of population limitation throughout the annual cycle will remain inadequate. We have described a novel migration strategy for a songbird, but studies of this kind are likely to reveal other atypical behaviors. Rusty Blackbirds spend over a quarter of their annual cycle at staging sites, and a large proportion repeatedly use the same sites and flyways. Thus, it is critical that these high-traffic sites are further identified and protected. Additional studies utilizing nanotags or other new technologies (e.g. archival GPS tags; Hallworth and Marra 2015) will help determine whether our observed staging behaviors of Rusty Blackbirds are consistent across their range. If consistent, the behaviors we observed show that it is crucial to incorporate stopover sites into conservation and management plans for Rusty Blackbird populations. It is possible that our site is an anomaly, demonstrating the best-case scenario for refueling potential in a geographic region intermediate between breeding and wintering grounds. Our site is also one of the few remaining wetlands in a landscape dominated by agriculture, as Ohio has lost >90% of its wetlands since European settlement (Dahl and Johnson 1991). The Midwest U.S. in general has lost >80% of its wetlands (Dahl and Johnson 1991), so the remaining

pockets are likely critical to migrant Rusty Blackbirds. Furthermore, with the planned development of wind farms underway on Lake Erie (Lake Erie Energy Development Corporation; U.S. Department of Energy 2017), nocturnal flights over the lake (72% of our spring departures) could expose a large proportion of the Rusty Blackbird population to collision mortalities (Loss et al. 2013). The next step in elucidating the pressures they face during migration is to understand their habitat use on these extended stopover events, and how their preferred habitat differs between spring and fall stopover events. This will help generate habitat management recommendations and establish conservation priorities that will allow wetland habitat managers to incorporate Rusty Blackbirds into their seasonal management plans. More broadly, our findings highlight the need to fully explore all aspects of species' annual cycles in order to understand the spatiotemporal nature of population limitation and habitat needs (Marra et al. 2015), to inform efficient and effective conservation action.

**Table 1.1.** Stopover departure and movement categorizations for all tagged Rusty Blackbirds. Total number of birds tagged and returned (n) is displayed for each season. Number of confirmed and probable diurnal (D) and nocturnal (N) migratory departures are shown. Total number of stopover relocations, migratory flybys of returned birds (tagged previous season), and predations (by owl or unknown raptor) are also shown.

Season	Confirmed Departure	Probable Departure	Unknown Departure Movement	Confirmed Relocation	Probable Relocation	Migratory Flyby	Predated
Fall 2015 (n=5)	0	2 (N)	3	4	1	0	0
Spring 2016 (n=30)	12 (N)	9 (N) 2 (D)	5	6	3	0	2
Fall 2016 (n=44)	2 (N)	17 (N) 1 (D)	17	26	4	6	1
Spring 2017 (n=28)	8 (N) 2 (D)	3 (N) 3 (D)	10	8	2	2	0



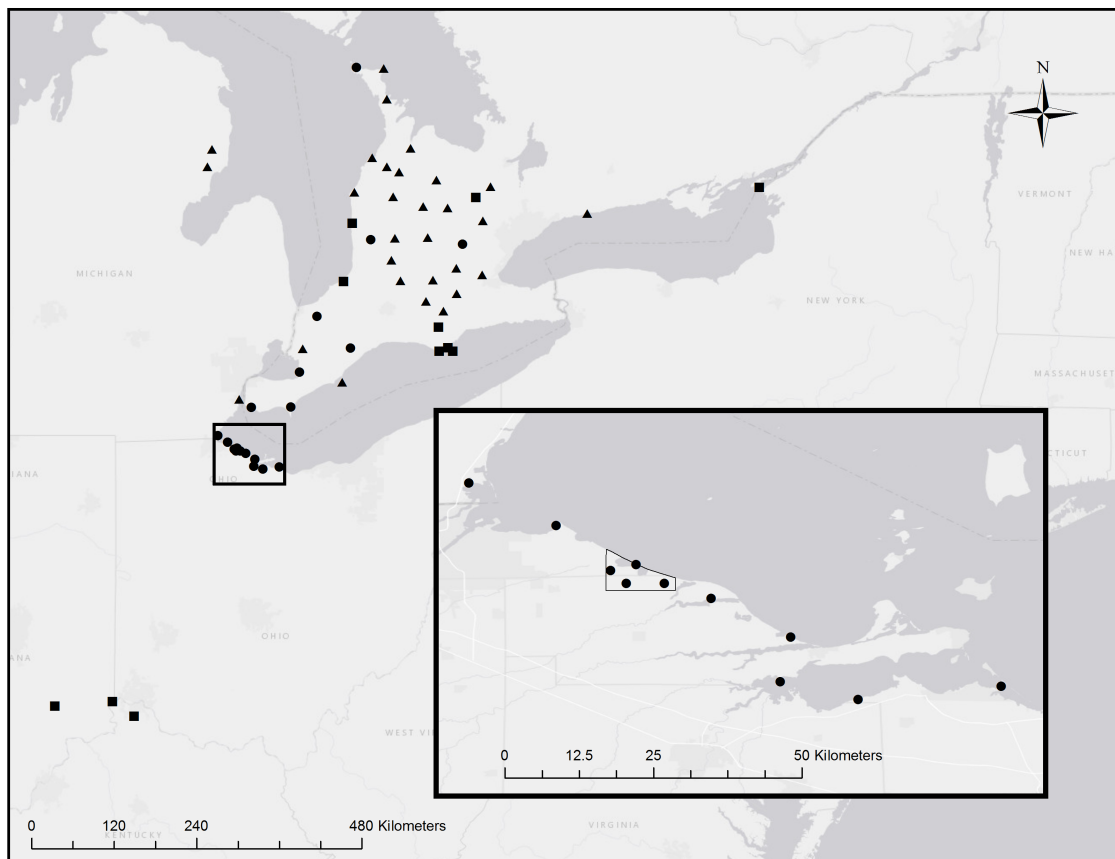
**Table 1.2.** Between-season site fidelity for Fall 2016 and Spring 2017. The total number of possible returning birds (n) is displayed for each season. This number is based on how many tags remain at the end of the previous season that should have sufficient battery life to last through the intervening stationary period and following migration. Of this total, the actual number of returned tagged birds that were detected anywhere in the North American Motus array is shown (n = 14 for both seasons). Number of return stopover visits to the study site, return flyovers, and stopovers in Ontario are shown. Thus, between-season site fidelity is displayed in parentheses as percentage of actual return detections that occurred for each category.

Season	Return detections in Motus array	Return stopovers > 1 day	Return flyovers	Ontario stopovers > 1 day
Fall 2016 (n = 33)	14	4 (29%)	6 (43%)	3 (21%)
Spring 2017 (n = 33)	14	5 (36%)	1 (7%)	1 (7%)

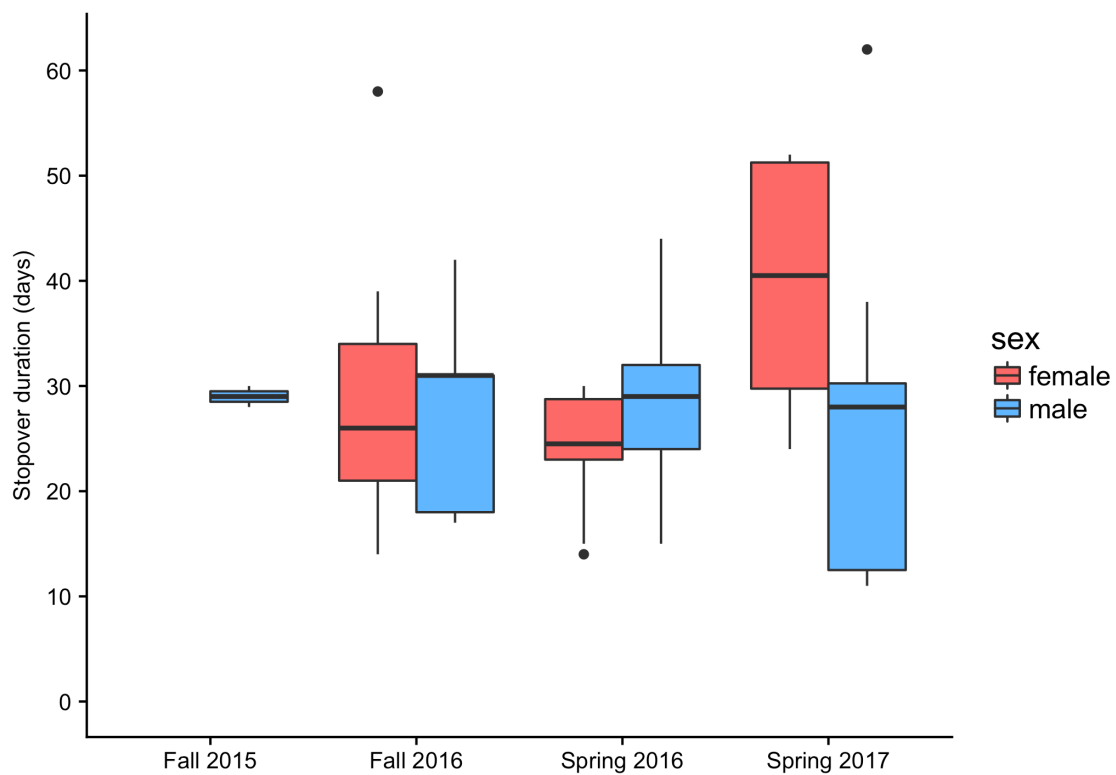
**Table 1.3.** Number of tagged individuals remaining on stopover each season for increasing number of stopover days. This table relates to the Cox Proportional Hazard departure probabilities for each season (Figure 1.4). The starting number of birds on stopover only includes those with confirmed or probable departures (see Table 1.1).

Stopover day	Individuals remaining	
	Fall	Spring
0	22	39
10	22	39
20	17	31
30	10	16
40	2	7
50	1	3
60	0	1

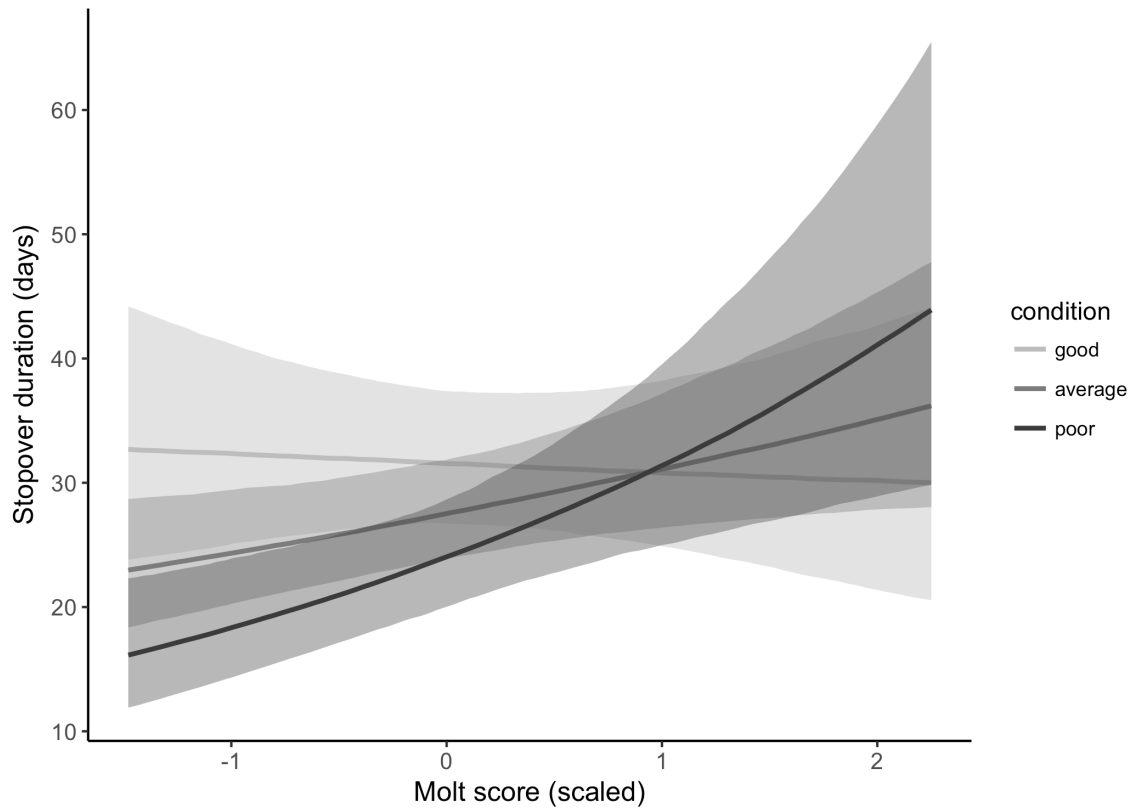
**Figure 1.1.** Location of the study site in northwest Ohio (Ottawa National Wildlife Refuge/Magee Marsh State Wildlife Area), and automated telemetry towers that detected Rusty Blackbirds. Towers that detected birds in spring are triangles; in fall are squares; and in both spring and fall are circles. The study site is outlined in black in the inset map. The four towers within the study site are the “local” array, while the other towers in the inset map make up the “regional” array. All other towers in the base map are part of the Motus Wildlife Tracking System array.



**Figure 1.2.** Boxplots of stopover duration (days) of tagged Rusty Blackbirds for males and females of each study season that were included in analyses (i.e. we had confirmed or probable departures). Sample size of each category as follows: Fall 2015: 2 males, 0 females; Fall 2016: 9 males, 11 females; Spring 2016: 13 males, 10 females; Spring 2017: 10 males, 6 females. Differences in stopover length between sexes in a given season were not significant (all  $P > 0.05$ ), but females had longer stopovers in Spring 2017 compared to Spring 2016 (Kruskal-Wallis test:  $\chi^2 = 5.5$ ,  $df = 1$ ,  $P = 0.02$ ).

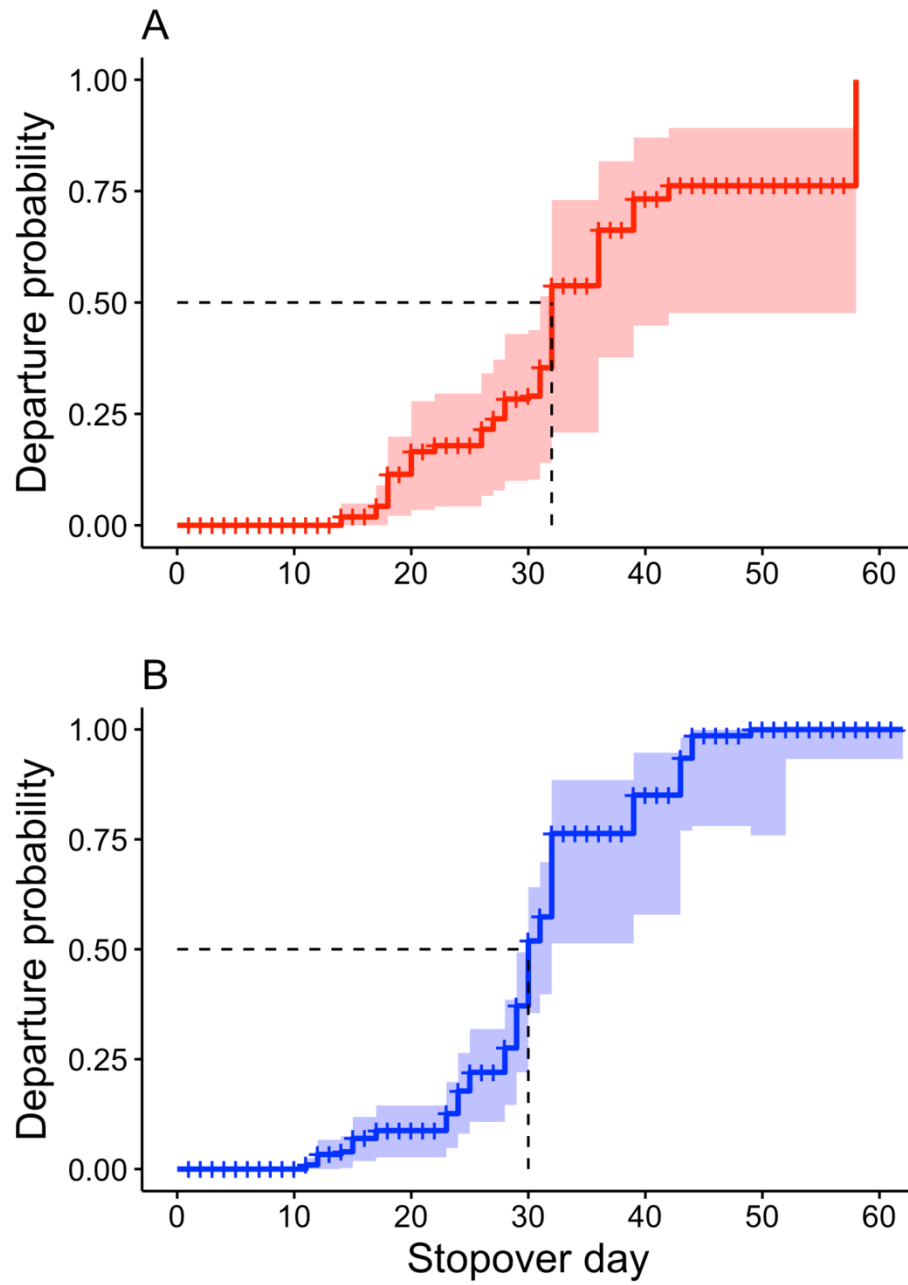


**Figure 1.3.** The marginal effect and 95% credible intervals of the interaction between body condition and molt score (condition X CCMI) on spring stopover duration of Rusty Blackbirds. “Average” condition is represented as the mean scaled mass index score; “good” condition is represented as plus one standard deviation from the mean; “poor” condition is represented as minus one standard deviation from the mean. Coefficients of the interaction variables are:  $\beta_{\text{int}} = -0.15, \{-0.27, -0.03\}$ ;  $\beta_{\text{ccmi}} = 0.14, \{0.03, 0.25\}$ ;  $\beta_{\text{condition}} = 0.14, \{0.04, 0.23\}$ .

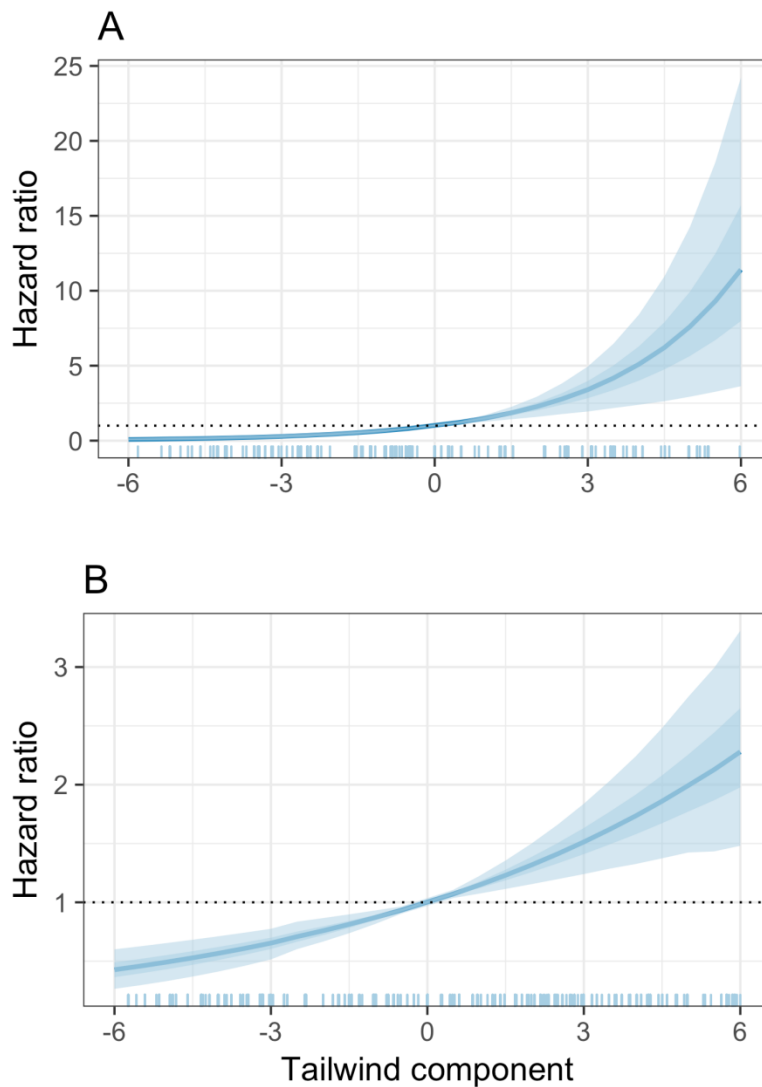


**Figure 1.4.** Daily probability of departure for fall (A) and spring (B) stopovers, as predicted by extended Cox Proportional Hazards models. Shaded areas represent 90% confidence intervals; dashed line represents day of median departure. The fall model included only tailwind as a relevant predictor, and significantly predicted likelihood of departure (Wald test = 18.3, d.f. = 1,  $p < 0.001$ ,  $n_{\text{events}} = 22$ ). Increasing tailwind was associated with increased daily probability of departure (Hazard Ratio (HR) = 1.51, 95% CI {1.25, 1.83}). The final spring model significantly predicted likelihood of departure (Wald test = 29.9, d.f. = 6,  $p < 0.001$ ,  $n_{\text{events}} = 39$ ), and included capture/arrival day (SJD), body condition, tailwind, and the interaction between sex and year (sex X year). Later capture days, increasing tailwind, and lower body condition were associated with higher probability of departure ( $HR_{\text{SJD}} = 1.07$ , {1.03, 1.11};  $HR_{\text{tailwind}} = 1.14$ , {1.06, 1.24};  $HR_{\text{condition}} = 0.85$ , {0.77, 0.95}). Males were less likely to depart on a given day than females in 2016 but more likely to depart in 2017 ( $HR_{\text{int}} = 3.5$ , {1.55, 7.9};  $HR_{\text{sexM}} = 0.02$ , {0.002, 0.21};  $HR_{\text{year2017}} = 0.48$ , {0.26, 0.89}).

Figure 1.4.



**Figure 1.5.** The effects of tailwind component on the hazard ratios for (A) fall and (B) spring departures, simulated for a range of tailwind conditions. Positive values represent increasing tailwind, negative values represent increasing headwinds. Increasing tailwind was a stronger predictor of departure in the fall ( $HR_{T-fall} = 1.51$ , 95% CI {1.25, 1.83}) than in the spring ( $HR_{T-spring} = 1.14$ , 95% CI {1.06, 1.24}). Shaded regions represent 50% and 90% confidence intervals.





## **Chapter 2: Fine-scale Habitat Selection of Rusty Blackbirds (*Euphagus carolinus*) on Stopover in the Western Lake Erie Basin**

### **Introduction**

Bird migration is a period of alternating flights and stopover events, as individuals travel several thousand kilometers over the course of several weeks between breeding grounds and wintering grounds. While the ultimate purpose of migration is to move between these two stationary periods, for most species the time spent on stopover events between flights is much greater than the time spent in flight (Alerstam 1993, Wikelski et al. 2003). These stopovers are critical for birds to rest and refuel during this energetically demanding period, but birds are also very vulnerable during these events. Mortality rates are highest during migration (Silllett and Holmes 2002, Klaassen et al. 2014), as refueling birds search for food at a high rate (Moore et al. 2017), often in an unfamiliar landscape, and are faced with increased predation pressure (Moore 1994) and resource competition with other birds (Moore and Yong 1991). Resource availability at stopover sites can have important fitness consequences by limiting the phenology of migrants, since birds that cannot locate abundant food will have to remain on stopover longer to refuel (Lupi et al. 2016, Moore et al. 2017). Therefore, it is key to migratory bird fitness that they select adequate habitats that optimize energetic needs and cover during these stopover events (Slager et al. 2015). For habitat specialists and species in decline, understanding habitat

use on stopover is crucial in developing conservation plans and ensuring that sufficient habitat is available to them during migration.

Stopover habitat selection is scale dependent (Moore et al. 2005). Migration occurs over a large geographic area and birds make decisions about where to stop based on different factors at different scales. Johnson (1980) described four orders of selection to characterize the varying stages of habitat selection. For example, at a geographic scale (Johnson's 1<sup>st</sup>-order selection), where an individual ends up at the end of a migratory flight is largely dependent on weather and geographic features such as various barriers to migration (Buler et al. 2007). Within a regional landscape (Johnson's 2<sup>nd</sup>-order selection), birds may search for easily identifiable features such as bodies of water or patches of dense forest. Once a particular habitat patch has been selected (Johnson's 3<sup>rd</sup>-order selection), further fine-scale selection is required to locate the best food and cover resources that patch has to offer (Johnson's 4<sup>th</sup>-order selection). Thus, as the scale narrows from geographic (100's of km) to within a patch (<10m), intrinsic habitat and vegetation characteristics become increasingly important to selection (Moore and Aborn 2000).

In order to demonstrate habitat selection, it is necessary to compare used habitat to available habitat (Jones 2001). For songbirds on stopover, researchers typically define available habitat as the temporary home range of an individual (measured by tracking birds with radio telemetry) and compare habitat variables at used locations with random locations within the home range (Yong et al. 1998, Tietz and Johnson 2007). Many migratory birds (e.g. songbirds) utilize a relatively small area once they have selected a

stopover site (Tietz and Johnson 2007, Buchanan 2008, Matthews and Rodewald 2010, Liu and Swanson 2015), so this method is appropriate even when birds remain on stopover for a short period of time. Flocking species, however, pose several challenges to the traditional methods of habitat selection analysis. First, wide-ranging movement behavior (e.g. between communal roosts and foraging areas) makes it difficult to consistently locate individuals in a logistically manageable study area, even though they have not left the broader stopover landscape (Farmer and Parent 1997, Ma et al. 2013). Second, their highly social behavior – and, thus, constant information exchange – makes their movement inherently dependent, and implies they largely lack a clearly bounded individualized home range (Barbaree et al. 2015). Due to these complications, habitat selection at an individual level is extremely difficult to unravel, particularly for 4<sup>th</sup>-order selection. Thus, research seeking to characterize important habitat variables must rely on examining individuals in the context of the flock and quantifying used sites in comparison to random available nearby sites.

The Rusty Blackbird (*Euphagus carolinus*) is a highly social migrant songbird that breeds across the boreal zone and winters in the southeast United States (Avery 2013). Their population has declined ~88% over the last 50 years, and has continued to decrease by ~5% per year (Greenberg and Matsuoka, 2010). The cause of this precipitous decline in such a widespread and previously common species is still largely obscured (Greenberg et al. 2011), although recent research has identified some factors that may be contributing to the decline. One important factor appears to be habitat loss on the wintering grounds (Luscier et al. 2010, Greenberg et al. 2011), as bottomland

hardwood forest was historically drained and cleared to make way for agriculture (Dahl and Johnson 1991). Rusty Blackbirds are traditionally considered habitat specialists (Avery 2013; but see DeLeon 2012), strongly associating with forested wetlands in the non-breeding season (Luscier et al. 2010). They primarily forage in flooded or saturated soils, so disturbances to natural flooding regimes by drainage and diversion of water can also reduce available habitat (Greenberg et al. 2011). Habitat loss and hydrological alterations may be an issue for migrating birds on stopover as well, but to date there have not been any studies examining their habitat use during migration. Furthermore, there have been no published studies that describe roosting habitat during the non-breeding season, although they do occasionally roost communally with Red-winged Blackbirds (*Agelaius phoeniceus*; Avery 2013).

In order to better understand Rusty Blackbird habitat needs during migratory stopover, we developed a habitat selection model for fine scale (Johnson's 4<sup>th</sup>-order selection) foraging behavior during both spring and fall migration. Due to the constraints of studying flocking species (detailed above), we did not quantify habitat selection on an individual home range basis. We instead used radio telemetry of tagged individuals as a way to consistently locate Rusty Blackbird flocks without biasing our observations toward easily accessible or previously known foraging areas. In this framework, we describe 4<sup>th</sup>-order habitat selection of highly mobile foraging flocks, where available habitat is defined as the entire study site (excluding deep open water and impermeable surfaces). We compared habitat characteristics between used foraging and paired random

locations within the same habitat patch to identify the most important variables for predicting fine scale use.

While Rusty Blackbirds are generally regarded as forested wetland specialists, research on the wintering grounds suggests that they are not strictly reliant on this habitat type, but more broadly rely on shallow water and wet leaf litter for foraging (Luscier et al. 2010, DeLeon 2012). During the winter, birds forage in flocks by wading in shallow water and flipping through leaf litter to locate aquatic invertebrates, seeds, and acorns (Avery 2013). Due to similarities in foraging behavior and environment, we hypothesized that Rusty Blackbirds would exhibit habitat preferences on stopover similar to those on the wintering grounds. We predicted that wet leaf litter, shallow water, tall woody shrub cover, and a lack of open grass, tall forbs, and herbaceous shrub cover would characterize Rusty Blackbird foraging locations in all habitat types. More specifically, in non-forested habitat types, we predicted Rusty Blackbirds to select areas near trees or habitat edges where leaf litter would be present and flock members could perch easily for more effective predator vigilance (Roberts 1996). Additionally, we predicted Rusty Blackbirds would select for sites of high dogwood (*Cornus* spp.) berry abundance in the fall, since they are anecdotally known to forage on dogwood berries during fall migration (Wright, pers.obs.). Lastly, in order to get a more complete picture of stopover resource needs, we describe habitat use of nocturnally roosting Rusty Blackbirds. Given the dearth of information on stopover in Rusty Blackbirds, our findings will be critical in conservation planning that takes into account the entire annual cycle of this species.

## Methods

### Study site

Our study site is a high-traffic stopover site in the western Lake Erie Basin in northern Ohio. Our selection of the site was based on data from the Rusty Blackbird Spring Migration Blitz (Evans et al. in prep), a citizen science-based effort (developed by the International Rusty Blackbird Working Group and implemented using eBird checklists) to closely monitor spring migration across the species' range from 2014 to 2016. The Blitz identified Ottawa National Wildlife Refuge/Magee Marsh Wildlife Area (41.608° N, 83.208° W), on the southwest shore of Lake Erie, as receiving among the highest number of migrant Rusty Blackbirds in North America. This site, consisting of a managed complex of wetlands approximately 28 km<sup>2</sup> in size, contains a substantial amount of suitable habitat (e.g. wet forest/shrublands/marsh edges; Avery 2013) for the species in a region that is dominated by agricultural development.

Ottawa NWR and Magee Marsh are composed of a variety of wetland habitat types, including submergent marsh, emergent marsh, wet prairie, wet-mesic prairie, dogwood-willow swamp, inundated shrub-swamp, wet-mesic flatwoods, floodplain forest, hardwood swamp, and mudflats (USFWS 2015). Submergent marsh was rarely used by Rusty Blackbirds, but consisted especially of American lotus (*Nelumbo lutea*) and a number of other submergent species such as *Elodea canadensis* and *Utricularia* spp. Emergent marshes were composed of primarily cattail (*Typha* sp.) interspersed with

stands of invasive *Phragmites* sp., but also included a number of other emergents such as swamp mallow (*Hibiscus* sp.), smartweed (*Polygonum* sp.), swamp loosestrife (*Decodon verticillatus*), flowering rush (*Butomus umbellatus*), bur-reed (*Sparganium* sp.), and beggarticks (*Bidens* sp.).

Rusty Blackbirds primarily used four general habitat types while foraging: dogwood-willow swamp, inundated shrub-swamp, wet prairie, and forested wetland. Dogwood-willow swamp was usually dominated by dogwood species, especially gray dogwood (*Cornus racemosa*), but included a variety of other dogwood species such as *C. sericea* and *C. drummondii*, as well as various *Salix* spp. Dogwood stands could occur in open habitat with no canopy cover (usually *C. racemosa*); in more forested areas with tall cottonwood (*Populus* sp.) overstory and hawthorn (*Crataegus* sp.) understory; or in very wet areas (usually *C. sericea*) with interspersed dead ash (*Fraxinus* sp.) trees or cottonwoods. Most road edges and ditches were lined with linear dogwood patches. Reed canary grass (*Phalaris arundinacea*) was a common invader of the understory/ground layer in dogwood, prairie, and emergent marsh habitats. Inundated shrub-swamp was almost uniformly buttonbush (*Cephalanthus occidentalis*), but could also include *Salix* spp. and some *Cornus* spp. and a varying amount of canopy cover. Prairie habitats were a mix of native grasses and sedges of varying heights <1.5m, especially bluejoint (*Calamagrostis canadensis*), but also included cordgrass (*Spartina* sp.), rushes (*Juncus* sp.), and milkweeds (*Asclepias* sp.). The forested patches (wet-mesic flatwoods, floodplain forest, hardwood swamp) were usually composed of a diverse mix of maple, oak, elm, ash, and hickory species. Large ash trees were nearly always dead as

a result of Emerald Ash Borer (*Agilus planipennis*) invasion (Hermes and McCullough 2014), and contributed to a large amount of the woody ground cover. The shrub layer was often sparse in forest patches, but could include multiflora rose and other *Rosa* spp., grapevines (*Vitis* sp.), autumn olive (*Elaeagnus umbellata*), honeysuckle (*Lonicera* sp.), dogwood, and reed canary grass.

### **Capture and tracking methods**

We captured Rusty Blackbirds during two spring seasons (2016 and 2017) and one fall season (2016). We captured birds passively (i.e. without playback or baiting) using mist nets by targeting reliable Rusty Blackbird foraging areas. All capture sites were located within 3 km of each other. We banded birds with uniquely numbered U.S. Geological Survey aluminum bands and plastic color bands for individual field identification.

We deployed 2.1g coded nanotags (model NTQB-6-1; Lotek Wireless Inc., Newmarket, Ontario) on a subset of all captured birds each season, using the leg-loop harness method of attachment (Rappole and Tipton 1991). We only deployed tags on individuals whose mass was > 52 grams, so tags were less than 4% of the body mass. These tags all broadcasted on the same frequency (166.380 MHz, pulse rate 6.1 seconds), but had unique digitally coded signatures to allow for individual identification by handheld receivers (model SRX800, Lotek Wireless Inc.). The battery life of these tags was approximately 9 months, allowing for repeat detections should individuals return to the site during subsequent migrations. All bird handling methods were approved by the



Institutional Animal Care and Use Committee of The Ohio State University (protocol# 201500000028).

We tracked birds by hand using 3- or 5-element Yagi directional antennas. We attempted to locate each tagged bird at least once per day during their stopover, but due to the wide-ranging behavior of individuals this was not always possible. We homed in on individuals to visually confirm behavior within the flock. When foraging flocks were located we marked a point with a handheld GPS (error +/- 3m) at the location of the first bird that was seen. We recorded the following information on each flock: time and date, tagged birds present, number of individuals, behavior (foraging, perched, flying, or combination of behaviors), and species composition of the flock (other blackbird species often present). To determine nocturnal roosting habitat, we searched the study site after sunset and triangulated positions of tagged individuals (i.e. estimated intersection of three directional bearings to the signal). We calculated positions and error ellipses using program LOAS (v 4.0.3., Ecological Software Solutions, LLC, Urnasch, Switzerland).

### **Habitat surveys**

We returned to a subset of visually confirmed foraging points to perform habitat surveys. Foraging habitat survey points were chosen non-randomly to avoid overlap with previous surveys and to represent all habitat types in use. In order to ensure that habitat surveys accurately reflected conditions at the time of foraging observations, surveys were completed within several days of the observation as often as possible. However, due to the difficulties of tracking birds in the fall (e.g. 71% of tagged birds made landscape-

scale ( $>10\text{km}$ ) movements during stopover), some surveys in this season were completed up to a month after the foraging observation. To determine fine-scale selection of habitat features within a patch, we paired all foraging habitat surveys with a random habitat survey completed in the same patch on the same day. This ensured that delayed surveys (in relation to observation times) maintained comparable conditions between used and random points. Random survey points were located at a randomly chosen distance between 25 and 125m from the foraging point, in a randomly chosen direction that also allowed the point to fall within the same habitat patch. We measured ground cover and shrub layer habitat variables in a 5m-radius around the survey point, and made tree basal area measurements in an 11.3m-radius around the point (James and Shugart, 1970). Herbaceous ground cover was considered to be plants  $<50\text{cm}$  in height, and shrub layer was from 50cm to 4m above ground. Some dogwood stems exceeded 4m, but dogwood was always included in the shrub layer; otherwise woody stems  $>4\text{m}$  in height with  $>5\text{cm}$  diameter at breast height (DBH) were considered trees. Ground cover variables included percent cover estimates of grass, sedge, forbs, wet leaf litter, dry leaf litter, moss, woody debris, shallow water ( $<10\text{ cm}$ ), deep water ( $>10\text{cm}$ ), and mud. We also estimated average leaf litter depth and water depth by taking 12 measurements of each within the 5m-radius plot, located at 1-, 3-, and 5-m increments from the plot center in each cardinal direction. Shrub layer variables included relative percent cover estimates of all species present (identified to genus); average, minimum, and maximum heights of all species; stem counts of woody shrub species; and total shrub cover estimated for the 5m-radius plot. Additionally, we measured dogwood leaf-out (to nearest mm) to track phenology in

the spring, and made a separate stem-count of berry-producing dogwoods (number of mature stems >2m) in the fall. We also attempted to estimate berry abundance in the fall by counting berries on the closest dogwood stem to plot center, but as Fall 2016 was a very low berry-producing year (Ron Huffman, Ottawa National Wildlife Refuge, pers. comm.), only a small number of plots had berries at the time of surveying. Canopy variables included an estimate of canopy cover using a densiometer at the center of the plot, an estimate of average canopy height using a range finder, and estimates of basal area of all trees (identified to genus or species). We estimated basal area per tree using a reach stick held at breast height to determine DBH size class (James and Shugart, 1970); size classes were 5-8cm, 8-23cm, 23-38cm, and 38-53cm (Martin et al. 1997). In addition to these vegetation and structural variables, we also measured distance to nearest edge of habitat using a range finder or gps unit (Garmin GPSMAP 64st), and estimated percent cover of each habitat type within the 11.3m-radius plot. Additionally, we performed habitat surveys at triangulated roosting locations with small (<500m<sup>2</sup>) error ellipses. Due to homogeneous habitat at these locations (*Typha/Phragmites* sp. emergent marsh), we did not pair roosting survey points with random survey points to demonstrate fine-scale habitat selection of roosting locations.

### **Statistical analysis**

Before performing analyses, we condensed measured habitat variables down to ~20 independent variables for analysis (Appendix B). Since birds were never seen foraging in trees, and only foraged on dogwood shrubs in the fall, we considered ground

cover and vegetation structure variables to be of primary importance in fine-scale stopover habitat selection. Shrub species were thus grouped into “woody shrub” or “herbaceous shrub” categories, and we calculated a total percent cover estimate and weighted mean height (based on relative cover of species) for each category. Tree species were grouped together to calculate total basal area for each plot; when calculating basal area, we used the mid-point of each size class as an approximation of DBH for each tree (Martin et al. 1997). We condensed percent cover of different habitat types within the plot into a single “mixed habitat” variable, which was the sum of all habitat types that were not the habitat type at plot center. We also excluded several habitat variables that had very low occurrences, such as mossy ground cover in both seasons, and berry counts and mud ground cover in the fall. We analyzed spring and fall habitat selection separately, and all analyses were performed in Program R (v 3.4.1, R Core Development Team 2017).

In preliminary analyses, we tested two random effects to determine whether or not we should use generalized linear mixed effects to model our data following Zuur et al. (2009). Specifically we tested if it was necessary to include random intercepts for individual bird and/or habitat type at plot center. We anticipated that the effect of the individual tagged bird would not be significant, since individuals were nearly always members of a larger flock, and multiple tagged individuals could be within a flock, regardless of which individual we used to locate the flock. The variance of both random effects equaled zero and had no effect on estimated coefficients, so we excluded the random effects and proceeded with analysis using generalized linear regression models

(GLM) with a binomial error distribution (logit link function). We performed model selection within an information theoretic approach to identify variables that best explained habitat selection (Burnham and Anderson 2002). Our *a priori* model set included the null model, global model, and all univariate models for each season, as well as all year interaction models in the spring. We also tested several models that included predicted habitat variable interactions. Specifically, since birds sometimes use woody debris to forage over deep water, we tested the interaction between woody debris and deep water cover, as well as average water depth. Due to the possibility of differing predation pressure in forests versus shrub or prairie patches, we tested interactions of woody and herbaceous shrub cover with tree basal area. We further included 20 multivariate models for each season based on hypothesized effects, which included several ground layer, shrub layer, and canopy layer models, as well as a number of mixed habitat layer models (see Appendix B for complete AIC<sub>c</sub> table and description of variables). We used variance inflation factors (VIFs) to identify significant multicollinearity between predictors, and eliminated variables with VIFs >5 from individual models as necessary. We ranked all models using Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>) and Akaike weights ( $w_i$ ). Since many of the top-ranked models were within 4.0  $\Delta$ AIC<sub>c</sub> (Tables 2.1 and 2.2), we used multimodal inference to obtain model-averaged estimates of variable coefficients and unconditional confidence intervals (Burnham and Anderson 2002). Following Buler et al. (2007) we scored the magnitude of variable effects in the top models, such that variables were considered to have a "strong" effect when their 95% confidence interval (CI) did not

overlap zero, a “moderate” effect when the 90% CI did not overlap zero, a “weak” effect when the 85% CI did not overlap zero, and no effect when the 85% CI overlapped zero. Variables that had an effect were included in a final “effects” model for each season (Table 2.3), and we report variable coefficients and respective odds ratios (exponentiation of coefficient) +/- relevant confidence intervals (95%, 90%, or 85%). We calculated the Hosmer-Lemeshow goodness-of-fit statistic for each final model (Hosmer and Lemeshow 1980), as well as Tjur’s  $R^2$  for logistic regression to describe the amount of variance explained by our final “effects” models (Tjur 2009). Finally, to determine if Rusty Blackbirds were selecting for proximity to trees in non-forested patches, we performed a separate GLM analysis on surveys in only non-forested patches and tested for the effects of canopy cover, basal area, and distance to edge.

## **Results**

We captured and deployed coded nanotags on 30 individuals in Spring 2016, 34 individuals in Fall 2016, and 22 individuals in Spring 2017. We homed in on tagged birds to locate foraging flocks at 218 independent points in Spring 2016, 118 points in Fall 2016, and 233 points in Spring 2017. We returned to perform habitat surveys and paired random surveys at 50 foraging points in Spring 2016 and 46 points in Spring 2017, for a total of 192 spring habitat surveys. In Fall 2016, we performed surveys at 41 foraging points and paired random points (82 habitat surveys total). Additionally, we returned to 11 triangulated roost points with small error ellipses ( $<500\text{m}^2$ ) to perform

habitat surveys. These roost locations were used repeatedly during stopover by at least 52% of all tagged Rusty Blackbirds (roosting sites were never located for the remaining 48%).

Dogwood-willow swamp was the most commonly used habitat type for foraging in the fall, with 68% of surveyed points occurring within this habitat, followed by emergent marsh (20%), inundated shrub-swamp (5%), and forested patches (5%).

Dogwood-willow swamp was also most commonly used in the spring (44% of surveyed points), followed by forested patches (39%), prairie (11%), and shrub-swamp (4%).

We ranked 47 habitat models by AIC<sub>c</sub> in the fall (Appendix B), and the top 7 models were within 4.0  $\Delta$ AIC<sub>c</sub> (Table 2.1). Five variables showed strong or moderate effects on habitat selection after multimodal averaging, and were included in our final “effects” model (Figure 2.1, Table 2.3). The final model did not show evidence of poor fit (Hosmer-Lemeshow goodness-of-fit test:  $\chi^2 = 8.26$ ,  $df = 8$ ,  $p = 0.41$ ), and explained 28% of the variation in used vs. random habitat (Tjur’s  $R^2 = 0.28$ ). Foraging points were positively associated with shallow water and dry leaf litter cover, and negatively associated with grass, forbs, and herbaceous shrub cover (Figure 2.1).

We ranked 69 habitat models in the spring (Appendix B), the top 12 of which were within 4.0  $\Delta$ AIC<sub>c</sub> (Table 2.2). Five variables showed strong or moderate effects on habitat selection, and one variable showed a weak effect (Figure 2.2, Table 2.3). Our final “effects” model did not show evidence of poor fit (Hosmer-Lemeshow goodness-of-fit test:  $\chi^2 = 9.45$ ,  $df = 8$ ,  $p = 0.31$ ), and explained 16% of the variation in used vs. random habitat (Tjur’s  $R^2 = 0.16$ ). Used foraging points were negatively associated with

grass cover and distance to edge of habitat, and positively associated with wet leaf litter cover, shallow water cover, woody shrub cover, and mixed habitat (Figure 2.2). There was some evidence for a weak interaction between year and wet litter in the top models ( $0.05 < p < 0.1$ ), however when comparing the effects model with and without the interaction term, the  $\Delta AIC_c = 0.16$ , so in the interest of parsimony we did not include this interaction in the final effects model.

When removing forested habitat patches from analyses in the spring data set, canopy cover was positively associated with foraging points (odds ratio (OR) and 95% CI = 1.03 {1.00, 1.05}) and distance to edge was negatively associated with foraging points (OR = 0.98 {0.97, 0.99}). There were no significant effects of canopy cover, basal area, or distance to edge in the fall (all ORs overlapping 1).

Roosting habitat in both seasons was primarily in emergent marsh, with 10 of 11 (91%) surveyed points occurring within monotypic *Phragmites* sp. or *Typha* sp. marsh patches. The other roost point was within a northern buttonbush (*Cephalanthus occidentalis*) patch with *Salix* sp. and dead *Fraxinus* sp. overstory, 13m from the edge of a *Phragmites* marsh. Mean shrub layer cover (*Phragmites*, *Typha*, and *Cephalanthus*) was 78%, with an average height of 2.3m.

## Discussion

Our results demonstrate that Rusty Blackbirds are selecting fine-scale (Johnson's 4<sup>th</sup> order; Johnson 1980) foraging habitat based on a variety of factors in multiple habitat



layers. Ground cover variables appear to be most important in selection. As food availability is thought to be ultimately responsible for fine-scale habitat use (Hutto 1985), it is not surprising that a ground forager such as the Rusty Blackbird would select preferred foraging areas based on ground cover characteristics. The shrub layer also played a role in habitat selection during both seasons, and trees were important in selecting foraging areas outside of forested patches in the spring. Furthermore, spring migrants also selected for proximity to edges and areas with a mixed habitat matrix. Taken together, these results show considerable complexity in Rusty Blackbird habitat preferences during migratory stopover.

Shallow water and leaf litter were the most important ground cover characteristics being selected for in both seasons. Rusty Blackbirds selected for wet litter in the spring and dry litter in the fall, but this disparity is likely due to precipitation differences. Total precipitation for the fall season (4.5 inches) was considerably less than the two spring seasons (mean 9.8 inches; Toledo Express Airport, Toledo, OH; <http://cdo.ncdc.noaa.gov>). As a result, wet leaf litter was much less available in the fall at only 24% of fall surveys, as opposed to 68% of spring surveys. Shallow water was also less available during the fall, at 32% of fall surveys versus 76% of spring surveys. However, instead of eliminating the effect of shallow water in the fall as was the case with wet leaf litter, this served to amplify the selection of shallow water. This selection amounts to flocks being twice as likely to forage in a location with only a 9% increase in shallow water cover in the fall, whereas in the spring, birds were twice as likely to forage in a location after a 54% increase in shallow water. Rusty Blackbirds have a fairly

diverse plant-based diet in the wintering period, including fruit, berries, pecan nuts, pine seeds, and acorn mast (Luscier et al. 2010, Avery 2013) in addition to a variety of arthropods. Most of these resources are also available during autumn migration, but are not specifically found in wet habitats. The strong selection of shallow water in the fall indicates that aquatic invertebrates, their main food item during the breeding period (Avery 2013), are still an important part of the Rusty Blackbird diet on autumn migration. During spring migration, emergent aquatic insects are an important part of the diet for other songbirds at our site (MacDade et al. 2011), so Rusty Blackbirds are likely exploiting this resource in the spring as well.

The strong avoidance of grass, forbs, and herbaceous shrub cover by Rusty Blackbirds in the fall met our predictions, based on habitat structure. These cover categories typically result in dense cover very close to the ground making it difficult for birds to walk around and forage easily. Forbs and herbaceous shrubs are probably not strongly avoided in the spring because they have not yet emerged or leafed out in the early spring when Rusty Blackbirds are on stopover. On the other hand, woody shrub cover at the study site, which consisted mainly of dogwood (*Cornus* sp., mean relative cover = 65%), was typically over 2m tall leaving ample room for birds to forage on the ground. Birds exhibited moderate selection for this characteristic in the spring, but did not appear to select for this in the fall. However, while denser stands of woody shrubs were not selected at the within-patch scale, birds were generally selecting this type of habitat (dogwood-willow swamp) more frequently in the fall than in the spring. This seemed to confirm our prediction that birds would be selecting for dogwood berry stands

in the fall, but the very low abundance of berries that season (berries present in only 15% of surveys) made it difficult to draw any conclusions from our berry counts. The low berry crop was probably due to a lack of local rainfall in the early spring and summer, which may have effected both flower and berry production (Ron Huffman pers. comm.). Berries are an important part of the diet for many autumn migrants (Parrish 1997), as they can supply birds with a high amount of fat and antioxidants (Alan et al. 2013). *Cornus racemosa* in particular has high fat content (35% dry mass, Smith et al. 2013); thus, as we detected a high use of berry producing habitat, though not selection of berries themselves, we suspect that this is an important food resource for fall migrant Rusty Blackbirds in years with more typical fruit crops. In addition, during our pilot season in Fall 2015, we observed many individuals congregating around and feeding on dogwood berries when they were more abundant.

Rusty Blackbirds showed a strong preference for edges and weak preference for mixed habitat in the spring. This is consistent with other studies that have found a diversity of migrant songbirds prefer foraging in edge-dominated habitats (Rodewald and Brittingham 2004, 2007). Forest edges often have a higher arthropod abundance than the interior (Jokimäki et al. 1998), and insects can be more active and visible along edges which are more exposed to sunlight (Rodewald and Brittingham 2007). Outside of forested habitats, edges and areas with some canopy cover may also have more leaf litter than surrounding areas, so access to litter-dwelling arthropods (Avery 2013) could be driving this selection for the ground-foraging Rusty Blackbird (Luscier et al. 2010, DeLeon 2012). However, another possible explanation for the preference of edge and

canopy cover outside of forests may be predation pressure. One of the key benefits of foraging in flocks is decreased risk of predation, both by “safety in numbers” (less chance of a given individual being predated), but also by improved predator detection as a result of group vigilance (Roberts 1996). Small groups of individuals within a flock of foraging Rusty Blackbirds would often take foraging breaks and fly up to a nearby tree to preen or rest (Wright pers. obs.). These individuals may inadvertently serve as temporary sentinels (McGowan and Woolfenden 1989), spotting predators long before ground-foraging birds. The selection of canopy cover and edges may demonstrate a reluctance to stray far from some form of tall vegetation from which potential predators can be spotted at a distance. Furthermore, edges often provide a higher degree of shrub cover (Rodewald and Brittingham 2004), where birds can take shelter from attacking predators.

We should note that our study site is a U.S. National Wildlife Refuge with relatively high quality native habitat. Thus, our results may not necessarily reflect fine-scale foraging habitat selection across the full spectrum of habitat quality available in the Rusty Blackbird migratory range. Our study site did not encompass any agricultural land, for instance, but Rusty Blackbirds are often seen foraging on agricultural fields in mixed flocks on the wintering grounds (Luscier et al. 2010). Furthermore, contrary to our results, an occupancy study on the wintering grounds found that Rusty Blackbird abundance was positively correlated with grass cover (DeLeon 2012), where birds were often seen foraging in flooded lawns. Grass cover at our site, however, usually did not consist of lawn-type cover but rather taller stands of reed canary grass, bluejoint, and other native grass species which produced relatively impenetrable structure compared to

lawns. Birds at our site were not totally averse to grass cover, however, as we witnessed several flocks foraging in flooded areas of native prairie. Our results can inform habitat management in protected areas or other intact native habitat. However, further research is needed to determine the preferences of this species in more disturbed/modified environments, and the relative quality of microhabitats therein.

Nocturnal roosting habitat use was starkly in contrast to diurnal foraging habitat. All roosting areas were located within or in very close proximity to emergent marsh, particularly in dense stands of *Typha* sp. and *Phragmites* sp. where birds were almost never seen foraging. This was somewhat unexpected, as there is evidence that Rusty Blackbirds roost on the ground in open fields with low dense vegetation, or in evergreen trees and shrubs in residential areas on the wintering grounds (Greenberg et al. 2011, Avery 2013). However, these microhabitats provide similar cover to *Typha/Phragmites* marsh, and these dense stands of marsh grass provide excellent cover from inclement weather and nocturnal predators. Furthermore, on the wintering grounds, Rusty Blackbirds often roost in mixed species congregations with Red-winged Blackbirds (Greenberg et al. 2011). Our study site has a high abundance of Red-winged Blackbirds and, indeed, most of the roosting sites we located were also shared by large flocks of this species. Since Rusty Blackbirds appear to show some seasonal flexibility with respect to roosting habitat, it may be that migrant Rusty Blackbirds cue in on large flocks of related birds to maximize safety during roosting.

Several studies of habitat use on the wintering grounds have concluded that Rusty Blackbirds are not as dependent on forested wetlands as previously supposed (Luscier

2010, DeLeon 2012, Borchert 2015), and our results support this conclusion for stopover habitat as well. Rather than being restricted to the patches of low-lying forests at our site, birds used a variety of wet shrub, prairie, marsh, and forested habitats. Large forest patches may be a visual cue for migrating Rusty Blackbirds at a landscape level, but in fine-scale selection flocks are more versatile in their habitat choices. These results suggest that wetlands with a variety of available habitat types may provide the best habitat for migrating birds on stopover. Rusty Blackbirds have diverse diet (Avery 2013) and nutritional requirements during migration, and a matrix of mixed wetland habitats could provide the resources to efficiently refuel during this energetically demanding period. During the spring, the presence of prealternate molt (Wright et al. in review) means they may also have separate nutrient requirements to meet other than refueling (McGraw 2007).

Our study has identified several important habitat characteristics that land managers can focus on to provide appropriate habitat for migrating Rusty Blackbirds. As a result of the vast extent of agricultural development around our study site and across the Midwest (Dahl and Johnson 1991), many of the habitat features Rusty Blackbirds select for are not readily available on the landscape. Thus, this species may need to be adaptable to alternative habitats, or tolerant to increased densities in currently preferred ones, to avoid continued population declines. A lack of available habitat in their migratory range could explain the large concentrations of Rusty Blackbirds at the site, as birds from around the region may funnel into the site as they search for suitable habitat. However, our results also do suggest that a fragmented landscape is useable for small

flocks of Rusty Blackbirds so long as appropriate shallow water habitat can be found.

Future studies of stopover habitat selection and behavior should be performed at a variety of other sites across their range, to determine if habitat needs differ in varying landscapes.

This will virtually complete our knowledge of Rusty Blackbird habitat requirements across their full annual cycle, and thus contribute to effective range-wide conservation efforts.

**Table 2.1.** AIC<sub>c</sub> table of top model set for fall habitat models predicting Rusty Blackbird stopover habitat selection. We used model averaging among the entire model set (n=47) to identify variables with a significant effect on fall habitat selection. See Appendix B for the full AIC<sub>c</sub> table and descriptions of variables.

Fall habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
grass + forbs + dry.litter + shallow + herb.shrub	99.26	0.00	0.26	-43.07	6
grass + forbs + shallow + herb.shrub	100.39	1.13	0.15	-44.80	5
grass + forbs + dry.litter + shallow + herb.shrub + mixed.hab	100.58	1.32	0.14	-42.53	7
grass + forbs + litter + shallow + herb.shrub	100.77	1.51	0.12	-43.83	6
grass + forbs + dry.litter + shallow + herb.shrub + canopy.cov	100.82	1.56	0.12	-42.65	7
grass + forbs + dry.litter + shallow + herb.shrub + basal.area	101.20	1.94	0.10	-42.84	7
grass + forbs + dry.litter + shallow + herb.shrub + total.shrub	101.65	2.39	0.08	-43.07	7
grass + forbs + litter + shallow + herb.shrub + mixed.hab + edge.dist	104.49	5.23	0.02	-43.26	8



**Table 2.2.** AIC<sub>c</sub> table of top model set for spring habitat models predicting Rusty Blackbird stopover habitat selection. We used model averaging among the entire model set (n=69) to identify variables with a significant effect on spring habitat selection. See Appendix B for the full AIC<sub>c</sub> table and descriptions of variables.

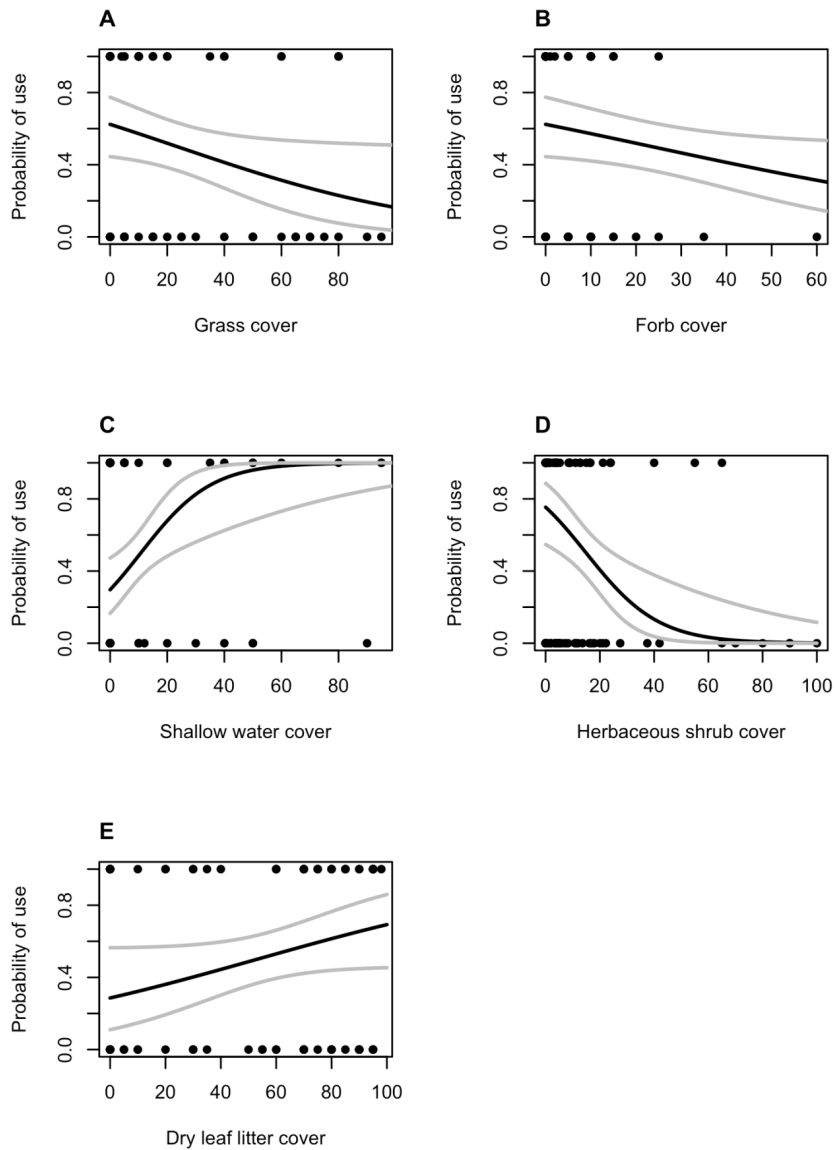
**Table 2.2.**

Spring habitat models	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
wet.litter + shallow + edge.dist + grass	245.45	0.00	0.15	-117.56	5
wet.litter*year + shallow + edge.dist + mixed.hab	245.71	0.27	0.13	-115.55	7
wet.litter*year + shallow + edge.dist	246.04	0.59	0.11	-116.79	6
wet.litter + shallow + edge.dist	246.05	0.60	0.11	-118.92	4
wet.litter + shallow + edge.dist + mixed.hab	246.13	0.68	0.10	-117.90	5
wet.litter*year + shallow + edge.dist + mixed.hab	246.40	0.95	0.09	-118.04	5
wet.litter + shallow + edge.dist + forbs	247.16	1.71	0.06	-118.42	5
wet.litter + dry.litter + shallow + edge.dist + grass	247.18	1.73	0.06	-117.36	6
wet.litter + shallow + edge.dist + herb.shrub	247.19	1.74	0.06	-118.43	5
wet.litter*year + shallow + woody.shrub	248.26	2.81	0.04	-117.90	6
wet.litter*year + shallow	248.76	3.31	0.03	-119.22	5
grass + forbs + wet.litter*year + shallow	249.42	3.97	0.02	-117.40	7
wet.litter + shallow + edge.dist + canopy.cov*year	250.36	4.91	0.01	-117.87	7

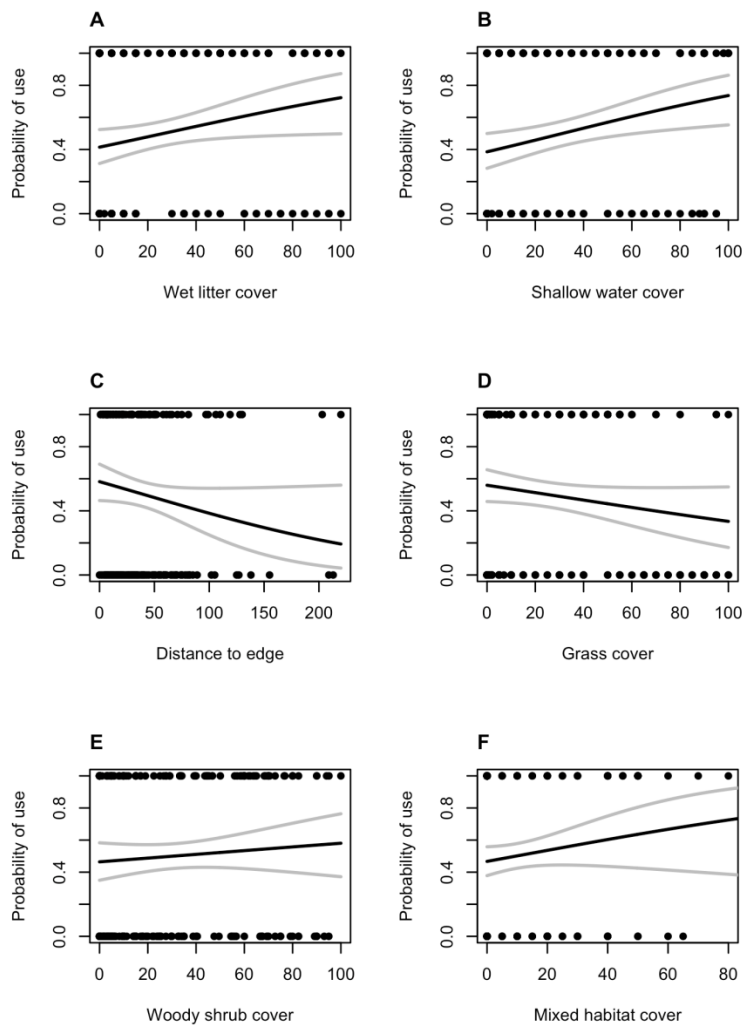
**Table 2.3.** Variables with significant effects on fine scale stopover habitat selection of Rusty Blackbirds in fall and spring, identified by multimodal inference. “GC” denotes ground cover variables. Effect size of variables was classified as strong, moderate, or weak, based on 95%, 90%, and 85% unconditional confidence intervals not overlapping zero. Odds ratios (exponentiation of the coefficient) are displayed with their relevant confidence intervals: 95% for strong effects, 90% for moderate effects, 85% for weak effects. Final habitat models incorporating these effects explained 28% of the variation in used vs. random habitat (Tjur’s  $R^2 = 0.28$ ) in the fall; and 16% of the variation in used vs. random habitat (Tjur’s  $R^2 = 0.16$ ) in the spring.

Season	Habitat variable	Effect size	Parameter effect	Odds ratio and confidence interval
Fall	GC Grass	Strong	-0.022	0.978 {0.957, 0.999}
	GC Forbs	Strong	-0.092	0.912 {0.832, 0.999}
	GC Shallow water	Strong	0.078	1.081 {1.020, 1.147}
	Herb. Shrub cover	Strong	-0.076	0.927 {0.882, 0.975}
	GC Dry litter	Moderate	0.018	1.018 {1.002, 1.036}
Spring	GC Wet litter	Strong	0.015	1.015 {1.003, 1.027}
	GC Shallow water	Strong	0.013	1.013 {1.002, 1.024}
	Distance to edge	Strong	-0.009	0.991 {0.982, 0.999}
	GC Grass	Moderate	-0.009	0.991 {0.982, 0.999}
	Woody shrub cover	Moderate	0.009	1.009 {1.000, 1.018}
	Mixed habitat	Weak	0.015	1.015 {1.000, 1.029}

**Figure 2.1.** Logistic regression plots (on the probability scale) of effects included in the final model for fall stopover habitat selection of Rusty Blackbirds. Grass (A), forb (B), shallow water (C), and herbaceous shrub cover (D) were all strong effects (95% confidence interval not overlapping zero). Dry leaf litter cover (E) exhibited a moderate effect (90% CI not overlapping zero).



**Figure 2.2.** Logistic regression plots (on the probability scale) of effects included in the final model for spring stopover habitat selection of Rusty Blackbirds. Wet leaf litter cover (A), shallow water cover (B), and distance to edge (C) were all strong effects (95% confidence interval not overlapping zero). Grass cover (D) and woody shrub cover (E) exhibited moderate effects (90% CI not overlapping zero). Amount of mixed habitat types within 11.3m plot (F) exhibited a weak effect on habitat selection (85% CI not overlapping zero).



### **Chapter 3: Conservation and Management Implications**

Many species of North American migrants are rapidly declining across their range (Robbins et al. 1989, Dunn 2002). These species are likely at highest risk of mortality during the migratory period (Sillett and Holmes 2002), so it is crucial that researchers and managers understand their behavior and habitat requirements during migration to identify factors potentially limiting population size. Our research has identified several unexpected stopover behaviors of a declining songbird, and demonstrated that more research is needed to understand migratory behaviors of other understudied passerines. The nocturnal flights and long spring stopover durations of our study species were both surprising results, and neither behavior would have been properly described without the use of a landscape-scale telemetry array. Including our work, relocations within the greater stopover landscape have now been documented for a number of songbirds (Mills et al. 2011, Taylor et al. 2011). Therefore, stopover studies that examine individual behaviors and habitat selection at a large spatial scale will be most useful in elucidating limitations for declining species on migration.

Our study specifically detailed the stopover behavior and habitat selection of Rusty Blackbirds at a high-traffic stopover site in the western Lake Erie basin. This is one of the most rapidly declining songbirds in North America (Niven et al. 2004), and as a widespread and once-common species it may be a particularly good indicator of threats other songbirds face on migration (NABCI 2014). We found that Rusty Blackbirds make

exceptionally long stopovers for a passerine during both migration seasons, and there was a considerable amount of site fidelity to the region between seasons. Furthermore, these stopover events often included a substantial amount of landscape-scale movement over a considerable spatial scale (~35km). Together with results of the Rusty Blackbird Blitz (Evans et al. in prep), which identified this region as having among the highest relative abundance during migration, our results indicate that the marsh region of the western Lake Erie basin is a critical feature of the annual cycle of Rusty Blackbirds.

Since a large percentage of native wetland habitat has disappeared over the last century as a result of urban and agricultural development (Dahl and Johnson 1991, Dahl 2011), it is important to identify high-quality stopover sites to ensure that they are not developed for anthropogenic use, and mitigate past losses through restoration. However, the landscape-scale use of individuals at our site suggests that Rusty Blackbirds are able to locate and utilize useable habitat within a fragmented landscape matrix. Thus, quality stopover sites may need to have a large, but not necessarily contiguous, area of available habitat. One way to identify these areas is to find regions that have multiple moderate to large blocks of intact wetlands in relatively close proximity (<35km; based on landscape relocations, Chapter 1). We should note that this describes our study region, so this assessment involves a certain degree of bias. Rusty Blackbird behavior at our site may be a function of the surrounding landscape, and different stopover behaviors are of course possible at other sites, with varying degrees of habitat isolation. Similar studies are needed along a gradient of wetland fragmentation to determine if these behaviors are consistent across their range, or are a function of habitat configuration.

Once appropriate stopover landscapes have been identified, managers must know what specific habitat variables Rusty Blackbirds prefer. The fine-scale habitat selection of Rusty Blackbirds at our site echoed our expectations, with access to shallow water and leaf litter being of primary importance for foraging. The use of a variety of wet habitats by flocks of Rusty Blackbirds provides further evidence that large blocks of forested wetlands are not necessary for adequate stopover habitat, and that a mixed wetland matrix including emergent marsh, mesic shrublands, and wet forest may be ideal to provide suitable habitat for both foraging and roosting birds. Their preference for edges also indicates that Rusty Blackbirds prefer areas with some degree of habitat complexity. During fall migration, sites with an abundance of dogwood or other high-fat content, berry-producing shrubs may be of particular importance to migrant Rusty Blackbirds, as is the case with many other migrant passerines (Tietz and Johnson 2007, Alan et al. 2013, Smith et al. 2013).

Rusty Blackbirds exhibited striking similarities in behavior to migrating shorebirds. Coupled with their reliance on shallow water (<10cm) for foraging, these results suggest that current hydrological management practices for shorebirds can be adapted or expanded to other habitat types to encourage Rusty Blackbird use during migration (Potter et al. 2007). Ensuring that wetland units are not too deep during the migratory period will allow Rusty Blackbirds to forage most effectively. Conversely, allowing forest or shrub units to flood periodically during migration will greatly increase the amount of habitat available to Rusty Blackbirds. While beavers (*Castor canadensis*) are considered a hindrance to effective land management in many areas, it may be



beneficial to allow a certain degree of beaver activity at some sites to create areas of shallow water within appropriate foraging habitat (Powell et al. 2014, Wright pers. obs.).

Our study also draws attention to the pressing conservation issue of the impacts of wind power development on volant animals. Wind turbines currently account for >300,000 mortalities of migrating birds per year (Loss et al. 2013, Erickson et al. 2014). With the planned development of off-shore wind energy on Lake Erie (U.S. Department of Energy 2017) and the Lake Erie marsh region (a Globally Important Bird Area), many nocturnally migrating birds will be at risk of collision with these huge moving structures (Kunz et al. 2007). Our research shows that most Rusty Blackbirds migrate at night and across the lake, placing them among the many species that are at risk of collision mortality. Our research also demonstrated that migratory departure decisions are dictated in large part by favorable tailwind conditions. As Dossman (2015) suggests, mortality rates to migrant birds could be greatly reduced by halting turbine operation during nights of favorable migratory conditions.

Rusty Blackbird populations are now a fraction of what they were a century ago, but they are still widespread and locally common in areas such as the western Lake Erie marsh region. Our study is the first to describe their life history, movement behavior, and habitat selection during migratory stopover, a critical period in their full annual cycle. Rusty Blackbirds at our site exhibited extensive molt during spring migration, as well as stopover durations and movement behaviors very similar to migrating shorebirds at staging sites. The Rusty Blackbird is the first passerine species known to exhibit this type of migration strategy. Our examination of their fine-scale habitat selection on

stopover confirmed their reliance on shallow water for foraging, but also demonstrated their preference for a matrix of mixed wetland habitat. The knowledge that our research has provided will inform conservation and management practices for Rusty Blackbirds across their migratory range. With appropriate action, crucial stopover habitat can be identified and protected to help slow or prevent further population declines.

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## Appendix A: Chapter 1 Supplemental Materials

**Table A.1.** Summary output of final Bayesian GLM model for fall stopover duration, from package ‘brms’ in Program R.

---

Family: negbinomial(log)  
Formula: duration ~ capdate  
Data: fall.stop.dep (Number of observations: 22)  
Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 4000  
ICs: LOO = 157.8; WAIC = 157.46; R2 = 0.29

### Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	10.84	2.50	5.77	15.82	2471	1.00
capdate	-0.03	0.01	-0.04	-0.01	2458	1.00

### Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
shape	25.03	17.73	7.58	66.90	1380	1.00



**Table A.2.** Summary output of final Bayesian GLM model for spring stopover duration, from package ‘brms’ for Program R.

---

Family: negbinomial(log)  
 Formula: duration ~ year \* sex + ccmi \* condition + SJD  
 Data: spring.stop.dep (Number of observations: 39)  
 Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 4000  
 ICs: LOO = 280.4; WAIC = 279.15; R2 = 0.63

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
Intercept	3.32	0.10	3.13	3.52	2216	1.00
year4	0.02	0.17	-0.31	0.36	1708	1.00
sexM	0.18	0.13	-0.08	0.44	2023	1.00
ccmi	0.14	0.06	0.03	0.25	2720	1.00
condition	0.14	0.05	0.04	0.23	4000	1.00
SJD	-0.02	0.00	-0.03	-0.01	4000	1.00
year4:sexM	-0.46	0.21	-0.87	-0.05	1576	1.00
ccmi:condition	-0.15	0.06	-0.27	-0.03	2412	1.00

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Eff.Sample	Rhat
shape	31.80	22.00	10.45	88.67	1621	1.00

## Appendix B: Chapter 2 Supplemental Materials

**Table B.1.** List and description of all habitat variables included in AIC<sub>c</sub> model selection.

Habitat variable	Description
grass	Ground cover (5m radius): % grass <50cm
sedge	Ground cover (5m radius): % sedge <50cm
forbs	Ground cover (5m radius): % forbs <50cm
wet.litter	Ground cover (5m radius): % wet leaf litter
dry.litter	Ground cover (5m radius): % dry litter
litter	Ground cover (5m radius): % wet and dry litter combined
woody	Ground cover (5m radius): % woody debris
shallow	Ground cover (5m radius): % shallow water <10cm deep
deep	Ground cover (5m radius): % deep water >10cm deep
mud	Ground cover (5m radius): % mud
litter.depth	Ground cover (5m radius): average of 12 leaf litter depth measurements (cm)
water.depth	Ground cover (5m radius): average of 12 water depth measurements (cm)

continued

continued

**Table B.1.** List and description of all habitat variables included in AIC<sub>c</sub> model selection.

Habitat variable	Description
shrub.ht	Shrub cover (5m radius): average shrub height of plot, calculated by weighted mean of shrub species heights
woody.shrub	Shrub cover (5m radius): total woody shrub cover, calculated by summing cover of woody shrub species
herb.shrub	Shrub cover (5m radius): total herbaceous shrub cover, calculated by summing cover of herbaceous shrub species
total.shrub	Shrub cover (5m radius): total shrub cover of plot, regardless of woody or herbaceous
berry.stems	Shrub cover (5m radius - fall only): count of mature dogwood stems >2m
dw.leafout	Spring only: length of leafout (mm), measured from twig of nearest dogwood stem to plot center
canopy.ht	Average canopy height of plot, determined by range finder
canopy.cov	Average canopy cover of plot, determined by densiometer reading at plot center
basal.area	Total basal area of plot (m <sup>2</sup> ), calculated by summing basal area of all trees within 11.3m radius
mixed.hab	Total percentage of other habitat types besides habitat type at plot center within 11.3m radius
edge.dist	Distance to nearest edge of habitat patch

**Table B.2.** Full AIC<sub>c</sub> model selection results for fall habitat models.

Fall habitat models	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
grass + forbs + dry.litter + shallow + herb.shrub	99.26	0.00	0.26	-43.07	6
grass + forbs + shallow + herb.shrub	100.39	1.13	0.15	-44.80	5
grass + forbs + dry.litter + shallow + herb.shrub + mixed.hab	100.58	1.32	0.14	-42.53	7
grass + forbs + litter + shallow + herb.shrub	100.77	1.51	0.12	-43.83	6
grass + forbs + dry.litter + shallow + herb.shrub + canopy.cov	100.82	1.56	0.12	-42.65	7
grass + forbs + dry.litter + shallow + herb.shrub + basal.area	101.20	1.94	0.10	-42.84	7
grass + forbs + dry.litter + shallow + herb.shrub + total.shrub	101.65	2.39	0.08	-43.07	7
grass + forbs + litter + shallow + herb.shrub + mixed.hab + edge.dist	104.49	5.23	0.02	-43.26	8
grass + forbs + litter + shallow + woody*deep + herb.shrub	109.99	10.73	0.00	-43.44	10
grass + forbs + dry.litter + shallow	111.50	12.24	0.00	-50.36	5
grass + forbs + litter	111.83	12.56	0.00	-51.65	4
herb.shrub	113.07	13.80	0.00	-54.46	2
grass	114.45	15.19	0.00	-55.15	2

continued

continued

**Table B.2.** Full AIC<sub>c</sub> model selection results for fall habitat models.

Fall habitat models	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
woody	114.48	15.22	0.00	-55.16	2
shrub.ht + herb.shrub	115.15	15.89	0.00	-54.42	3
herb.shrub + berry.stems	115.21	15.95	0.00	-54.45	3
shrub.ht*basal.area	115.38	16.12	0.00	-53.43	4
litter.depth	115.47	16.21	0.00	-55.66	2
litter	115.68	16.42	0.00	-55.76	2
null model	115.73	16.47	0.00	-56.84	1
basal.area	115.81	16.54	0.00	-55.83	2
herb.shrub*basal.area	115.94	16.68	0.00	-53.71	4
forbs	116.05	16.79	0.00	-55.95	2
shallow	116.26	16.99	0.00	-56.05	2
dry.litter	116.61	17.35	0.00	-56.23	2
edge.dist*basal.area	116.69	17.43	0.00	-54.08	4

continued

continued

**Table B.2.** Full AIC<sub>c</sub> model selection results for fall habitat models.

Fall habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
edge.dist	116.72	17.46	0.00	-56.28	2
woody.shrub	116.78	17.52	0.00	-56.31	2
wet.litter	117.38	18.12	0.00	-56.62	2
berry.stems	117.45	18.19	0.00	-56.65	2
mixed.hab	117.46	18.20	0.00	-56.66	2
sedge	117.52	18.26	0.00	-56.68	2
total.shrub	117.60	18.33	0.00	-56.72	2
canopy.ht	117.65	18.39	0.00	-56.75	2
canopy.cov	117.71	18.45	0.00	-56.78	2
shrub.ht	117.74	18.48	0.00	-56.79	2
deep	117.76	18.50	0.00	-56.80	2
water.depth	117.82	18.56	0.00	-56.83	2
canopy.cov + basal.area	117.83	18.57	0.00	-55.76	3

continued

continued

**Table B.2.** Full AIC<sub>c</sub> model selection results for fall habitat models.

Fall habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
woody*deep	117.87	18.61	0.00	-54.68	4
woody*water.depth	118.44	19.18	0.00	-54.96	4
woody.shrub*basal.area	118.83	19.57	0.00	-55.16	4
grass + sedge + forbs + wet.litter + dry.litter + woody + deep + shallow	118.86	19.60	0.00	-49.18	9
woody.shrub + berry.stems	118.93	19.67	0.00	-56.31	3
grass + sedge + forbs + litter + woody*deep + shallow	119.26	20.00	0.00	-49.38	9
shrub.ht + woody.shrub + herb.shrub + berry.stems	119.56	20.30	0.00	-54.38	5
canopy.ht + canopy.cov + basal.area	119.89	20.63	0.00	-55.68	4
global model	123.98	24.72	0.00	-40.21	17

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
wet.litter + shallow + edge.dist + grass	245.45	0.00	0.15	-117.56	5
wet.litter*year + shallow + edge.dist + mixed.hab	245.71	0.27	0.13	-115.55	7
wet.litter*year + shallow + edge.dist	246.04	0.59	0.11	-116.79	6
wet.litter + shallow + edge.dist	246.05	0.60	0.11	-118.92	4
wet.litter + shallow + edge.dist + mixed.hab	246.13	0.68	0.10	-117.90	5
wet.litter*year + shallow + edge.dist + mixed.hab	246.40	0.95	0.09	-118.04	5
wet.litter + shallow + edge.dist + forbs	247.16	1.71	0.06	-118.42	5
wet.litter + dry.litter + shallow + edge.dist + grass	247.18	1.73	0.06	-117.36	6
wet.litter + shallow + edge.dist + herb.shrub	247.19	1.74	0.06	-118.43	5
wet.litter*year + shallow + woody.shrub	248.26	2.81	0.04	-117.90	6
wet.litter*year + shallow	248.76	3.31	0.03	-119.22	5
grass + forbs + wet.litter*year + shallow	249.42	3.97	0.02	-117.40	7
wet.litter + shallow + edge.dist + canopy.cov*year	250.36	4.91	0.01	-117.87	7

continued



continued

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
wet.litter + shallow	250.46	5.01	0.01	-122.17	3
wet.litter*year	251.08	5.63	0.01	-121.43	4
wet.litter	253.83	8.38	0.00	-124.88	2
shallow	254.66	9.22	0.00	-125.30	2
shallow*year	257.34	11.89	0.00	-124.56	4
grass + sedge + forbs + wet.litter + dry.litter + woody + deep + litter.depth + shallow + mud	261.56	16.11	0.00	-119.05	11
grass	264.92	19.48	0.00	-130.43	2
forbs	265.02	19.58	0.00	-130.48	2
litter.depth	266.14	20.69	0.00	-131.04	2
litter	266.26	20.81	0.00	-131.10	2
total.shrub	266.61	21.16	0.00	-131.27	2
edge.dist	266.91	21.47	0.00	-131.42	2
dry.litter	267.14	21.70	0.00	-131.54	2

continued

continued

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
woody.shrub	267.20	21.75	0.00	-131.57	2
edge.dist*basal.area	267.50	22.05	0.00	-129.64	4
mixed.hab	267.51	22.06	0.00	-131.72	2
woody	267.61	22.17	0.00	-131.78	2
canopy.ht	267.77	22.32	0.00	-131.85	2
null model	268.19	22.74	0.00	-133.08	1
edge.dist*year	268.23	22.78	0.00	-130.01	4
litter.depth*year	268.28	22.83	0.00	-130.03	4
shrub.ht	268.29	22.85	0.00	-132.11	2
woody.shrub + herb.shrub	268.54	23.09	0.00	-131.21	3
woody.shrub*basal.area	268.72	23.27	0.00	-130.25	4
forbs*year	268.96	23.52	0.00	-130.38	4
grass*year	269.00	23.55	0.00	-130.39	4

continued

continued

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
basal.area	269.01	23.57	0.00	-132.48	2
canopy.cov	269.17	23.72	0.00	-132.55	2
shrub.ht*basal.area	269.31	23.86	0.00	-130.55	4
canopy.cov*year	269.34	23.89	0.00	-130.56	4
herb.shrub	269.77	24.32	0.00	-132.85	2
mud	269.94	24.49	0.00	-132.94	2
litter*year	269.96	24.51	0.00	-130.87	4
deep	270.01	24.56	0.00	-132.97	2
water.depth	270.06	24.61	0.00	-133.00	2
sedge	270.20	24.75	0.00	-133.07	2
dw.leafout	270.23	24.78	0.00	-133.08	2
canopy.ht*year	270.71	25.27	0.00	-131.25	4
woody.shrub*year	270.78	25.33	0.00	-131.28	4

continued

continued

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
canopy.cov + basal.area	270.87	25.43	0.00	-132.37	3
global model	270.88	25.44	0.00	-112.99	20
dry.litter*year	271.00	25.55	0.00	-131.39	4
woody*deep	271.05	25.61	0.00	-131.42	4
woody*year	271.32	25.88	0.00	-131.55	4
woody*water.depth	271.40	25.95	0.00	-131.59	4
mixed.hab*year	271.62	26.18	0.00	-131.70	4
canopy.ht + canopy.cov + basal.area	271.88	26.43	0.00	-131.83	4
basal.area*year	272.04	26.59	0.00	-131.91	4
herb.shrub*basal.area	272.22	26.77	0.00	-132.00	4
sedge*year	272.26	26.81	0.00	-133.06	3
shrub.ht*year	272.42	26.98	0.00	-132.11	4
shrub.ht + woody.shrub + herb.shrub + dw.leafout	272.62	27.17	0.00	-131.15	5

continued

continued

**Table B.3.** Full AIC<sub>c</sub> model selection results for spring habitat models.

Spring habitat models	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$	Log-likelihood	$k$
herb.shrub*year	273.74	28.29	0.00	-132.76	4
deep*year	273.77	28.32	0.00	-132.78	4
mud*year	274.09	28.64	0.00	-132.94	4
water.depth*year	274.12	28.68	0.00	-132.96	4
dw.leafout*year	274.38	28.93	0.00	-133.08	4