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RESEARCH ARTICLE

Automated telemetry reveals staging behavior in a declining migratory passerine

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ABSTRACT

Migratory birds spend most of their journeys at stopover sites where they rest and refuel. Many migrants are in steep decline, and understanding their behavior within and among migrations is crucial for developing effective conservation strategies across the full annual cycle. One of the most rapidly declining songbirds in North America is the Rusty Blackbird (*Euphagus carolinus*; 85–95% decline over the past 50 yr), and stopover ecology is a major gap in our knowledge of its annual cycle. We utilized an automated telemetry array in western Lake Erie and the Motus Wildlife Tracking System to track landscape-scale movements, stopover duration, departure behavior, and between-season site fidelity in this species. We found that stopover duration during both fall and spring was nearly 1 mo (mean = 25.5 days)—exceptionally long for a passerine. During spring, birds in both poor condition and high degree of molt had longer stopovers, post-departure flights were relatively long for a songbird, and tailwinds predicted departure in both seasons. Many individuals made landscape-scale (10–35 km) relocations during stopover. Site fidelity was high for a passerine, in terms of both route and stopover site. Taken together, these behaviors describe a migration strategy that largely matches the staging behavior of shorebirds. Lastly, we found that Rusty Blackbirds migrate directly across Lake Erie and migrate primarily at night, which might expose them to mortality from offshore wind development. Collectively, our results indicate that high-quality stopover habitat may be critically important to Rusty Blackbird populations. More broadly, our results highlight the need to expand the scale of stopover studies, and to further explore all aspects of species' annual cycles to understand potential limiting factors on populations.

Keywords: Euphagus carolinus, migration, Motus, Rusty Blackbird, staging, stopover

La télémétrie automatisée révèle un comportement de halte migratoire chez un passereau migrateur en déclin

RÉSUMÉ

La majorité du voyage des oiseaux migrateurs se passe dans les haltes migratoires, où les oiseaux se reposent et se ravitaillent. Plusieurs espèces migratrices sont en fort déclin; ainsi, comprendre leur comportement pendant une migration et d'une migration à l'autre est essentiel afin de développer des stratégies de conservation efficaces tout au long du cycle annuel. L'un des oiseaux chanteurs dont le déclin est le plus rapide en Amérique du Nord est *Euphagus carolinus* (85-95 % de déclin au cours des 50 dernières années). L'écologie de halte migratoire constitue une lacune majeure dans nos connaissances sur son cycle annuel. Nous avons utilisé un réseau de télémétrie automatisée dans l'est du lac Érié et le Système de surveillance faunique Motus pour suivre les déplacements à l'échelle du paysage, la durée de la halte migratoire, le comportement de départ et la fidélité au site entre les saisons chez cette espèce. Nous avons trouvé que la durée de halte migratoire en automne et au printemps était près d'un mois (moyenne = 25,5 jours), ce qui est exceptionnellement long pour un passereau. Au printemps, les oiseaux en mauvaise condition physique et fortement en mue faisaient une halte plus longue, les vols après le départ étaient relativement longs pour un oiseau chanteur et les vents arrières prédisaient le moment de départ au cours des deux saisons. Plusieurs individus se sont relocalisés à l'échelle du paysage (10-35 km) au cours de leur halte migratoire. La fidélité au site était élevée pour un passereau, à la fois en termes de trajet et de site de halte migratoire. Ensemble, ces comportements décrivent une stratégie de migration similaire au comportement de halte migratoire des limicoles. Enfin, nous avons révélé qu'*E. carolinus* migre directement par-dessus le lac Érié, et principalement la nuit, ce qui l'expose potentiellement à une mortalité due au développement éolien au large des côtes. Collectivement, nos résultats indiquent qu'un habitat de halte migratoire de qualité élevée peut être essentiel pour les populations d'*E. carolinus*. De façon plus générale, nos résultats mettent en lumière le besoin d'élargir l'échelle des études sur les haltes migratoires et d'explorer davantage tous les aspects du cycle annuel des espèces afin de comprendre les facteurs limitants potentiels des populations.

Mots-clés : Euphagus carolinus, halte migratoire, migration, Motus, rassemblement

INTRODUCTION

Each spring and fall, hundreds of species of North American birds migrate thousands of kilometers between their breeding and wintering grounds. For many species, these migrations are completed as quickly as is energetically possible (Alerstam et al. 2003), and their annual cycle is essentially 2 stationary periods punctuated by 2 periods of rapid movement. Those periods of rapid movement, in turn, are punctuated by stopover events when birds stop to quickly refuel (for several hours to several days) before continuing on their migration (Newton 2008). In fact, the majority of a bird's time and energy during the migratory period is spent on these stopover events, rather than on actual migratory flights (Wikelski et al. 2003). As such, the protection of stopover habitat, and the identification of key stopover sites, is essential to the conservation of declining bird species (Buler and Moore 2011, Cohen et al. 2017).

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 lasting up to several weeks, often referred to as "staging" events (Warnock 2010), occur in numerous shorebird and waterfowl species (Warnock 2010, Ma et al. 2013, Bengtsson et al. 2014) and have been increasingly documented in passerines (reviewed in McKinnon et al. 2013). These events could be driven by various 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 spent refueling 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. For species that make extended stopovers at specific sites and where stopover can fulfill multiple functions, habitat conservation is especially critical (Sheehy et al. 2011).

Stopover duration can vary between individuals of a species as a result of intrinsic and extrinsic factors. Energy reserves are often an important intrinsic factor, because birds arriving with lower fat content must remain on stopover longer to replenish reserves to an adequate level for further migration (Deppe et al. 2015, Lupi et al. 2016). In addition, duration may vary in an age- or sex-specific manner, 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 vs. young birds (Newton 2008, McKinnon et al. 2016). Extrinsic environmental factors such as weather and geography also influence stopover dynamics. For instance, favorable wind conditions influence departure time in some species (e.g., Mitchell et al. 2015, Dossman et al. 2016), and rainfall may drive food availability, and therefore refueling rates, thus influencing stopover duration and survival (Halupka et al. 2017). Individual stopover duration is largely determined by the interplay of these intrinsic and extrinsic factors, as a bird's behavior on stopover will depend on its geographic location, environmental conditions, and internal drivers (Cohen et al. 2014, Deppe et al. 2015).

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). In relation to other stages in the annual cycle, the highest mortality in migrant species is thought to take place during migration (Sillett and Holmes 2002, Klaassen et al. 2014). However, migration is one of the least understood stages of a bird's annual cycle, largely because of the difficulties of studying individuals during a period of large-scale movement (Marra et al. 2015). Such is the case for the Rusty Blackbird (*Euphagus carolinus*), a once common species that has experienced 85–95% declines over the past 50 yr (Niven et al. 2004) and shows qualitative evidence of declines dating to the 19th century (Greenberg and Droege 1999). Recently, numerous studies have attempted 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., Luscier 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 methylmercury 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 can form large congregations in some areas but remain diffuse across most of their migratory range (Rusty Blackbird Spring Migration Blitz; Evans 2016). However, we have no information on how individuals utilize stopover sites and whether specific stopover sites play an important role in their annual cycle. During the nonbreeding period, Rusty Blackbirds are a flocking species strongly associated with forested wetland habitat (Luscier et al. 2010). Given that large expanses of forested wetland have been developed for agriculture (Dahl and Johnson 1991), it is possible that migrant Rusty Blackbirds aggregate in traditional high-quality habitat sites, much like the example of Red Knots in Delaware Bay (Gillings et al. 2009).

Our overarching goal was to describe Rusty Blackbird stopover biology by using a large, automated telemetry array to track movement behavior 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), as well as extrinsic factors (wind, temperature, and precipitation conditions) at the stopover site. By tracking the movements and stopover duration of individuals, we sought to determine where Rusty Blackbirds sit within the spectrum of migratory strategies. We predicted that stopover duration would be (1) longer in fall than in spring, because 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. Because males are under greater pressure to return to the breeding grounds to establish territories (Morbey and Ydenberg 2001), we predicted (3) that males would arrive sooner than females in spring, but we expected no such relationship in fall. Because 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) that younger birds would arrive later than older birds in fall. Lastly, we expected (5) that most migratory departures would occur diurnally (Avery 2013); and (6) that among extrinsic environmental variables, migratory departure would be best predicted by wind conditions, with increasing tailwinds predicting departure (Dossman et al. 2016). In addition to testing these predictions, we describe other poorly known behaviors of Rusty Blackbirds such as flight speed, movement behavior during stopover, and site fidelity between seasons. The results fill a large gap in our knowledge of the full annual cycle of this species, which is critical to understanding its ecology and the causes of its population declines.

METHODS

Study Site
We captured Rusty Blackbirds over the course of 4 migration seasons from fall 2015 to spring 2017 at a high-traffic stopover site in northern Ohio, USA: Ottawa National Wildlife Refuge and Magee Marsh State Wildlife Area (41.608°N, 83.208°W; Figure 1). The Rusty Blackbird Spring Migration Blitz (Evans 2016), a citizen science–based effort, identified this area on the southwestern shore of Lake Erie as receiving among the highest numbers of migrant Rusty Blackbirds in North America. This site consists of a managed complex of wetlands ~28 km^2 in size, containing a substantial amount of relatively suitable habitat (e.g., wet forest/shrublands; Avery 2013) for the species in a region dominated by agricultural development. The geographic location of the site (situated adjacent to a large body of water) likely concentrates many migrants, which may partly explain the high volume of Rusty Blackbirds. The study site is also at the northern edge of

the wintering range of Rusty Blackbirds, but eBird reports (Sullivan et al. 2009) suggest that numbers of overwintering birds in the area are typically low.

Capture Methods
We captured birds passively using mist nets (60 mm mesh) by targeting reliable Rusty Blackbird foraging areas. Capture effort was irregular, depending on weather conditions and the ease of locating foraging flocks, but generally consisted of opening six 12 m nets for 4–8 hr on capture days. During fall, we captured birds on 4 days in late October 2015 and on 6 days between October 9 and November 14, 2016. During spring, we captured birds on 6 days between March 15 and April 19, 2016, and on 4 days between March 12 and April 14, 2017. Because of difficulties in targeting specific individuals, no dedicated effort was made to recapture individuals over the course of their stopover. 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 determined age and sex using feather and eye characteristics (Pyle 1997, Mettke-Hofmann et al. 2010). We measured a standard suite of morphometrics in each individual, of which mass (±0.1 g) and wing chord (±0.5 mm) were included in the final analysis. We also examined each bird for flight feather and body molt; for birds captured in spring, we recorded body molt using a variation of Greenwood et al.'s (1983) method of combined contour molt index (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 0–100 (Wright et al. 2018). Molt was rare in fall, so we did not employ this detailed method for fall-captured birds.

Automated Radio Telemetry
We deployed 2.1 g coded nanotags (model NTQB-6-1; Lotek Wireless, Newmarket, Ontario, Canada) on a subset of all captured birds each season, using a leg-loop harness (Rappole and Tipton 1991) with 1.5 mm diameter stretch bead cord (Stretch Magic brand) melted to itself with a soldering iron. These tags broadcast on the same frequency (166.380 MHz, pulse rate 6.1–10.1 s) but have unique digitally coded signatures to allow for individual identification. Battery life of tags was estimated at approximately 9–12 mo depending on the pulse rate, allowing for repeat detections should individuals return to the site during subsequent migrations.

We used an array of automated telemetry towers to track tagged birds (Figure 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
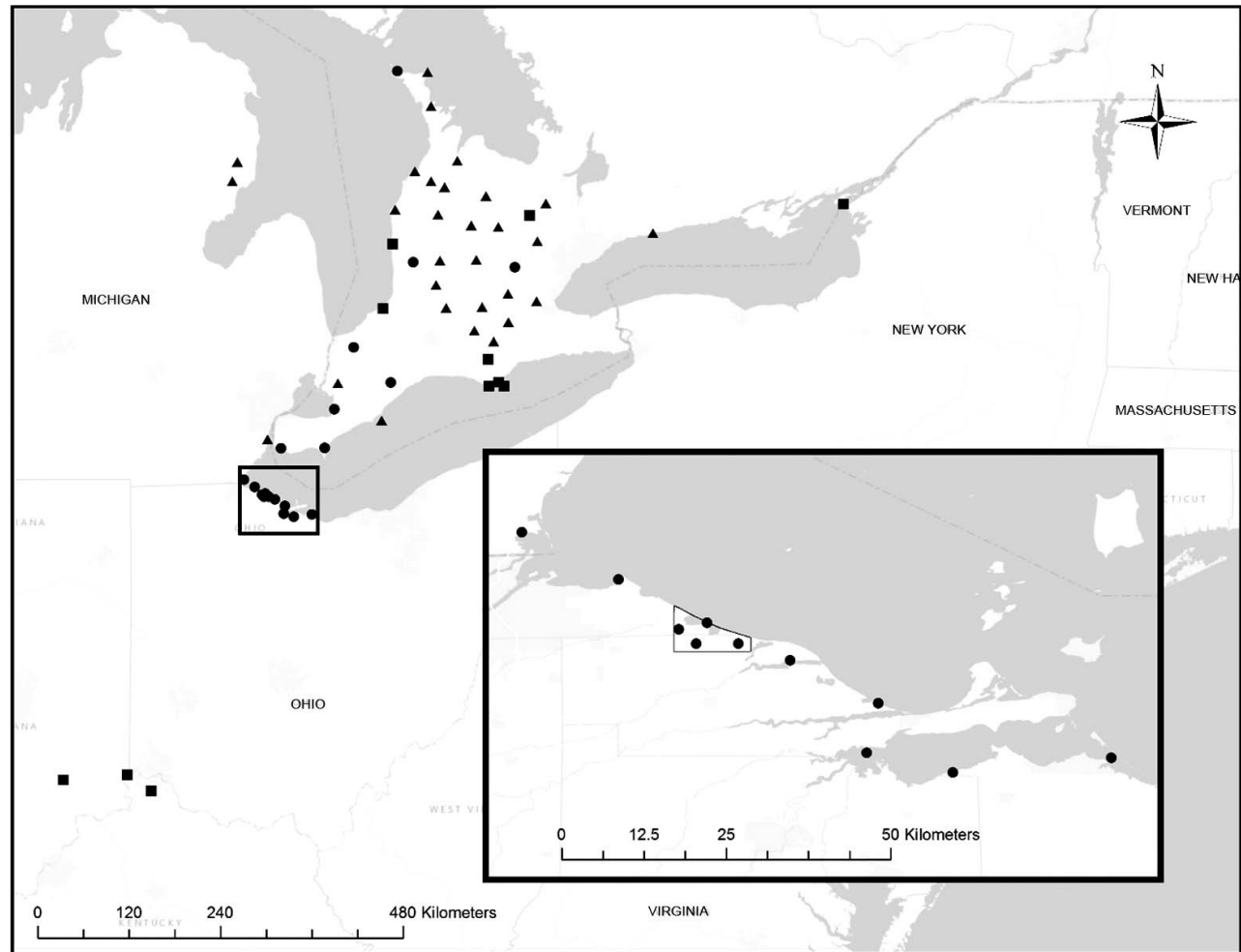
FIGURE 1. Location of the study site on Lake Erie in northwest Ohio, USA (Ottawa National Wildlife Refuge–Magee Marsh State Wildlife Area), and of automated telemetry towers that detected Rusty Blackbirds. Towers that detected birds are represented by triangles for spring, squares for fall, and circles for both spring and fall detections. The study site where birds were captured is outlined in black within the inset map. The four towers within the study site are the "local" array; the other towers within the inset map make up the "regional" array. All other towers are part of the broader Motus Wildlife Tracking System.

consisted of 4 towers surrounding the main capture site (i.e. Ottawa NWR/Magee Marsh WA), providing full coverage of the area. The "regional" array consisted of 7 additional towers spread out over 75 km to the west and east of the study site, along the southwestern shore of Lake Erie. In addition to our local and regional arrays, we used data collected from the Motus Widlife Tracking System array (Taylor et al. 2017) in Michigan and Indiana, USA, and Ontario, Canada. Motus is a collaborative network of >300 automated telemetry stations that coordinates data sharing among researchers, to which we contribute. The towers outside the local array allowed us to monitor large-scale movements and confirm departure events. All local and regional array towers, and most relevant Motus towers, were active throughout the entire duration of the study period, including intervening winters and summers.

The exact deployment of Motus towers at the time of data collection can be found at http://www.motus.org/data/receivers.

The towers in the local and regional arrays each consisted of 2–4 nine-element Yagi antennas mounted 9 m above ground, connected to a Lotek receiver (model SRX 600, 800, or DL). Under ideal conditions (birds flying above trees, no obstructions between tag and tower), the detection range can 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 is <500 m (J. R. Wright personal observation). 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 s. For every tag detection, receivers recorded the tag ID, time, antenna of detection, and signal strength.

Movement and Departure Categorization

There was great variability in the movements of tagged birds; therefore, 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, because Rusty Blackbirds forage during the day and roost at night, we categorized diurnal and nocturnal detections separately. Lastly, we distinguished between "local" birds (tagged present season) and "returned" birds (tagged previous season). 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.

Diurnal detections. We categorized the tower detections during daytime as follows:

- *To/from roost.* This was 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.
- *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.
- *Sporadic.* When birds left the local array, they could go undetected for days, then return at seemingly random intervals in the regional array. This meant they were somewhere in the area but at the fringe of the tower's detection range. We considered these types of detections evidence of stopover relocation.
- *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).
- *Diurnal departure.* Similar to a migratory flyby, but for local birds. If a local bird was detected flying by multiple towers in an appropriate migratory direction and was never detected again, this was considered a probable migratory departure.
- *Absence.* The absence of any detections from the local array for >2 days, followed by the return of detections, indicated that the bird was not utilizing the study site

and was considered a probable temporary stopover relocation.

Nocturnal detections. We categorized the tower detections at night as follows:

- *On roost.* If a bird was roosting very close to a tower, it could be detected either for part of the night or for the entire night. In this case, it was always detected the following morning, leaving the roost.
- *Disturbed from roost.* Birds were occasionally detected briefly during the night, probably because of some disturbance on the roost. In this case, the birds were always detected the following morning at the same tower, leaving the roost.
- *Nocturnal migratory flyby.* This is the same type of detection as the diurnal migratory flyby, occurring only at night.
- *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.

Movement categorization. Our criteria for determining when birds made migratory departures, stopover relocations, or unknown movements (Table 1) were as follows:

- *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 or night. Given the geographic coverage of the Motus array (i.e. few towers south of the study area), we classified very few fall movements as "confirmed departures."
- *Probable departure.* A "diurnal" or "nocturnal departure," not subsequently followed by Motus array detections.
- *Confirmed relocation.* We detected birds by the first 3 diurnal categories (most often "sporadic") in the regional array after they had left the local array.
- *Probable relocation.* "Absence" from the array for >2 days, followed by subsequent detections in either the local or the regional array.
- *Unknown movement.* When the final detections of birds were indistinguishable from the first 3 diurnal detection categories, we were unable to categorize the apparent end of stopover as a true departure vs. stopover relocation.
- *Migratory flyby.* Either diurnal or nocturnal "migratory flyby" of a returning bird.

Statistical Analysis

We excluded birds with unknown departures from analyses of stopover duration and departure behavior.

TABLE 1. Stopover departure and movement categorizations for all tagged Rusty Blackbirds at western Lake Erie, Ohio, USA, including returned birds. Numbers represent confirmed and probable diurnal (D) and nocturnal (N) migratory departures and total numbers of stopover relocations, migratory flybys of returned birds (tagged previous season), and predations (by owl or unknown raptor).

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

Because different evolutionary and ecological factors drive fall and spring migration (Alerstam et al. 2003), we analyzed the 2 seasons separately. Intrinsic explanatory variables included day of capture, sex, age, body condition, and molt score (spring only). Fat score was also recorded, but we removed it from analyses because it had no relationship with response variables and was collinear with body condition. 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). Because the slopes of the body size–mass relationship were not different for males and females ($P > 0.05$), we pooled the 2 sexes. Since no consistent effort was made to recapture birds, we do not have a measure of fuel deposition rate; thus, body condition upon initial capture is our only proxy for fuel load. Additionally, because very few captured birds were lean (fat score $= 0$; $n = 5$ birds) and we did not have access to a long-term dataset of migrant Rusty Blackbirds, we were unable to use lean body mass to calculate arrival fuel loads as other studies have done (e.g., Delingat et al. 2008, Bulyuk 2012). Capture day (or arrival day (i.e. ordinal day) for returning birds, hereafter "capture/arrival") was correlated with sex in 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 mean $= 0$ and SD $= 1$. To test for year effects in spring, we included year and all 2-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. We tested additional 2-way interaction terms as appropriate, including interactions of age, sex, and body condition with capture day and molt score. Returned birds (spring $n = 2$, fall $n = 2$) were not captured again upon return; thus, we had several missing values for body condition and spring molt score. In order to avoid removing relevant data from analyses, we generated these few missing values using multiple imputation by Gibbs sampling (package "mice" for R;

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

Stopover duration. We calculated minimum stopover duration (date and 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 ("brms" package; Bürkner 2017) in R 3.4.1 (R Core Team 2017). Because there was evidence of overdispersion in our dataset (dispersion $= 6.7$; function "dispersiontest" in package "AER" for R; Kleiber and Zeileis 2008), we used a negative binomial error distribution with a log link function and flat priors for our models. Model evaluation was performed using leave-one-out 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 the convergence and fit of our final models by 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 4 Markov chain Monte Carlo chains of 2,000 iterations each (burn-in $= 1,000$, 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 (Therneau and Grambsch 2000; 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. We performed CPH analysis using the "survival" (Therneau 2015) and "survminer" (Kassambara and Kosinski 2017) packages for R.

Meteorological data for the duration of each season were obtained from the Toledo Express Airport (Toledo, Ohio; http://cdo.ncdc.noaa.gov; 48 km west of the study area), where multiple weather variables are recorded multiple times per hour. We tested the effects of temperature (°C), visibility (0–10 miles), cloud cover (4 categories, from clear to overcast), precipitation (inches), and tailwind (see below) on the probability of departure, as

TABLE 2. Between-season site fidelity for fall 2016 and spring 2017, western Lake Erie, Ohio, USA. The total possible number of 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. Among 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), along with numbers of return stopover visits to the study site, return flyovers, and stopovers in Ontario. Between-season site fidelity is displayed in parentheses as the 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%)

well as endogenous variables such as age, sex, 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. Because 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 when departure events didn't occur, weather conditions (except precipitation) were taken as the average of conditions for the median hour of departure for all birds that season (2300 hours for each season). The tailwind component was calculated following Safi et al. (2013), using the following formula: tailwind $= V_w * \cos(\beta)$, where V_w is wind speed and β is the difference between the bird's track direction and the wind direction. Increasing positive values represent greater tailwind, whereas 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, nonsignificant 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 >1 indicate greater probability of departure and shorter stopover durations, whereas HRs <1 indicate lower probability of departure and longer stopover durations. Because 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. We used nonparametric 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. For all birds with confirmed departures or multiple detections on a returning flight, we calculated minimum distance traveled in a single migratory flight and corresponding flight speed. These flights are considered "minimum distance" because they rely only on positive tower detections and therefore are not necessarily complete flights. Distance traveled was measured as the great-circle distance between the 2 farthest automated telemetry towers where birds were detected (package "geosphere" for 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 whether flight speed or distance was related to tailwind conditions on departure. Lastly, we calculated between-season stopover site fidelity (Table 2) 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 vs. those that did not stop.

RESULTS

We deployed nanotags on 5 and 34 birds in fall (2015 and 2016, respectively), and on 30 and 22 birds in spring (2016 and 2017, respectively). In fall, we tracked 19 after-hatch-year birds (11 females, 8 males) and 20 hatch-year birds (6 females, 14 males). In spring, we tracked 38 after-second-year birds (14 females, 24 males) and 14 second-year birds (8 females, 6 males).
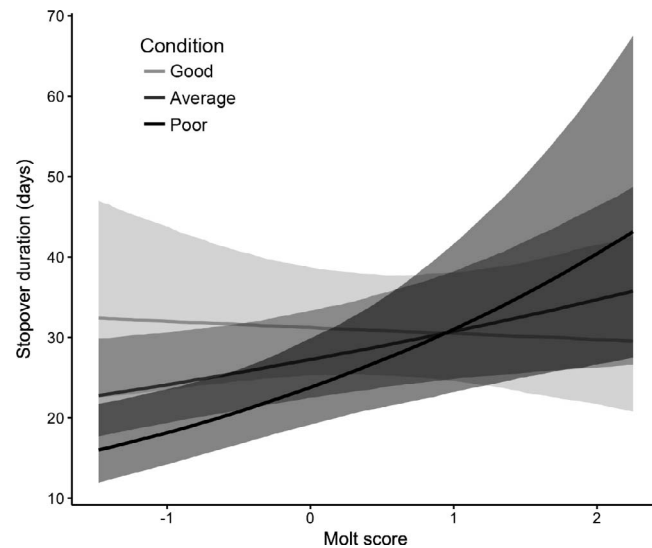
Stopover Duration
The mean ($\pm$ SE) minimum stopover duration for all tagged birds was 25.7 ± 1.6 days in fall (range: 2–58 days) and 25.3 ± 1.8 days in spring (range: 3–62 days; Figure 2). Including returned birds in fall 2016 and spring 2017 (Table 2), we obtained confirmed or probable departures for 22 birds in fall and 39 birds in spring (Table 1). The final model for fall stopover duration included only
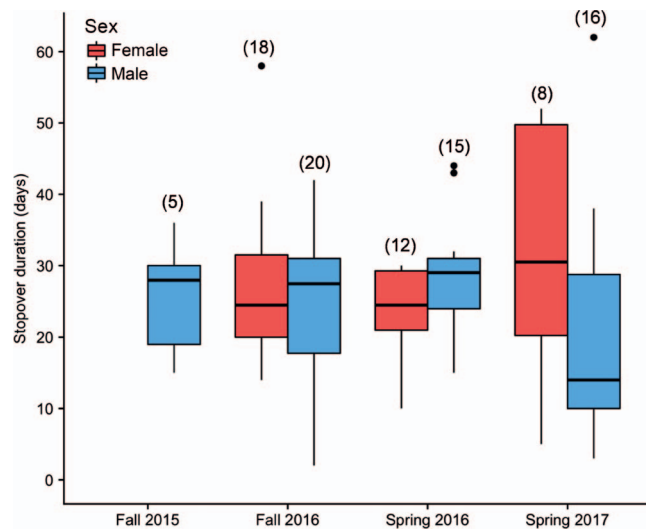
FIGURE 2. Box plots representing quartiles and medians of stopover duration (days) for tagged female (red) and male (blue) Rusty Blackbirds during each study season in western Lake Erie, Ohio, USA. Numbers in parentheses are sample size. None of the differences in stopover length between sexes or between seasons were significant (all $P > 0.05$).


FIGURE 3. The marginal effect and 95% credible intervals (shaded areas) of the interaction between body condition and molt score (condition $\times$ CCMI) on spring stopover duration of Rusty Blackbirds (western Lake Erie, Ohio, USA). "Average" condition is represented as the mean scaled mass index score (medium gray); "good" condition is represented as $+1$ SD from the mean (light gray); "poor" condition is represented as -1 SD from the mean (dark gray).

capture/arrival day as a predictor of stopover length (Appendix A and B). 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 [CI]: -0.04 to -0.01; effective sample size $>2,000$; $\hat{R} = 1$). The low explanatory power of this model probably indicates that other factors than those we measured are responsible for variation in stopover lengths (e.g., breeding origin of birds). For the spring season, our final model included capture/arrival day (SJD), the interaction between sex and year (sex $\times$ year), and the interaction between body condition and molt score (condition $\times$ CCMI; Appendix B). This model explained 63% of the variation in stopover length (Bayesian $R^2 = 0.63$; all effective sample sizes $>1,500$; all $\hat{R} = 1$). Stopovers were shorter for later capture/arrival dates ($\beta_{SJD} = -0.02$, 95% CI: -0.03 to -0.01), and males had longer stopovers than females in 2016 but shorter stopovers in 2017 ($\beta_{int} = -0.46$, 95% CI: -0.87 to -0.05; $\beta_{sex} = 0.18$, 95% CI: -0.08 to 0.44; $\beta_{year} = 0.02$, 95% CI: -0.31 to 0.36; Figure 2). Higher molt scores (CCMI) resulted in longer stopovers when birds were in relatively poor condition (Figure 3), but this effect was absent from birds that were in better condition ($\beta_{int} = -0.15$, 95% CI: -0.27 to -0.03; $\beta_{ccmi} = 0.14$, 95% CI: 0.03–0.25; $\beta_{condition} = 0.14$, 95% CI: 0.04–0.23; Figure 3). Although stopover length tended to differ between the sexes in spring, sample sizes were small and not consistent between the 2 seasons, so more years of data are needed to clarify the effect of sex on stopover duration.

Departure Behavior

Nearly all fall departures (95%) and 82% of spring departures occurred at night. The median time of nocturnal departure in all seasons was 2300 hours, while the median time of diurnal departure was 0700 hours. Of 39 known spring departure flights, 28 (72%) crossed Lake Erie, while the remainder went around the lake. It is important to note that the distribution of Motus towers may have biased these results toward more known lake crossings. Our final CPH model predicting probability of departure (Figure 4A) in fall included only tailwind as a relevant variable (tailwind increased with increasing daily probability of departure; hazard ratio [HR] = 1.51, 95% CI: 1.25–1.83; Figure 5). Our final spring model (Figure 4B) included capture/arrival day (SJD), body condition, tailwind, and the interaction between sex and year (sex $\times$ year). Later capture days, increasing tailwind, and lower body condition were associated with higher probability of departure ($HR_{SJD} = 1.07$, 95% CI: 1.03–1.11; $HR_{tailwind} = 1.14$, 95% CI: 1.06–1.24; $HR_{condition} = 0.85$, 95% CI: 0.77–0.95). Because of differences in sample size by sex and year, it is difficult to draw any conclusions regarding the influence of sex on departure behavior.

Stopover Relocations

Among a total of 49 fall stopovers, 35 birds (71%) made confirmed or probable stopover relocations; among a total of 58 spring stopovers, 19 birds (33%) made confirmed or
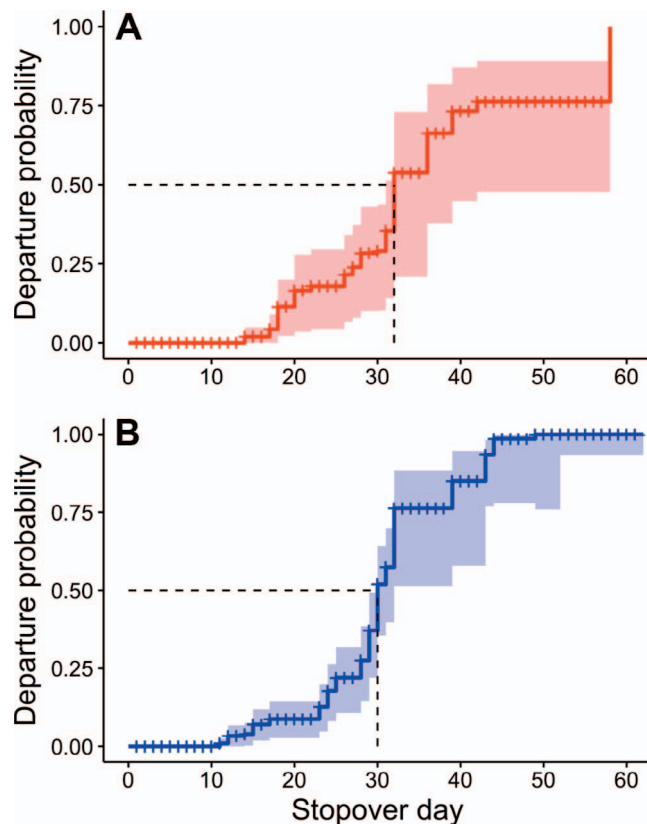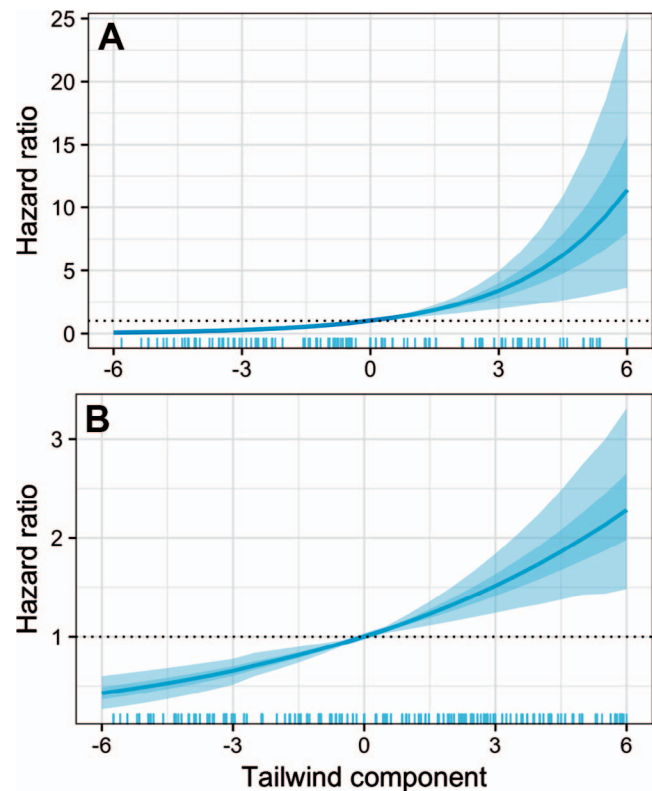
FIGURE 4. Daily probability of departure for fall (**A**) and spring (**B**) stopovers, as predicted by extended Cox proportional hazards models (western Lake Erie, Ohio, USA). Shaded areas represent 90% confidence intervals; dashed line represents day of median departure. The fall model, including only tailwind as a relevant predictor, significantly predicted the likelihood of departure (Wald test = 18.3, df = 1, $P \ll 0.001$, $n_{events} = 22$). The final spring model significantly predicted likelihood of departure (Wald test = 29.9, df = 6, $P \ll 0.001$, $n_{events} = 39$) and included capture/arrival day (standardized Julian day), body condition, tailwind, and the interaction between sex and year (sex × year).

FIGURE 5. The effects of the tailwind component on the hazard ratios for fall (**A**) and spring (**B**) departures from western Lake Erie, Ohio, USA, 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 fall than in spring. Shaded regions represent 50% and 90% confidence intervals.

probable relocations (Table 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 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 that of birds that did not relocate (Kruskal-Wallis test: $\chi^2 = 11$, df = 1, $P = 0.0009$).

Arrivals

Julian day of capture/arrival did not differ significantly 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 fall. In 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 ± SE = 86.9 ± 2.5 days) arrived significantly earlier than females (mean ± SE = 100 ± 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 migratory movements. 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 hr^{-1}), with a median distance of 257 km. Overland flight speeds (not accounting for wind conditions) ranged from 8 to 88 km hr^{-1} (the latter flight a distance of 356 km), with a median flight speed of 49 km hr^{-1}. Tailwind at departure did not explain flight speed or distance traveled, 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 0.29 (95% CI: 0.05–0.52) for spring 2015–fall 2016 and 0.36 (95% CI: 0.11–0.61) for

fall 2016–spring 2017 (Table 2). We also calculated migratory-route fidelity, incorporating birds that flew over the site but did not stop (Table 2), which was 0.71 (95% CI: 0.48–0.95) for fall 2016 and 0.43 (95% CI: 0.17–0.69) for spring 2017. Outside of our regional array, the Motus array detected 5 additional stopover events >1 day in Ontario, which ranged in duration from 3 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 spring migratory direction) and stopping for an additional 11 days.

DISCUSSION

Our results clearly indicate that Rusty Blackbirds are not among those passerines that undertake rapid migrations punctuated only by short refueling stopovers. Individuals may have made brief refueling stops before or after stopping at our high-use site, but overall the behavior we observed at our site is not characteristic of typical passerine stopovers. In fact, we found that Rusty Blackbirds spent 5× longer on stopover, on average, than parulid warblers at the same site (Dossman et al. 2016). In spring this long duration is likely due to an interaction with prealternate molt, drawing a parallel with some shorebird systems (Lourenço and Piersma 2015, Wright et al. 2018). Additionally, 87% of tagged birds departed at night, overturning the previously held assumption that Rusty Blackbirds are diurnal migrants (Avery 2013). The high proportion (72%) of birds crossing Lake Erie (∼50 km) suggests that it is not a significant barrier to migration for this species, given that there is an alternative route around the lake in close proximity (Gesicki et al. 2016). Collectively, our study describes an unusual migration system in songbirds that highlights the importance of specific stopover areas to conservation efforts for this declining species, similar to recent findings in some Neotropical migrants (Bayly et al. 2018).

The migratory behavior of Rusty Blackbirds differs from most documented passerine strategies and therefore may be more analogous to shorebird systems. Rusty Blackbirds share several important life-history characteristics with many shorebirds as well: they are a highly social mixed-species flocking bird and are habitat specialists that rely heavily on a particular type of wetland (Luscier et al. 2010). Furthermore, while their migratory distance is shorter than that of many shorebirds, they differ from their close relatives (e.g., Brewer's Blackbird [*Euphagus cyanocephalus*]) in being an obligate migrant breeding in the northern boreal zone. As such, it is perhaps more appropriate to draw on shorebird stopover terminology to describe the function of our study site. While there is some debate on classification of shorebird refueling sites, one widely accepted distinction is between staging 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, duration on site is relatively long, and site fidelity is high. Stopover areas, by contrast, are usually lower-quality sites that birds utilize irregularly and only for short periods after migratory flights, using them to refuel before moving on to a staging area (Warnock 2010). Although the behaviors of Rusty Blackbirds do not exactly reflect shorebird staging and migration, we conclude—on the basis of observed patterns of stopover duration, migratory flights, and site fidelity—that they exhibit a variant of the staging migratory strategy.

Rusty Blackbirds utilize southwestern Lake Erie for variable but lengthy bouts of staging in both fall and spring. Average minimum staging duration was more than twice as long as many 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, Chernetsov 2012, Rush et al. 2014, Liu and Swanson 2015). However, recent geolocator studies (reviewed in McKinnon et al. 2013) have documented long stopovers (defined as >7 days in McKinnon et al. 2013) in some passerines in certain key regions (e.g., 19 days for Red-eyed Vireos [*Vireo olivaceus*] in Colombia; Callo et al. 2013), and it appears possible that many Nearctic–Neotropical migrants exhibit such patterns while migrating through Central and South America (Bayly et al. 2018). In both migrations, staging length was negatively associated with capture/arrival day, which suggests that birds captured later had already been at the site for a time. Thus, we may be underestimating the length of staging bouts for birds captured later in the season, although another possibility is a trade-off between staging arrival and duration. One important variable that may have explained variation in staging length, which we were not able to include in our models, is the geographic origin and destination of migrating birds. This is an important aspect of linking stopover strategies to other stages of the annual cycle (Paxton and Moore 2017) that future studies should seek to address using stable hydrogen isotopes or GPS loggers.

The lengthy staging events observed here run counter to the expectation that birds should minimize the amount of time spent migrating by maximizing fuel deposition on stopover (Alerstam et al. 2003). Stopover length is usually dependent on the energetic condition of the individual (Goymann et al. 2010), in that birds with depleted energy reserves must stop longer to recoup those losses. Expected flight distance is also a determinant of stopover length, and some shorebirds make exceptionally long staging events, accumulating >50% of their body mass in fat stores, prior to long flights (Warnock 2010). We were not able to directly measure fuel deposition in the present study, but it seems unlikely that Rusty Blackbirds require these lengthy staging events for refueling alone. Although the recorded

migratory flights of >400 km are substantially longer than typical passerine migratory flights (150–270 km; Wikelski et al. 2003, Hall-Karlsson and Fransson 2008, Stutchbury et al. 2009), they are not comparable to the long-distance, nonstop flights of shorebirds (and some passerines) associated with crossing major marine boundaries (thousands of kilometers; e.g., Gill et al. 2009, Warnock 2010, Alves et al. 2016, Gómez et al. 2017). Further physiological studies are needed to clarify the role that fuel deposition plays in determining Rusty Blackbird staging behavior.

One explanation for lengthy staging events in spring is molt. Nearly all (98%) Rusty Blackbirds at our site undergo a partial prealternate molt of contour feathers (Wright et al. 2018). The need to both molt and refuel could conflict energetically, necessitating longer staging events. Our finding that birds in relatively poor condition and heavy molt had longer staging events supports this idea. Body molt is an energetically costly activity, due to reduced effectiveness of thermal insulation (Piersma et al. 1995) and increased metabolic rates (Lindström et al. 1993). Several shorebird species undergo prealternate or presupplemental molt at staging areas, including Great Knots (*Calidris tenuirostris*; Battley et al. 2006, Peng et al. 2015), Black-tailed Godwits (*Limosa limosa*; Lourenço and Piersma 2015), and Bar-tailed Godwits (*L. lapponica*; Piersma and Jukema 1993). In fall, some passerines undergo their prebasic molt at stopover sites in the Mexican monsoon region (Leu and Thompson 2002, Pyle et al. 2009); however, this molt includes flight-feather replacement and thus is not directly comparable. Nevertheless, prealternate molt-migration, previously undocumented in a passerine (Wright et al. 2018), likely plays a role in the unusual strategy (among passerines) of staging behavior in spring.

Although they are of similar length, the long staging events by Rusty Blackbirds in fall and spring probably have different evolutionary and ecological drivers (Nilsson et al. 2013), and molt could also explain this contrast. We did not observe molt in fall; thus, birds are not completing 2 potentially conflicting physiological tasks, as in spring. Since there is no breeding-associated selective pressure on early arrival, selection on refueling rate is likely weaker in fall, resulting in longer stopover durations and slower flights in fall (McKinnon et al. 2013, Nilsson et al. 2013). In addition, fall migration is less physiologically stressful, because levels of testosterone and corticosterone are lower than in spring (O'Reilly and Wingfield 1995). Tøttrup et al. (2012) found that Red-backed Shrikes (*Lanius collurio*) also make long stopovers during fall migration (average 53 days) and suggested that this is a third resident stage of the annual cycle (which they also considered staging behavior), when birds exploit favorable foraging conditions following late summer rains. Likewise, Rusty Blackbirds consume highly abundant dogwood (*Cornus* spp.) berries in early

autumn, and 68% of autumn foraging observations occurred in dogwood stands (J. R. Wright personal observation). In a study utilizing light-level geolocators (Johnson et al. 2012), 3 individuals tagged in Alaska made stops of ~1 mo on fall migration, and preliminary data from 2 GPS archival tags deployed and recovered in Northern Alberta show similar patterns during spring and fall (L. L. Powell personal observation), suggesting range-wide consistency and multiple stationary periods.

The prevalence of relocations within the greater landscape indicates that staging Rusty Blackbirds are not limited to a single, tightly bound home range. Social species typically move around staging and 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 often relocated to sites 20–35 km apart. Resource availability and competition could explain these relocations in spring, as most relocations occurred early in the season, when density of aquatic invertebrates is lower (MacKenzie and Kaster 2004, MacKenzie et al. 2004). This is consistent with the result that males were more likely to relocate than females because they arrived at the site earlier in the season. Similarly, Mills et al. (2011) found that landscape-scale stopover relocations by thrushes in the genus *Catharus* were most likely to occur early in the stopover period (~30% of total minimum stopover time). In contrast to our findings, the thrushes made these movements nocturnally, and Mills et al. (2011) interpreted the movements as avoidance of predation risk. Rusty Blackbirds may be able to mitigate predation risk by flocking and thereby gain the benefit of exploring habitats in daylight. The fragmented nature of the landscape, with large expanses of farmland between wetland habitats, could explain the large distances traveled. In general, landscape-scale movements of passerines on stopover are poorly understood, but these movements further highlight the need to expand the scale at which stopover and staging behavior is quantified (Mills et al. 2011, Taylor et al. 2011).

Site fidelity is an important aspect of a staging site (Warnock 2010), because high rates indicate the importance of specific sites to individuals and populations. Due in part to higher costs of wind-drift compensation, fidelity of passerines to particular stopover sites is expected to be low compared to larger-bodied species (Catry et al. 2004). Estimates range from 0.3% return rates for Tennessee Warblers (*Oreothlypis peregrina*; Winker et al. 1991, Vogt et al. 2012) to 12.9% for habitat specialists such as Eurasian Reed-Warblers (*Acrocephalus scirpaceus*; Catry et al. 2004). Shorebirds generally exhibit high site fidelity to staging locations between seasons (Harrington et al. 1989), 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 (~30% both seasons), though

our sample size is small ($n = 9$ returns). Several other returning individuals migrated past the site without stopping, especially in fall. Given our findings on landscape-scale movements, this suggests that fidelity is better measured at larger spatial scales. For instance, it's possible that Rusty Blackbirds have adequate staging areas on the north shore of Lake Erie and need not stop after crossing.

Rusty Blackbirds spend over a quarter of their annual cycle at staging sites, often repeatedly using the same sites and flyways. Thus, it is critical that these high-traffic areas are identified and protected. The behaviors we observed show that it is crucial to incorporate staging sites into conservation plans for Rusty Blackbirds. It is possible that our site is an anomaly, demonstrating the best-case scenario for refueling potential in an optimal geographic region. The site is also one of the few remaining wetlands in a landscape dominated by agriculture. Ohio and the midwestern United States have lost >80% of their wetlands since European settlement (Dahl and Johnson 1991), so remaining pockets are likely critical to the species. Therefore, determining preferred staging habitats, including season-specific needs (e.g., fall fruit availability), is critical to habitat conservation. Furthermore, with planned wind-farm development on Lake Erie (Lake Erie Energy Development Corporation; U.S. Department of Energy 2017), nocturnal cross-lake flights (72% of our spring departures) could expose a large proportion of the population to collision mortalities (Loss et al. 2013).

Our results demonstrate the necessity of examining individual behaviors of migrants at multiple spatial scales. Without such studies, our understanding of population dynamics throughout the annual cycle will remain inadequate (Marra et al. 2015, Paxton and Moore 2017). We have described an unusual migration strategy for a songbird, but studies of this kind are likely to reveal other atypical behaviors. Exploration of all aspects of species' annual cycles is critically needed in order to understand the spatiotemporal nature of population limitation and habitat needs (Marra et al. 2015) to inform efficient and effective conservation action.

ACKNOWLEDGMENTS

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APPENDIX A

Summary output of final Bayesian generalized linear model for fall stopover duration of Rusty Blackbirds at western Lake Erie, Ohio, USA, from package 'brms' in Program R.

Family: negbinomial(log)

Formula: duration $\sim$ 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

	Estimate	Est. Error	95% CI	Eff. Sample	$\hat{R}$
Population-level effects					
Intercept	10.84	2.50	5.77 to 15.82	2,471	1.00
Capdate	−0.03	0.01	−0.04 to −0.01	2,458	1.00
Family-specific parameters					
Shape	25.03	17.73	7.58 to 66.90	1,380	1.00

APPENDIX B

Summary output of final Bayesian generalized linear model for spring stopover duration of Rusty Blackbirds at western Lake Erie, Ohio, USA, from package "brms" for R.

Family: negbinomial(log)

Formula: duration $\sim$ 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

	Estimate	Est. Error	95% CI	Eff. Sample	$\hat{R}$
Population-level effects					
Intercept	3.32	0.10	3.13 to 3.52	2,216	1.00
Year4	0.02	0.17	−0.31 to 0.36	1,708	1.00
SexM	0.18	0.13	−0.08 to 0.44	2,023	1.00
CCMI	0.14	0.06	0.03 to 0.25	2,720	1.00
Condition	0.14	0.05	0.04 to 0.23	4,000	1.00
SJD	−0.02	0.00	−0.03 to −0.01	4,000	1.00
Year4:SexM	−0.46	0.21	−0.87 to −0.05	1,576	1.00
CCMI:Condition	−0.15	0.06	−0.27 to −0.03	2,412	1.00
Family-specific parameters					
Shape	31.80	22.00	10.45 to 88.67	1,621	1.00