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Research article

Local weather and endogenous factors affect the initiation of migration in short- and medium-distance songbird migrants

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Migratory birds employ a variety of mechanisms to ensure appropriate timing of migration based on integration of endogenous and exogenous information. The cues to fatten and depart from the non-breeding area are often linked to exogenous cues such as temperature or precipitation and the endogenous program. Shorter distance migrants should rely heavily on environmental information when initiating migration given relatively close proximity to the breeding area. However, the ability to fatten and subsequently depart may be linked to individual circumstances, including current fuel load and body size. For early and late departing migrants, we investigate effects of temperature, precipitation, lean body mass, fuel load and day of year on the initiation of migration (i.e. fuel load and departure timing) from the non-breeding region by analyzing 21 years of banding data for four species of short- and medium-distance migrants. Temperatures at the non-breeding area were related to temperatures at potential stopover areas. Despite local cues being predictive of conditions further north, the amount variation explained by local weather conditions in our models differed by species and temporal period but was low overall (< 33% variation explained). For each species, we also compared lean body mass and fuel load between early and late departing migrants, which showed mixed results. Our combined results suggest that most individuals migrating short or medium distances in our study did not time the initiation of migration with local predictive cues alone, but rather other factors such as lean body mass, fuel load, day of year, which may be a proxy for the endogenous program, and those beyond the scope of our study also influenced the initiation of migration. Our study contributes to understanding which factors influence departure decisions of short- and medium-distance migrants as they transition from the non-breeding to the migratory phase of the annual cycle.

Keywords: departure decisions, house wren *Troglodytes aedon*, ruby-crowned kinglet *Corthylio calendula*, swamp sparrow *Melospiza georgiana*, weather, white-throated sparrow *Zonotrichia albicollis*



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Introduction

Appropriate timing of arrival at the breeding area is critical to match the local phenology of resources and maximize reproductive success in migratory birds (Lack 1968, Winkler et al. 2014). Migratory birds employ a variety of mechanisms to ensure appropriate timing of migration and arrival, which are based on the integration of endogenous and exogenous information. For example, individuals use photoperiod as an initial predictive cue and a 'Zeitgeber' for endogenous circannual rhythms initiating the developmental phase of spring migration, including the completion of prenuptial molt, initiation of pre-migratory fattening, and migratory departure (Wingfield 1983, Berthold 1984, Schwabl and Farnier 1989, Dawson et al. 2001, Ramenofsky 2011). Additional endogenous factors, such as individual-specific traits (e.g. age, sex, body size, fuel stores), may impact the ability to compete for resources and influence the decision to engage in migratory flight (Ellegren 1991, Moore et al. 2003, Jakubas and Wojczulanis-Jakubas 2010, Smolinsky et al. 2013, Sjöberg et al. 2015, Zenzal et al. 2021). In contrast, exogenous factors, such as temperature or precipitation, can influence the decision to fatten and depart from the non-breeding area by directly affecting food abundance and, subsequently, an individual's ability to deposit fuel for long-distance flights (Wingfield 1983, Studds and Marra 2011, Ramenofsky 2012, Tøttrup et al. 2012).

Observations suggest that individuals making long- versus shorter-distance migrations differ in the degree to which they rely on exogenous versus endogenous information when making departure decisions (Butler 2003, Lehikoinen et al. 2004, Tøttrup et al. 2010, Cohen et al. 2015). Individuals moving short or medium distances, which use non-breeding areas closer to their breeding grounds (i.e. north of the Tropic of Cancer within the Nearctic-Neotropical migration system; (DeGraaf and Rappole 1995, Carlisle et al. 2004)) compared to long-distance migrants, experience climatic changes and weather patterns at the non-breeding area that may be relatively similar to conditions at their prospective breeding area. Individuals migrating short or medium distances may thus be able to more accurately predict the advancement of spring at the breeding area based on local environmental cues such as temperature and precipitation, allowing more reliance on local cues when making departure decisions compared to individuals migrating long distances. On the other hand, individuals migrating long distances spend the non-breeding season further from the breeding area (i.e. south of the Tropic of Cancer) (DeGraaf and Rappole 1995, Carlisle et al. 2004) and experience climatic conditions independent of those at the breeding area, which are not reliable cues for making departure decisions. Therefore, the departure decision of an individual migrating a long distance is thought to be influenced more by endogenous circannual rhythm, and less so by local predictive cues, than that of an individual migrating a shorter distance (Butler 2003, Lehikoinen et al. 2004, Tøttrup et al. 2010, Cohen et al. 2015). This hypothesis is supported by observations of higher variation in migration

timing of individuals migrating short versus long distances (Mason 1995, Jonzén et al. 2006, Rubolini et al. 2007, Knudsen et al. 2011). Some tracking studies provide further support by showing high repeatability of migratory departure timing across years in long-distance migratory birds (Vardanis et al. 2011, Stanley et al. 2012), but more recent studies do not (Hasselquist et al. 2017, Amélineau et al. 2021, Conklin et al. 2021). The difference in the value of available local predictive cues on which to base migratory departure decisions is the basis of phenological mismatch. Individuals that mistime arrival at the breeding area and do not match their breeding phenology with that of local resources suffer reproductive costs (Both and Visser 2001, Coppack and Both 2002, Both et al. 2006, Winkler et al. 2014).

Individuals migrating shorter distances may aim to time departure from the non-breeding area based on endogenous or exogenous cues, but their ability to depart may be dependent on their ability to secure resources sufficient to initiate migration. An individual with insufficient fuel stores may be forced to remain at the non-breeding area longer or be limited in their migratory movements (Marra et al. 1998, Studds and Marra 2005, 2011, Woodworth et al. 2014, Zenzal et al. 2021), which may delay arrival at the breeding area and negatively impact fitness (Both and Visser 2001, Coppack and Both 2002, Both et al. 2006, Winkler et al. 2014). Factors such as current fuel stores and body size have been shown to influence access to resources (Brown and Maurer 1986, Moore et al. 2003, Funghi et al. 2015, Francis et al. 2018), which are needed to initiate migratory flights. Individuals able to gain priority access to resources or high quality non-breeding habitats will be able to quickly fuel and depart earlier, which may enable early access to limited breeding resources (i.e. territory, mate) and increase the likelihood of reproductive success (Lozano et al. 1996, Smith and Moore 2005, McKellar et al. 2013). Of course, mass gain increases later in the non-breeding season as they ready themselves for migratory departure (Hou et al. 2015, Risely et al. 2015, Hou and Welch 2016, Bayly et al. 2020) and those spending the non-breeding season in temperate North America may find greater resource abundance later in spring when arthropods tend to be more abundant compared to earlier in the season.

Most studies investigating the departure decisions of migratory songbirds use data collected at stopover sites during passage (Dänhardt and Lindström 2001, Dierschke and Delingat 2001, Marra et al. 2005, Deppe et al. 2015, Sjöberg et al. 2015, Dossman et al. 2016, Packmor et al. 2020) or from the breeding area in terms of stable isotope samples or tracking technologies (Woodworth et al. 2016, 2017, Cooper et al. 2017, Ouweland and Both 2017). Few studies have directly examined departure from the non-breeding area (Marra et al. 1998, Studds and Marra 2005, 2011, Gordo 2007). Therefore, for most species, relationships between endogenous and exogenous factors and the decision to initiate migration remains poorly understood. More observations from the non-breeding area would not only increase understanding of the decision to initiate migration, but would also shed light on how much of the observed

migration phenology is influenced by the timing of departure from the non-breeding area versus adjustments made during passage (Tøttrup et al. 2008).

In this study, we investigate the relationships between local predictive environmental cues at the non-breeding area (i.e. temperature and precipitation) and endogenous factors (day of year, fuel load, lean body mass (LBM)) on the decision to depart on migration by analyzing 21 years of banding data for four species that migrate short and medium distances. Our first objective was to test whether temperature and precipitation from the non-breeding grounds are correlated with temperature and precipitation, respectively, at potential stopover and breeding areas. A positive correlation between non-breeding conditions and those further north would suggest individuals may benefit if using local predictive cues for departure decisions. Our second objective was to examine which endogenous and local weather variables have the strongest association with departure decisions for individuals departing early and late in the season. We analyzed early- and late-departing individuals separately as these groups may represent different attributes (i.e. age, sex, breeding latitude) and may operate under different pressures (Marra and Holmes 2001, Moore et al. 2003, Conklin et al. 2010). Thus, we predict early-departing individuals will have strong associations with body size (due to priority access to resources) and temperature (if correlated with temperatures further north), while late-departing individuals will have strong associations with fuel load. Our third objective was to determine if fuel stores and body size differ between early and late departing individuals. We predict early-departing individuals will be of larger body size but carrying lower fuel loads compared to late-departing individuals due to resources being more abundant later in spring.

Methods

Study site and focal species

Our study site is uniquely positioned to investigate decisions surrounding migratory departure from the non-breeding area as it is located on the northwestern coast of the Gulf of Mexico (near Johnson Bayou, LA, USA; 29°45'N, 93°37'W). Birds were captured using 28–30 mist nets (12 or 6 × 2.6 m; 30-mm mesh) as part of a long-term banding operation in a coastal chenier forest embedded within a wetland landscape (see Barrow et al. 2000 and Lain et al. 2017 for habitat description). Netting was conducted daily from 7:00 to 16:00 CST from late March until early May 1993–2014, excluding 1997. Each captured individual was fitted with a U.S. Geological Survey aluminum leg band, had subcutaneous fat assessed according to Helms and Drury (1960), unflattened wing chord (0.5 mm) and mass (0.1 g) measured, as well as age and sex determined when possible (Pyle 1997). Permission to capture wild birds was granted by the U.S. Bird Banding Laboratory (permit no. 21221) and the Louisiana Department of Wildlife and Fisheries (permit no. LNHP-15-040). All protocols were

approved by the University of Southern Mississippi institutional animal care and use committee (protocol no. 11092210).

We included short- and medium-distance migrant species in our analyses based on the following criteria: 1) stationary non-breeding range is restricted to continental North America and does not reach into Central America, 2) non-breeding and breeding ranges do not overlap at the study site, and 3) we captured ≥ 10 individuals during at least 5 of the 21 years sampled, which was based on the methods of past studies analyzing long-term banding datasets (Paxton et al. 2014, Cohen et al. 2015, Lain et al. 2017). The following four species within our dataset met the above criteria and were used to assess the importance of endogenous factors and local weather on migratory departure decisions: white-throated sparrow *Zonotrichia albicollis*, swamp sparrow *Melospiza georgiana*, ruby-crowned kinglet *Corthylio calendula* and house wren *Troglodytes aedon*. While it is apparent we captured birds that did not reside during the non-breeding season at our study site, we believe they likely resided in the region during the non-breeding season and were exposed to similar exogenous conditions (Falls and Kopachena 2020, Hebert and Mowbray 2020, Johnson 2020, Swanson et al. 2021), thus they likely pass through our site shortly after departure and their behavior should closely represent departure behavior (i.e. timing).

Bird data

For each focal species, we were interested in determining which factors influence the decision to depart on migration. We analyzed captures from the study site on days encompassing the first or last 25% of total captures, which made up the early and late temporal periods, respectively. From our banding data and a mark–recapture approach (below), we used capture date and fuel load as our indicators of departure from the non-breeding area. For capture date, we used the ordinal date of final capture of retrapped birds or initial capture of birds never retrapped to determine when individuals departed the study area (all presented calendar dates are based on non-leap years). To estimate fuel load for each species, we followed methods described by Ellegren (1992) using wing chord, fat score and body mass of all initial captures from our study site. Following this method, we first performed a regression between body mass and fat score for each 1 mm wing chord class. After eliminating any wing chord classes with low sample sizes ($n < 10$), we then used a second regression between the remaining wing chord classes and intercepts generated during the first set of regressions. The second regression provides the equation parameters to estimate mean LBM, which was subtracted from each individual's final capture mass. Any individual without a mass or wing chord measurement at capture were omitted from further analysis.

Weather data

We assumed temperature and precipitation are linked to resource availability and serve as a proxy for phenological cues

used by our focal species (Studds and Marra 2011, Wood and Pidgeon 2015, Burnside et al. 2021). We collected monthly mean temperature (°C) and total precipitation (cm) data for the months of February, March, April and May 1993–2014 from NOAA's National Centers for Environmental Information for the non-breeding area as well as potential breeding areas and stopover locations (Fig. 1). We selected the Louisiana and extreme eastern Texas coasts along the Gulf of Mexico to represent the non-breeding region for all species (Fig. 1), which includes our banding station in southwest Louisiana. For each species, we sampled conditions from

potential breeding and stopover areas guided by eBird abundance maps of each species using data from 1993 to 2014 (eBird 2021) since we are unaware of any population-specific tracking data from our non-breeding area to better justify connectivity. We selected areas of highest abundance used exclusively for breeding or stopover that were north of our non-breeding area during April and June for stopover and breeding areas, respectively. For each non-breeding, breeding and stopover region, we averaged climatic data for each species from stations found within our defined spatial extents (Fig. 1). We only included weather station locations without



Figure 1. Location of weather stations in the non-breeding, stopover and breeding areas for (A) house wren *Troglodytes aedon*, (B) ruby-crowned kinglet *Corthylio calendula*, (C) swamp sparrow *Melospiza georgiana* and (D) white-throated sparrow *Zonotrichia albicollis*.

missing temperature and precipitation data over the temporal scope of this study.

Site persistence models

In our study, accuracy in departure date and fuel load are critical in investigating departure decisions. To make the most prudent inferences, we need to know how long individuals persist after initial capture and their daily fueling rates (sensu [Schaub et al. 2001](#), [Moore et al. 2017](#)). We followed methodology similar to that described in [Moore et al. \(2017\)](#) and used a mark–recapture modeling approach to estimate the amount of time our focal species remained at the study site after initial capture. The model's estimates can help determine the most likely date of departure, especially for individuals only captured once, and allows us to adjust fuel loads based on the fuel deposition rates of birds recaptured at our study site, which accounts for changes in fuel load after capture (Supporting information). Fuel deposition rates are calculated by subtracting fuel load at final capture from fuel load recorded during the initial capture and dividing the difference by the number of bird use days, which generates a rate in grams per day.

We ran capture–mark–recapture models ([White and Burnham 1999](#)) to estimate persistence, which provided better estimates of departure date and fuel load. For each focal species, we used the capture history of every individual to generate model estimates. We attempted to estimate year-specific persistence measures for each species, but this was not always possible. If sample sizes in an individual year were too low, we grouped years within species in sequential order until we had enough samples. Across species, this approach resulted in 21 individual years with enough data to estimate persistence and 11 groups of years (Supporting information). We attempted to include age and sex in the analyses but over 75% of individuals were recorded with a non-specific age or sex class, which typically resulted in inadequate sample sizes to run the models. In the few instances where sample sizes were adequate, age and sex were never in the final best model. Therefore, we pooled data across sex and age.

'Survival' estimates generated from the mark–recapture models represent daily probabilities of persistence for the 21 individual years and 11 groups of years (Supporting information), modified for imperfect capture probability since birds were not always recaptured despite being present at the site on subsequent days. Generated 'survival' estimates were converted into persistence estimates (number of days) using the life expectancy formula that estimates expected stopover duration after the initial capture ([Efford 2005](#)). While most recaptured birds remained at the study site beyond the modeled estimates of persistence, those only captured once, which accounted for 63% of our data, would have been biased with earlier departure dates – supporting our decision to address imperfect recapture probability.

We scrutinized candidate models that incorporated effects of mass and ordinal date at initial capture day on daily persistence and recapture probability using Akaike's information

criterion adjusted for small sample sizes (AICc; [Burnham and Anderson 2002](#)). We first ran all the possible models ($n = 16$) for each of the 21 individual years and 11 groups of years and input models with sufficient sample size that did not result in singularities in the estimates or terms that were not significant into the AICc model selection. In some cases, this approach resulted in only the model with a constant daily persistence probability being considered (Supporting information). However, the persistence estimates from the constant only models were similar to models where we pooled data across all years for each species (i.e. one estimate per species).

Statistical analysis

We tested our first objective, that annual temperature and precipitation ($n = 22$ years) may be correlated between the non-breeding area and breeding as well as stopover areas, using Spearman Rank correlations analyzing each month separately for each species. We included all region and month combinations where an individual might use a local cue to predict conditions further north (i.e. each test included one variable from the non-breeding area). We considered any correlation test with an absolute value of $\rho \geq 0.60$ to exhibit a meaningful relationship between factors, opposed to evaluating p-values, which may be spurious given the number of tests ([Rice 1989](#)).

To test our second objective, which examines the relationship between endogenous factors and local weather on the initiation of migration (departure date and fuel load), we used partial least squares regressions (PLSR) to analyze each species and temporal period (early or late) separately. PLSR is a non-parametric approach, which combines characteristics of multiple regression and principal components analysis, that allows small sample sizes and highly correlated predictor variables, while performing at least as similarly as, or better than, either parent test ([Abdi 2007](#), [Carrascal et al. 2009](#), [Hair et al. 2019](#)). In each species PLSR model, we specified 2 components and input our response variable as departure date or fuel load with predictor variables consisting of monthly temperatures and precipitation for the non-breeding area as well as LBM. Fuel load and departure day exchanged roles as predictor and response variables ([Table 1, 2, 3 and 4](#)). We included weather conditions for the month in which an individual was captured as well as the previous month. We offset monthly weather condition bins by 7 days to account for birds departing early in the month likely experiencing conditions more similar to the previous month (i.e. birds captured during: 8 February–7 March assigned February conditions, 8 March–7 April assigned March conditions and 8 April–7 May assigned April conditions). For each model, we present the meaningful independent variables, which are based on the amount of weight they contribute to each component of the model. Variable component weights > 0.2 when squared are considered important ([Carrascal et al. 2009](#)). Model goodness of fit is assessed using the R^2 statistic for explained variation and goodness of prediction assessed using the Q^2

Table 1. Results from partial least squares regression (PLSR) for the departure day and fuel load models in the first quarter and last quarter of house wren *Troglodytes aedon* departures from southwest Louisiana. Mean and standard deviation of each variable is also provided. W_1 = weight of predictor variable based on the first component, W_2 = weight of predictor variable based on the second component. Weights > 0.2 when squared and $Q^2 > 0.0975$ are shown in bold (see text).

	First 25% of final captures					Last 25% of final captures				
	Departure day model		Fuel load model		Mean (\pm SD)	Departure day model		Fuel load model		Mean (\pm SD)
	W_1	W_2	W_1	W_2		W_1	W_2	W_1	W_2	
Lean body mass (g)	0.62	0.01	0.01	0.48	10.02 \pm 0.12	-0.75	0.03	0.07	0.38	9.95 \pm 0.13
Previous precipitation (cm)	-0.09	0.04	0.44	0.45	8.95 \pm 5.06	-0.06	-0.45	0.08	0.40	6.51 \pm 3.16
Previous temperature ($^{\circ}$ C)	0.65	0.14	-0.47	-0.42	13.59 \pm 1.39	-0.10	0.40	0.57	-0.17	15.34 \pm 1.93
Current precipitation (cm)	0.27	-0.90	0.48	-0.06	9.97 \pm 6.14	-0.13	-0.31	0.67	-0.11	8.26 \pm 5.58
Current temperature ($^{\circ}$ C)	0.20	0.24	0.54	-0.55	16.37 \pm 1.92	0.45	-0.52	-0.14	0.67	19.71 \pm 0.80
Departure day	NA	NA	-0.26	0.29	85 \pm 4	NA	NA	0.44	0.46	110 \pm 5
Fuel load (g)	-0.26	-0.32	NA	NA	0.97 \pm 0.67	0.45	0.51	NA	NA	1.24 \pm 1.03
R ²	0.09	0.01	0.16	0.02		0.18	0.02	0.19	0.03	
Q ²	-0.09	-0.27	-0.11	-0.24		0.03	-0.07	-0.04	-0.09	

statistic for predictive power based on cross-validation where $Q^2 > 0.0975$ indicates predictive model significance.

To address our third objective, which directly compares fuel load and LBM between temporal periods, we used species-specific Mann–Whitney U-tests and adjusted alpha to account for multiple comparison testing using the Holm–Bonferroni correction (Mann and Whitney 1947, Holm 1979). All statistics were performed in the R statistical language (www.r-project.org). Our first objective was addressed by leveraging packages ‘dplyr’, ‘Reshape2’ and ‘Hmisc’ (Wickham 2007, Harrell and Dupont 2021, Wickham et al. 2021). Our second objective was addressed by using the ‘pls-depot’ package (Sanchez 2012). Results are reported as mean \pm standard deviation.

Results

Regional weather relationships

Spearman Rank correlations for the various spatiotemporal combinations found temperatures at non-breeding areas during certain months to exhibit meaningful associations with species-specific geographic regions further north across all species (Fig. 2), but precipitation at the non-breeding area did not display any meaningful relationships ($\rho < 0.60$) with

conditions further north. House wren and white-throated sparrow non-breeding region temperatures during February, March and April were positively correlated with stopover region temperatures occurring within the same month ($p < 0.01$, $\rho \geq 0.60$; Fig. 2A and E). House wren also had a positive correlation between breeding and non-breeding region temperatures in March ($p < 0.01$, $\rho = 0.61$; Fig. 2B). For ruby-crowned kinglet and swamp sparrow, non-breeding region temperatures in March and April were positively correlated with stopover area temperatures occurring within the same month ($p < 0.01$, $\rho \geq 0.61$; Fig. 2C and D). All other combinations that included non-breeding area temperature did not result in a meaningful relationship ($\rho < 0.60$).

Local weather and endogenous factors on departure decisions

Local weather

Based on the departure dates (Supporting information; Table 1, 2, 3 and 4) of the first 25% of departures by our focal species, we were able to determine associations between early season departure day and local weather variables. For house wren ($n = 41$), we found temperature during the month before departure to show strong positive association with departure day in the first component, while precipitation the month of departure had a strong negative association

Table 2. Results from partial least squares regression (PLSR) for the departure day and fuel load models in the first quarter and last quarter of ruby-crowned kinglet *Corthylio calendula* departures from southwest Louisiana. Mean and standard deviation of each variable is also provided. W_1 = weight of predictor variable based on the first component, W_2 = weight of predictor variable based on the second component. Weights > 0.2 when squared and $Q^2 > 0.0975$ are shown in bold (see text).

	First 25% of final captures					Last 25% of final captures				
	Departure day model		Fuel load model		Mean (\pm SD)	Departure day model		Fuel load model		Mean (\pm SD)
	W_1	W_2	W_1	W_2		W_1	W_2	W_1	W_2	
Lean body mass (g)	-0.25	0.87	0.28	-0.64	5.64 \pm 0.16	-0.05	-0.40	0.14	0.41	5.62 \pm 0.13
Previous precipitation (cm)	0.76	0.18	-0.01	0.69	12.10 \pm 4.78	-0.05	-0.03	-0.41	-0.73	8.94 \pm 4.52
Previous temperature ($^{\circ}$ C)	-0.26	-0.15	0.19	0.28	12.56 \pm 1.77	0.51	-0.66	-0.48	0.29	14.97 \pm 2.72
Current precipitation (cm)	-0.25	-0.09	-0.15	0.13	8.78 \pm 6.02	0.17	-0.38	-0.13	0.28	9.40 \pm 4.46
Current temperature ($^{\circ}$ C)	0.04	0.43	-0.65	-0.15	15.57 \pm 2.03	0.74	0.51	-0.47	0.37	18.16 \pm 1.96
Departure day	NA	NA	-0.67	-0.07	82 \pm 4	NA	NA	-0.58	0.10	101 \pm 6
Fuel load (g)	-0.48	0.01	NA	NA	0.60 \pm 0.41	-0.39	0.00	NA	NA	0.44 \pm 0.43
R ²	0.26	0.03	0.13	0.01		0.32	0.02	0.14	0.03	
Q ²	0.09	-0.24	-0.07	-0.22		0.20	-0.29	0.04	-0.13	

Table 3. Results from partial least squares regression (PLSR) for the departure day and fuel load models in the first quarter and last quarter of swamp sparrow *Melospiza georgiana* departures from southwest Louisiana. Mean and standard deviation of each variable is also provided. W_1 = weight of predictor variable based on the first component, W_2 = weight of predictor variable based on the second component. Weights > 0.2 when squared and $Q^2 > 0.0975$ are shown in bold (see text).

	First 25% of final captures					Last 25% of final captures				
	Departure day model		Fuel load model		Mean (\pm SD)	Departure day model		Fuel load model		Mean (\pm SD)
	W_1	W_2	W_1	W_2		W_1	W_2	W_1	W_2	
Lean body mass (g)	0.21	-0.28	0.83	-0.10	14.59 \pm 0.41	-0.83	0.10	0.67	0.67	14.39 \pm 0.35
Previous precipitation (cm)	0.28	-0.28	0.05	-0.14	11.59 \pm 5.21	-0.41	0.05	0.14	0.08	6.75 \pm 3.18
Previous temperature ($^{\circ}$ C)	-0.06	0.80	-0.17	-0.92	11.91 \pm 2.41	-0.08	0.53	-0.40	0.28	15.68 \pm 2.00
Current precipitation (cm)	-0.35	-0.04	0.14	0.07	8.95 \pm 5.22	0.09	0.75	-0.38	0.47	8.33 \pm 5.37
Current temperature ($^{\circ}$ C)	-0.38	0.27	0.06	0.29	15.89 \pm 2.18	0.23	-0.10	0.46	-0.43	19.55 \pm 0.84
Departure day	NA	NA	0.51	-0.17	86 \pm 3	NA	NA	0.13	0.26	110 \pm 4
Fuel load (g)	0.78	0.35	NA	NA	1.64 \pm 1.06	0.28	0.37	NA	NA	2.02 \pm 1.20
R ²	0.05	0.01	0.16	0.01		0.04	0.01	0.11	0.02	
Q ²	0.00	-0.05	0.11	-0.04		-0.01	-0.03	0.06	-0.01	

in the second component (Table 1, 5 and Fig. 3A). For ruby-crowned kinglets ($n = 61$), we found precipitation during the month before departure to show a strong positive association with departure day in the first and second component, respectively (Table 2, 5 and Fig. 4A). Our swamp sparrow ($n = 159$) model found departure day to be positively associated with temperature during the month before departure in the second component, which suggests little influence of local weather conditions on this species (Table 3, 5 and Fig. 5A). In white-throated sparrows ($n = 115$), we identified meaningful associations between departure day and conditions during the month of departure, such that there was a positive association with precipitation in the first component and a negative association with temperature in the second component. (Table 4, 5 and Fig. 6A).

Based on the departure fuel loads (Supporting information; Table 1, 2, 3 and 4) of the first 25% of departures by our focal species, we were able to determine associations between early season departure fuel load and local weather variables. In house wren, fuel load was strongly positively associated with temperature and precipitation during the month of departure and strongly negatively associated with temperature the month before departure in the first component. Interestingly, we found a conflict in the second component where house wren fuel load was strongly negatively

associated with temperature the month of departure in the second component; precipitation the month of departure showed a strong positive association with fuel load in the second component (Table 1, 5 and Fig. 3B). For the ruby-crowned kinglet model, temperature the month of departure in the first component was negatively associated with fuel load; precipitation the month before departure was positively associated with fuel load in the second component (Table 2, 5 and Fig. 4B). The swamp sparrow model only identified temperature the month prior to departure in the second component to be negatively associated with fuel load, which suggests little influence of local weather conditions on this species (Table 3, 5 and Fig. 5B). The white-throated sparrow model found a negative association in the first component between fuel load and precipitation during the month before departure, while there was a positive association with temperature the month of departure in the second component (Table 4, 5 and Fig. 6B).

From the departure dates (Supporting information; Table 1, 2, 3 and 4) of the last 25% of departures by our focal species, we were able to determine associations between departure dates late in the season and local weather variables. In house wren ($n = 38$), temperature during the month of departure was positively associated with departure day in the first component. In the second component, precipitation the

Table 4. Results from partial least squares regression (PLSR) for the departure day and fuel load models in the first quarter and last quarter of white-throated sparrow *Zonotrichia albicollis* departures from southwest Louisiana. Mean and standard deviation of each variable is also provided. W_1 = weight of predictor variable based on the first component, W_2 = weight of predictor variable based on the second component. Weights > 0.2 when squared and $Q^2 > 0.0975$ are shown in bold (see text).

	First 25% of final captures					Last 25% of final captures				
	Departure day model		Fuel load model		Mean (\pm SD)	Departure day model		Fuel load model		Mean (\pm SD)
	W_1	W_2	W_1	W_2		W_1	W_2	W_1	W_2	
Lean body mass (g)	-0.14	-0.66	0.43	0.66	23.75 \pm 0.75	0.10	-0.11	0.19	0.06	23.70 \pm 0.67
Previous precipitation (cm)	0.20	-0.18	-0.19	0.23	9.58 \pm 5.63	0.42	-0.14	0.36	-0.18	9.84 \pm 5.50
Previous temperature ($^{\circ}$ C)	0.44	-0.16	-0.78	-0.02	13.05 \pm 1.49	-0.06	-0.19	0.17	0.22	16.24 \pm 1.73
Current precipitation (cm)	0.80	0.26	-0.28	0.53	8.85 \pm 4.98	-0.33	0.37	-0.03	0.93	9.74 \pm 5.40
Current temperature ($^{\circ}$ C)	0.32	-0.49	-0.31	0.28	16.15 \pm 2.13	0.40	-0.66	0.53	-0.15	19.78 \pm 1.26
Departure day	NA	NA	-0.06	0.38	84 \pm 4	NA	NA	0.72	0.17	110 \pm 4
Fuel load (g)	-0.09	0.45	NA	NA	0.99 \pm 1.59	0.74	0.60	NA	NA	1.96 \pm 1.84
R ²	0.04	0.01	0.10	0.01		0.09	0.01	0.11	0.03	
Q ²	-0.01	-0.07	0.01	-0.03		-0.01	-0.09	-0.01	-0.10	

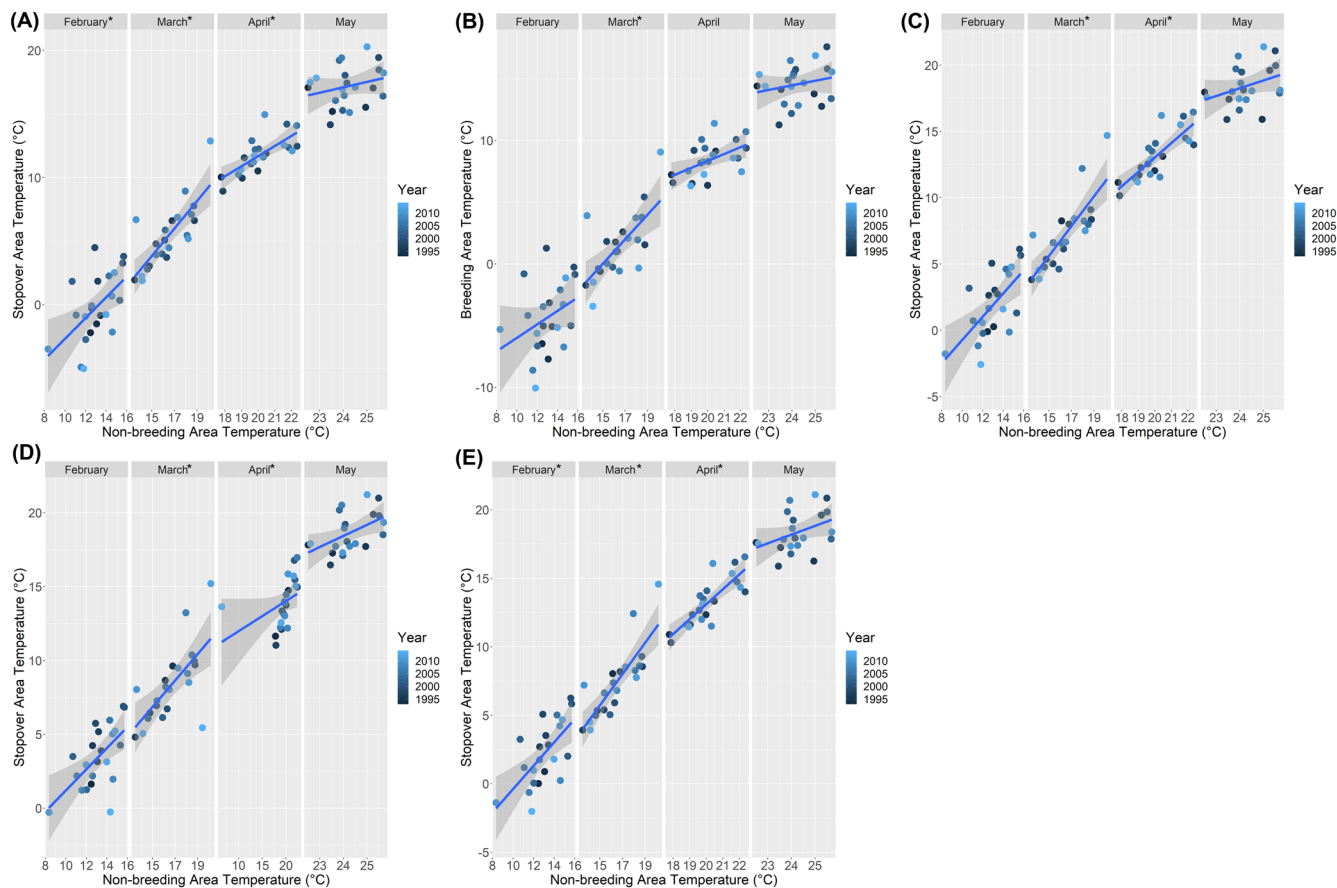


Figure 2. Relationships between temperature at the non-breeding area and temperature at the stopover (A) and breeding (B) areas for house wren *Troglodytes aedon* as well as stopover areas for ruby-crowned kinglet *Corthylio calendula*, (C) swamp sparrow *Melospiza georgiana*, (D) white-throated sparrow *Zonotrichia albicollis*, (E) shaded area around trendline indicates 95% confidence intervals and an asterisk (*) indicates $|\rho| \geq 0.60$.

month prior to departure and temperature during the month of departure were negatively associated with departure day (Table 1, 5 and Fig. 3C). For ruby-crowned kinglets ($n = 56$), local weather variables were the only ones found to be important by the departure day model. Departure day was positively associated with temperature during both the month of and the month before departure in the first component. In the second component, temperature during the month of departure was positively associated with departure day, but temperature the month before departure was negatively related to departure day (Table 2, 5 and Fig. 4C). For swamp sparrows ($n = 165$), we only found local weather variables to be associated with departure day in the second component, which included positive associations with temperature the month prior to departure and precipitation the month of departure (Table 3, 5 and Fig. 5C). Similar to swamp sparrow, the white-throated sparrow ($n = 105$) model only found local weather conditions to be important in the second component, which included a negative association with temperature the month of departure (Table 4, 5 and Fig. 6C).

From the departure fuel loads (Supporting information; Table 1, 2, 3 and 4) of the last 25% of departures by our

focal species, we were able to determine associations between departure fuel loads late in the season and local weather variables. In our house wren model, we found positive associations with temperature the month before departure occurred and precipitation during the month of departure in the first component and temperature during the month of departure in the second component (Table 1, 5 and Fig. 3D). For ruby-crowned kinglets, we found negative associations with temperature the month of and prior to departure in the first component as well as the previous month's precipitation in the second component (Table 2, 5 and Fig. 4D). The swamp and white-throated sparrow models both found fuel load to be positively associated with temperature and precipitation during the month of departure in the first and second components, respectively (Table 3, 4, 5 and Fig. 5D, 6D).

Endogenous factors

Using data from departure dates (Supporting information; Table 1, 2, 3 and 4) of the first 25% of departures by our focal species, we were able to determine associations between early season departure day and various endogenous factors. For the house wren model, we only found a meaningful positive

Table 5. The percent of information each local weather variable has on the first and second components when departure day and fuel load are the response variables for the first 25% and last 25% of birds departing within each focal species. In parenthesis, positive signs indicate a positive relationship between the response and predictor variable and negative signs indicate a negative relationship between the response and predictor variable.

Species	Departure group	Predictor variable	Departure day		Fuel load	
			Percent of information in component 1	Percent of information in component 2	Percent of information in component 1	Percent of information in component 2
House wren	Early	Current precipitation	7% (+)	81% (-)	23% (+)	< 1% (-)
	Early	Previous precipitation	1% (-)	< 1% (+)	19% (+)	20% (+)
	Late	Current precipitation	2% (-)	10% (-)	45% (+)	1% (-)
	Late	Previous precipitation	< 1% (-)	20% (-)	1% (+)	16% (+)
	Early	Current temperature	4% (+)	6% (+)	29% (+)	30% (-)
	Early	Previous temperature	42% (+)	2% (+)	22% (-)	18% (-)
	Late	Current temperature	20% (+)	27% (-)	2% (-)	45% (+)
	Late	Previous temperature	1% (-)	16% (+)	32% (+)	3% (-)
Ruby-crowned kinglet	Early	Current precipitation	6% (-)	1% (-)	2% (-)	2% (+)
	Early	Previous precipitation	58% (+)	3% (+)	< 1% (-)	48% (+)
	Late	Current precipitation	3% (+)	14% (-)	2% (-)	8% (+)
	Late	Previous precipitation	< 1% (-)	< 1% (-)	17% (-)	53% (-)
	Early	Current temperature	< 1% (+)	18% (+)	42% (-)	2% (-)
	Early	Previous temperature	7% (-)	2% (-)	4% (+)	8% (+)
	Late	Current temperature	55% (+)	26% (+)	22% (-)	14% (+)
	Late	Previous temperature	26% (+)	44% (-)	23% (-)	8% (+)
Swamp sparrow	Early	Current precipitation	12% (-)	< 1% (-)	2% (+)	< 1% (+)
	Early	Previous precipitation	8% (+)	8% (-)	< 1% (+)	2% (-)
	Late	Current precipitation	1% (+)	56% (+)	14% (-)	22% (+)
	Late	Previous precipitation	17% (-)	< 1% (+)	2% (+)	1% (+)
	Early	Current temperature	14% (-)	8% (+)	< 1% (+)	8% (+)
	Early	Previous temperature	< 1% (-)	64% (+)	3% (-)	85% (-)
	Late	Current temperature	5% (+)	1% (-)	21% (+)	19% (-)
	Late	Previous temperature	1% (-)	28% (+)	16% (-)	8% (+)
White-throated sparrow	Early	Current precipitation	64% (+)	7% (+)	8% (-)	28% (+)
	Early	Previous precipitation	4% (+)	3% (-)	4% (-)	5% (+)
	Late	Current precipitation	11% (-)	14% (+)	< 1% (-)	86% (+)
	Late	Previous precipitation	18% (+)	2% (-)	13% (+)	3% (-)
	Early	Current temperature	10% (+)	24% (-)	10% (-)	8% (+)
	Early	Previous temperature	19% (+)	3% (-)	61% (-)	< 1% (-)
	Late	Current temperature	16% (+)	44% (-)	28% (+)	2% (-)
	Late	Previous temperature	< 1% (-)	4% (-)	3% (+)	5% (+)

association between departure day and LBM in the first component (Table 1, 6 and Fig. 3A). For ruby-crowned kinglet, we found a meaningful negative association between departure day and fuel load in the first component and a positive association of LBM in the second component (Table 2, 6 and Fig. 4A). Like the house wren model, the swamp sparrow departure day model only found one strong association, which was positive with fuel load in the first component (Table 3, 6 and Fig. 5A). The white-throated sparrow model only showed meaningful associations in the second component, which were positive between departure date and fuel load but negative with LBM (Table 4, 6 and Fig. 6A).

Using data from departure fuel loads (Supporting information; Table 1, 2, 3 and 4) of the first 25% of departures by our focal species, we were able to determine associations between early season departure day and various endogenous factors. In the house wren and white-throated sparrow models, we only found a positive association between fuel load and LBM in the second component (Table 1, 4, 6

and Fig. 3B, 6B). The ruby-crowned kinglet model showed a strong negative association between fuel load and departure day as well as LBM in the first and second components, respectively (Table 2, 6 and Fig. 4B). For swamp sparrow, we found meaningful positive associations with LBM and departure day in the first component (Table 3, 6 and Fig. 5B).

From the departure dates (Supporting information; Table 1, 2, 3 and 4) of the last 25% of departures by our focal species, we were able to determine associations between departure dates late in the season and endogenous factors. For house wren, LBM was negatively associated with departure day in the first component, but fuel load was positively associated with departure day in both the first and second components (Table 1, 6 and Fig. 3C). In the swamp sparrow model, the first component contained the only meaningful relationship, which was the negative association with LBM (Table 3, 6 and Fig. 5C). The white-throated sparrow model identified positive relationships between departure day and

fuel load in both the first and second components (Table 4, 6 and Fig. 6C). The ruby-crowned kinglet model showed no important relationships between departure day and endogenous factors (Table 2, 6 and Fig. 4C).

From the departure fuel loads (Supporting information; Table 1, 2, 3 and 4) of the last 25% of departures by our focal species, we were able to determine associations between departure fuel loads late in the season and endogenous factors. Fuel load in the house wren model only showed a positive association with departure day in the second component (Table 1, 6 and Fig. 3D). We found a negative association between fuel load and departure day in the first component of the ruby-crowned kinglet model (Table 2, 6 and Fig. 4D). For swamp sparrow, we found fuel load to be positively associated with

LBM in the first and second components (Table 3, 6 and Fig. 5D). In the white-throated sparrow model, we found fuel load and departure day to have a positive association in the first component (Table 4, 6 and Fig. 6D).

Fuel load and lean body mass during early and late departures

To address our third objective, we compared species-specific fuel load and LBM between the first 25% and last 25% of birds to depart. While house wren showed no significant difference in fuel load ($W=592$; $p=0.07$; adjusted $\alpha=0.03$; Supporting information) or LBM ($W=1008.5$; $p=0.02$; adjusted $\alpha=0.02$; Supporting information) between early

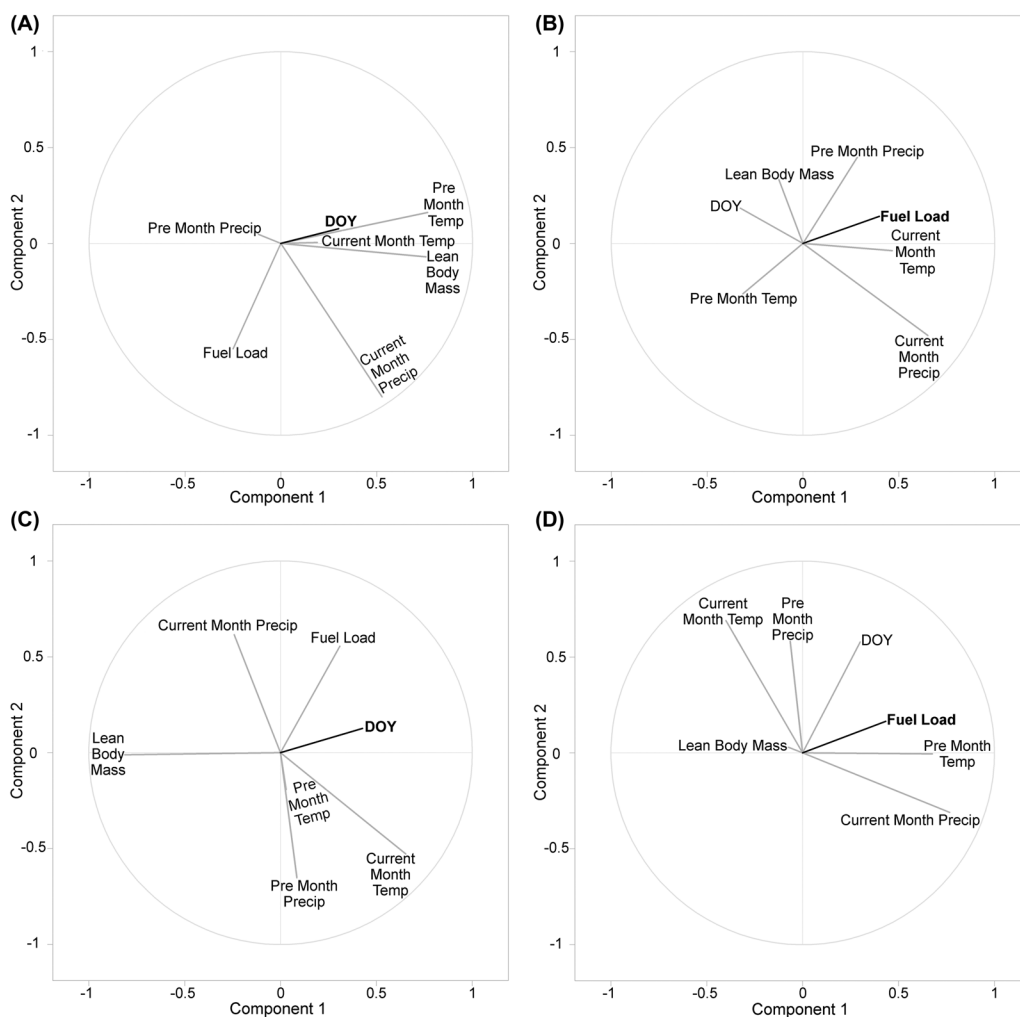


Figure 3. Circle of correlations based on the partial least squares regression for house wren *Troglodytes aedon* departure behaviors. Response variables appear in black and predictor variables appear in gray. Predictor variables in the same direction as the response variable indicate a positive relationship, while those opposite (i.e. 180°) indicate a negative association; predictor variables perpendicular (i.e. 90°) to the response variable signify no relationship. Longer lines specify a stronger influence on (predictors) or relationship with (response) the component(s). Within each plot, 'DOY' = departure day; 'current month precip/temp' = mean precipitation or temperature, respectively, the month of departure; 'pre month precip/temp' = mean precipitation or temperature, respectively, the month before departure; 'lean body mass' = mass of individuals without fuel; and 'fuel load' = mass of individuals above or below lean body mass. (A) Departure day model for first 25% of departures, (B) fuel load model for first 25% of departures, (C) departure day model for the last 25% of departures and (D) fuel load model for the last 25% of departures.

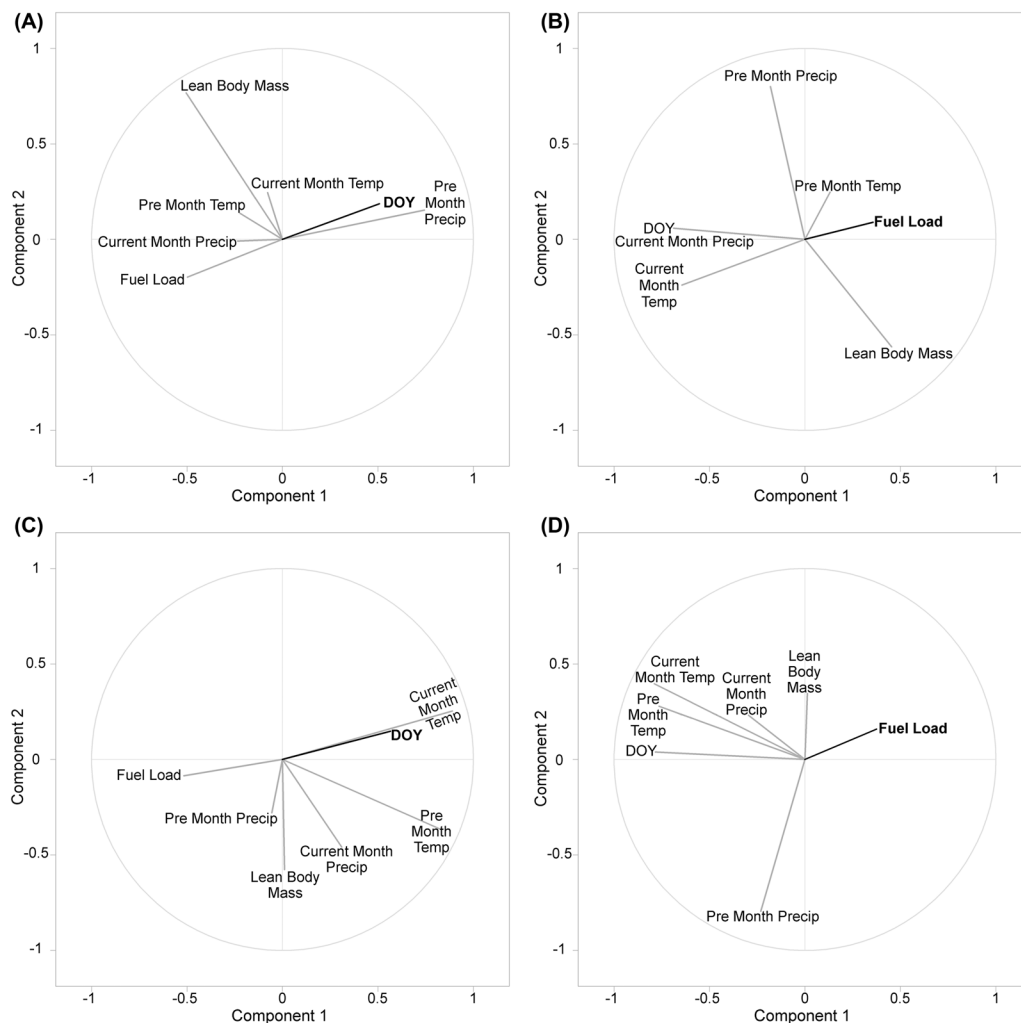


Figure 4. Circle of correlations based on the partial least squares regression for ruby-crowned kinglet *Corthylio calendula* departure behaviors. Response variables appear in black and predictor variables appear in gray. Predictor variables in the same direction as the response variable indicate a positive relationship, while those opposite (i.e. 180°) indicate a negative association; predictor variables perpendicular (i.e. 90°) to the response variable signify no relationship. Longer lines specify a stronger influence on (predictors) or relationship with (response) the component(s). Within each plot, ‘DOY’ = departure day; ‘current month precip/temp’ = mean precipitation or temperature, respectively, the month of departure; ‘pre month precip/temp’ = mean precipitation or temperature, respectively, the month before departure; ‘lean body mass’ = mass of individuals without fuel; and ‘fuel load’ = mass of individuals above or below lean body mass. (A) Departure day model for first 25% of departures, (B) fuel load model for first 25% of departures, (C) departure day model for the last 25% of departures and (D) fuel load model for the last 25% of departures.

and late departing individuals, differences appeared to approach significance. Early departing house wrens tended to be slightly larger but carry less fuel (Table 1, Supporting information; see previous section for all sample sizes) compared to later departing wrens. Ruby-crowned kinglets showed no difference in LBM between early and late departing birds ($W = 1784.5$; $p = 0.68$; Table 2, Supporting information), but we detected a marginally significant difference between fuel load with early departing individuals carrying more fuel than late departing individuals ($W = 2040.5$; $p = 0.07$; $\alpha = 0.05$; Table 2, Supporting information). Swamp sparrow differed in both fuel load ($W = 11\ 012$; $p = 0.01$; adjusted $\alpha = 0.02$; Table 3, Supporting information) and LBM ($W = 17\ 052$; $p < 0.01$; adjusted $\alpha = 0.01$; Table 3, Supporting information)

between the early and late departure periods. Early departing swamp sparrows tended to be larger but carry less fuel compared to individuals departing later (Table 3). White-throated sparrow showed a similar difference with fuel load greater in late departing individuals ($W = 3869.5$; $p < 0.01$; adjusted $\alpha = 0.01$; Table 4, Supporting information), but LBM did not differ ($W = 6176$; $p = 0.77$; Table 4, Supporting information) between the early and late departure periods.

Discussion

When resource availability is synchronized to allow timely arrival with sufficient energy stores at the breeding area,

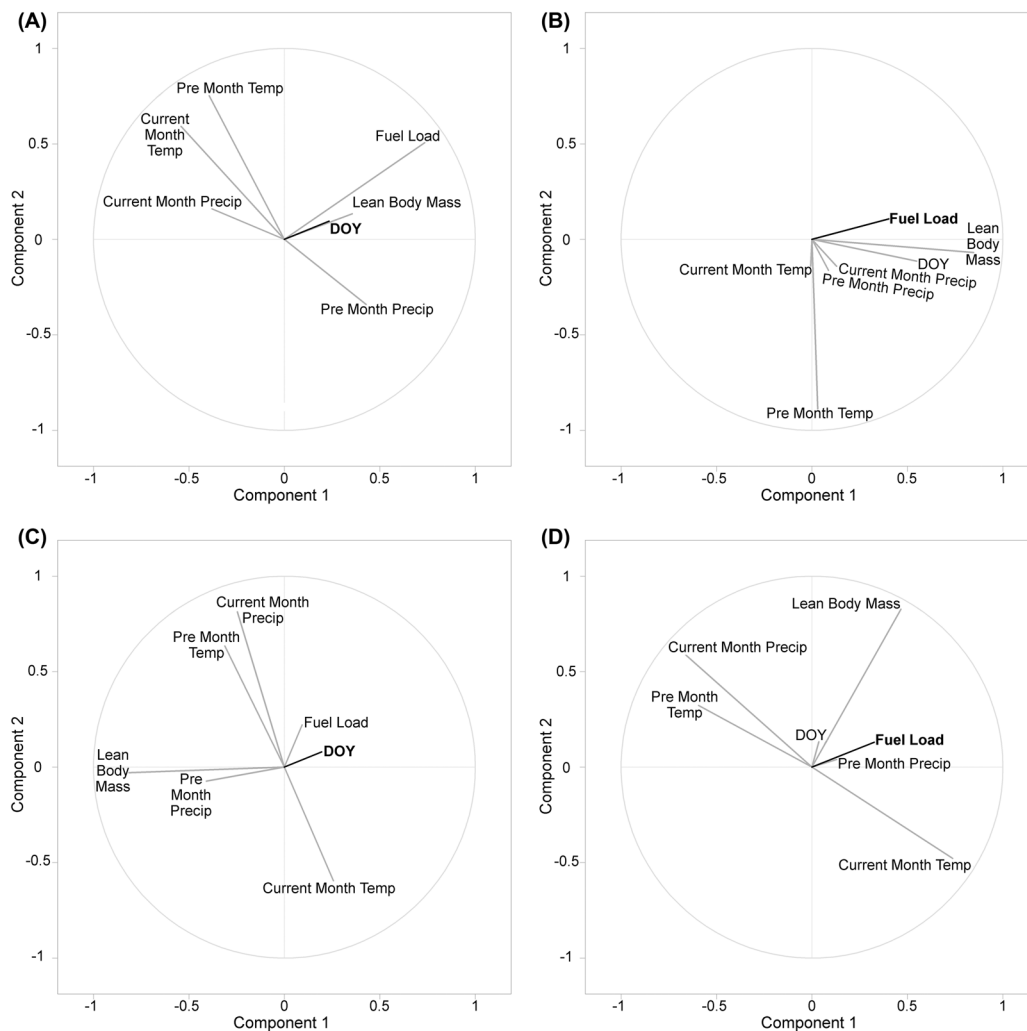


Figure 5. Circle of correlations based on the partial least squares regression for swamp sparrow *Melospiza georgiana* departure behaviors. Response variables appear in black and predictor variables appear in gray. Predictor variables in the same direction as the response variable indicate a positive relationship, while those opposite (i.e. 180°) indicate a negative association; predictor variables perpendicular (i.e. 90°) to the response variable signify no relationship. Longer lines specify a stronger influence on (predictors) or relationship with (response) the component(s). Within each plot, 'DOY' = departure day; 'current month precip/temp' = mean precipitation or temperature, respectively, the month of departure; 'pre month precip/temp' = mean precipitation or temperature, respectively, the month before departure; 'lean body mass' = mass of individuals without fuel; and 'fuel load' = mass of individuals above or below lean body mass. (A) Departure day model for first 25% of departures, (B) fuel load model for first 25% of departures, (C) departure day model for the last 25% of departures and (D) fuel load model for the last 25% of departures.

migratory animals should enjoy greater reproductive success and associated fitness benefits (Lack 1968, Smith and Moore 2003, 2005, Winkler et al. 2014). Given their relatively close proximity to the breeding area, individuals migrating short or medium distances should be able to time their spring arrival with local resource phenology (Winkler et al. 2014). These individuals should be more reliant on local environmental cues and adjust non-breeding area departure timing with resource availability further north, at both stopover and breeding areas (Butler 2003, Lehikoinen et al. 2004, Tøttrup et al. 2008, Cohen et al. 2015). Indeed, all focal species at the non-breeding area in our study would benefit from relying on local predictive cues because non-breeding area

temperatures during most months were positively correlated with temperatures at potential stopover areas, and potential breeding area temperatures for the house wren, during the same month. Despite local cues being predictive of conditions further north for our four focal species, the amount variation explained by local weather conditions in our models differed by species and temporal period but was low overall ($< 32\%$ variation explained). Only the ruby-crowned kinglet departure day model for the last 25% of birds found local weather conditions to be the only important predictor variables, which was only one of two models to exhibit predictive power. All other models included non-weather predictor variables. These results suggest that most individuals migrating

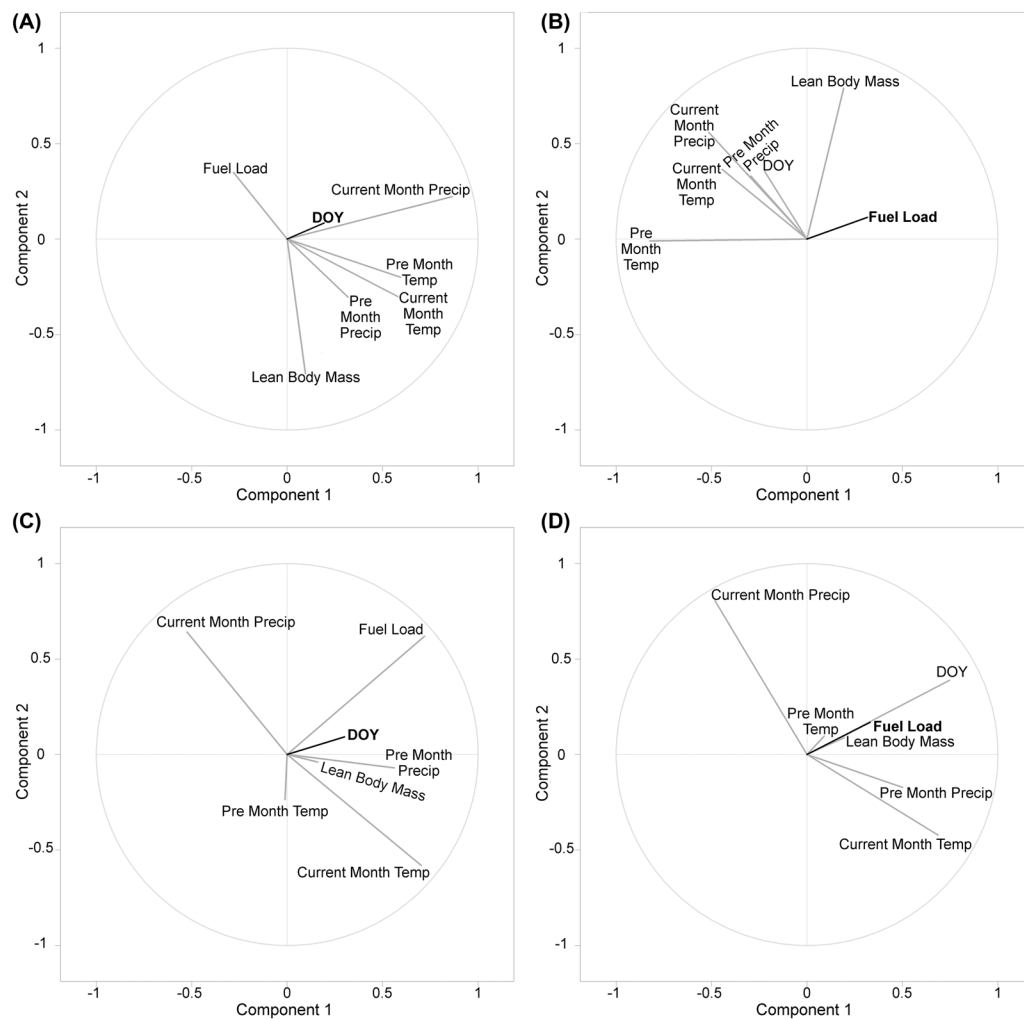


Figure 6. Circle of correlations based on the partial least squares regression for white-throated sparrow *Zonotrichia albicollis* departure behaviors. Response variables appear in black and predictor variables appear in gray. Predictor variables in the same direction as the response variable indicate a positive relationship, while those opposite (i.e. 180°) indicate a negative association; predictor variables perpendicular (i.e. 90°) to the response variable signify no relationship. Longer lines specify a stronger influence on (predictors) or relationship with (response) the component(s). Within each plot, 'DOY' = departure day; 'current month precip/temp' = mean precipitation or temperature, respectively, the month of departure; 'pre month precip/temp' = mean precipitation or temperature, respectively, the month before departure; 'lean body mass' = mass of individuals without fuel; and 'fuel load' = mass of individuals above or below lean body mass. (A) Departure day model for first 25% of departures, (B) fuel load model for first 25% of departures, (C) departure day model for the last 25% of departures and (D) fuel load model for the last 25% of departures.

short or medium distances in our study did not time the initiation of migration with local predictive cues alone, but rather other factors such as body size, fuel load, day of year, which may be a proxy for the endogenous program, and those beyond the scope of our study (e.g. breeding latitude, winds aloft, previous year temperatures) also influenced the initiation of migration.

Local weather

Local environmental cues, such as temperature and precipitation, are most reliable to inform initial departure decisions when non-breeding areas are in relatively close proximity to breeding areas. Indeed, temperatures in our non-breeding

area were indicative of temperatures en route and, to a lesser degree, breeding areas over a 21-year period. However, precipitation in the non-breeding area was not related to precipitation in the northern geographic regions, which is possibly due to differences in the type of precipitation between non-breeding and northern regions during our seasonal period (i.e. rain versus snow). The relationship with temperature is important because arthropod abundance in temperate habitats increases with warming temperatures during late winter and early spring (Diggs et al. 2011, Wood and Pidgeon 2015). There is also a link between precipitation and food abundance, but this linkage is more important in dryer regions (Morrison and Bolger 2002) as well as during fruit production (Karr 1976). Given these relationships, our data

Table 6. The percent of information each endogenous factor has on the first and second components when departure day and fuel load are the response variables for the first 25% and last 25% of birds departing within each focal species. In parenthesis, positive signs indicate a positive relationship between the response and predictor variable and negative signs indicate a negative relationship between the response and predictor variable.

Species	Departure group	Predictor variable	Departure day		Fuel load	
			Percent of information in component 1	Percent of information in component 2	Percent of information in component 1	Percent of information in component 2
House wren	Early	Departure day	NA	NA	7% (-)	8% (+)
	Early	Lean body mass	38% (+)	< 1% (+)	< 1% (+)	23% (+)
	Early	Fuel load	7% (-)	10% (-)	NA	NA
	Late	Departure day	NA	NA	19% (+)	21% (+)
	Late	Lean body mass	56% (-)	< 1% (+)	< 1% (+)	14% (+)
	Late	Fuel load	20% (+)	26% (+)	NA	NA
Ruby-crowned kinglet	Early	Departure day	NA	NA	45% (-)	< 1% (-)
	Early	Lean body mass	6% (-)	76% (+)	8% (+)	41% (-)
	Early	Fuel load	23% (-)	< 1% (+)	NA	NA
	Late	Departure day	NA	NA	34% (-)	1% (+)
	Late	Lean body mass	< 1% (-)	16% (-)	2% (+)	17% (+)
	Late	Fuel load	15% (-)	0% (+)	NA	NA
Swamp sparrow	Early	Departure day	NA	NA	26% (+)	3% (-)
	Early	Lean body mass	4% (+)	8% (-)	69% (+)	1% (-)
	Early	Fuel load	61% (+)	12% (+)	NA	NA
	Late	Departure day	NA	NA	2% (+)	7% (+)
	Late	Lean body mass	69% (-)	1% (+)	45% (+)	45% (+)
	Late	Fuel load	8% (+)	14% (+)	NA	NA
White-throated sparrow	Early	Departure day	NA	NA	< 1% (-)	14% (+)
	Early	Lean body mass	2% (-)	44% (-)	18% (+)	44% (+)
	Early	Fuel load	< 1% (-)	20% (+)	NA	NA
	Late	Departure day	NA	NA	52% (+)	3% (+)
	Late	Lean body mass	1% (+)	1% (-)	4% (+)	< 1% (+)
	Late	Fuel load	55% (+)	36% (+)	NA	NA

suggest that if short- and medium-distance migrants spending the non-breeding season along the northern Gulf of Mexico began to fuel for migration when resources become locally available, they would likely experience similar resource availability en route but less so at the breeding area.

While species- and temporal-specific differences did exist in the amount of variation explained by local weather cues to make departure related decisions, we documented some commonalities across species and/or temporal periods. For example, we found in all species but kinglet that temperatures during the month before departure appeared to have an inverse relationship with fuel load in early departing individuals. Temperature the month of departure explained meaningful variation in the first or second components of the fuel load models across all species for late departing individuals, with all species but kinglets showing a positive relationship. A positive relationship between fuel load and temperatures during the month of departure may be indicative of an increase in arthropod prey abundance (sensu Morrison and Bolger 2002, Diggs et al. 2011, Wood and Pidgeon 2015). Overall, wrens and kinglets had more information explained by weather variables compared to the sparrow species, which may be due to sparrows being much less reliant on arthropods during the non-breeding season compared to wrens or kinglets (Falls and Kopachena 2020, Hebert and Mowbray 2020, Johnson 2020, Swanson et al. 2021). Alternatively,

differences we observed may be due to differences in 1) body size as kinglets and wrens are smaller than either sparrow species or 2) sample sizes, which were approximately three to four times greater for the sparrow species compared to kinglets and wrens, respectively. Interestingly, we found temperature during the month of departure to be positively associated with ruby-crowned kinglet departure day during the late period, opposite the pattern found for fuel load during both temporal periods. The contrasting effect of temperature during the month of departure in ruby-crowned kinglets, when both fuel load and departure day behave as response variables may be a result of the positive association between temperature and bird abundance (Leptien and Bock 1976). During warmer months, a higher abundance of individuals in the non-breeding area could depress fuel loads (Moore and Yong 1991, Kelly et al. 2002, Zenzal and Moore 2019) and, consequently, delay the initiation of migration.

Endogenous cues

Despite evidence of individual variation (Conklin et al. 2010, 2021), change in photoperiod is considered one of the strongest drivers in the endogenous program that migratory birds use to initiate migratory fueling and movements (Wingfield 1983, Berthold 1984, Schwabl and Farner 1989, Dawson et al. 2001, Ramenofsky 2011, Ramenofsky and

Németh 2014). Therefore, it is not surprising that over half of the models investigating fuel load found a relationship with day of year, which suggests some reliance on the endogenous program to build fuel stores and depart by individuals migrating shorter distances. The species-specific differences in the use of local predictive cues we observed may be due to differences in breeding habitat, distance to the breeding area, migratory strategies, prey preferences or ability to secure resources. Given the overall low amount of variation explained by the departure date and fuel load models for most species, it may be that most individuals migrating shorter distances initiate migration with little respect to local weather cues and adjust their pace of migration as they encounter environmental conditions further north, similar to long-distance migrants (Tøttrup et al. 2008, Cohen et al. 2015).

Individual circumstances (i.e. fuel load and body size) appeared to be important in the initiation of migration across all species. For example, LBM was the variable to explain the most variation in the first component of 1) departure date and fuel load for late departing swamp sparrows, 2) fuel load for early departing swamp sparrows and 3) departure day in late departing house wrens. Despite LBM being important with respect to the decision to depart, we only found LBM in swamp sparrow to differ between early and late periods. Larger body size tends to convey dominance (Brown and Maurer 1986, Funghi et al. 2015, Francis et al. 2018), which suggests larger individuals may be able to gain priority access to resources or higher quality non-breeding habitats and subsequently gain fuel faster before migrating earlier. In our study, larger bodied individuals within a species tended to initiate migration earlier. It is possible that there is a latitudinal trend in body size (i.e. larger-bodied individuals breed further north and initiate migration earlier) and/or larger-bodied individuals may have been able outcompete smaller individuals for food and migrate earlier. While our results may infer a sex-dependent migration strategy where larger bodied males leave earlier as they are under greater time selection compared to smaller bodied females, which may favor energy or risk minimization, our inability to determine the sex of the majority of captured birds does not allow us to disentangle this potential pattern.

Fuel load explained departure day in late departing house wrens and white-throated sparrows as well as early departing swamp sparrows, such that individuals carried more fuel later in the season. Additionally, in all species but kinglet, we found late departing individuals tended to carry more fuel compared to those initiating migration earlier in the season. Interestingly, fuel load also had a strong inverse relationship with departure day in early departing kinglets, which may explain the lack of difference in fuel load between early and late departing individuals. The relationship between fuel load and the decision to migrate is no surprise as numerous other studies have also documented this relationship during the migratory and pre-migratory phases (Lindstrom and Alerstam 1992, Marra et al. 1998, Studds and Marra 2005, 2011, Deppe et al. 2015, Sjöberg et al. 2015, Dossman et al. 2016, Zenzal et al. 2021; but see Zenzal et al. 2018). The difference

in condition may suggest that early-departing migrants may be attempting to minimize time while late-departing migrants may be attempting to minimize the energetic cost of migration (sensu Alerstam and Lindström 1990, Lindstrom and Alerstam 1992, Alerstam 2011). Alternatively, differences in fuel load may simply be a result of greater resource abundance later in the season.

Conclusions

It is clear from our study that behavioral decisions related to the initiation of migration (i.e. hyperphagia and departure from the wintering area) are based on a complex set of cues for individuals migrating short or medium distances. While we did find that local predictive cues vary in the degree to which they are associated with the initiation of spring migration for most species and temporal periods, other factors, such as the endogenous program, internal circumstance and factors beyond the scope of our study (e.g. breeding latitude, winds aloft, previous year temperatures), are clearly at play and, in some cases, appear stronger than local weather cues. For example, fuel load in early departing swamp sparrows, departure day in early and late departing swamp sparrows, and departure day in early departing white-throated sparrows were only explained by non-weather variables in the first component. While individuals may use local cues to gauge the optimal time for departure, other factors may influence an individual's ability to depart as found in other non-breeding systems (Marra et al. 1998, Studds and Marra 2005). Indeed, when our models were able to predict departure day in late departing ruby-crowned kinglets and early departing swamp sparrows, the most important variables were temperature for kinglets and LBM as well as departure day for swamp sparrows. Our study contributes to our understanding of factors that influence the departure decisions of species migrating short and medium distances as they transition from the non-breeding to the migratory phase of the annual cycle.

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2jm63xsss> (Zenzal et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Abdi, H. 2007. Partial least squares regression (PLS regression). – In: Salkind, N. J. (ed.), *Encyclopedia of measurement and statistics*. Sage, pp. 740–744.
- Alerstam, T. 2011. Optimal bird migration revisited. – *J. Ornithol.* 152: 5–23.
- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, P. D. E. (ed.), *Bird migration*. Springer, pp. 331–351.
- Amélineau, F., Delbart, N., Schwemmer, P., Marja, R., Fort, J., Garthe, S., Elts, J., Delaporte, P., Rousseau, P., Duraffour, F. and Bocher, P. 2021. Timing of spring departure of long distance migrants correlates with previous year's conditions at their breeding site. – *Biol. Lett.* 17: 20210331.
- Barrow, W. C., Chen, C. C., Hamilton, R. B., Ouchley, K. and Spengler, T. J. 2000. Disruption and restoration of en route habitat, a case study: the Chenier Plain. – *Stud. Avian Biol.* 20: 71–87.
- Bayly, N. J., Norris, D. R., Taylor, P. D., Hobson, K. A. and Morales-Rozo, A. 2020. There's no place like home: tropical overwintering sites may have a fundamental role in shaping migratory strategies. – *Anim. Behav.* 162: 95–204.
- Berthold, P. 1984. The endogenous control of bird migration: a survey of experimental evidence. – *Bird Study* 31: 19–27.
- Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – *Nature* 411: 296–298.
- Both, C., Bouwhuis, S., Lessells, C. M. and Visser, M. E. 2006. Climate change and population declines in a long-distance migratory bird. – *Nature* 441: 81–83.
- Brown, J. H. and Maurer, B. A. 1986. Body size, ecological dominance and Cope's rule. – *Nature* 324: 248–250.
- Burnham, K. P. and Anderson, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. – Springer.
- Burnside, R. J., Salliss, D., Collar, N. J. and Dolman, P. M. 2021. Birds use individually consistent temperature cues to time their migration departure. – *Proc. Natl Acad. Sci. USA* 118: e2026378118.
- Butler, C. J. 2003. The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. – *Ibis* 145: 484–495.
- Carlisle, J. D., Stock, S. L., Kaltenecker, G. S. and Swanson, D. L. 2004. Habitat associations, relative abundance and species richness of autumn landbird migrants in southwestern Idaho. – *Condor* 106: 549–566.
- Carrascal, L. M., Galván, I. and Gordo, O. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. – *Oikos* 118: 681–690.
- Cohen, E. B., Németh, Z., Zenzal Jr., T. J., Paxton, K. L., Diehl, R. H., Paxton, E. H. and Moore, F. R. 2015. Spring resource phenology and timing of songbird migration across the Gulf of Mexico. – In: Wood, E. M. and Kellerman, J. L. (eds), *Studies in avian biology*. CRC Press, pp. 63–82.
- Conklin, J. R., Battley, P. F., Potter, M. A. and Fox, J. W. 2010. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. – *Nat. Commun.* 1: 67.
- Conklin, J. R., Lisovski, S. and Battley, P. F. 2021. Advancement in long-distance bird migration through individual plasticity in departure. – *Nat. Commun.* 12: 4780.
- Cooper, N. W., Hallworth, M. T. and Marra, P. P. 2017. Light-level geolocation reveals wintering distribution, migration routes and primary stopover locations of an endangered long-distance migratory songbird. – *J. Avian Biol.* 48: 209–219.
- Coppack, T. and Both, C. 2002. Predicting life-cycle adaptation of migratory birds to global climate change. – *Ardea* 55: 369–378.
- Dänhardt, J. and Lindström, A. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. – *Anim. Behav.* 62: 235–243.
- Dawson, A., King, V. M., Bentley, G. E. and Ball, G. F. 2001. Photoperiodic control of seasonality in birds. – *J. Biol. Rhythms* 16: 365–380.
- DeGraaf, R. M. and Rappole, J. H. 1995. *Neotropical migratory birds: natural history, distribution and population change*. – Cornell Univ. Press.
- Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenzal, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton, E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, D. and

- Cochran, W. W. 2015. Fat, weather and date affect migratory songbirds' departure decisions, routes and time it takes to cross the Gulf of Mexico. – *Proc. Natl Acad. Sci. USA* 112: E6331–E6338.
- Dierschke, V. and Delingat, J. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. – *Behav. Ecol. Sociobiol.* 50: 535–545.
- Diggs, N. E., Marra, P. P. and Cooper, R. J. 2011. Resource limitation drives patterns of habitat occupancy during the nonbreeding season for an omnivorous songbird. – *Condor* 113: 646–654.
- Dossman, B. C., Mitchell, G. W., Norris, D. R., Taylor, P. D., Guglielmo, C. G., Matthews, S. N. and Rodewald, P. G. 2016. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. – *Behav. Ecol.* 27: 567–574.
- eBird 2021. eBird: an online database of bird distribution and abundance (web application). – eBird.
- Efford, M. G. 2005. Migrating birds stop over longer than usually thought: comment. – *Ecology* 86: 3415–3418.
- Ellegren, H. 1991. Stopover ecology of autumn migrating bluethroats *Luscinia s. svecica* in relation to age and sex. – *Ornis Scand.* 22: 340–348.
- Ellegren, H. 1992. Estimated effects of age and sex on the fat-free body mass of autumn migrating bluethroats *Luscinia s. svecica*. – *Ardea* 80: 255–259.
- Falls, J. B. and Kopachena, J. G. 2020. White-throated sparrow *Zonotrichia albicollis*. – In: Poole, A. F. (ed.), *Birds of the world*, 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.whtspa.01>.
- Francis, M. L., Plummer, K. E., Lythgoe, B. A., Macallan, C., Currie, T. E. and Blount, J. D. 2018. Effects of supplementary feeding on interspecific dominance hierarchies in garden birds. – *PLoS One* 13: e0202152.
- Funghi, C., Leitão, A. V., Ferreira, A. C., Mota, P. G. and Cardoso, G. C. 2015. Social dominance in a gregarious bird is related to body size but not to standard personality assays. – *Ethology* 121: 84–93.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. – *Clim. Res.* 35: 37–58.
- Hair, J. F., Risher, J. J., Sarstedt, M. and Ringle, C. M. 2019. When to use and how to report the results of PLS-SEM. – *Eur. Busin. Rev.* 31: 2–24.
- Harrell Jr, F. E. and Dupont, C. 2021. Hmisc: harrell miscellaneous. – R package ver. 4.5-0, <https://cran.r-project.org/web/packages/Hmisc/>.
- Hasselquist, D., Montràs-Janer, T., Tarka, M. and Hansson, B. 2017. Individual consistency of long-distance migration in a songbird: significant repeatability of autumn route, stopovers and wintering sites but not in timing of migration. – *J. Avian Biol.* 48: 91–102.
- Hebert, J. A. and Mowbray, T. B. 2020. Swamp sparrow *Melospiza georgiana*. – In: Rodewald, P. G. (ed.), *Birds of the world*, 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.swaspa.01>.
- Helms, C. W. and Drury, W. H. 1960. Winter and migratory weight and fat field studies on some North American buntings. – *Bird-Banding* 31: 1–40.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. – *Scand. J. Stat.* 6: 65–70.
- Hou, L. and Welch, K. C. 2016. Premigratory ruby-throated hummingbirds, *Archilochus colubris*, exhibit multiple strategies for fuelling migration. – *Anim. Behav.* 121: 87–99.
- Hou, L., Verdirame, M. and Welch, K. C. 2015. Automated tracking of wild hummingbird mass and energetics over multiple time scales using radio frequency identification (RFID) technology. – *J. Avian Biol.* 46: 1–8.
- Jakubas, D. and Wojczulanis-Jakubas, K. 2010. Sex- and age-related differences in the timing and body condition of migrating reed warblers *Acrocephalus scirpaceus* and sedge warblers *Acrocephalus schoenobaenus*. – *Naturwissenschaften* 97: 505–511.
- Johnson, L. S. 2020. House wren *Troglodytes aedon*. – In: Poole, A. F. (ed.), *Birds of the world*, 1.0. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.houwre.01>.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. and Stenseth, N. C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. – *Science* 312: 1959–1961.
- Karr, J. R. 1976. Seasonality, resource availability and community diversity in tropical bird communities. – *Am. Nat.* 110: 973–994.
- Kelly, J. F., DeLay, L. S. and Finch, D. M. 2002. Density-dependent mass gain by Wilson's warblers during stopover. – *Auk* 119: 210–213.
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., Ranta, E., Rubolini, D., Sparks, T. H., Spina, F., Studds, C. E., Sæther, S. A., Tryjanowski, P. and Stenseth, N. C. 2011. Challenging claims in the study of migratory birds and climate change. – *Biol. Rev.* 86: 928–946.
- Lack, D. 1968. Ecological adaptations for breeding birds. – Methuen.
- Lain, E. J., Zenzl, T. J., Moore, F. R., Barrow, W. C. and Diehl, R. H. 2017. Songbirds are resilient to hurricane disturbed habitats during spring migration. – *J. Avian Biol.* 48: 815–826.
- Lehikoinen, E., Sparks, T. H. and Zalakevicius, M. 2004. Arrival and departure dates. – *Adv. Ecol. Res.* 35: 1–31.
- Lepthien, L. W. and Bock, C. E. 1976. Winter abundance patterns of North American kinglets. – *Wilson Bull.* 88: 483–485.
- Lindstrom, A. and Alerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. – *Am. Nat.* 140: 477–491.
- Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. – *J. Avian Biol.* 27: 164–170.
- Mann, H. B. and Whitney, D. R. 1947. On a test of whether one of two random variables is stochastically larger than the other. – *Ann. Math. Stat.* 18: 50–60.
- Marra, P. P. and Holmes, R. T. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. – *Auk* 118: 92–104.
- Marra, P. P., Francis, C. M., Mulvihill, R. S. and Moore, F. R. 2005. The influence of climate on the timing and rate of spring bird migration. – *Oecologia* 2: 307–315.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Mason, C. F. 1995. Long-term trends in the arrival dates of spring migrants. – *Bird Study* 42: 182–189.
- McKellar, A. E., Marra, P. P. and Ratcliffe, L. M. 2013. Starting over: experimental effects of breeding delay on reproductive

- success in early-arriving male American redstarts. – *J. Avian Biol.* 44: 495–503.
- Moore, F. R. and Yong, W. 1991. Evidence of food-based competition among passerine migrants during stopover. – *Behav. Ecol. Sociobiol.* 28: 85–90.
- Moore, F. R., Covino, K. M., Lewis, W. B., Zenzal, T. J. and Benson, T. J. 2017. Effect of fuel deposition rate on departure fuel load of migratory songbirds during spring stopover along the northern coast of the Gulf of Mexico. – *J. Avian Biol.* 48: 123–132.
- Moore, F. R., Mabey, S. and Woodrey, M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. – In: Berthold, P., Gwinner, E. and Sonnenschein, E. (eds), *Avian migration*. Springer, pp. 281–292.
- Morrison, S. A. and Bolger, D. T. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. – *Oecologia* 133: 315–324.
- Ouwehand, J. and Both, C. 2017. African departure rather than migration speed determines variation in spring arrival in pied flycatchers. – *J. Anim. Ecol.* 86: 88–97.
- Packmor, F., Klinner, T., Woodworth, B. K., Eikenaar, C. and Schmaljohann, H. 2020. Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? – *Mov. Ecol.* 8: 6.
- Paxton, K. L., Cohen, E. B., Paxton, E. H., Németh, Z. and Moore, F. R. 2014. El Niño-Southern oscillation is linked to decreased energetic condition in long-distance migrants. – *PLoS One* 9: e95383.
- Pyle, P. 1997. Identification guide to North American birds: Columbidae to Ploceidae. – Slate Creek Press.
- Ramenofsky, M. 2011. Hormones in migration and reproductive cycles of birds. – In: Norris, D. O. and Lopez, K. H. (eds), *Hormones and reproduction of vertebrates*. Academic Press, pp. 205–237.
- Ramenofsky, M. 2012. Reconsidering the role of photoperiod in relation to effects of precipitation and food availability on spring departure of a migratory bird. – *Proc. R. Soc. B* 279: 15–16.
- Ramenofsky, M. and Németh, Z. 2014. Regulatory mechanisms for the development of the migratory phenotype: roles for photoperiod and the gonad. – *Horm. Behav.* 66: 148–158.
- Rice, W. R. 1989. Analyzing tables of statistical tests. – *Evolution* 43: 223–225.
- Risely, A., Blackburn, E. and Cresswell, W. 2015. Patterns in departure phenology and mass gain on African non-breeding territories prior to the Sahara crossing in a long-distance migrant. – *Ibis* 157: 808–822.
- Rubolini, D., Møller, A. P., Rainio, K. and Lehikoinen, E. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. – *Clim. Res.* 35: 135–146.
- Sanchez, G. 2012. plsdepot: partial least squares (PLS) data analysis methods. – <https://github.com/gastonstat/plsdepot>.
- Schaub, M., Pradel, R., Jenni, L. and Lebreton, J.-D. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. – *Ecology* 82: 852–859.
- Schwabl, H. and Farner, D. S. 1989. Endocrine and environmental control of vernal migration in male white-crowned sparrows, *Zonotrichia leucophrys gambelii*. – *Physiol. Zool.* 62: 1–10.
- Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. and Muheim, R. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. – *Anim. Behav.* 104: 59–68.
- Smith, R. J. and Moore, F. R. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. – *Oecologia* 134: 325–331.
- Smith, R. J. and Moore, F. R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. – *Behav. Ecol. Sociobiol.* 57: 231–239.
- Smolinsky, J. A., Diehl, R. H., Radzio, T. A., Delaney, D. K. and Moore, F. R. 2013. Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. – *Behav. Ecol. Sociobiol.* 67: 2041–2051.
- Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A. and Stutchbury, B. J. M. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. – *PLoS One* 7: e40688.
- Studds, C. E. and Marra, P. P. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. – *Ecology* 86: 2380–2385.
- Studds, C. E. and Marra, P. P. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. – *Proc. R. Soc. B* 278: 3437–3443.
- Swanson, D. L., Ingold, J. L. and Wallace, G. E. 2021. Ruby-crowned kinglet *Regulus calendula*. – In: *Birds of the world*, 1.1. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.ruckin.01.1>.
- Tøttrup, A. P., Kasper, T., Kalle, R., Reuven, Y., Esa, L. and Carsten, R. 2008. Avian migrants adjust migration in response to environmental conditions en route. – *Biol. Lett.* 4: 685–688.
- Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C. and Thorup, K. 2010. Local temperature fine-tunes the timing of spring migration in birds. – *Integr. Comp. Biol.* 50: 293–304.
- Tøttrup, A. P., Klaassen, R. H. G., Kristensen, M. W., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. and Thorup, K. 2012. Drought in Africa caused delayed arrival of European songbirds. – *Science* 338: 1307–1307.
- Vardanis, Y., Klaassen, R. H. G., Strandberg, R. and Alerstam, T. 2011. Individuality in bird migration: routes and timing. – *Biol. Lett.* 7: 502–505.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: S120–S139.
- Wickham, H. 2007. Reshaping data with the reshape package. – *J. Stat. Softw.* 21: 1–20.
- Wickham, H., François, R., Henry, L. and Müller, K. 2021. dplyr: a grammar of data manipulation. – R package ver. 1.0.5, <https://dplyr.tidyverse.org/>.
- Wingfield, J. C. 1983. Environmental and endocrine control of avian reproduction: an ecological approach. – In: Mikami, S., Homma, K. and Wada, M. (eds), *Avian endocrinology: environmental and ecological perspectives*. Japan Scientific Societies/Springer, pp. 265–288.
- Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., McNamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D. and Piersma, T. 2014. Cues, strategies and outcomes: how migrating vertebrates track environmental change. – *Mov. Ecol.* 2: 10.
- Wood, E. M. and Pidgeon, A. M. 2015. Extreme variations in spring temperature affect ecosystem regulating services provided by birds during migration. – *Ecosphere* 6: art216.

- Woodworth, B. K., Francis, C. M. and Taylor, P. D. 2014. Inland flights of young red-eyed vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. – *J. Avian Biol.* 45: 387–395.
- Woodworth, B. K., Newman, A. E. M., Turbek, S. P., Dossman, B. C., Hobson, K. A., Wassenaar, L. I., Mitchell, G. W., Wheelwright, N. T. and Norris, D. R. 2016. Differential migration and the link between winter latitude, timing of migration and breeding in a songbird. – *Oecologia* 181: 413–422.
- Woodworth, B. K., Wheelwright, N. T., Newman, A. E., Schaub, M. and Norris, D. R. 2017. Winter temperatures limit population growth rate of a migratory songbird. – *Nat. Commun.* 8: 14812.
- Zenzal Jr, T. J., Johnson, D., Moore, F. R. and Németh, Z. 2022. Data from: Local weather and endogenous factors affect the initiation of migration in short- and medium-distance songbird migrants. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.2jm63xsss>.
- Zenzal Jr, T. J. and Moore, F. R. 2019. Resource use and defence by ruby-throated hummingbirds during stopover. – *Behaviour* 156: 131–153.
- Zenzal Jr, T. J., Moore, F. R., Diehl, R. H., Ward, M. P. and Deppe, J. L. 2018. Migratory hummingbirds make their own rules: the decision to resume migration along a barrier. – *Anim. Behav.* 137: 215–224.
- Zenzal Jr, T. J., Ward, M. P., Diehl, R. H., Buler, J. J., Smolinsky, J., Deppe, J. L., Bolus, R. T., Celis-Murillo, A. and Moore, F. R. 2021. Retreat, detour or advance? Understanding the movements of birds confronting the Gulf of Mexico. – *Oikos* 130: 739–752.