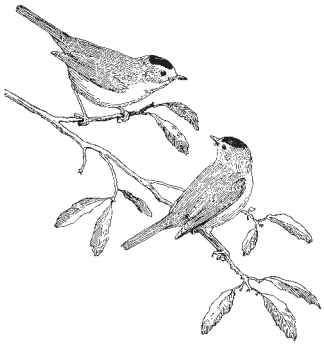

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Refueling performance of migratory passerines stopping at an inland stopover site in the Connecticut River Valley

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ABSTRACT—Migratory landbirds are in decline across North America as factors like habitat loss and climate change pose significant challenges across the annual cycle. Migration is a period of especially high mortality as birds must navigate new landscapes to find suitable foraging habitat and deal with ecological barriers, predation, and competition along the way. Stopover sites where birds can rest and refuel are crucial for successful migration. Refueling performance is linked to a variety of factors including season, migratory distance, habitat quality, and body condition upon arrival. Here, we used plasma triglyceride to investigate how season, progression of season (ordinal day), and breeding latitude influenced the stopover refueling performance of 7 migratory songbird species during fall and spring migration at an inland site in the Connecticut River Valley in western Massachusetts. We found that Swainson's Thrushes (*Catharus ustulatus*) and White-throated Sparrows (*Zonotrichia albicollis*) had greater refueling performance in spring, while Gray Catbirds (*Dumetella carolinensis*) showed increased refueling performance in fall, suggesting that birds refuel differently at the same site and experience different pressures between seasons during migration. Progression of season did not influence refueling performance for most species in either season, but in fall the refueling performance of Gray Catbirds increased as the season progressed, while the refueling performance declined as the fall season progressed for Yellow-rumped Warblers (*Setophaga coronata*). We used stable isotopes to examine how breeding latitude influenced refueling performance for a subset of Gray Catbirds and found that, contrary to our expectations, Gray Catbirds nearer to their breeding destination in spring had greater refueling performance, suggesting that birds may try to improve their body condition directly before arriving at their breeding grounds to increase their reproductive competitiveness. Our results show that refueling performance of songbirds passing through inland stopover sites varies across species and can be influenced by a variety of factors including season and breeding latitude. *Received 5 April 2022. Accepted 29 May 2023.*

Key words: deuterium, plasma triglycerides, songbird migration, stable isotopes, stopover.

Desempeño del reabastecimiento de aves terrestres migratorias durante paradas de descanso en un sitio del interior del valle del río Connecticut

RESUMEN (Spanish)—En América del Norte, las aves migratorias terrestres están declinando ya que factores como la pérdida de hábitat y el cambio climático representan desafíos significativos a lo largo del ciclo anual. La migración es un período de mortalidad

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elevada debido a que las aves deben navegar nuevos paisajes para encontrar hábitats de forrajeo y a la vez lidiar con barreras ecológicas, depredación y competencia. Los sitios de parada, donde las aves descansan y se reabastecen, son cruciales para una migración exitosa. La efectividad del reabastecimiento está vinculada con varios factores, incluyendo la temporada, la distancia de migratoción, la calidad del hábitat y la condición corporal al llegar. Usamos triglicéridos del plasma para investigar la influencia de la temporada, la progresión de la temporada (día ordinal), y la latitud de reproducción sobre la efectividad de reabastecimiento durante paradas para 7 especies de aves migratorias terrestres durante la migración de otoño y primavera en un sitio de parada interior en el valle del río Connecticut en el oeste de Massachusetts. Encontramos que *Catharus ustulatus* y *Zonotrichia albicollis* tuvieron mejor efectividad de reabastecimiento en la primavera, mientras que *Dumetella carolinensis* tuvo mejor efectividad en el otoño, sugiriendo que en un mismo sitio las aves se reabastecen de manera diferente y están sujetas a diferentes presiones entre temporadas de migración. La progresión de la temporada no influyó en la efectividad de reabastecimiento para la mayoría de las especies en ninguna de las temporadas, pero en otoño la efectividad de reabastecimiento de *Dumetella carolinensis* aumentó con el avance de la temporada, mientras que para *Setophaga coronata* disminuyó con el avance de la temporada. Utilizamos isótopos estables para examinar la influencia de latitud de reproducción sobre la efectividad de reabastecimiento para un subconjunto de *Dumetella carolinensis* y encontramos que, contrario a nuestras expectativas, los individuos más cercanos a sus destinos reproductivos en primavera tuvieron mayor efectividad de reabastecimiento, sugiriendo que las aves posiblemente mejoran condición corporal antes de llegar a sus áreas de reproducción para aumentar su competencia reproductiva. Nuestros resultados muestran que la efectividad de abastecimiento en aves terrestres que pasan a través de áreas de paradas interiores varia por especie y puede ser influenciada por una variedad de factores incluyendo temporada y latitud de reproducción.

Palabras clave: deuterio, isótopos estables, migración de aves terrestres, sitios de parada, triglicéridos en plasma.

In North America, more than 350 bird species migrate annually from their summer breeding grounds to their wintering grounds in the tropics, taking advantage of seasonal changes in resource availability. Avian migration is characterized by an alternating pattern of active flight periods, during which energy is expended, and stopover periods, where energy reserves are replenished as birds prepare for their next migratory flight. The majority of the energetic cost (Wikelski et al. 2003) and time of migration is spent at stopover (Hedenström and Alerstam 1997, Schmaljohann et al. 2012). During stopover, birds rest and refuel for the next leg of their journey and can wait for unfavorable weather conditions to pass before continuing. Stopover periods can directly influence the success of migration in terms of survival and reproductive performance (Norris and Taylor 2006, Moore 2018).

Stopover sites have been characterized by the density of birds using the site (Buler and Dawson 2014), time spent at the site (Liu and Swanson 2015), and by mass gained at the site (refueling rate; Schaub and Jenni 2001). Refueling rate is an important way to characterize a stopover site and has conventionally been measured using a body mass/time of day regression (Dunn 2001, 2002), but more recently has been measured using plasma metabolite profiling (Guglielmo et al. 2005). The regression method requires a large number of birds to be sampled and infers mass gained or lost at stopover for a whole population during a given day, while plasma metabolite profiling allows for measurement of the refueling performance of an individual.

The level of plasma triglyceride (TRIG) has been validated to assess the refueling performance of migrant birds at stopover, even among species with diverse feeding habits (Guglielmo et al. 2005). Plasma metabolite concentrations change rapidly in response to changes in feeding, making TRIG indicative of an individual's refueling performance at the specific time and location sampled (Zajac et al. 2006), which can be helpful in comparing refueling rates between sites (Guglielmo et al. 2002, Smith and McWilliams 2010, Ogden et al. 2013, Hoh et al. 2018), between sexes (Guglielmo et al. 2002, Seewagen et al. 2013, Hays et al. 2018), and between years (Seaman et al. 2006). Refueling rate is partially endogenously controlled according to the circannual rhythm (Berthold 1996) but is also greatly influenced by other factors including magnetic cues (Fransson et al. 2001), stopover habitat quality (Seaman et al. 2006, Smith et al. 2015), and presence of invasive plant species at stopover sites (Arizaga et al. 2013).

Much of the body of stopover ecology research has focused on sites where migrants concentrate to refuel and rest before or after crossing an ecological barrier like open water (Goymann et al. 2010, Deppe et al. 2015, Smetzer and King 2020) or urban matrices (Matthews and Rodewald 2010, Seewagen et al. 2011). However, birds at coastal sites often spread inland before continuing their migration (Smolinsky et al. 2013, Woodworth et al. 2014), and inland geographical features like

mountain ranges (Williams et al. 2001) and river valleys (Cormier et al. 2013, Kirsch et al. 2013) can also concentrate populations of migrants. Inland sites may even provide safer and more high-quality stopover habitat than coastal sites (Woodworth et al. 2014), and yet inland stopover ecology has been understudied. Inland stopover sites in eastern North America are of particular importance because greater volumes of land birds pass through the eastern half of the United States than the western half. Even species that spend a majority of the summer in western North America often follow migratory paths that take them through the eastern coast (Hobson and Kardynal 2015, DeLuca et al. 2019). Stopover sites near major water bodies and those embedded within developed or agricultural lands have high migrant bird density during fall migration and therefore are of great conservation importance (Buler and Dawson 2014).

The Connecticut River Valley serves as a major inland migration corridor providing stopover habitat within the Atlantic flyway (Litwin and Lloyd-Evans 2006, Tatten 2021). We picked 2 sites at the lower end of the valley within which to investigate factors influencing the refueling performance of birds migrating through this area. The Connecticut River is the longest river in New England and flows south from New Hampshire for 653 km, emptying into the Long Island Sound. Previous surveys of this watershed have found that spring migrant songbirds concentrate toward the southern end of the river system, then disperse north in lower numbers, and that they use sites closest to the river most often (Litwin and Lloyd-Evans 2006).

We used TRIG to investigate the refueling performance of 7 species of migratory songbirds in the Connecticut River valley during spring and fall migration and specifically focused on 3 questions regarding the influence of differences in season, timing, and migratory distance on refueling rate. Although there is also evidence for territorial competition on the wintering grounds (Powell et al. 2021), spring migration has long been hypothesized to be faster than fall migration due to increased selective pressure to arrive early at the breeding grounds to secure territories and mates (Kokko 1999, Nilsson et al. 2013). Overall rates of passerine migration tend to be significantly faster in the spring (Stutchbury et al. 2009), largely due to reductions in stopover duration rather than differences in actual flight speed (Nilsson et al. 2013). The increased daylight hours available for foraging (Bauchinger and Klaassen 2005) and more favorable winds in spring (Nussbaumer et al. 2022) also may contribute to more rapid spring migration. Within each season, birds migrating later operate under greater time constraints. Stopover duration decreases as the migratory season proceeds in both the spring (Yong and Moore 1997) and the fall (Ktitorov et al. 2010, Smith and McWilliams 2014). Migratory speed increases later in fall migration (Bensch and Nielsen 1999), likely because later migrants face urgent time constraints as moving south means avoiding harsher northern temperatures and declining resource availability. Although a consistent relationship between date and refueling rate has not been firmly established (Schaub and Jenni 2001, Eikenaar et al. 2016), we expect that progression of season influences refueling performance at stopover. Migratory distance may also impact fuel deposition rate in some circumstances (Schmaljohann et al. 2016, Hays et al. 2018). Larger fuel loads should allow an individual to fly longer distances before stopping over, and thereby increase the overall pace of migration. We hypothesized that (1) migrants will have increased refueling performance in spring compared to fall, (2) migrants arriving later within an individual season in both spring and fall will have greater refueling performance, and (3) birds with more northerly breeding grounds will have greater refueling performance during stopover in the spring.

Methods

Study site description

Our study used data from birds captured during fall and spring migration at 2 sites: Orchard Hill, on the University of Massachusetts Amherst campus in Amherst, MA (42°23′47″N, 72°31′05″W), and the Fort River Division of the Silvio O. Conte National Fish and Wildlife Refuge in Hadley, MA (42°20′30″N, 72°33′51″W) (Fig. 1). Sites were chosen to best capture migratory species based on 2 main criteria: (1) they consisted of some shrubland and herbaceous habitat, and (2) there were

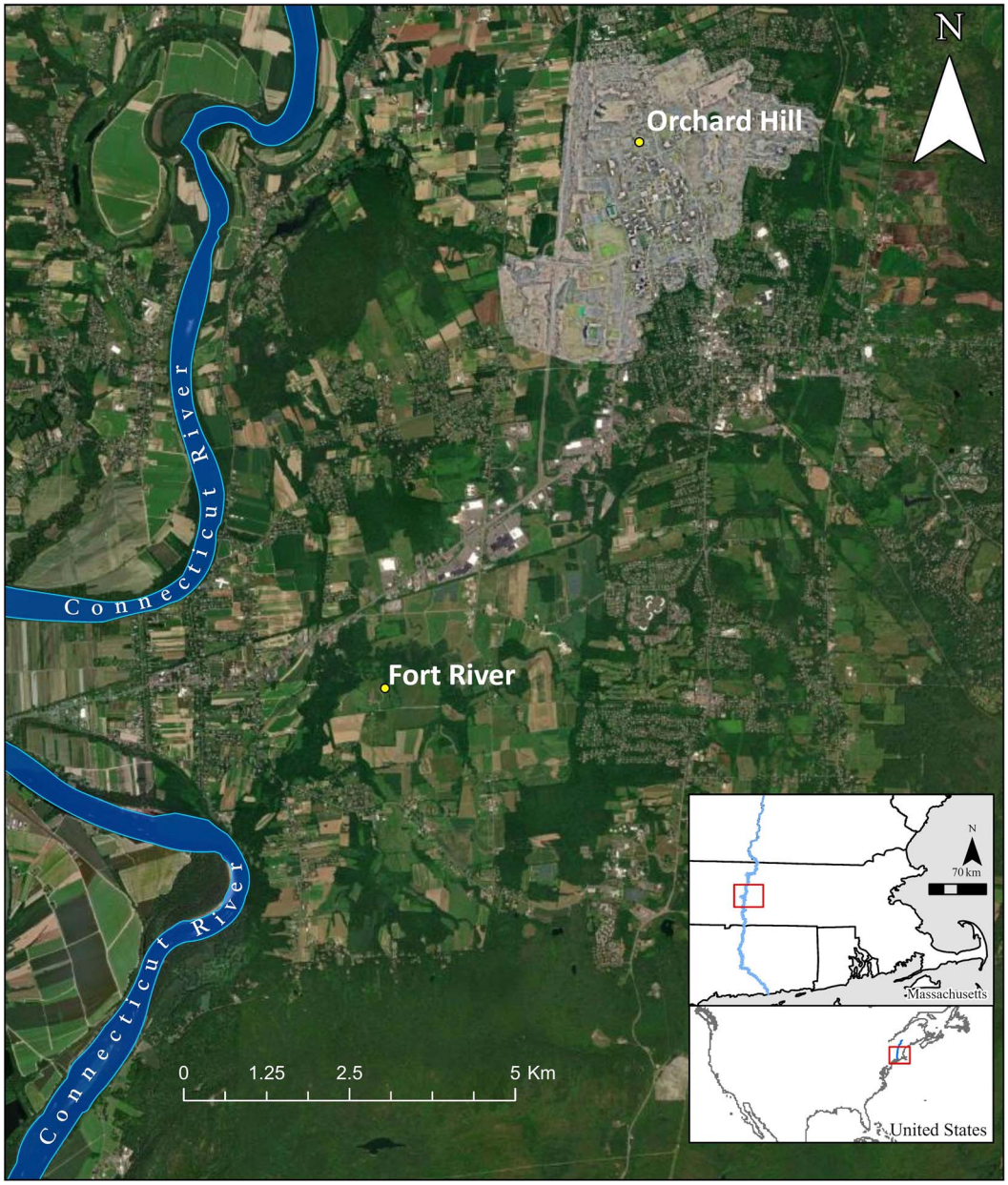

Figure 1. Study sites in western Massachusetts in relation to the Connecticut River. Inset maps show the location of the study area within New England and within the United States.

open or semi-open canopy conditions (Tatten 2021). These conditions typically yield higher mist net capture rates because migratory birds forage within shrublands due to food availability.

The Fort River Division is a protected conservation area managed by the U.S. Fish and Wildlife Service and consists of floodplain forest, open shrublands, and northeastern hardwood forest. Dominant plant species include red maple (*Acer rubrum*), sugar maple (*A. saccharum*), quaking aspen (*Populus tremuloides*), multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*), sumac (*Rhus* sp.), and dogwood (*Cornus* sp.) species. Orchard Hill is a fragmented deciduous

habitat with patches of forested area as well as open grassland dispersed within a developed college campus landscape. Dominant plant species include black raspberry (*Rubus* sp.), sugar maple, sumac, and dogwood species. Each site was individually chosen based on the criteria above, and dominant habitat type between the 2 sites was relatively similar. The sites are 7.17 km apart.

Bird capture and sample collection

We used data from a migration monitoring banding station that operated in 2017–2018 and amassed information from over 1,300 individual birds migrating through the Connecticut River Valley in fall and spring. Data were not collected expressly for the purpose of this project. Because the composition of birds captured was variable, and due to missing morphometric data, we selected species from the dataset for this study based on the sample size with complete morphometric and plasma metabolite data available.

The 7 focal species we selected for this study are Gray Catbird (*Dumetella carolinensis*; $n = 102$), Hermit Thrush (*Catharus guttatus*; $n = 26$), Northern Waterthrush (*Parkesia noveboracensis*; $n = 17$), Swainson's Thrush (*Catharus ustulatus*; $n = 21$), White-throated Sparrow (*Zonotrichia albicollis*; $n = 23$), Wood Thrush (*Hylocichla mustelina*; $n = 17$), and Yellow-rumped Warbler (*Setophaga coronata*; $n = 23$), for a total of 229 samples.

Birds were captured from 13 September to 20 October 2017, and from 2 to 26 May 2018, during the morning hours (from approximately sunrise to 1100 h EST) in nylon mist nets checked every 10 min. We determined age as hatch year or after hatch year (HY/AHY) in fall, and after hatch year or after second year (AHY/ASY) in spring (Pyle 1997). We weighed birds to 0.01 g on a digital scale, measured tail length, bill width, and wing chord, and scored fat on a 9-point scale (Kaiser 1993) and pectoral muscle on a 4-grade scale (Bairlein 1995). We banded birds with USGS aluminum leg bands before release. For birds captured more than once, we only included data from the first capture in our analyses. All data collection was permitted by the U.S. Geological Survey (Bird Banding Laboratory banding permits 23979 and 23140) and conducted under the approval of the University of Massachusetts Institutional Animal Care and Use Committee (#2015-0019).

Body condition index

We used a principal component analysis (PCA) created separately for each species to incorporate 3 distinct measures of body condition into 1 discrete variable to represent body condition in our models (Maggini et al. 2013). This PCA included body mass, fat score, and muscle score. PC1 explained 49.8–60.4% of the variation in the original data and is our body condition index.

Plasma triglyceride

We collected a blood sample (<10% of total body volume) from most birds captured via brachial venipuncture using a heparinized microcapillary tube, then stored the sample in an Eppendorf tube on ice in a cooler until nets were closed for the day (max 6 h). We assumed birds were in the net since the last time the net was checked, and conservatively measured "maximum bleed time" as the time elapsed between the previous net check and blood sampling. At the end of the banding effort each day, blood samples were spun in a centrifuge at 10,000 rpm for 10 min. Plasma was then transferred into a cryogenic vial and stored at −80°C for up to 3 months until analysis.

We measured glycerol and total triglyceride (Sigma Aldrich F6428 and Sigma Aldrich T2449, respectively) sequentially by quantitative determination. To increase plasma volumes, samples were diluted 3-fold with 0.9% NaCl. Triglyceride assays were run in duplicate in 400 µL flat bottom 96-well microplates and read at 540 nm in a microplate spectrophotometer (BioTek Synergy H1 Hybrid Multi-Mode Reader), with all CV <15% (Guglielmo et al. 2005).

Stable isotopes

Stable isotope analysis is a widely accepted method for investigating migratory connectivity because the ratio of deuterium (δ^2H) to hydrogen varies in a latitudinal gradient across North America according to well-established gradients in precipitation, with δ^2H decreasing as latitude increases. This isotopic signature is incorporated into the keratinized tissue of feathers. By analyzing this ratio in a

feather and comparing it to well established continental isotopic clines, it is possible to determine the approximate location where the feather was grown, likely approximating breeding location (Hobson and Wassenaar 1997). Deuterium analysis has been used to differentiate long-distance and short-distance migrant populations within species (Kelly et al. 2002, Hays et al. 2018).

We collected a tail feather (R3) from birds for stable isotope analysis of deuterium (δ^2H). Tail feather collection was somewhat inconsistent as it was not the priority of the data collection effort, and of our selected study species, the greatest number of feather samples were available from Gray Catbirds. Therefore, we selected 90 Gray Catbird feathers (65 from fall and 25 from spring) for deuterium analysis, based on the availability of measures of body condition (mass, wing chord, fat, and muscle) as well as plasma triglyceride data. Of this subset, 21 birds were captured at Fort River while the other 69 were captured at Orchard Hill.

Feathers were washed 5 times with a 2:1 chloroform:methanol solution to remove contaminants, and then dried in a fume hood and stored in clean envelopes. Analyses were performed on a Thermo Delta V isotope-ratio mass spectrometer (IRMS) interfaced to a Temperature Conversion Elemental Analyzer (TC/EA) at the Cornell University Stable Isotope Laboratory (COIL). Across the sample run, the standard deviation for the internal keratin standard was 1.9‰. The corrected isotope delta value for δ^2H measured against a primary reference scale, in this case, Vienna Standard Mean Ocean Water (V-SMOW), is written as δ^2H vs. VSMOW. δ^2H vs. VSMOW = [(hydrogen isotope ratio$_{sample}$/ hydrogen isotope ratio$_{standard}$) − 1] × 1,000. Delta values are measured in units of per mil (‰). For samples taken in the fall, breeding latitude gives information on how far that individual has flown to arrive at the stopover site, while in the spring, it informs approximately how much farther the individual must travel to arrive at their breeding grounds.

Statistical analyses and covariate selection

We conducted species-specific analyses to evaluate the effects of (1) season (spring vs. fall), (2) progression of season (ordinal day within spring and fall, separately), and (3) distance to/from the breeding grounds (breeding latitude, or δ^2H value) on variation in plasma triglyceride. Triglyceride concentrations were $\log_{10}(x+1)$ transformed to normalize the data. We constructed multiple linear regression models with normalized triglyceride as the response variable and either season, ordinal day, or δ^2H as the main effect of interest in each analysis. We also included time since sunrise, body condition index, and wing chord as covariates in every model. We chose these covariates because plasma metabolites have been shown to be affected by time of day (Guglielmo et al. 2005, Ogden et al. 2013), body mass (Schaub and Jenni 2001; Guglielmo et al. 2002, 2005), and body condition (Paxton and Moore 2017, Hoh et al. 2018). Additionally, fuel deposition rate has also shown to be correlated with body size (Lindström et al. 1990).

Bleed time, or the time between extracting a bird from the mist net and blood sampling, can influence refueling index values likely because capture stress (Jenni-Eiermann and Jenni 1991, Liu and Swanson 2014) and elapsed time (Zajac et al. 2006) have been shown to affect plasma metabolite levels. During sampling, nets were checked every 10–20 min to minimize this effect, and we tested to ensure that bleed time did not confound our analyses. There was no significant relationship between maximum bleed time and TRIG for any species, so we did not include bleed time as a covariate in our models.

Although we aged birds in the field during sample collection, we chose not to include age as a covariate in our models. While differences in foraging efficiency exist between age groups (Vanderhoff and Eason 2008), other authors have reported no difference in TRIG between juveniles and adults captured in the fall (Seewagen et al. 2013) or spring (Beauchamp et al. 2020). We aged birds as either HY or AHY in the fall, and a 2-sample *t*-test of differences in $\log_{10}(x+1)$ transformed triglyceride showed no significant difference between these 2 age classes ($t = -1.9135$, df = 28.263, $P = 0.07$). Due to our small sample sizes, we prioritized limiting the number of covariates included in our models to the greatest extent possible.

When modeling season as the main effect of interest, we created models for each of the 4 species for which sufficient data in both spring and

fall data were available (Gray Catbird, Swainson's Thrush, White-throated Sparrow, and Wood Thrush). When modeling progression of season (ordinal day) as the main effect of interest, models were run for each species using a spring subset and a fall subset. For 3 species (Hermit Thrush, Northern Waterthrush, and Yellow-rumped Warbler), available data were from only one season, and therefore only one progression of season analysis (spring or fall) was conducted. We did not create progression of season models for species where the single-season subset had a sample size of $n < 15$ due to concerns about overparametrized results. When modeling distance to/from the breeding grounds (δ^2H value), we used the subset of Gray Catbirds ($n = 90$) for which stable isotope analysis was performed and created separate models for fall and spring.

We used R 3.6.2 to conduct all analyses (R Core Team 2019). We carried out regressions using function *lm* in package *stats*, then used the function *dredge* in package *MuMIn* (Bartón 2019) to generate a full submodel set (including the null model), and candidate models were ranked based on Akaike's information criterion for small sample sizes (AICc). All models with ΔAICc < 2 were considered top models (Burnham and Anderson 2002, Symonds and Moussalli 2011), and we also present the null model for use in assessing the explanatory power of the top models. For explanatory variables in the top model sets, we averaged parameter estimates across models using the function *model.avg*, rather than basing conclusions on a single "best" model. Model averaging yielded estimates of the regression coefficient for each parameter. We used conditional averages as is recommended when investigating a particular factor of interest, as is the case here (Grueber et al. 2011).

Results

In fall 2017, total sampling effort was 162.5 net-hours at Fort River and 1,103.67 net-hours at Orchard Hill, totaling 1,266.17 net-hours. In spring 2018, sampling effort was 443.33 net-hours at Fort River and 473.33 net-hours at Orchard Hill, totaling 916.66 net-hours. Out of the data available from this sampling effort, we selected a dataset that includes 229 individuals of our focal species, with 149 captured in fall 2017 and 80 captured in spring 2018. In the fall, 20 birds were captured at Fort River and 129 birds were captured at Orchard Hill. In the spring, 23 birds were captured at Fort River and 57 birds were captured at Orchard Hill. There was greater sampling effort in fall 2017 than spring 2018, and at Orchard Hill compared to Fort River. This resulted in a disparity in sample size between seasons and sites purely based on uneven sample collection.

Gray Catbirds were the most abundant species in both seasons ($n = 102$). Mean mass, wing

Table 1. Summary of mean values of mass and wing chord ± SD, mean values of plasma triglyceride concentration ± SD, median fat score, and sample sizes for each species from data collected during fall migration 2017 and spring migration 2018 at 2 inland sites in the Connecticut River Valley.

	Mass (g)	Wing chord (mm)	Triglyceride (mmol/L)	Median fat score	*n*
Fall 2017					
Gray Catbird	40.2 ± 3.46	88.0 ± 2.79	1.45 ± 0.90	1	72
Hermit Thrush	30.3 ± 1.93	88.6 ± 5.44	1.25 ± 0.45	1	26
Swainson's Thrush	32.8 ± 3.27	96.5 ± 3.15	1.16 ± 0.46	1	6
Wood Thrush	57.5 ± 4.03	105.3 ± 3.78	0.92 ± 0.51	0	6
White-throated Sparrow	24.9 ± 1.58	70.7 ± 4.41	1.06 ± 0.64	2	16
Yellow-rumped Warbler	12.2 ± 1.16	70.7 ± 2.65	1.03 ± 0.53	2	23
Spring 2018					
Gray Catbird	36.3 ± 2.75	89.9 ± 3.66	0.97 ± 0.50	1	30
Northern Waterthrush	17.3 ± 1.47	74.6 ± 2.48	1.82 ± 1.10	2	17
Swainson's Thrush	30.5 ± 2.00	96.9 ± 2.67	1.92 ± 0.63	2	15
Wood Thrush	49.0 ± 5.48	105.6 ± 4.52	1.73 ± 1.72	0	11
White-throated Sparrow	26.8 ± 2.34	69.0 ± 2.94	2.25 ± 0.73	2	7

Table 2. Migratory passerines at a stopover site in the Connecticut River Valley. Age structure of dataset, per species for each season.

	Fall 2017		Spring 2018	
	HY	AHY	SY	ASY
Gray Catbird[a]	63	9	18	11
Hermit Thrush	23	3	–	–
Northern Waterthrush	–	–	11	6
Swainson's Thrush	6	0	5	10
Wood Thrush	6	0	7	4
White-throated Sparrow	14	2	6	1
Yellow-rumped Warbler	15	8	–	–
Totals	127	22	47	32

[a] We excluded from this table 1 spring Gray Catbird marked as "AHY."

chord, plasma triglycerides, and sample sizes for each species are presented in Table 1. Age distribution in both seasons is presented in Table 2. The proportion of fat birds (fat scores ≥2) and proportion of birds with full pectoral muscle (muscle scores ≥2) are presented in Table 3. Mean maximum bleed time across all species was 18.91 ± 0.5 min (range: 2–34 min), while the mean minimum bleed time was 5.91 ± 0.06 min (range: 0–32 min).

Seasonal differences

Season and body condition explained variation in triglyceride for all species. For catbirds, a negative parameter coefficient for season indicated greater TRIG values in fall compared with spring, while the opposite was true for the other 3 species (Fig. 2). Time since sunrise explained variation in triglyceride for all species except Wood Thrush. Birds captured later in the day and those with greater body condition index values were associated with greater TRIG. The inclusion of the null model as a top model for Wood Thrush indicated that the parameters we selected were unable to sufficiently explain variation in triglyceride for this species.

Fall season progression

Day 277 (4 Oct) was the median date of sample collection in the fall. Ordinal day was only retained in the top models for the Gray Catbird and Yellow-rumped Warbler, and parameter estimates indicated that Gray Catbirds captured later in the season had greater TRIG, while the opposite was true for Yellow-rumped Warblers (Fig. 2). In Gray Catbird, Hermit Thrush, and White-throated Sparrow models, time since sunrise helped to explain variation in TRIG, and greater TRIG was associated with capture later in the day. Body condition explained variation in triglyceride in Gray Catbird and Yellow-rumped Warbler models, and birds in better body condition were associated with greater TRIG.

Spring season progression

Day 130 (10 May) was the median date of sample collection in spring. Out of the 3 species, ordinal day was only retained in the top models for Northern Waterthrush (Supplemental Table S3). However, as the null model was a top model for both Northern Waterthrush and Swainson's Thrush, we conclude that ordinal day did not explain variation in TRIG for any species in the

Table 3. Body condition of migratory passerines during spring and fall migration at 2 stopover sites in the Connecticut River Valley. Proportion of fat birds (scored ≥2) (compared with lean birds) and birds with full pectoral muscles (scored ≥2) (compared birds with depleted pectoral muscles) for each study species, per season.

	Fall 2017		Spring 2018	
	Fat (%)	Full muscles (%)	Fat (%)	Full muscles (%)
Gray Catbird	34.7	72.2	46.7	73.3
Hermit Thrush	46.2	69.2	–	–
Northern Waterthrush	–	–	52.9	47.1
Swainson's Thrush	33.3	100	66.7	20
Wood Thrush	16.7	100	9.09	45.5
White-throated Sparrow	56.3	93.8	71.4	85.7
Yellow-rumped Warbler	60.9	82.6	–	–

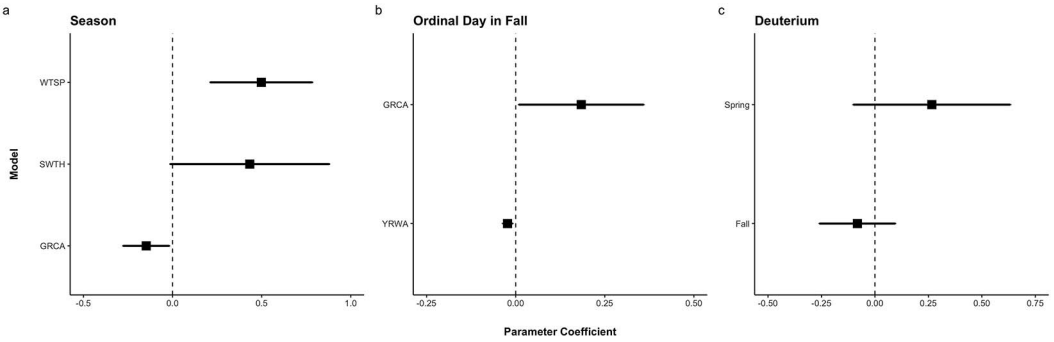

Figure 2. Model averaged parameter coefficients with 95% confidence intervals are shown for each main effect of interest on TRIG. Models that included the null model in the top model set are excluded here as we determined that this was an indication the given parameters were unable to sufficiently explain variation in TRIG. Panels display the parameter coefficients for season (a), fall ordinal day (b), and breeding latitude as determined by deuterium (c, for a fall and spring subset of Gray Catbirds). Parameter coefficients can be found in Supplemental Table S5.

spring. In Gray Catbird models, time since sunrise and wing chord explained variation in TRIG, with birds captured later in the day and those with shorter wing chord associated with greater TRIG.

Breeding latitude

For fall birds, the mean δ^2H value was −76.13‰ ± 0.81‰ (range: −91.06‰ to −58.67‰), and for spring birds the mean δ^2H value was −75.12‰ ± 1.55‰ (range: −88.31‰ to −57.58‰). The mean δ^2H value of catbirds sampled at Orchard Hill was −76.23‰ ± 0.76‰ (range −91.06‰ to −63.89‰), while the mean δ^2H value of catbird sampled at Fort River was −74.61‰ ± 1.83‰ (range −88.31‰ to −57.58‰).

In both fall and spring models with δ^2H as the main effect of interest, δ^2H was retained in the top model sets and helped to explain variation in TRIG (Fig. 2). Gray Catbirds with a more southern breeding latitude were associated with greater TRIG in spring. In fall, Gray Catbirds with a more northern breeding latitude were associated with greater TRIG.

Time since sunrise and wing chord were also included in both top model sets, with parameter estimates indicating that birds captured later in the day and those with shorter wings had greater TRIG. Body condition was only retained in the fall model, and birds with better body condition showed increased TRIG.

Discussion

Our results indicate that variation in refueling performance at inland stopover sites in the Connecticut River Valley is affected by different factors, including migratory season, progression of season, and distance to/from the breeding grounds, but that results are not uniform across species.

We found support for seasonal differences in the refueling performance of migratory songbirds stopping over in the Connecticut River Valley. We expected to see greater TRIG in the spring for all species due to increased pressure to arrive early on the summer breeding grounds and found this to be the case for Swainson's Thrushes and White-throated Sparrows. However, we found the opposite in Gray Catbirds, which displayed greater TRIG in fall than spring. Season did not play a role in determining variation in TRIG for Wood Thrushes.

For many Nearctic–Neotropical migratory species, refueling performance (measured using body mass–time of day regression or plasma triglycerides) during stopover is higher in the spring than the fall (Morris and Glasgow 2001, Seewagen et al. 2013). However, across different stopover sites along an entire migratory route, refueling indices are sometimes higher in fall than spring (Schaub and Jenni 2001), indicating that other factors besides season, such as food availability, competition, predation risk, and proximity to ecological barriers, are site-specific and likely

influence refueling rate. Others have found seasonal differences in stopover duration and usage of stopover habitat along the Connecticut River including at Fort River (Tatten 2021), including migrants making shorter stopovers and traveling at faster rates in spring compared to fall.

We expected to see elevated refueling performance in spring because birds experience increased pressure to arrive early to the breeding grounds in addition to increased daylight hours in which to forage (Bauchinger and Klaassen 2005). Contrary to these expectations, we found that for Gray Catbirds, greater TRIG was associated with fall capture in our model. It is unclear to us why catbirds differed from other species in this assessment because this species experiences the same time constraints and increased daylight hours in spring as the other species we assessed. While we cannot determine exactly why this species behaved differently, some factors that may have influenced our results include higher stress levels in the fall and seasonal dietary plasticity.

White-throated Sparrows and Swainson's Thrushes captured at the same stopover site in spring and fall do not vary in mean body mass between seasons (Smith 2013). The body mass (or body mass index) of Gray Catbirds, however, is significantly increased during fall migration compared to spring migration as well as the wintering and breeding periods (Oberkircher and Pagano 2018, DeMoranville et al. 2019). The elevated TRIG we saw for catbirds during fall migration may be related to the documented increase in body mass in the fall for this species specifically. Additionally, Gray Catbirds display elevated heterophil/lymphocyte ratios in the spring compared to fall and summer, indicating increased stress (Oberkircher and Pagano 2018). Another measure of stress response, corticosterone, has been associated with lower TRIG in migrant birds (Liu and Swanson 2014). Elevated stress response in the spring may help to explain the lower TRIG we saw in the spring for this species.

Seasonal plasticity in diet could also help explain the increased fall refueling rate for Gray Catbirds. In spring and summer, songbirds rely mostly on insects as a food source, while in the fall many exhibit high levels of frugivory (Bairlein 2002). For example, Blackpoll Warblers (*Setophaga striata*) and White-throated Sparrows have significantly greater TRIG at stopover sites with greater fruit crops and higher densities of fruiting shrubs and vines (Smith et al. 2015). While we did not quantify measurements of resource availability between sites or seasons here, it is possible that in our study system high densities of fruiting shrubs and vines allowed Gray Catbirds to refuel at higher rates solely in the fall, since this resource is largely unavailable until the beginning of summer. The percentage of fruit in the diet of Gray Catbirds varies throughout the year, from 20% in the spring to up to 81% in the fall (Martin et al. 1951), indicating that catbirds could be seasonally exploiting berries as an abundant resource during fall but not spring migration. However, Swainson's Thrush, Wood Thrush, and White-throated Sparrow also employ frugivory during fall migration (Parrish 1997, Billerman et al. 2020) and could be exploiting fruit resources in the fall as well, so seasonal frugivory is not sufficient to explain the differences in seasonal refueling performance that we found.

We expected to see TRIG concentrations increase as both seasons progressed for all species, since later arriving migrants are under greater time constraints and may decrease their stopover duration in order to increase their migratory speed and "catch up," necessitating elevated refueling performance. Our results regarding the impact of seasonal progression on TRIG were inconclusive. In fall, later capture date was associated with higher TRIG for Gray Catbirds, while the opposite was true for Yellow-rumped Warblers, and ordinal day did not influence variation in TRIG for the remaining species.

Gray Catbirds may be refueling differentially later in the fall season due to more urgent time constraints, and it is also worth noting that within our study system they are likely shorter distance migrants. Kelly et al. (2002) reported that in the fall, short distance migrants migrate later on average than long distance conspecifics. Gray Catbirds moving through the site later in the season may represent a shorter distance migrant population who are only increasing their refueling

performance in preparation for migratory flight at this time.

For Yellow-rumped Warblers, TRIG was negatively associated with capture date. Hays et al. (2018) similarly reported that the refueling index of migrating Wilson's Warblers (*Cardellina pusilla*) decreased with capture date during fall migration. For most warblers, one could speculate that lower refueling index later in the fall season may be explained by decreasing insect abundance as the fall season continues. Yellow-rumped Warblers, however, have unique gastrointestinal modifications allowing them to efficiently digest waxy berries like bayberry and wax-myrtle, and can therefore maintain more northern wintering ranges than closely related species (Place and Stiles 1992). We therefore would not expect decreasing insect abundance to have as strong of an effect on this species compared with other passerines. One possibility is that this proficiency for metabolizing wax-coated berries may be allowing Yellow-rumped Warblers to remain at our study sites throughout the fall season and even into the wintering period. Terrill and Ohmart (1984) theorize that Yellow-rumped Warblers exhibit a great deal of plasticity in terms of their migratory timing, maintaining a physiological state that allows them to winter as far north as possible while moving southward if conditions (such as cold weather fronts) become unfavorable. Perhaps the Yellow-rumped Warblers that we captured later in the fall season are refueling at a lower rate because these birds are not imminently migrating south, instead choosing to stay at or near our study sites until conditions become less favorable. Observationally, Yellow-rumped Warblers have been seen at Fort River as late in the fall season as 20 November.

Contrary to our expectations, progression of spring season did not influence variation in TRIG in any of our species. While ordinal day was retained in the top model set for Northern Waterthrush, we concluded that the given parameters did not influence refueling rate for this species based on the inclusion of the null model in the top model set. Previous studies similarly found that energetic condition did not vary with time of spring for Northern Waterthrush (Slager et al. 2015), lending support to this finding. We also note that some of our study species are within their breeding range during spring capture, which may influence the relationships we found, since we could not discern between birds that are breeding in the study area and birds that are just passing through.

We did not create a prediction for the effect of distance from the breeding ground on TRIG in the fall since selective pressure for fast migration in fall is less intense than spring. However, other authors have also hypothesized that migratory decision making, such as the timing of nocturnal departure (Müller et al. 2018), can be affected by the distance remaining to the destination rather than total migration distance. In fall, we found that Gray Catbirds from more northern breeding latitudes, who we assume have traveled farther to arrive at the capture site, were associated with greater TRIG values. Similarly, Hays et al. (2018) found that the refueling index of Wilson's Warblers increased with decreasing δ^2H during fall migration.

Birds breeding at more southern latitudes, who have traveled shorter distances before arriving at our capture site, have likely just begun their migratory journey. We speculate that these birds are only recently getting into their migratory disposition, while individuals breeding at more northern latitudes are likely already in their full migratory disposition when arriving at the capture site and consequently may be upregulating their fuel deposition.

In the spring, we expected to see Gray Catbirds from more northern breeding latitudes, and therefore with longer distances remaining to their breeding destination, show increased refueling performance at stopover because individuals with longer distances remaining should minimize stopover duration to increase their migratory efficiency. Contrary to this prediction, we found that Gray Catbirds with more southern breeding latitudes, and consequently less distance remaining to their summer grounds, had greater TRIG. Black-and-white Warblers (*Mniotilta varia*) nearer to their breeding destination during spring migration also displayed greater migratory condition, higher refueling rates, and longer stopover durations compared

to conspecifics migrating to breeding destinations farther from the capture site (Paxton and Moore 2017). Birds nearer to their breeding destination may prepare for breeding by accumulating energy stores before arrival. Breeding and the behaviors associated with it, such as territory defense, nest building, and egg laying, are energetically expensive, and consequently an individual's body condition upon arrival can directly affect their reproductive success. American Redstarts (*Setophaga ruticilla*) who arrive at their breeding grounds with higher fat loads experience gains in reproductive success in terms of increased clutch size, egg volume, and nestling mass (Smith and Moore 2003). Additionally, birds migrating to more distant breeding grounds may refuel at lower rates in order to minimize their fuel load and thereby minimize the energetic cost of their next migratory flight.

Stable hydrogen isotope analysis of feathers collected at stopover allowed us to gain insight into approximate breeding destination of the Gray Catbirds we captured. However, deuterium analysis did not allow for great specificity in determining exact breeding grounds, and without the use of external trackers like radio tags or geolocators, we were unable to determine local scale movements of the birds we studied. We do not know the fate of these birds after release and were unable to determine the length of stopover and whether individuals embarked on long distance migratory flight when they departed or left the site to complete foraging movements at a more local scale.

We recognize that interpretation of our results is limited by the small sample sizes for most of our species (except for Gray Catbirds), and by the fact that we are basing our analyses on a single year of data. These limitations are acceptable for an individual-level, exploratory study such as this, but replication is needed across years and with larger samples before we can confidently detect patterns from the effects we report here. We aimed to present specific and local data about refueling performance of landbird migrants at an inland site, noting that nearly 60% of landbird species are experiencing population decline (Rosenberg et al. 2019) and that conservation of deciduous forest stopover sites within highly altered landscapes is of particular importance due to high concentrations of migrant birds (Guo et al. 2023).

Although we did not quantify site differences and were unable to examine how differences in site impacted refueling rate due to the limitations of small sample sizes, we recognize that these differences may exist. Data were collected primarily at 2 sites which, while largely similar in dominant habitat type and vegetation, may still differ in overall habitat quality and resource availability. Habitat quality has been shown to influence refueling rate (Smith et al. 2015), and it would be interesting to investigate if our study species refuel differentially at these sites in the context of seasonal variation as well. Overall, our findings support the idea that these inland sites in the Connecticut River Valley provide high-quality stopover habitat for migratory species, as TRIG increased as the day progressed in at least one season for the majority of our study species.

It seems clear that a complex mixture of factors helps to determine the refueling rate of an individual during migratory stopover. Our results provide support for the idea that differences in refueling performance exist between seasons, across the progression of a single season, and as distance to or from the breeding grounds changes. These differences appear to be species specific, and trends were not broadly applicable across all species. The relationship between body condition and refueling rate at stopover has previously been a well-established focus of study, but our study and others provide evidence that other extrinsic factors such as migration phenology and distance also play an important role in determining how migrants use stopover sites, and particularly how they refuel at stopover. Here we were unable to link individuals to their wintering grounds, but examining species-specific refueling rates over the entire annual cycle would offer a more nuanced view of the migratory strategies of specific populations. This is especially important from a conservation approach as there is widespread recognition that migratory species are declining more rapidly than nonmigratory species (Rosenberg et al. 2019), and impactful conservation efforts must strive to encompass a holistic

view of crucial habitats across the annual cycle (Mehlman et al. 2005, Faaborg et al. 2010).

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Literature cited

Arizaga J, Unamuno E, Clarabuch O, Azkona A. 2013. The impact of an invasive exotic bush on the stopover ecology of migrant passerines. Animal Biodiversity and Conservation. 36:1–11.

Bairlein F. 1995. Manual of field methods: European-African songbird migration network. Wilhelmshaven (Germany): European Science Foundation.

Bairlein F. 2002. How to get fat: Nutritional mechanisms of seasonal fat accumulation in migratory songbirds. Naturwissenschaften. 89:1–10.

Bartón K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. https://CRAN.R-project.org/package=MuMIn

Bauchinger U, Klaassen M. 2005. Longer days in spring than in autumn accelerate migration speed of passerine birds. Journal of Avian Biology. 36:3–5.

Beauchamp AT, Guglielmo CG, Morbey YE. 2020. Stopover refueling, movement and departure decisions in the White-throated Sparrow: The influence of intrinsic and extrinsic factors during spring migration. Journal of Animal Ecology. 89:2553–2566.

Bensch S, Nielsen B. 1999. Autumn migration speed of juvenile Reed and Sedge warblers in relation to date and fat loads. Condor. 101:153–156.

Berthold P. 1996. Control of bird migration. London (UK): Chapman and Hall.

Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS. 2020. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://birdsoftheworld.org/bow/home

Buler JJ, Dawson DK. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. Condor. 116:357–370.

Burnham KP, Anderson DR. 2002. Model selection and inference: A practical information-theoretic approach. New York (NY): Springer.

Cormier RL, Gardali T, Wood JK. 2013. Assessing migratory stopover site quality for birds during fall migration along two California rivers. Western North American Naturalist. 73:72–79.

DeLuca WV, Woodworth BK, Mackenzie SA, Newman AEM, Cooke HA, et al. 2019. A boreal songbird's 20,000 km migration across North America and the Atlantic Ocean. Ecology. 100:e02651.

DeMoranville KJ, Corder KR, Hamilton A, Russell DE, Huss JM, Schaeffer PJ. 2019. PPAR expression, muscle size and metabolic rates across the Gray Catbird's annual cycle are greatest in preparation for fall migration. Journal of Experimental Biology. 222(14): jeb198028.

Deppe JL, Ward MP, Bolus RT, Diehl RH, Celis-Murillo A, et al. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences. 112:E6331–E6338.

Dunn EH. 2001. Mass change during migration stopover: A comparison of species and sites. Journal of Field Ornithology. 72:419–432.

Dunn EH. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin. 114:368–379.

Eikenaar C, Fritzsch A, Kämpfer S, Schmaljohann H. 2016. Migratory restlessness increases and refuelling rate decreases over the spring migration season in Northern Wheatears. Animal Behaviour. 112:75–81.

Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications. 20:398–418.

Fransson T, Jakobsson S, Johansson P, Kullberg C, Lind J, Vallin A. 2001. Magnetic cues trigger extensive refuelling. Nature. 414:35–36.

Goymann W, Spina F, Ferri A, Fusani L. 2010. Body fat influences departure from stopover sites in migratory birds: Evidence from whole-island telemetry. Biology Letters. 6:478–481.

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. 2011. Multimodel inference in ecology and evolution: Challenges and solutions. Journal of Evolutionary Biology. 24:699–711.

Guglielmo CG, Cerasale DJ, Eldermire C. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology. 78:116–125.

Guglielmo CG, O'Hara PD, Williams TD. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living Western Sandpipers. Auk. 119:437–445.

Guo F, Buler JJ, Smolinsky JA, Wilcove DS. 2023. Autumn stopover hotspots and multiscale habitat associations of migratory landbirds in the eastern United States.

Proceedings of the National Academy of Sciences. 120:e2203511120.

Hays QR, Morbey YE, Hobson KA, Lyons JE, Guglielmo CG. 2018. Effects of migration distance and sex on stopover timing and refueling by Wilson's Warblers. Journal of Field Ornithology. 89:149–164.

Hedenström A, Alerstam T. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. Journal of Theoretical Biology. 189:227–234.

Hobson KA, Kardynal KJ. 2015. Western Veeries use an eastern shortest-distance pathway: New insights to migration routes and phenology using light-level geolocators. Auk. 132:540–550.

Hobson KA, Wassenaar LI. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia. 109:142–148.

Hoh CM, Pagano SS, Norment CJ. 2018. Spatial variation in White-throated Sparrow (*Zonotrichia albicollis*) refueling rate near a migratory barrier. Wilson Journal of Ornithology. 130:891–901.

Jenni-Eiermann S, Jenni L. 1991. Metabolic responses to flight and fasting in night-migrating passerines. Journal of Comparative Physiology B. 161:465–474.

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. Journal of Field Ornithology. 64:246–255.

Kelly JF, Atudorei V, Sharp ZD, Finch DM. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia. 130:216–221.

Kirsch EM, Heglund PJ, Gray BR, McKann P. 2013. Songbird use of floodplain and upland forests along the upper Mississippi River corridor during spring migration. Condor. 115:115–130.

Kokko H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology. 68:940–950.

Ktitorov P, Tsvey A, Mukhin A. 2010. The good and the bad stopover: Behaviours of migrant Reed Warblers at two contrasting sites. Behavioral Ecology and Sociobiology. 64:1135–1143.

Lindström Å, Hasselquist D, Bensch S, Grahn M. 1990. Asymmetric contests over resources for survival and migration: A field experiment with Bluethroats. Animal Behaviour. 40:453–461.

Litwin T, Lloyd-Evans T. 2006. The Silvio O. Conte National Fish and Wildlife Refuge Neotropical Migrant Bird Stopover Habitat Survey. Northampton (MA): Smith College [cited 3 Feb 2022]. www.science.smith.edu/stopoverbirds/index.html

Liu M, Swanson DL. 2014. Stress physiology of migrant birds during stopover in natural and anthropogenic woodland habitats of the Northern Prairie region. Conservation Physiology. 2:1–14.

Liu M, Swanson DL. 2015. Stopover duration, movement patterns and temporary home ranges of fall migrant Yellow-rumped Warblers *Setophaga coronata* in native and anthropogenic woodlands of the Northern Prairie region, USA. Journal of Avian Biology. 46:452–461.

Maggini I, Spina F, Voigt CC, Ferri A, Bairlein F. 2013. Differential migration and body condition in Northern Wheatears (*Oenanthe oenanthe*) at a Mediterranean spring stopover site. Journal of Ornithology. 154:321–328.

Martin AC, Zim HS, Nelson AL. 1951. American wildlife and plants: A guide to wildlife food habits. New York (NY): Dover Publications Inc.

Matthews SN, Rodewald PG. 2010. Movement behaviour of a forest songbird in an urbanized landscape: The relative importance of patch-level effects and body condition during migratory stopover. Landscape Ecology. 25:955–965.

Mehlman DW, Mabey SE, Ewert DN, Duncan C, Abel B, et al. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. Auk. 122:1281–1290.

Moore FR. 2018. Biology of landbird migrants: A stopover perspective. Wilson Journal of Ornithology. 130:1–12.

Morris SR, Glasgow JL. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin. 113:202–210.

Müller F, Eikenaar C, Crysler ZJ, Taylor PD, Schmaljohann H. 2018. Nocturnal departure timing in songbirds facing distinct migratory challenges. Journal of Animal Ecology. 87:1102–1115.

Nilsson C, Klaassen RHG, Alerstam T. 2013. Differences in speed and duration of bird migration between spring and autumn. American Naturalist. 181:837–845.

Norris DR, Taylor CM. 2006. Predicting the consequences of carry-over effects for migratory populations. Biology Letters. 2:148–151.

Nussbaumer R, Schmid B, Bauer S, Liechti F. 2022. Favorable winds speed up bird migration in spring but not in autumn. Ecology and Evolution. 12(8):e9146.

Oberkircher MC, Pagano SS. 2018. Seasonal variation in chronic stress and energetic condition in Gray Catbirds (*Dumetella carolinensis*) and Song Sparrows (*Melospiza melodia*). Auk. 135:83–90.

Ogden LJE, Martin K, Williams TD. 2013. Elevational differences in estimated fattening rates suggest that high-elevation sites are high-quality habitats for fall migrants. Auk. 130:98–106.

Parrish JD. 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. Condor. 99:681–697.

Paxton KL, Moore FR. 2017. Connecting the dots: Stopover strategies of an intercontinental migratory songbird in the context of the annual cycle. Ecology and Evolution. 7:6716–6728.

Place AR, Stiles EW. 1992. Living off the wax of the land: Bayberries and Yellow-rumped Warblers. Auk. 109:334–345.

Powell LL, Ames EM, Wright JR, Matthiopoulos J, Marra PP. 2021. Interspecific competition between resident

and wintering birds: Experimental evidence and consequences of coexistence. Ecology. 102:e03208.

Pyle P. 1997. Identification guide to North American birds. Part 1. Bolinas (CA): Slate Creek Press.

R Core Team. 2019. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.r-project.org/

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, et al. 2019. Decline of the North American avifauna. Science. 366:120–124.

Schaub M, Jenni L. 2001. Variation of fuelling rates among sites, days, and individuals in migrating passerine birds. Functional Ecology. 15:584–594.

Schmaljohann H, Fox JW, Bairlein F. 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. Animal Behaviour. 84:623–640.

Schmaljohann H, Meier C, Arlt D, Bairlein F, van Oosten H, et al. 2016. Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. Behavioral Ecology. 27:321–331.

Seaman DAA, Guglielmo CG, Elner RW, Williams TD. 2006. Landscape-scale physiology: Site differences in refueling rates indicated by plasma metabolite analysis in free-living migratory sandpipers. Auk. 123:563–574.

Seewagen CL, Guglielmo CG, Morbey YE. 2013. Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behavioral Ecology. 24:634–642.

Seewagen CL, Sheppard CD, Slayton EJ, Guglielmo CG. 2011. Plasma metabolites and mass changes of migratory landbirds indicate adequate stopover refueling in a heavily urbanized landscape. Condor. 113:284–297.

Slager DL, Rodewald PG, Heglund PJ. 2015. Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). Behavioral Ecology and Sociobiology. 69:1809–1819.

Smetzer JR, King DI. 2020. Intrinsic markers reveal breeding origin and geographically-structured migration timing of two songbird species at a coastal stopover site. Animal Migration. 7:42–51.

Smith AD, McWilliams SR. 2014. What to do when stopping over: Behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behavioral Ecology. 25:1423–1435.

Smith RJ, Moore FR. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia. 134:325–331.

Smith SB. 2013. A physiological assessment of seasonal differences in spring and autumn migration stopover at Braddock Bay, Lake Ontario. Condor. 115:273–279.

Smith SB, McWilliams SR. 2010. Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. Auk. 127:108–118.

Smith SB, Miller AC, Merchant CR, Sankoh AF. 2015. Local site variation in stopover physiology of migrating songbirds near the south shore of Lake Ontario is linked to fruit availability and quality. Conservation Physiology. 3:1–14.

Smolinsky JA, Diehl RH, Radzio TA, Delaney DK, Moore FR. 2013. Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. Behavioral Ecology and Sociobiology. 67: 2041–2051.

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, et al. 2009. Tracking long-distance songbird migration by using geolocators. Science. 323:896.

Symonds MRE, Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology. 65: 13–21.

Tatten JM. 2021. Factors influencing stopover and movement of migratory songbirds within the Silvio O. Conte National Fish and Wildlife Refuge [master's thesis]. Amherst (MA): University of Massachusetts, Amherst.

Terrill SB, Ohmart RD. 1984. Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). Auk. 101:427–438.

Vanderhoff EN, Eason PK. 2008. Comparisons between juvenile and adult American Robins foraging for mulberry fruit. Wilson Journal of Ornithology. 120:209–213.

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH. 2003. Costs of migration in free-flying songbirds. Nature. 423:704.

Williams TC, Williams JM, Williams PG, Stokstad P. 2001. Bird migration through a mountain pass studied with high resolution radar, ceilometers, and census. Auk. 118:389–403.

Woodworth BK, Francis CM, Taylor PD. 2014. Inland flights of young Red-eyed Vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. Journal of Avian Biology. 45:387–395.

Yong W, Moore FR. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk. 114:263–278.

Zajac RM, Cerasale DJ, Guglielmo CG. 2006. The rapid response of plasma metabolites to changes in feeding rate in a small passerine *Wilsonia pusilla*. Journal of Avian Biology. 37:405–408.