



# The effects of diet-shifting from invertebrates towards fruit on the condition of autumn-migrant *Catharus* thrushes

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## Abstract

Migration is an energetically challenging and risky life history stage for many animals, but could be supported by dietary choices *en route*, which may create opportunities to improve body and physiological condition. However, proposed benefits of diet shifts, such as between seasonally available invertebrates and fruits, have received limited investigation in free-living animals. We quantified diet composition and magnitude of autumn diet shifts over two time periods in two closely-related species of migratory songbirds on stopover in the northeastern U.S. (Swainson's thrush [*Catharus ustulatus*], long-distance migrant,  $N=83$ ; hermit thrush [*C. guttatus*], short-distance migrant,  $N=79$ ) and used piecewise structural equation models to evaluate the relationships among (1) migration timing, (2) dietary behavior, and (3) morphometric and physiological condition indices. Tissue isotope composition indicated that both species shifted towards greater fruit consumption. Larger shifts in recent weeks corresponded to higher body condition in Swainson's, but not hermit thrushes, and condition was more heavily influenced by capture date in Swainson's thrushes. Presence of "high-antioxidant" fruits in fecal samples was unrelated to condition in Swainson's thrushes and negatively related to multiple condition indices in hermit thrushes, possibly indicating the value of fruits during migration is related more to their energy and/or macronutrient content than antioxidant content. Our results suggest that increased frugivory during autumn migration can support condition, but those benefits might depend on migration strategy: a longer-distance, more capital-dependent migration strategy could require stricter regulation of body condition aided by increased fruit consumption.

**Keywords** Stopover · Songbird · Seasonal frugivory · Antioxidants · Stable isotope analysis

## Introduction

For many animals, migration is an energetically intensive life history stage that requires extended bouts of activity absent from other parts of their annual cycle (Dingle 2014). Although migration can provide multiple benefits (e.g., increased resource abundance), it can also be a major source of mortality (Rockwell et al. 2017), and so there is substantial pressure to prepare for these challenges as

effectively as possible. Preparation for migration very often involves improving body condition through the substantial accumulation of fat and muscle, which is used to fuel and perform long-distance movements (Evans et al. 1992; Alerstam 2011). Not only is body condition a key determinant of survival during migration, such as when crossing ecological barriers (Ward et al. 2018), it can also have numerous non-lethal consequences including delaying migratory departures and arrivals or reducing subsequent reproductive output (Smith and Moore 2003; Cooper et al. 2015). Thus, understanding the factors that determine body condition is central to the study of migration and the conservation of migratory species.

Building muscle and fuel stores in preparation for migration requires the input of external energy and nutrients, meaning that body condition is closely linked to diet. Although certain diet items, such as fruits and other immobile foods, may support condition by limiting foraging costs (Vanderhoff and Eason 2007; Vissoto et al. 2019), one of

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the most important links between diet and condition is the nutritional quality of diet items (Bairlein 1996, 2004; Smith and McWilliams 2010). The nutritional value of fruits may be particularly relevant to migration, as seasonally available diet items potentially contain high concentrations of carbohydrates (Guglielmo et al. 2017), fats (Smith et al. 2015), or anthocyanins (hydrophilic phenolic compounds that have strong antioxidant properties; Halliwell and Gutteridge 2007). Each of these nutrients may support increases in body condition: carbohydrates and fats are accessible and dense energy sources (Klasing 1998), whereas antioxidants relieve tradeoffs in the allocation of energy and other limited resources towards maintenance, growth, and recovery from oxidative damage associated with aerobic metabolism (Beaulieu and Schaefer 2013; Cooper-Mullin and McWilliams 2016; Eikenaar et al. 2017). Migratory songbirds are an excellent system to study the relationships between migratory and nutritional behavior (particularly regarding fruit), because (1) there is a well-documented shift from primarily consuming arthropods during the breeding season to including greater amounts of fruits and seeds during autumn migration among many species in the northern hemisphere (Parrish 1997; Gagnon and Hobson 2009) and (2) there is evidence that songbirds perceive and select foods based on anthocyanins, carbohydrates, and fats (Marshall et al. 2016).

Given the potential for links between fruit consumption and migratory success, a range of previous studies have addressed this topic in songbirds. One approach to investigating the influence of fruit on body condition has involved feeding captive birds diets with varying proportions of fruit, and generally revealed positive relationships between proportion of fruit and condition (Bairlein 2004; Nwaogu et al. 2020; but see Parrish 2000; Pierce and McWilliams 2004). Many studies have also investigated this question in the wild, finding, for example, positive associations between fruit abundance and migrant presence (Parrish 2000; Tietz and Johnson 2007), higher body condition in areas with more fruit resources available (Oguchi et al. 2017; Rojas et al. 2019), and species-level correlations between fruit consumption and condition (Parrish 1997). Finally, studies that reconstructed diets of individual birds have sometimes (González-Varo et al. 2022), but not always (Vitz and Rodewald 2012; McKinnon et al. 2017), found positive relationships between fruit consumption and body condition. While these and related studies have made considerable progress in advancing our understanding of the patterns and consequences of seasonal frugivory, they have nevertheless been limited in their ability to provide detailed insights into the timing and scope of diet shifts, and the influence of those factors on condition. Variation in the timing of diet shifts may accelerate or delay preparation for migration and produce downstream impacts on the overall pace and probability

of successfully completing migratory journeys (Cooper et al. 2015). Accordingly, investigating the timing of dietary behavior and its consequences addresses a key gap in current knowledge of the relationships between nutrition and migration.

There is a wide range of physiological adjustments songbirds can make in preparation for migration in addition to increasing body condition. For example, long-distance flight requires high levels of aerobic output and correspondingly high levels of oxygen transport (Butler and Woakes 1990; Yap et al. 2018). This demand can be supported by increasing the cellular fraction of blood (hematocrit), which has been observed in a variety of migratory bird species (Fair et al. 2007). Similarly, the content of oxygen-binding hemoglobin within red blood cells can be modulated (Calbet et al. 2006), which has also been observed in migratory birds (Minias et al. 2014). Beyond adjustments to aerobic metabolism, migration often exposes songbirds to novel stressors including pathogens and parasites (Bush and Clayton 2018; Hegemann et al. 2018), predators (Alerstam 2011; Samraoui et al. 2022), and inclement weather (La Sorte et al. 2015; Ward et al. 2018). The negative effects of these factors may be ameliorated by physiological responses such as changes to the immune system (e.g. heterophil/lymphocyte ratio; Buehler et al. 2010; Matson et al. 2012) or corticosterone-mediated stress responses (Müller et al. 2011; Ramos et al. 2018). Although some studies have investigated such aspects of physiological condition in the context of diet composition (Pryke et al. 2012; Koch et al. 2018; Oberkircher and Pagano 2018), few have done so in a migratory context and, like body condition, the relationships between physiological condition and the timing of diet shifts are largely unknown.

We investigated the relationships between the timing and magnitude of diet shifts, as well as recent diet composition, and body and physiological condition in two closely-related songbird species, with the primary goal of determining whether shifts towards higher fruit consumption during fall migration were related to condition and whether those relationships were contingent on the recency of the shift. Given the potential benefits of fruits as a source of antioxidants for birds, we also sought to determine whether condition was related to consumption of the subset of fruit species with higher quantities of antioxidants. We expected that our results would show a positive relationship between both shifts towards fruits and overall fruit consumption and condition, consistent with previous findings, and we expected that shifts would be more beneficial shortly before migratory flight, such as on stopovers. We also expected that consumption of high-antioxidant fruits would support improved condition, possibly via the mechanisms of reduced damage or faster recovery from migratory flight.

## Materials and methods

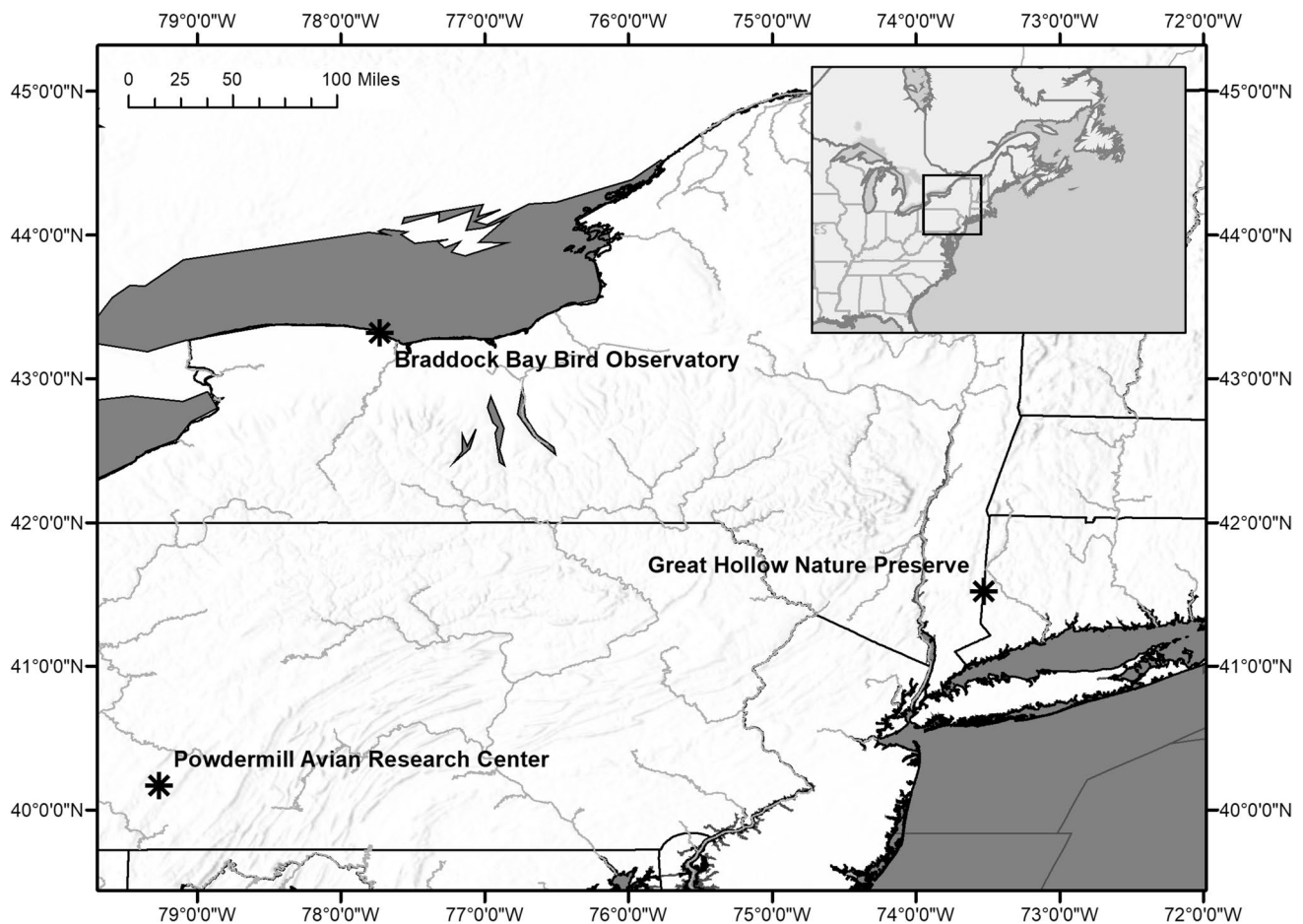
### Study sites

We collected samples from birds at three sites in the north-eastern United States along the eastern migratory flyway (Fig. 1): Braddock Bay Bird Observatory in Rochester, NY (43.3222 N, 77.7166 W), Great Hollow Nature Preserve and Ecological Research Center in New Fairfield, CT (41.5105 N, 73.5242 W), and Powdermill Avian Research Center in Rector, PA (40.1632 N, 79.2668 W). All three sites are dominated by mature northern hardwood forests (Ferree and Anderson 2013), with the landscape surrounding Great Hollow and Powdermill including some patches of early successional, former agricultural land. Corresponding to their shared forest community type, all of our study sites had very similar complements of fruiting plants, including high quality natives such as dogwood (*Cornus* spp.) and viburnum (*Viburnum* spp.), as well as

similar complements of non-native shrubs such as buckthorn (*Rhamnus* spp.), bush honeysuckle (*Lonicera* spp.), and barberry (*Berberis* spp.) (Utech 1999; Smith et al. 2015).

### Study species

We investigated the impacts of diet shifts in two closely related species of *Catharus* thrushes that have both been regularly used in studies on avian migration and stopover ecology: Swainson's thrush (*Catharus ustulatus*, SWTH) and hermit thrush (*C. guttatus*, HETH). Both species are medium-sized (~30 g) songbirds that primarily use interior forest habitats and consume omnivorous diets (Strong et al. 2005; Carter et al. 2021). Swainson's thrushes are long-distance migrants, breeding in boreal and high elevation hardwood and spruce/fir forests throughout Canada and parts of the northern United States and wintering in Central and South America (Mack and Yong 2020). Hermit thrushes, in contrast, are typically shorter-distance migrants, breeding in



**Fig. 1** Swainson's thrush and hermit thrush sampling locations at Braddock Bay Bird Observatory (Rochester, NY), Great Hollow Nature Preserve and Ecological Research Center (New Fairfield, CT), and Powdermill Avian Research Center (Rector, PA), September–November, 2021

northern hardwood and coniferous forests of North America and wintering in the southern United States and northern parts of Central America (Dellinger et al. 2020). Swainson's thrushes do not breed at any of our study sites, but there are records of hermit thrushes breeding at both Great Hollow and Powdermill, which led us to exclude several individuals captured at Powdermill before October 1 as potential non-migrants (see below). Both species molt flight feathers in the post-breeding period prior to migration, with the majority of individuals completing molt before mid-September for Swainson's thrushes (Mack and Yong 2020) and the end of September for hermit thrushes (Dellinger et al. 2020).

### Bird capture and sample collection

We collected samples from birds captured between September 4th and November 10th 2021 as part of normal fall banding operations at Powdermill and Braddock Bay, and project-specific efforts at Great Hollow. Birds were captured in mist nets opened from 15 to 30 min before to approximately 5–6 h after sunrise, as permitted by weather. Following extraction from nets, we placed each bird in a paper bag lined with a plastic tray and a rubberized hardware cloth grate to facilitate the collection of fecal samples (Knutie and Gotanda 2018). Birds remained in the paper bag until they were processed (~5–30 min), at which time we collected the following information and samples: age (hatch-year, after-hatch-year), weight (to the nearest 0.1 g), unflattened wing chord (to the nearest mm), total tarsus length (to the nearest 0.1 mm), fat score (0–7 scale, modified from Kaiser [1993] to have a maximum score of seven rather than eight), ~100  $\mu$ L of blood collected into heparinized capillary tubes from the brachial vein following puncture with a 26.5 or 27.5 gauge needle, and a single R1 (first from center) tail feather, typically the first tail feathers to be molted in passerines (Pyle 1997). After we fitted birds with an aluminum United States Geological Survey numbered band and released them we scraped any fecal liquids and solids left on the plastic tray into a 2 mL microcentrifuge tube and stored fecal and blood samples on ice until they could be returned to the lab (no more than 5 h). Feather samples were stored in paper envelopes or plastic sandwich bags until analysis. In total, we collected matched feather, blood, and fecal samples from 41 individuals at Great Hollow (SWTH,  $N=23$ ; HETH,  $N=21$ ), 62 individuals at Braddock Bay (SWTH,  $N=35$ ; HETH,  $N=27$ ), and 79 individuals at Powdermill (SWTH:  $N=46$ ; HETH,  $N=33$ ).

### Sample processing and hematology

Upon returning to the lab, fecal samples were stored at  $-20$  °C, while feather samples were kept at room temperature in a box to minimize exposure to light. When

sample volume allowed at Great Hollow and Braddock Bay, we used ~15  $\mu$ L of whole blood to prepare smears on glass microscope slides and an additional 8  $\mu$ L to measure hemoglobin (mmol/L) with a HemoPoint H2 point-of-care device (Stanbio Laboratory, Boerne, TX, USA), which we also used to estimate hematocrit (%) at Braddock Bay. At all sites, the remaining blood was centrifuged at 12,000  $g$  for 10 min to separate plasma and red blood cells (RBC) fractions, and at Great Hollow we used fractionated capillary tubes to estimate hematocrit. We transferred blood fractions to cryogenic tubes and then stored them at  $-80$  °C until analysis. Frozen blood and fecal samples collected at Braddock Bay and Powdermill were temporarily stored on site, before being shipped overnight to Great Hollow in insulated containers filled with dry ice and ice packs frozen to  $-80$  °C, respectively.

Air-dried blood smears were fixed with methanol and then stained using a Quick III Wright-Giemsa solution kit (VWR International, Radnor, PA, USA) or a Fisher Healthcare PROTOCOL Hema 3 Wright-Giemsa manual staining system (Fisher Scientific). We subsequently used smears to estimate heterophil/lymphocyte ratio by viewing slides under oil immersion at 1000 $\times$  magnification. Due to differences in staff time and resources between study sites, at Braddock Bay this involved counting leukocytes until 100 total were identified, and then calculating heterophil/lymphocyte ratio (Oberkircher and Pagano 2018), whereas at Great Hollow, the heterophil/lymphocyte ratio was calculated from total counts of cells identified in 100 randomly placed fields of view along the fringe of the smear. Estimated heterophil/lymphocyte ratio was positively correlated between methods in a random subset of smears assessed using both approaches ( $r_{18}=0.64$ ,  $P=0.004$ ). We obtained measurements of heterophil/lymphocyte ratio for a total of 86 individuals (SWTH,  $N=42$ ; HETH,  $N=44$ ), hematocrit for a total of 72 individuals (SWTH,  $N=38$ ; HETH,  $N=34$ ), and hemoglobin for a total of 86 individuals (SWTH,  $N=45$ ; HETH,  $N=41$ ).

### Fecal analysis

We dissected fecal samples in order to produce a quantitative estimate of the composition of the recent diet of our study animals. Although this method can be biased towards more durable diet items (e.g., arthropod exoskeletons, fruit skins), its results are usually qualitatively similar to estimates produced by other methods and is generally considered a valuable tool in trophic ecology (Nielsen et al. 2018; Carter et al. 2021). Each sample was thawed and spread into a thin, translucent layer over a 2 mm  $\times$  2 mm reference grid, with clumped materials untangled and solids diluted with distilled water as necessary. We then viewed samples under a dissecting microscope and identified fruit flesh, skin, and seeds through comparison to reference samples collected at



Great Hollow and Braddock Bay and Kirkbride et al. (2000). Durable fragments of arthropod exoskeletons were identified following Marshall (2006). We estimated relative diet proportions of fruits and arthropods in a given sample by counting the number of grid cells containing material from each of those sources and calculating their respective percent of total occupied cells. We also classified each sample as either containing or not containing “high-antioxidant” fruit based on the unambiguous positive detection of flesh, skin, or seeds from a fruit with a total phenolic concentration > 1000 mg/L gallic acid equivalents, a sufficiently high cutoff to distinguish fruits from the cluster at or below median phenolic concentration of local taxa (Sood 2015; Marinaş et al. 2021).

### Stable isotope analysis

We used stable isotope analysis of tissues with different turnover times to construct a timeline of diet composition and corresponding shifts in diet for individual thrushes. Tissues differ in the rate at which they incorporate dietary isotopes and the corresponding time period over which diet signals are integrated, meaning that tissues with slower turnover rates can provide information about dietary behavior further back in an animal’s history (Vander Zanden et al. 2015; Carter et al. 2019). Accordingly, we selected plasma to represent diet within the week prior to collection (Hobson and Clark 1993; Lourenço et al. 2015), RBC to represent diet approximately 2–3 weeks prior to collection (Hobson and Clark 1993; Bauchinger and McWilliams 2009; Lourenço et al. 2015), and feathers, an inert tissue after they are grown, to represent post-breeding diet up to several months prior to collection (Chamberlain et al. 1997; Gómez et al. 2018). To prepare plasma and RBC samples, we first defrosted and then pipetted 10 and 5  $\mu\text{L}$  aliquots, respectively, into weighed tin capsules. We then dried samples for 24 h in a 55 °C oven before reweighing and crimping capsules. For feather samples, we first removed recently-added preen oils by washing samples with petroleum ether (Hobson and Clark 1992; Carter et al. 2021), allowed them to dry, and then cut small ( $\sim 1 \text{ mm}^2$ ) pieces from the tip of the feather, which we then weighed and sealed into tin capsules. All weights for stable isotope analysis were measured to the nearest 0.01 mg.

We sent plasma, RBC, and feather samples to the University of New Mexico Center for Stable Isotopes for analysis of carbon and nitrogen elemental and isotopic composition, which took place in June 2022. Sample composition was measured using a Costech 4010 elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) coupled with a Thermo Scientific Delta V mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA) via a ConFlo IV interface. Isotope values are presented in delta per mille ( $\delta\text{‰}$ ) notation, relative to International

Atomic Energy Agency standards Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N (AIR) for nitrogen. Unknown samples were evaluated by comparison with a curve of regularly validated internal standards, including periodically interspersed casein standards, which had across-run standard deviations of 0.05 $\text{‰}$  for carbon and 0.03 $\text{‰}$  for nitrogen.

### Estimating diet shifts

To investigate the dietary behavior of thrushes, we quantified the magnitude of shifts between tissues in isotope values corrected to represent diet composition. We used literature diet-tissue discrimination factors collated by Ruhl et al. (2020) from Hobson and Bairlein (2003), Pearson et al. (2003), and Evans Ogden et al. (2004) to correct isotope values to represent diet. The values of carbon discrimination factors ( $\Delta^{13}\text{C}$ ) were 2.7 $\text{‰}$  for feathers, 2.0 $\text{‰}$  for RBC, and 0.5 $\text{‰}$  for plasma, whereas the values of nitrogen discrimination factors ( $\Delta^{15}\text{N}$ ) were 4.0 $\text{‰}$  for feathers, 3.0 $\text{‰}$  for RBC, and 3.0 $\text{‰}$  for plasma (Ruhl et al. 2020). After applying discrimination factors, we calculated the magnitude of diet shifts for individuals as the Euclidean distance between tissues in carbon–nitrogen isotope space. With three tissues, we considered diet shifts during two time periods: an early (less recent) shift represented by the distance between feather and RBC samples and a late (more recent) shift represented by the distance between RBC and plasma samples. Although there are multiple sources of variation in the isotope composition of diet items, nitrogen isotope ratios are reliably related to trophic level (Hobson and Clark 1992; Carter et al. 2019). We compared diet shifts between thrush species using linear mixed effects models with site as a random intercept and degrees of freedom estimated with a Satterthwaite approximation.

### Condition indices

We used fat score and size-corrected body mass to measure body condition. Although related, these measures provide complementary information, with fat score more directly indicative of fuel stores (Herremans et al. 2009) and size-corrected body mass representing a more holistic measure that includes lean mass. We calculated size-corrected body mass by conducting a principal component analysis of unflattened wing chord, tarsus length, and body mass (Hays et al. 2018; Frauendorf et al. 2021). The first component represented structural size and accounted for 60.8% of the total variance in the dataset. Therefore, we extracted scores for the second component (PC2; 27.1% of total variance) as our condition index for each individual. We used our measures of hemoglobin, hematocrit, and heterophil/lymphocyte ratio as indices of physiological condition, reflective of aerobic

capacity (Fair et al. 2007; Minias 2015) and chronic stress (Buehler et al. 2010; Matson et al. 2012), respectively. After confirming that model assumptions were met, we compared condition indices between thrush species using linear mixed effects models with site as a random intercept and degrees of freedom estimated with a Satterthwaite approximation.

### Structural equation models

We used piecewise structural equation models via the *psem* function in the ‘piecewiseSEM’ package (Lefcheck 2016) to quantify the relationships between timing, diet composition, and thrush condition. This approach has been recommended for complex ecological and physiological systems (Cohen et al. 2012) and has been previously used to investigate the consequences of songbird diets (DeMoranville et al. 2020; Nwaogu et al. 2020). As our foremost objective was to evaluate the impact of diet on condition, we did not consider multiple causal models, but instead focused on a single, relatively saturated model and judged the importance of variables based on their involvement in significant relationships within that model.

Our model contained three levels: timing variables, diet variables, and condition variables. Timing variables included date of capture (Julian date) and the time (hours after sunrise) at which a given bird was captured and sampled. Diet variables included the magnitude of early and late diet shifts, proportion of fruit in fecal samples, and the presence of high-antioxidant fruits. Condition variables included size-corrected body mass (PC2), fat score, hematocrit, hemoglobin, and heterophil/lymphocyte ratio. Our model included all timing and diet variables as predictors of each condition variable as well as capture date as a predictor for all diet variables and capture time as a predictor for proportion of fruit and “high-antioxidant” fruit presence. We did not include links between capture time and either early or late shift magnitude as both of these variables would be largely set prior to the day of capture and therefore unaffected by timing. Among the diet variables we considered links between variables adjacent in time (early shift magnitude and late shift magnitude, late shift magnitude and proportion of fruit, proportion of fruit and high-antioxidant fruit presence) but presumed that variables were otherwise independent.

Piecewise SEM models are constructed as a series of linear models within a glm framework (Lefcheck 2016). Accordingly, we formatted all models for use with the *lmer* or *glmer* function from the package ‘lme4’, as appropriate, and included site as a random intercept in each model. We used this random effect to account for potential variation among sites (e.g., differences in fruit availability or competition for fruit resources) that we were unable to quantify and for which we had no clear directional predictions. Age

was not related to any condition variable in preliminary analyses and therefore excluded from subsequent SEMs. Despite the flexibility of the glm framework, the heavy right skew in fat score and heterophil lymphocyte ratio prevented us from being able to meet the assumptions of the models and estimate standardized coefficients for models including those variables. We therefore applied a log + 1 transformation to fat score and a log transformation to heterophil/lymphocyte ratio to normalize their residuals and conducted analyses involving them with the *lmer* function. We analyzed SEMs separately for SWTH and HETH to evaluate whether the effect of dietary behavior on condition differed between long-distance and short-distance migrants. Due to the inconsistent sample sizes for our condition variables, we also fitted separate SEMs for size-corrected body mass, fat score, hematocrit, hemoglobin, and heterophil/lymphocyte ratio. Relationships among timing and diet variables were almost entirely consistent among models for different condition variables and so in the results we present estimates from the models with the largest sample sizes (size-corrected body mass and fat score). Global goodness-of-fit tests using a Fisher’s *C* statistic aggregated from tests of directed separation indicated that none of our models were missing significant relationships among variables (all  $P > 0.106$ ). All analyses were conducted with the R programming language (version 4.1.3; R Core Team, Vienna, Austria) and used an alpha level of 0.05.

## Results

### Thrush captures and condition

The migration of SWTH peaked approximately 1 month earlier than for HETH (Table 1, Fig. S1), with a median capture date of September 17th for SWTH (Julian date = 260) versus October 21st for HETH (Julian date = 294). SWTH also tended to be captured earlier in the day than HETH, with a median capture time 1.5 h after sunrise as opposed to 2.5 h after sunrise (Table 1, Fig. S1). At capture, average body condition was somewhat lower for SWTH than HETH as indicated by size-corrected body mass (PC2;  $T_{157.9} = -5.49$ ,  $P < 0.001$ ) and fat score ( $T_{160} = -2.03$ ,  $P = 0.044$ ), but the range of values for SWTH fully encompassed those for HETH in both metrics (Table 1, Fig. S2). By contrast, physiological condition was more consistent between individual SWTH and HETH, with near complete overlap in hemoglobin and hematocrit and minor separation between species in heterophil/lymphocyte ratio (all  $P > 0.22$ ; Table 1, Fig. S2).

**Table 1** Timing and condition of migrating Swainson’s (SWTH) and hermit (HETH) thrushes

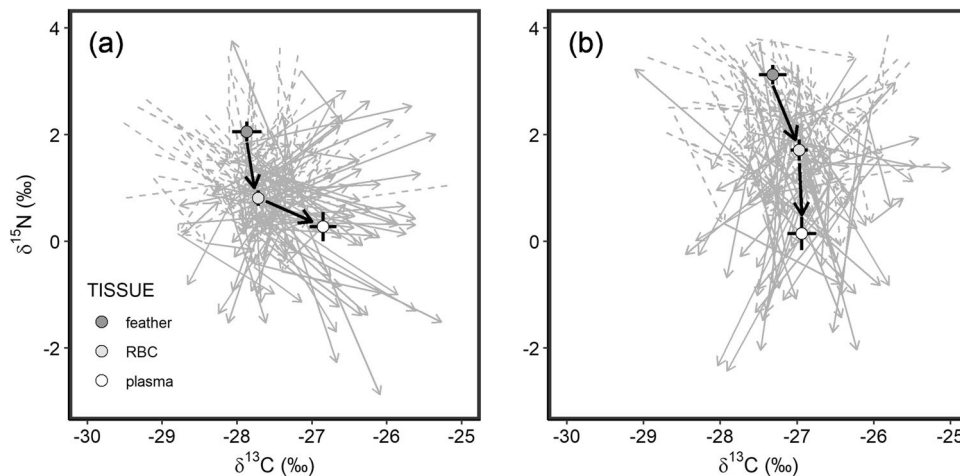
	HETH			SWTH		
	<i>N</i>	<i>Median</i>	<i>Range</i>	<i>N</i>	<i>Median</i>	<i>Range</i>
<i>Timing variables</i>						
Capture date (Julian date)	79	294 (Oct 21)	271–314 (Sep 28–Nov 10)	83	260 (Sep 17)	247–288 (Sep 4–Oct 15)
Capture time (hours after sunrise)	79	2.5	0.1–6.0	83	1.5	0.1–5.0
<i>Condition variables</i>						
Size-corrected body mass (PC2)	79	1.1 ± 2.1	–4.0–6.6	83	–1.1 ± 3.0	–6.2–18.7
Fat score (0–7 scale)	79	1.4 ± 0.9	0–4	83	1.2 ± 1.1	0–7
Hemoglobin (mmol/L)	44	10.7 ± 1.1	6.8–13.2	42	10.5 ± 1.5	7.4–13.7
Hematocrit (%)	34	49.5 ± 3.0	42.0–54.8	38	49.5 ± 3.1	40.3–55.8
Heterophil/lymphocyte ratio	41	0.73 ± 0.81	0.04–3.45	45	0.51 ± 0.64	0.03–3.06

Study animals were captured in fall 2021 during stopover in Rochester, NY, New Fairfield, CT, and Rector, PA

**Diet shifts and recent diet composition**

The position of thrush tissues in isotope space differed between SWTH and HETH, with SWTH feathers and RBC generally more depleted in <sup>13</sup>C and <sup>15</sup>N than those tissues in HETH (Fig. 2). Despite these differences, the separation of corrected isotope values among tissues indicated that SWTH and HETH made substantial changes in their diet over time, with both species shifting towards lower tropic-level, plant-derived foods. The magnitude of the late diet shift (RBC to plasma) was greater in HETH than SWTH ( $T_{158,3} = 2.65, P = 0.009$ ), but the magnitude of the early diet shift (feather to RBC) was consistent between species ( $T_{158,1} = 1.00, P = 0.320$ ) and the overall scale of early and late shifts was similar (Fig. 2).

Combined, we detected nine orders of arthropods in the feces of SWTH and HETH, including (in order of frequency) Hymenoptera, Araneae, Coleoptera, Orthoptera, Diptera, Lepidoptera, Acari, Dermaptera, and Hemiptera. Meanwhile, we detected thirteen genera of fruits in the feces of SWTH and HETH: *Berberis, Ilex, Vitis, Viburnum, Rosa, Elaeagnus, Cornus, Lonicera, Celastrus, Rhamnus, Phytolacca, Euonymus, and Lindera*, in descending order of frequency (Table S1). Of these fruit genera, *Ilex, Vitis, Viburnum, Phytolacca, and Rhamnus* met our threshold to be considered “high-antioxidant” fruits. As with diet shifts and physiological condition, relative proportion of fruit in thrush diets was highly consistent between species: fruit remnants made up  $60.5 \pm 35.1\%$  (mean ± SD) of SWTH fecal samples and  $62.3 \pm 31.4\%$  of HETH fecal samples. Fecal samples



**Fig. 2** Isotope values of feathers, red blood cells (RBC), and plasma of migratory Swainson’s thrushes (A) and hermit thrushes (B), respectively representing diet up to several months prior to capture, approximately 2–3 weeks prior to capture, and approximately 1 week prior to capture. Symbols with error bars depict population mean

(± SE) isotope values for each tissue and heavy arrows depict population-level diet shifts. Light arrows depict shifts for individual birds: dashed lines are shifts between feather and RBC (early shift), whereas solid lines are shifts between RBC and plasma (late shift)

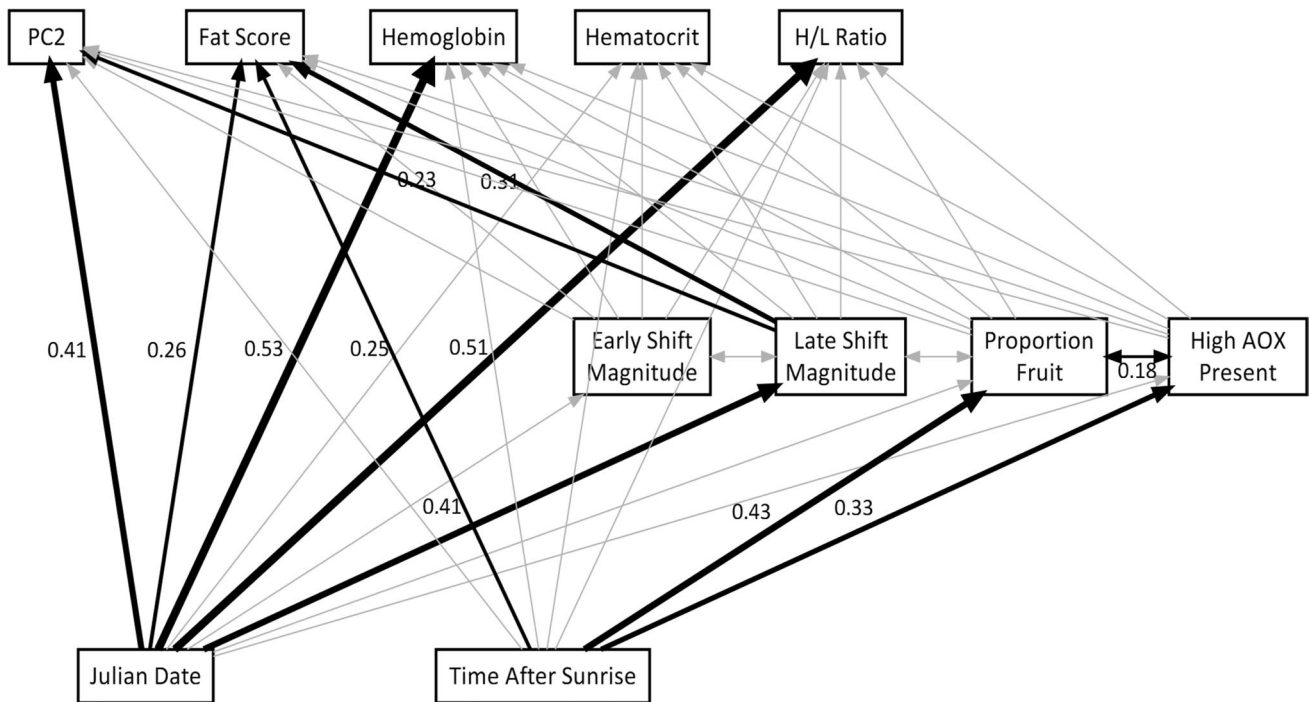
from eight individuals of each species were entirely composed of fruit, while fecal samples from fourteen SWTH and eight HETH were entirely composed of arthropod remnants, and the frequency of different fruit species in fecal samples did not differ between SWTH and HETH ( $X^2_{13} = 7.09$ ,  $P = 0.898$ ). We detected remnants of high-antioxidant fruits in the feces of 46.8% of HETH sampled, but only 33.7% of SWTH ( $X^2_1 = 2.19$ ,  $P = 0.139$ ).

**Relationships among timing, diet, and condition variables**

Our structural equation model indicated that seasonal progression had a strong positive influence on SWTH condition (Fig. 3, Table S2), with significant paths between capture date and size-corrected body mass (standardized coefficient:  $\beta = 0.41$ ,  $P = 0.002$ ), fat score ( $\beta = 0.26$ ,  $P = 0.047$ ), hemoglobin ( $\beta = 0.53$ ,  $P = 0.002$ ), and heterophil/lymphocyte ratio ( $\beta = 0.51$ ,  $P = 0.016$ ). Body condition was also positively impacted by dietary behavior, with size-corrected body mass ( $\beta = 0.23$ ,  $P = 0.038$ ) and fat score ( $\beta = 0.31$ ,  $P = 0.008$ ) significantly increasing

according to the magnitude of late diet shifts. The magnitude of late diet shifts was itself positively influenced by capture date ( $\beta = 0.41$ ,  $P = 0.002$ ). Fat score increased with time after sunrise ( $\beta = 0.25$ ,  $P = 0.046$ ), but this effect was unrelated to the positive influence of time on proportion of fruit in fecal samples ( $\beta = 0.43$ ,  $P = 0.005$ ) and consumption of high-antioxidant fruits ( $\beta = 0.33$ ,  $P = 0.015$ ).

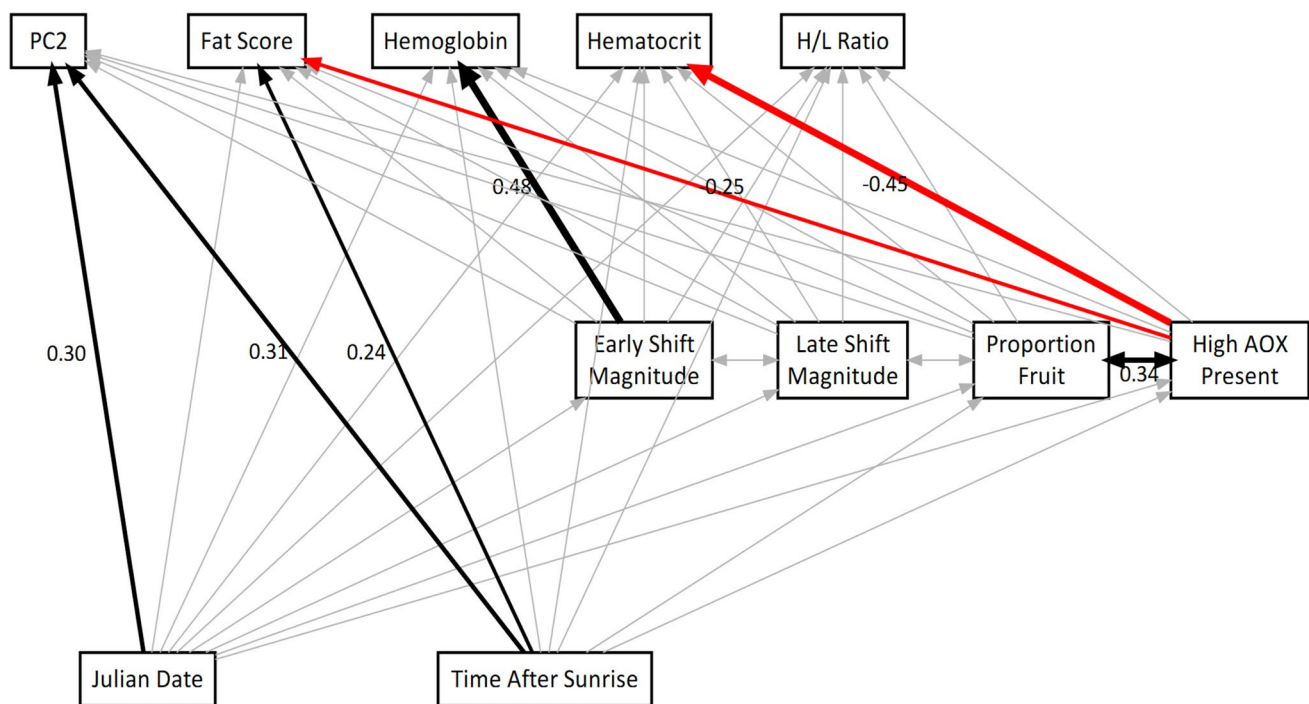
In contrast to SWTH, our structural equation model showed far less influence of seasonal progression on HETH condition (Fig. 4, Table S3), with only a single significant effect of capture date on size-corrected body mass ( $\beta = 0.30$ ,  $P = 0.044$ ). As with SWTH, HETH fat score increased over the course of the morning ( $\beta = 0.24$ ,  $P = 0.038$ ), but unlike SWTH, size-corrected body mass also increased over time ( $\beta = 0.31$ ,  $P = 0.006$ ). Diet shifts did not impact body condition in HETH as in SWTH, but the magnitude of early diet shifts was positively related to HETH physiological condition, in terms of hemoglobin concentrations ( $\beta = 0.48$ ,  $P = 0.011$ ). Both body and physiological condition were affected by recent diet in HETH, as indicated by negative effects of high-antioxidant fruit consumption on fat score ( $\beta = -0.25$ ,  $P = 0.039$ ) and hematocrit ( $\beta = -0.45$ ,  $P = 0.014$ ).



**Fig. 3** Relationships among timing of capture (Julian date, time after sunrise), diet (early shift magnitude, late shift magnitude, proportion fruit, high-antioxidant fruit presence), and condition (size-adjusted body mass [PC2], fat score, hemoglobin, hematocrit, heterophil/lymphocyte ratio) variables in Swainson’s thrushes (*Catharus ustulatus*) during fall migration. Relationships were evaluated with confirmatory

path analysis and numerical values are standardized coefficients for significant relationships. Black lines indicate positive relationships, while grey lines indicate relationships included in the causal model, but found to be non-significant. Double-headed arrows denote correlational relationships





**Fig. 4** Relationships among timing of capture (Julian date, time after sunrise), diet (early shift magnitude, late shift magnitude, proportion fruit, high-antioxidant fruit presence), and condition (size-adjusted body mass [PC2], fat score, hemoglobin, hematocrit, heterophil/lymphocyte ratio) variables in hermit thrushes (*Catharus guttatus*) during fall migration. Relationships were evaluated with confirmatory

path analysis and numerical values are standardized coefficients for significant relationships. Black lines indicate positive relationships and red lines indicate negative relationships, while grey lines indicate relationships included in the causal model, but found to be non-significant. Double-headed arrows denote correlational relationships

## Discussion

Dietary decisions have the potential to greatly influence condition and subsequent performance outcomes for songbirds and other migratory species during migration and beyond, but the individual-level consequences of diet shifts towards fruit have received limited attention in the wild. We combined several methods of diet analysis with multiple morphometric and hematological condition indices to examine the interrelationships among fall frugivory, seasonal progression, and condition in two closely related migratory songbirds. We found that greater shifts from invertebrate- to fruit-based diets in the near-term, but not earlier in a bird's migration history, were positively associated with body condition. Contrary to expectations, though, this pattern was only apparent in the long-distance migrant, Swainson's Thrush, which also exhibited stronger positive relationships between seasonal progression and condition than its short-distance migrant congener, the hermit thrush. Surprisingly, the presence of particularly high-antioxidant fruit species in recent diets had no positive relationship with condition in the long-distance migrant and was actually negatively associated with some measures of condition in the short-distance migrant. Overall, our results demonstrate that shifting diets

to include larger amounts of fruit is beneficial to fall migratory condition in natural contexts, but not universally across species, and likely as a source of energy or macronutrients more so than a source of antioxidants.

## Diet shifts and thrush condition

Consistent with findings of shifts towards plant-based resources by fall-migrant songbirds that may continue throughout the entire migratory period (McKinnon et al. 2017; Gómez et al. 2018), both of our study species exhibited substantial differences between tissues in isotope space that signaled shifts from invertebrates towards fruit (e.g., progressively lower  $\delta^{15}\text{N}$  values). The reliable presence of both early and late shifts in our study demonstrates that individuals continue to adjust their diets over the course of the fall. Ongoing diet shifts throughout the fall may partly be a response by birds to changing resource availability as different fruit species ripen and are consumed (Cullen et al. 2020; Gallinat et al. 2020). Changing fruit availability also may help explain the different trajectories of diet shifts in SWTH and HETH: despite considerable geographic overlap in breeding ranges (Dellinger et al. 2020; Mack and Yong 2020), the breeding and post-fledging, pre-migration habitats

used by SWTH and HETH remain largely segregated by elevation and forest type (Holmes and Robinson 1988). Such spatial segregation creates opportunities for these species to exploit different food resources in the post-fledging and early migratory period before converging into shared stopover habitats during fall migration, consistent with the overlap between SWTH and HETH in plasma isotope values representative of areas where they are known to co-occur.

Although declining arthropod availability throughout the fall migratory period may explain much of the variation in dietary behavior by migratory thrushes, diet shifts may also be the product of active dietary decisions, which could be motivated by the positive effects of these decisions on condition. Seasonal frugivory has long been proposed to be an important strategy for migratory preparation (Bairlein 2004; Smith and McWilliams 2010) and has received support in studies at the landscape (Tietz and Johnson 2007; Oguchi et al. 2017), population (Parrish 1997; González-Varo et al. 2022), and individual (Nwaogu et al. 2020) levels. Consistent with these results, we found that the magnitude of recent diet shifts was positively related to both indices of body condition in SWTH, and was, in fact, the strongest influence on fat score we observed. Thus, our results support the hypothesis that shifting diets from invertebrates towards fruits during fall migration is an effective behavioral mechanism for songbirds to increase their condition, and ultimately improve migratory performance.

Alternately or collectively, there are several related mechanisms by which diet shifts could have this functional effect. The simplest is that feeding on fruits generally involves much lower foraging costs than preying on invertebrates (Vanderhoff and Eason 2007; Vissoto et al. 2019), thereby benefiting overall energy balance. Alternately, life history stages may be associated with different nutritional requirements and diets high in fruit may contain a macronutrient (i.e. carbohydrate, fat, protein) profile better suited for migratory fattening (e.g., high carbohydrate and fat; Langlois and McWilliams 2010). A recent study by Blendinger et al. (2022) demonstrated dietary matching of macronutrient targets in a community of overwintering Swainson's thrushes and other songbirds, which highlights the plausibility of this mechanism for migratory thrushes. Fruits may also be beneficial based on their micronutrient composition, and particularly the inclusion of antioxidant compounds (Beaulieu and Schaefer 2013; Cooper-Mullin and McWilliams 2016). Our study was not designed to effectively distinguish between these possibilities, but the lack of any positive relationship between "high-antioxidant" fruit consumption and condition (see below) does not support the idea that the benefit of shifting diets towards fruits is related to antioxidants. Similarly, the inclusion of fruits as an additional, low-effort energy source suggests that dietary diversity is the most beneficial aspect of diet shifts, which

is somewhat inconsistent with the emphasis on shift magnitude in our study. Accordingly, we conclude that shifting diets towards fruit is a valuable strategy for migratory songbirds to improve body condition and that this effect is most likely due to the macronutrient composition of fruits. Interestingly, the shift positively associated with condition in SWTH involved substantial changes in  $\delta^{13}\text{C}$  values, which are most reliably linked to plant photosynthetic pathway and may suggest that our birds were shifting between plant communities, as well as from invertebrates to fruits, in order to meet macronutrient targets. Such a shift could be related to increasing use of resources from  $\text{C}_4$  grasslands or aquatic resources, both of which are enriched in  $^{13}\text{C}$  (Gannes et al. 1998; Cloern et al. 2002; Carter et al. 2019).

While diet shifts may be an important dietary strategy for migration, we found no influence of early diet shift magnitude on body condition. This may be due to the rapid accumulation and loss of fat and lean mass by songbirds during migration (Jenni and Jenni-Eiermann 1998; McWilliams et al. 2004; Bayly et al. 2021), which likely prevent the accumulation of benefits and make diet shifts most effective as a short-term strategy for birds on limited-duration migration stopovers. It remains possible that diet shifts have longer-term benefits in the post-breeding period prior to the start of migration, but evidence for such positive effects is scarce (Vitz and Rodewald 2012) and their impact would likely be limited in scope.

Somewhat surprisingly, we found few associations between the magnitude of diet shift towards fruits and our hematological condition indices. Previous studies have documented relationships between diet quality and hematocrit and hemoglobin (Fair et al. 2007; Pryke et al. 2012), and matching that expectation we found a positive relationship between early diet shifts and hemoglobin in HETH. This may be best explained by a tradeoff in protein allocation to molt and hemoglobin synthesis (Piersma et al. 1996; Minias et al. 2014), which was mitigated by an earlier molt with a correspondingly larger estimated diet shift. It remains unclear why this might apply to HETH and not to SWTH, but it is possible there was less variation in the timing of molt among SWTH than HETH in our study populations. However, despite reports of positive relationships between diet and hematological variables (as with hemoglobin in our study), the influence of diet quality on songbird hematology has been inconsistent across studies (Fair et al. 2007; Minias 2015) and multiple studies have failed to find any influence of diet quality on heterophil/lymphocyte ratios (Koch et al. 2018; Oberkircher and Pagano 2018). Overall, it appears the physiological condition of our study species during fall migration is less closely related to dietary behavior than is body condition, perhaps due to the slower changes of blood cells than fat stores in migrants (Jenni and Jenni-Eiermann 1998; Bauchinger and McWilliams 2009).

## Effects of antioxidant consumption

Contrary to our expectations, the presence of high-antioxidant fruits in recent diets did not have a positive relationship with body or physiological condition in either species and was actually negatively related to fat score and hematocrit in HETH. Dietary antioxidants are proposed to improve condition in migratory songbirds by reducing the energy and resources needed to prepare for and recover from the oxidative byproducts of aerobic metabolism (Beaulieu and Schaefer 2013; Cooper-Mullin and McWilliams 2016; Eikenaar et al. 2017), thereby allowing more energy to be devoted to improving condition. Although the lack of observable benefits in our study could be explained by the limitations inherent to our characterization of diets based on the presence rather than abundance of high-antioxidant fruits in feces, there are several other interpretations. These include efficient neutralization of oxidative damage by the well-developed endogenous antioxidant system commonly found in songbirds (Cooper-Mullin and McWilliams 2016) or low levels of oxidative stress, which did not necessitate large tradeoffs in energy allocation (McWilliams et al. 2021). If oxidative damage is related to flight duration and speed (Costantini et al. 2008, 2013), the benefits of antioxidant consumption would likely remain low for HETH, as a short-distance migrant (Skríp et al. 2015), but might increase for long-distance migrant SWTH as they make longer flights en route to Central and South America.

For HETH in our study, the lack of benefits to consuming the subset of fruit species with high antioxidant levels was compounded by negative associations with fat score and hematocrit. This finding is perhaps best explained by the fact that phenolics are a broad category of compounds (Halliwell and Gutteridge 2007), and consequently our use of a threshold level of total phenolics produced a coarse indicator of antioxidant quality. Included in total phenolics may have been many plant secondary metabolites (Ingersoll et al. 2010) that can have negative effects on songbirds, such as reduced digestive efficiency (Levey and Martinez del Rio 2001) and protein assimilation (Bairlein 1996), leading to constraints on protein and energy allocation. It is not immediately obvious why this effect would apply to HETH and not SWTH, but the consumption of high-antioxidant fruits was somewhat more frequent in HETH than SWTH, which may have been more careful in their selection of fruits and avoided those with disruptive secondary metabolites. Alternatively, this could also be the result of seasonal changes in high-antioxidant fruit availability coinciding with earlier passage by SWTH than HETH. Regardless, our study provides little evidence that antioxidant consumption benefits migrating songbird condition and may suggest that indiscriminate fruit consumption could actually have negative effects.

## Migration strategy, time constraints, and regulation of condition

Perhaps the most striking result in our study was the difference between species in the regulation of condition. Long-distance migration often selects for a time-minimizing strategy (Lindstrom and Alerstam 1992; La Sorte et al. 2015; Monti et al. 2018; Bayly et al. 2021), which ensures the entire distance can be covered, increases the chances of acquiring quality territories on breeding and wintering grounds (Marra 2000; Rushing et al. 2016), and reduces exposure to threats such as inclement weather (La Sorte et al. 2015; Ward et al. 2018), predators (Alerstam 2011; Samraoui et al. 2022), and pathogens and parasites (Bush and Clayton 2018; Hegemann et al. 2018). Accordingly, the adoption of a more time-minimizing strategy by SWTH (a long-distance migrant) than HETH (a short-distance migrant) could largely explain the more prominent relationships between migratory timing and condition in SWTH, including the strongest effects observed in this study (capture date with hemoglobin and heterophil/lymphocyte ratio). Furthermore, the direction of these relationships (increasing condition and stress over time) is consistent with previously documented increases in condition over migratory periods (Minias et al. 2014; Hays et al. 2018; Stepniewska et al. 2020), and may be due to the greater time constraints associated with later passage. While a similar mechanism could be responsible for the relationship between capture date and size-corrected body mass in HETH, the lack of corresponding changes in other condition indices combined with the later capture dates of HETH suggest that this could also be the result of a shift towards a wintering phenotype with increased thermogenic capacity (Petit and Vézina 2014). Some HETH overwinter as far north as our study sites (Delinger et al. 2020), making thermoregulatory adjustments a potential necessity for those individuals.

Parallel with, and likely complimentary to variation in time-minimization during migration, SWTH and HETH may also vary in the length of their migratory steps and corresponding reliance on stored fuel (i.e., their position on a continuum between capital and income migration; Evans and Bearhop 2022). Assuming that SWTH make longer flights than HETH throughout migration and not only when crossing substantial barriers (Cohen et al. 2015; Ward et al. 2018), it follows that they would need to build up larger fuel stores and musculature prior to departure. In this context, shifting diets to include more fruits would be more beneficial to SWTH than HETH as an additional source of energy. Similarly, elevated energy demands in SWTH would increase the benefits of carefully optimizing macronutrient intake to maximize fat storage, and therefore explain the positive relationship between late diet shifts and body condition in SWTH, but not HETH. These benefits would

likely increase as the migratory season progresses, leading to greater diet shifts later in the migratory period and our observed positive relationship between capture date and late-shift magnitude. Interestingly, the apparent lack of benefits to diet shifting in HETH is consistent with the previous finding that another relatively short-distance migrant, the yellow-rumped warbler (*Setophaga coronata*), does not track macronutrient targets in its diet (Marshall et al. 2016), and so this may suggest a general relationship between nutritional and migration strategies.

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**Author contribution statement** WAC conceived the study and WAC, SSP, and CLS designed its methodology. WAC and SSP collected the samples used in this study and WAC conducted the laboratory analyses with contributions from SSP on hematological analyses. WAC analyzed the data and drafted the original manuscript. WAC, SSP, and CLS contributed to editing the manuscript.

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**Data availability** All datasets used in this study are available from the authors upon request.

## Declarations

**Conflict of interest** The authors declare no conflicts of interest.

**Ethical approval** All methods involving live birds were conducted under the appropriate USGS Bird Banding Lab permits (Great Hollow: #23755; Braddock Bay: #20539-Q; Powdermill: #8231) and approved by the Rochester Institute of Technology's Institutional Animal Care and Use Committee (proposal #2019-1).

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