Research Article

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Fuel loads of Neotropical migrant songbirds on autumn passage through the Darién region of Colombia: Influence of migratory distance, route, ENSO, age and body size

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Abstract: Available energy stores determine stopover length, migration speed and likely survival in migrating birds. We measured energy stores by estimating fuel load in 11 species of Neotropical migrant songbirds in the Darién of Colombia over five years. We evaluated 1) whether individuals flying further from breeding origin arrived with smaller fuel loads, 2) if the ENSO (El Niño-Southern Oscillation) cycle affected fuel load and 3) if species known to migrate mostly overwater arrived with less fuel relative to those migrating overland. Breeding origin, inferred from feather $\delta^2\text{H}$ values, only had a significant positive effect on fuel load in Swainson's Thrush (*Catharus ustulatus*). Veery (*Catharus fuscescens*) and Swainson's thrush had higher and lower fuel loads, respectively, in El Niño years. Multi-species mixed-effects models revealed support for larger fuel loads in larger-bodied species and in species taking overwater routes, contrary to our prediction. Across species, we found no support for common effects of breeding origin or ENSO on fuel loads, in contrast to community-wide effects of migration route and body-size. In general, the variables considered here explained little of the variance in fuel loads, suggesting that inter-individual differences likely have a greater impact than broad-scale factors in our study system.

1 Introduction

As a group and throughout the World, long-distance migrant birds are declining at faster rates than short-distance migrants and resident species [1, 2]. Why this group appears to be more vulnerable than other groups of birds is still open to speculation. Breeding origin is one factor that can influence survivorship [3, 4], with longer migrations involving greater risks [5]. Other authors have hypothesized that long-distance migrants are exposed to greater climatic variability, including tropical storms and hurricanes [6]. For Neotropical migratory birds that cross the Gulf of Mexico and the Caribbean Sea, such factors are also linked to the El Niño Southern Oscillation (ENSO) [7, 8]. Migratory success in songbirds has also been linked to experience, with younger, more inexperienced birds expected to have lower survival during migratory episodes [9].

To date, few studies have attempted to determine which factors might influence the success of long-distance migration despite migration accounting for up to 80% of annual mortality in small migratory passerines [6, 10, 11]. Migratory birds are typically available for study before or after migration or at key stopover sites where they refuel [3, 4, 12–20]. Birds from more northerly populations, or those making over-water crossings, might be expected to arrive at stopover sites with relatively lower fuel loads than those from southerly populations or those traveling overland where they are able to make more frequent stops [21]: particularly in a rapidly changing world where dependence on geographically restricted stopover habi-

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tats can increase the chance of habitat availability becoming a limiting factor [22]. Longer migration distances and/or more stopovers *en route* can also presumably expose individuals to more stochastic events influencing survivorship and predation [10, 16, 23, 24]. Finally, age or experience, migration route and weather are factors known to affect survivorship of migrants.

Body condition is a term used to describe the nutrient and energy stores available to an individual to allocate towards life processes, with the assumption that condition is positively related to health and fitness [25, 26]. As the absolute nutritional state of an individual is difficult to obtain, body condition indices (BCIs) calculated using combinations of body morphometrics are often applied as approximate measures of nutritional condition [27, 28]. More direct, and non-invasive, approaches to quantifying body condition include the use of quantitative magnetic resonance (QMR) [29] but that approach is typically difficult at remote field sites. An alternative is to estimate fuel load, a measure of the amount of energy stored by a bird during migration [3, 4] and therefore an appropriate proxy for fuel loads in migrating birds [30]. Fuel load is derived from the relationship linking a bird's lean body mass (LBM) with some measure of physical size, such that positive values imply that an individual has fuel loads above and beyond its LBM. When expressed as a percentage of LBM, fuel load is corrected for differences in size between individuals/species, and can therefore be used to compare fuel reserves among species.

Many species of Neotropical migrants undertake long-distance migrations towards wintering sites located in South America but precise routes can vary greatly. Some species such as Veery (*Catharus fuscescens*), Black-poll Warbler (*Setophaga striata*) and Bobolink (*Dolichonyx oryzivorus*) are known for making long over-water crossings [13, 23, 31, 32], while others such as Canada Warbler (*Cardellina canadensis*) and Mourning Warbler (*Geothlypis philadelphia*) tend to follow the Central American landmass more closely [33]. If part of the risk of over-water crossings is that birds exhaust energy reserves in the absence of feeding opportunities, then birds taking such routes are expected to have a higher probability of exhausting their energy reserves relative to birds migrating largely overland.

As reviewed by McCabe and Guglielmo [34], juveniles generally tend to experience poorer body condition compared to adults during migration. This has been linked to slower migration speed [35–37] and longer duration at stopovers than adults [38–42]. Indeed, for some species, adults often arrive at stopover locations in better condition, while juveniles may arrive lighter and with less fat

[32, 43, 44], but these differences are not always observed [45]. If juveniles remain less skilled foragers during migration, they may be able to compensate by increasing foraging time to achieve similar overall energy intake to adults or, alternatively, they may store larger energy reserves to compensate for errors generated through inexperience. Several studies found refueling differences between juvenile and adult passerines during stopover on fall migration [38, 40, 44, 46–49]; but for different findings see [50, 51].

The El Niño Southern Oscillation Index (ENSO), the periodic variation in winds and sea-surface temperatures over the tropical eastern Pacific Ocean, affects much of the tropics and subtropics [52]. The warming phase or El Niño results in reduced rainfall across much of Central and northern South America and reduces productivity, while the cooling phase, La Niña, gives rise to increased rainfall and is linked to increased productivity. How this climatic variability affects bird migration remains poorly understood, especially in the Neotropics [8]. The ENSO cycle may affect the fuel load of Neotropical birds arriving at stopover sites by increasing or decreasing the availability of food resources necessary for the successful completion of migration [8]. Migrants that depend on insects for refueling during stopover may not be strongly affected by El Niño because in the tropics, insects are generally considered to be abundant year-round [53], although in strongly seasonal tropical habitats this may not be true. In contrast, migrants that depend on fruit resources for refueling may be affected by El Niño when fruit becomes scarce due to dry conditions which inhibit fruiting in tropical forests [8].

To determine which factors most strongly influence fuel loads and therefore vulnerability during migration in Neotropical migratory landbirds, we evaluated the impact of several factors on arrival fuel loads in a group of 11 Neotropical migrants moving through a major stopover region [3, 14, 21], the Darién, in northwestern Colombia on fall migration. This region concentrates populations of migratory landbirds from across their North American breeding ranges and therefore provides a snapshot of fuel loads from multiple breeding populations [20]. We aimed to determine: 1) whether individuals from northern origins that travel further to reach the Darién, arrive with smaller fuel loads than those from southern origins, 2) if migrants are affected by the ENSO cycle, whereby El Niño years result in smaller fuel loads on arrival relative to La Niña years, and 3) if species known to migrate mostly over water arrived with lower fuel loads relative to those that migrate mostly overland.

Figure 1: Location of study site in the Darién region of northwest Colombia: Tacarcuna Nature Reserve, Sapzurro, Chocó, Colombia.

2 Methods

2.1 Study site and data collection

We studied a group of 11 long-distance migrants: Red-eyed Vireo (*Vireo olivaceus*), Veery, Swainson's Thrush, Gray-cheeked Thrush (*Catharus minimus*), Yellow Warbler (*Setophaga petechia*), Northern Waterthrush (*Parkesia noveboracensis*), Mourning Warbler, Canada Warbler (*Cardellina canadensis*), Prothonotary Warbler (*Protonotaria citrea*), Scarlet Tanager (*Piranga olivacea*) and Summer Tanager (*Piranga rubra*), at a constant-effort mist-net station in the Tacarcuna Nature Reserve, Chocó, Colombia (08 ° 39'41.53"N, 77 ° 22'06.74"W; ~100 m asl). The reserve lies within an important stopover region described in previous publications [14, 21] for Neotropical migrants and in a major migration corridor for raptors and aerial insectivores [54]. The station was located near the village of Sapzurro close to the border of Colombia and Panama (Figure 1). Habitat consisted of seasonal tropical humid forest interspersed with small clearings for agriculture and houses. Fall migration was monitored between 2011 to 2015 using 8 to 15 mist-nets (12 or 18 m long, 32-mm mesh) between mid-September and early November. Nets were positioned strategically to maximize captures and the number of nets and their location were kept virtu-

ally constant among days and years. Nets were opened daily beginning at dawn and remained open for 4.5 h on average, and were checked every 30-40 min. Captured birds were banded with uniquely coded Porzana-made metal bands (band reporting website: www.aselva.co). For all species, we recorded date and time of capture, age and sex, visible subcutaneous fat score (range 0 to 8), pectoral muscle score (range 0-3), wing chord (± 1 mm), and body mass (± 0.1 g) using an electronic balance (Fast Weigh digital pocket scale, model M-500). In addition, we collected the first primary feather of a subset of individuals from each species to determine breeding origins based on stable hydrogen isotope ($\delta^2\text{H}_i$) analyses. See Table 1 for sample sizes of captured birds and for the number of individuals for which a feather was collected.

We prepared feather samples in the Environment Canada stable isotope laboratory at the National Hydrology Research Centre (NHRC) in Saskatoon, Canada. Each feather sample was soaked for 5 h in 2:1 chloroform:methanol solution then rinsed and dried in a fume hood for 48 h [55]. The impact of exchangeable hydrogen on isotopic measurements was corrected using the comparative equilibration method [56]. Within analytical runs, Environment Canada keratin reference standards CBS (caribou [*Rangifer tarandus*] hoof = -197‰) and KHS (kudu [*Tragelaphus spp.*] horn = -54.1‰) were used to account for exchangeable H and to calibrate samples. H

isotopic measurements were performed on H_2 gas derived from high temperature (1350°C on glassy carbon) flash pyrolysis of $350 \pm 10 \mu\text{g}$ of distal-vane feather subsamples in silver capsules. Resulting H gas was separated in a Eurovector 3000 (Milan, Italy) elemental analyzer and introduced into an Isoprime (Crewe, UK) continuous-flow isotope-ratio mass spectrometer. All results are reported for non-exchangeable H expressed in the typical delta (δ) notation, in units per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. Based on within-run replicate ($N = 5$) measurements of laboratory keratin standards, measurement precision was estimated to be $\pm 2\text{‰}$.

2.2 Fuel loads and lean body mass

To describe fuel loads, we first generated a linear regression equation describing lean body mass (LBM) in each species, using body mass and wing length data from a group of individuals with no visible fat deposits (fat score = 0). LBM represented the average body mass of a bird with no visible fat for a given wing length. Taking the LBM equation for each species, we calculated fuel load for each individual using the following equation that expresses fuel reserves as a percentage of LBM [30]: Fuel load = $((\text{body mass} - \text{LBM}) / \text{LBM}) * 100$, where LBM was calculated for each individual based on its wing length. Expressing fuel load as a percentage of LBM allows for interspecies comparisons regardless of body size [57].

Figure 2. Fuel loads were not influenced by breeding origin in most species based on δ_2H_f values in feathers of 11 species of Neotropical migrants captured on fall migration (2011 – 2015) in the Tacarcuna Nature Reserve, Darién, Colombia. For one species, Swainson's Thrush, fuel loads increased with shorter migratory distances (positive relation between fuel loads and δ_2H_f values, more positive (δ_2H_f) values indicate more southerly origins).

2.3 Climate conditions-ENSO

For the years 2011–2015, average Southern Oscillation index (SOI) values were derived from monthly index data available through the National Oceanic and Atmospheric Administration's Climate Prediction Center [58]. The SOI was used to measure the strength of ENSO in Mexico and Central America (where stopover sites expected to be used by most species including those that make overseas crossings prior to arriving in the Darien are located), as has been done in previous climate studies [59, 60]. A strong positive value indicates La Niña conditions (high precipitation), and a strong negative value indicates El Niño conditions (low precipitation). Within the period of study, there was both a strong La Niña event (2011) and a strong El Niño event (2015; one of the strongest events in the previous 65 years). We carried out a model selection process using AIC values [61, 62] to determine the support for SOI

variables calculated using different groups of months (e.g. 12 months prior to and including October [peak month of migration for most species] and 6 months prior to and including October) for each species and included the top ranked variable in subsequent analyses.

2.4 Modelling fuel load on arrival

To evaluate those factors influencing arrival fuel loads, we created three model sets in which fuel load on arrival was the response variable. Modelling was carried out in the program R version 3.3.3 [63] and model selection was carried out using Akaike's information criterion (AIC), comparing Δ_i values, where Δ_i was the difference between each model and the model with the lowest AIC (i.e. $\Delta_i = \text{AIC} - \text{minimum AIC}$).

Figure 3. A relationship between fuel loads and the El Niño Southern Oscillation was absent for most of the 11 species of Neotropical migrants captured on fall migration in the Tacarcuna Nature Reserve, Chocó, Colombia. When controlling for age and hour of capture, Veery had significantly lower fuel loads in wetter La Niña years, while Swainson's Thrush showed the opposite pattern. The continuous variable fuel load includes negative values indicating that fuel loads have been exhausted, while positive values > 5 indicate adequate fuel loads for continuing migration. The SOI index includes negative values (< -0.5) representing El Niño conditions (low precipitation inducing drier conditions in the Caribbean basin), and positive values (> 0.5) representing La Niña conditions (high precipitation).

Table 1. Summary table of sample size by species and the coefficients for significant effects of breeding origin, age, and the ENSO cycle on the fuel loads of 11 migratory landbirds captured during fall migration in the Tacarcuna Nature Reserve, Chocó, Colombia over five years (2011–2015). Results and sample sizes come from two analyses, a first using only birds for which an analysis of stable hydrogen isotopes was carried out to infer breeding origin and a second for which all birds captured were included (results for Age, SOI, Year, Top model, R^2). We report whether there was support for significant effects of year on fuel loads, regardless of whether these could be explained by the SOI index or not.

Species	N (isotopes)	Breeding Origin	Age (HY)	SOI index	Year	Top Model	R^2 (adj)
Veery	870 (218)	-	-1.715*	-0.665*	YES	SOI+Age+Hour	0.019
Gray-cheeked Thrush	914 (152)	-	-	-	YES	Hour	0.037
Swainson's Thrush	2115 (306)	0.0539*	-	1.344***	YES	SOI+Hour	0.030
Red-eyed Vireo	1495 (170)	-	-1.5398**	-	-	Age+Hour	0.020
Yellow Warbler	136 (105)	-	-	-	-	Hour	0.008
Northern Waterthrush	135 (77)	-	-	-	-	Hour	0.034
Prothonotary Warbler	288 (151)	-	-	-	-	SOI+Hour	0.010
Mourning Warbler	304 (146)	-	-	-0.532	YES	SOI+Hour	0.014
Canada Warbler	158 (46)	-	-	-	-	Hour	0.046
Summer Tanager	119 (34)	-	-	-	YES	Hour	0.031
Scarlet Tanager	103 (61)	-	-	-	-	Null	-

Significance of coefficients: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, italics $P < 0.1$

2.4.1 Breeding origin

To evaluate the effect of breeding origin on fuel load, we analyzed each species individually using only those individuals with a $\delta^2\text{H}_f$ value and a model set that also accounted for possible effects of year, age and hour of capture on fuel loads, where: Breeding origin – was the continuous $\delta^2\text{H}_f$ value as a proxy for breeding latitude; Age – a two-level factor, HY: hatch year <1 year old and AHY: after hatch year >1 year old; Year – a five-level factor covering the years 2011 through 2015; Hour – capture hour of individuals converted into a continuous numeric variable. Models included various combinations of the explanatory variables through additive effects.

2.4.2 ENSO and age

To evaluate the effect of the ENSO cycle and age on fuel load, we used the full capture dataset for each species and ran a model set accounting for the possible effects of capture hour on fuel loads. We also ran models with the five-level factor Year to determine whether significant variation in fuel load existed that may or may not be accounted for by the ENSO cycle. Models included various combinations of the variables described above and the additional explanatory variable: SOI – a continuous value reflecting

average SOI values during 12 months of 6 months prior to and including October of the year of capture.

2.4.3 Migration route and body size

To examine the effect of migration route on fuel loads, we combined data across all species and created a third model set (Table 2) including various combinations of the explanatory variables: Body Size – a continuous variable taken as the mean LBM value by species, as an estimate of body size; Migration Route – a two-level factor, over land (migrating mostly by land) and over water (migrating mostly over water); Breeding Origin – the mean $\delta^2\text{H}_f$ value by species; ENSO – a continuous variable based on the SOI index; and Species – a categorical variable. Models were run as mixed-effect models in the package lme4 [64] in Program R, including species as a random effect and all other variables as fixed effects. We included the variable lean body mass as a standard measure of body size in small passerines, as body size may influence the ability of birds to cope with adverse conditions such as wind, with smaller, lighter birds being less able to counteract strong winds. Migration routes were based on a literature review of the most probable route of migration for the majority of individuals of each species during fall migration [4, 23, 65–67]. We assigned migration routes as follows: primar-

Table 2. Multi-species analysis using mixed effect models to determine how fuel load varies as a function of the variables: breeding origin (Origin), ENSO index, migration route (overland vs. overwater), species (S) and body size (mean lean body mass by species) on arrival at the Tacarcuna Nature Reserve, Chocó, Colombia during fall migration (years 2011- 2015). Models are ordered by the relative support they received from Akaike Information Criteria. The variable species (1|S), corresponds to a random effect.

Model (Fuel load =)	K	AICc	Delta_AICc	AICcWt
Migration Route + Body Size + ENSO + (1 S)	6	49539.63	0	0.35
Migration Route + Body Size + (1 S)	5	49540.15	0.52	0.27
Migration Route + Body Size + Origin + (1 S)	6	49541.88	2.25	0.12
Migration Route + ENSO + (1 S)	5	49543.47	3.84	0.05
Body Size + (1 S)	4	49543.54	3.91	0.05
Migration Route + (1 S)	4	49543.94	4.31	0.04
Origin + Body Size + ENSO + (1 S)	6	49543.98	4.34	0.04
Origin + Body Size + (1 S)	5	49544.39	4.76	0.03
Migration Route + Origin + (1 S)	5	49545.86	6.23	0.02
ENSO + (1 S)	4	49546.73	7.1	0.01
Null + (1 S)	3	49547.17	7.54	0.01
Migration Route: ENSO + (1 S)	5	49547.79	8.15	0.01
Origin	4	49548.40	8.77	0

ily overland species - Canada Warbler, Mourning Warbler, Scarlet Tanager, Summer Tanager, Yellow Warbler; primarily over water - Red-eyed Vireo (a trans-Gulf migrant), Veery, Swainson's Thrush, Gray-cheeked Thrush, Prothonotary Warbler (a trans-Gulf migrant and trans-Caribbean

migrant), and Northern Waterthrush (a trans-Gulf, circum-Gulf, and trans-Caribbean migrant).

3 Results

6637 individuals of eleven study species were considered for analysis, of which 1466 individuals were sampled for stable isotopes in order to infer breeding origin (see Table 1 for sample sizes by species). There was considerable variation in arrival fuel load both within and between species, with values ranging from -20% LBM to 45% LBM. Averaged across species, 38% of individuals arrived at the study site with a body mass below our lean body mass estimates and typically had no visible fat reserves. The following sections summarize which of the factors predicted to affect fuel loads influenced the eleven species examined in this study.

Figure 4: Arrival fuel loads of 11 species of Neotropical migrants grouped by their primary migratory route: over land via Mexico and Central America or trans-Gulf/trans-Caribbean before arrival at the Tacarcuna Nature Reserve, Chocó, Colombia during fall migration (years 2011- 2015). Fuel loads were larger in species traveling overwater and in birds of larger body size e.g. Swainson's Thrush (SWTH) and Veery (VEER). Boxplots describe the inter-quartile range, whiskers the 97.5% quartiles and individual points represent outliers.

3.1 Breeding origin (surrogate for migratory distance)

We found support for an effect of breeding origin (as inferred from $\delta^2\text{H}_t$ values, with more positive values indicating shorter distances [20]) in just one species, the Swainson's Thrush (Table 3). Swainson's Thrush showed

increasing fuel loads as migratory distance decreased in line with more likely southern origins.

3.2 ENSO cycle

There was support for an effect of the SOI variable on fuel load in Veery and Swainson's Thrush, with the 95% confidence intervals for coefficients excluding zero in both species. In Swainson's Thrush the coefficient was positive, indicating that individuals migrating during El Niño years arrived with lower fuel loads than individuals migrating during La Niña years (Table 3) (Figure 3). The opposite trend was true for Veery, with birds arriving with larger fuel loads in El Niño years. In a third species, the Mourning Warbler, there was support for an effect of SOI, however, the 95% confidence intervals for the coefficient marginally overlapped with zero. Like Veery, the coefficient was negative in Mourning Warblers.

3.3 Age

There was support for age effects in Red-eyed Vireo and Veery (Table 2), with hatch-year (HY) individuals generally arriving with lower fuel loads than AHY individuals.

3.4 Effect of migration route & body size

Among the mixed effects models including all eleven species there were two top models (Table 2), which included the variables Migration Route, Body Size and ENSO. However, only the 95% confidence intervals for migration route and body size excluded zero, both having a positive effect on fuel load, such that fuel loads were larger in species with overwater routes and in larger bodied species (Table 3). There was no support for a community wide influence of breeding origin in these models. The effect of body size was such that for each 10 g increase in lean body mass, fuel load was predicted to increase by 2.5%, while fuel loads in species using overwater routes were predicted to be 3.8% higher than species using overland routes on average.

4 Discussion

Our analysis of five-years of data from long-distance Neotropical migrant songbirds during fall migration revealed

Table 3. Model coefficients (SE) from the top mixed effects model describing the variation in fuel loads across 11 Neotropical migrant songbirds captured on fall migration in the Tacarcuna Nature Reserve, Chocó, Colombia, between 2011 and 2015.

	Dependent variable: Fuel load
Migration Route (Overwater)	3.809** (1.431)
Body Size (LBM)	0.254** (0.091)
ENSO (SOI12)	0.136 (0.086)
Constant	-0.412 (1.82)
Observations	6637
Log Likelihood	-24763.81
Akaike Inf. Crit.	49539.62
Bayesian Inf. Crit.	49580.42

Significance of coefficients: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

that fuel loads at a migratory stopover in the Darién region of Colombia were affected by several factors. These included migration distance, climatic events like the El Niño–Southern Oscillation (ENSO), age, body size and migration route. However, the influence of these factors varied considerably among species and, in general, migration distance and ENSO effects on fuel loads were not as strong as we predicted for most species. Further, the direction of likely relationships varied among species, as was the case for ENSO for example, implying potentially species-dependant responses to these variables. In contrast, strong support for body size being a determinant of fuel loads for the suite of migratory species examined, suggests that physical processes may have greater influence than either migration distance or climatic variation [34]. Migration route also influenced fuel load, with birds taking over water routes arriving in better condition than those traveling primarily overland, contrary to our prediction. Age was only significant in a few species, suggesting that there are not universal patterns among age classes affecting all species either. Taken together, our study points to the complexity of the multiple factors affecting avian migration and stopover ecology and underlines the need for long-term monitoring of avian migration, especially in the tropics [68].

4.1 Effect of migration distance (breeding origin) on fuel loads

We only found evidence for an effect of breeding origin (as revealed by estimates of breeding latitude provided by feather $\delta^2\text{H}$ analysis) on fuel loads in Swainson's Thrush. As predicted, Swainson's Thrush with likely southern origins arrived in better condition to our site than birds from more northern origins. Although breeding origin appeared among the top models (within 2 AIC values) for six of eleven species (including Swainson's Thrush), it was often ranked below the null model, indicating a very weak effect if it was present at all. Sample sizes varied from 34 to 306 among species for the breeding origin analysis and it was only in the species with the largest sample size that there was support for an effect. This suggests that increased sample sizes could help to determine the prevalence of migration distance effects on fuel loads but given the lack of support for an effect in species with samples sizes >100 , it is likely that migration distance does not have a strong influence on fuel loads in migratory landbirds arriving at a stopover site. Indeed, given the number of species examined, that one species would show a significant relationship with breeding origin is to be expected by chance alone.

The lack of relationship between fuel loads and breeding origin may also arise because of the method we used to calculate lean body mass, in which we used wing length as a measure of body size. If wing length but not overall body size increases with migration distance, as observed in certain species [69], then we may have underestimated the fuel loads of birds with more northerly origins. However, we found no evidence for a negative relationship between wing length and $\delta^2\text{H}_f$ values among the 11 study species, as would be expected if the above is true.

4.2 Effect of the ENSO cycle on fuel loads

Few studies have evaluated the direct effects of El Niño events in tropical forest animals [8, 70] but variable community-level fruit production has been found to induce fluctuations in the abundance of species of frugivorous mammals in Panama [70]. In Costa Rica, the fuel loads of insectivorous Eastern Wood-Pewees improved during spring migrations coinciding with El Niño, whereas frugivorous Swainson's Thrushes and Traill's Flycatchers experienced reduced condition during El Niño years [8]. However, it is unclear how general these patterns are and particularly how the ENSO cycle might affect different species during the migration period. We found a discern-

able effect of the ENSO cycle on two species, Veery and Swainson's Thrush, and it is notable that the direction of the effect differed between the two. In Veery, individuals arrived with lower fuel loads during La Niña conditions, contrary to our expectation for a largely frugivorous species [21]. Meanwhile, the Swainson's Thrush, also a largely frugivorous species showed higher fuel loads in (wetter) La Niña years.

Other frugivorous species (on fall migration) in this study, such as Gray-cheeked Thrush, Scarlet Tanager and Red-eyed Vireo, also failed to follow the expected pattern, although in the Gray-cheeked Thrush there were significant differences in fuel loads between years. Such variation among ecologically similar species suggests that other factors may be at play and these are likely related to differences in migration routes and the location of stopover sites, which expose species to different conditions. It is notable that in Costa Rica, Swainson's Thrushes on spring migration showed the opposite pattern [8] to that recorded in fall birds in the Darién.

Five of eleven species in this study showed significant differences in fuel loads between years (Table 1), however, in two species the ENSO cycle did not explain this variation and in two of the remaining three, the SOI index we used only explained part of the variation (as evidenced by stronger support for models with the categorical variable Year versus the continuous variable SOI). These results imply that even where inter-annual variation exists, the ENSO cycle can only explain part of it and likely other factors such as the presence of tropical storms in the Caribbean basin or conditions at distant stopover sites influence arrival fuel loads in our study region during fall migration. Finally, we cannot rule out that effects were masked by the high inter-individual variation in our data and the limited number of years available. Generating more years of data under differing ENSO conditions may help to clarify this point.

4.3 Effect of age on fuel loads

Fuel loads were influenced by age in Red-eyed Vireo and Veery. HY individuals of Veery and Red-eyed Vireo arrived in the Darién with lower fuel loads than AHY birds, as we had predicted based on the expectation that younger birds are less experienced [49, 71] and require more time to gain migratory fuel, migrate with lower fuel loads, stay longer at stopover sites, and take longer to complete their journeys [34, 71]. Further, AHY birds are expected to be more efficient when foraging, not only due to their greater experience, but also because they may be socially dominant

over HY birds throughout the non-breeding season [72, 73].

4.4 Effect of migration route and body size on fuel loads

Contrary to our prediction, species with primarily overwater routes did not have lower fuel loads than those migrating primarily overland. Indeed, the opposite pattern was true, with species using overwater routes having 3.8% larger fuel loads on average. We can only speculate as to why this might be the case and a number of factors may explain the larger fuel loads such as the need for a greater buffer in energy reserves when migrating overwater. Alternatively, those species migrating overwater may migrate in longer flight stages and therefore generally carry more reserves than those travelling overland – this is relevant if some individuals had already refuelled to the north of our study site following overwater flights. Interpretation of this result is further complicated by the fact that actual routes adopted by the different species that pass through the Darién have not been well documented. Nonetheless, among the *Catharus* thrushes for which geolocators have described the migration routes of disparate populations [23, 74, 75], Veery and Swainson's Thrush [21] showed no clear difference in condition, despite the trans-Caribbean route adopted by Veery and the trans-Gulf/Central American route used by most Swainson's Thrushes.

In addition to migration route, body size also had a significant effect on fuel load in our multi-species model. Our results showed that larger species (e.g. Veery, Gray-cheeked Thrush, Swainson's Thrush) arrived in better condition than smaller individuals/species (e.g. Northern Waterthrush, Mourning Warbler, Yellow Warbler, and Canada Warbler). In terms of flight efficiency, bigger birds have higher aspect ratios than smaller birds, which promote greater flight efficiency [76]. In general, smaller birds have lower lift to drag ratios than larger ones, as well as having higher basal metabolism [76], both of which translate into a higher energy expenditure in order to cover a given distance. Reduced lift [76] also means that smaller birds may be less able to counteract unfavorable wind directions, making them more vulnerable to storms over water.

5 Conclusions

Our study is the first attempt to understand how a suite of factors may affect fuel loads in a diverse group of migratory landbirds at a migratory bottleneck that have completed a significant proportion of their migration. Aside from body size and migration route, no one factor was found to be common to all eleven of our study species and more importantly, the direction of effects often differed among species. The relatively weak signal when using fuel loads as an indicator of condition suggests that high individual variation in fuel load may be hiding more general patterns. It also suggests that we did not include all the sources of variation in our models and future studies should examine ways to incorporate adverse weather conditions such as tropical storms and headwinds, as well as estimating the distance that birds must cover to reach their final destination [4], for example. Importantly, the lack of clear patterns implies that the factors that directly impact migratory condition through body mass are species dependent and cannot be summarized in general relationships. This has important implications for understanding which species are most vulnerable to events or changes during migration. While we can conclude that, in general, smaller bodied species will likely be more vulnerable to shifting wind patterns or loss of stopover habitat, few other factors were as clear cut.

It was surprising to find opposite responses to predictions regarding the ENSO cycle among species and while this may in part be due to high variation between individual strategies that could hide more general patterns, it suggests that the impacts of climate change [5], for example, will not be unidirectional but instead depend on the location of individual species/population's stopover sites. Another important finding from this study, is that increasing migration distance does not necessarily make individuals more vulnerable to the rigors of migration or at least when fuel loads are considered an indicator of vulnerability to starvation or other lethal events. Alternative explanations for the steeper declines observed in long-distance migrants include a higher potential for phenological mismatch at more distant points on the globe [77] or a lower cumulative survival probability in birds that migrate farther as they typically spend more days on migration and daily survival probability is generally lower during migration [10].

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