Mass gain and stopover dynamics among migrating songbirds are linked to seasonal, environmental, and life-history effects

Devin R. de Zwaan,1,2,3,* Andrew Huang,2 Quinn McCallum,3,4 Kiirsti Owen,3,5 Myles Lamont,3,6 and Wendy Easton2

1 Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada
2 Environment and Climate Change Canada, Pacific Wildlife Research Centre, Delta, British Columbia, Canada
3 WildResearch Society, Vancouver, British Columbia, Canada
4 Department of Zoology, Faculty of Science, University of British Columbia, Vancouver, British Columbia, Canada
5 Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada
*Corresponding author: drdezwaan@gmail.com

ABSTRACT

During migration, birds must stopover at refueling sites to replenish energy stores, with the rate of refueling linked to stopover length, migration speed, and the timing of critical life stages, such as breeding. Under optimal migration theory, birds are expected to maximize fuel intake and minimize stopover length (the time minimization hypothesis). Within a multi-species framework, we demonstrate that time minimization behavior is context-dependent, as refueling rate, stopover length, and departure decisions vary between seasons, among species with different ecological traits (e.g., diet and migration distance), and in response to density-dependent factors and prevailing environmental conditions. Using long-term banding data (10 years) from southwestern British Columbia, Canada, we investigated the ecological processes shaping stopover dynamics among 5 warbler (Parulidae) and 5 sparrow species (Passerellidae). Specifically, we assessed variation in fuel deposition rates (FDRs) as well as the associations between mass gain, stopover length, and departure probability. FDR was greater in insectivorous warblers during spring migration and in species migrating long distances. FDR responded positively to temperature and habitat productivity, but negatively to precipitation events, particularly for insectivorous, long-distance migrants during spring migration. Similarly, density-dependent refueling rate was only observed in insectivores and long-distance migrants during spring migration, where higher densities of foliage-gleaning insectivores were associated with a lower FDR. Stopover duration was more closely associated with body condition upon arrival and subsequent mass gain than direct environmental effects, especially during northward spring migration, providing support for time minimization and a mass threshold influencing departure decisions. These results highlight that refueling rates and stopover quality vary among species depending on their life-history strategies, with particular implications for long-distance, migratory insectivores, which may be most susceptible to climate shifts.

Keywords: climate change, fat accumulation, fuel deposition rate, lean body mass, refueling rate, seasonal migration strategies, stopover duration, weather effects

LAY SUMMARY

• Linking differences in stopover behavior among migratory songbirds to ecological traits helps us understand habitat use patterns and identify conservation priorities beyond the breeding site.
• Over a 10-year volunteer-led study in southwestern British Columbia, Canada, mass gain was the highest in insectivorous warblers, during spring migration, and for long-distance migrants.
• Temperature, precipitation, habitat productivity, and density-dependent factors strongly influenced mass gain, particularly for insectivores during spring migration.
• Stopover duration and departure probability during spring were more closely linked to arrival body condition and mass gain than weather, providing support for a fat accumulation threshold and selection for short stopovers.
• We highlight how the use and importance of stopover sites vary among species depending on life-history strategies, with implications for long-distance, migratory insectivores which may be particularly sensitive to habitat degradation and climate change.
Le gain de masse corporelle et la dynamique des escales chez les oiseaux chanteurs migrateurs sont liés aux effets saisonniers, environnementaux et du cycle vital

RÉSUMÉ
Pendant la migration, les oiseaux doivent faire escale sur des sites de ravitaillement pour reconstituer leurs réserves d'énergie, le taux de ravitaillement étant lié à la durée de l'escale, à la vitesse de migration et au moment des étapes importantes de leur vie, comme la reproduction. Selon la théorie de la migration optimale, les oiseaux sont censés maximiser l'absorption d'énergie et limiter au minimum la durée de l'escale (l'hypothèse de la « minimisation du temps »). Dans un système multispecifique, nous démontrons que le comportement de minimisation du temps dépend du contexte, car le taux de ravitaillement, la durée de l'escale et les décisions de départ varient d'une saison à l'autre, entre les espèces ayant des caractéristiques écologiques différentes (p. ex., régime alimentaire, distance de migration) et en réponse à des facteurs dépendant de la densité et aux conditions environnementales qui prévalent. À l'aide de données de bagage à long terme (10 ans) provenant du sud-ouest de la Colombie-Britannique, au Canada, nous avons étudié les processus écologiques qui façonnent la dynamique des escales chez cinq espèces de parulines (Parulidae) et cinq espèces de bruants (Passerellidae). Plus précisément, nous avons évalué la variation des taux de dépôt de graisses (FDR), ainsi que les associations entre le gain de masse corporelle, la durée de l'escale et la probabilité de départ. Les FDR étaient plus élevés chez les parulines insectivores au cours de la migration printanière et chez les espèces migrant sur de longues distances. Les FDR ont réagi positivement à la température et à la productivité de l'habitat, mais négativement aux épisodes de précipitation, particulièrement pour les espèces insectivores migrant sur de longues distances lors de la migration printanière. De même, un taux de ravitaillement dépendant de la densité n'a été observé que chez les espèces insectivores et celles migrant sur de longues distances pendant la migration printanière, alors que des densités supérieures d'espèces insectivores glanant sur le feuillage étaient associées à des FDR plus faibles. La durée de l'escale était plus étroitement associée à la condition corporelle à l'arrivée et au gain de masse corporelle subseqüent qu'aux effets environnementaux directs, particulièrement pendant la migration printanière vers le nord, ce qui favoriserait la minimisation du temps et un seuil de masse corporelle influençant les décisions de départ. Ces résultats soulignent que les taux de ravitaillement et la qualité de l'escale varient entre les espèces selon leurs stratégies de cycle vital, avec des implications particulières pour les espèces insectivores migrant sur de longues distances, qui peuvent être les plus sensibles aux changements climatiques.

Mots-clés: changements climatiques, EVI, accumulation de graisses, taux de dépôt de graisses, masse corporelle maigre, taux de ravitaillement, stratégies de migration printanière et automnale, durée de l’escale, effets météorologiques

INTRODUCTION
Migration is a widespread, yet energetically costly, life-history strategy, during which conditions impacting body condition can profoundly influence subsequent fitness (Berthold et al. 2003, Newton 2008). To balance energy budgets, birds must select stopover sites to refuel, while avoiding sub-optimal conditions or risky habitats (Sillett and Holmes 2002). Optimal migration theory assumes birds limit their time at stopovers to reduce risks in unfamiliar habitats and increase migration speed (time-minimization hypothesis; Alerstam and Lindström 1990), particularly in spring where early arrival at breeding sites is linked to territorial advantages and greater reproductive success (Harrison et al. 2011, Morrison et al. 2019). Given that energy accumulation is slower than energy loss during flight, >70% of migration is spent replenishing fat stores at stopovers (Hedenström and Alerstam 1997, Linscott and Senner 2021). As such, the fuel deposition rate (FDR) is likely the primary driver of stopover duration (Alerstam and Lindström 1990), influencing migration speed, phenotype, and reproductive success (Hedenström 2008, Nilsson et al. 2013, Schmaljohann 2018). Assessing what drives variation in FDR and stopover dynamics is critical to understanding habitat use and identifying conservation priorities beyond the breeding site (Schaub and Jenni 2000).

Many species experience strong selective pressure on FDR and stopover duration (Chernetsov 2012, Schmaljohann 2018). Under the time-minimization hypothesis, body condition on arrival and stopover length should be minimally correlated as individuals are under pressure to elevate FDR and continue migration (Lindström and Alerstam 1992, Alerstam 2011, Bayly et al. 2019). Alternatively, a strong association between initial condition and stopover duration suggests that FDR is inflexible or constrained in some way as birds recover energy (Bayly et al. 2021). Both predict that individuals must reach an energy threshold prior to departure (Schaub et al. 2008, Bayly et al. 2013). Several factors can influence FDR; therefore, testing associations between initial condition, FDR, and stopover duration can highlight important ecological mechanisms acting within stopover habitats.

Environmental factors are often strongly associated with FDR and stopover dynamics (Newton 2008, Chernetsov 2012). High FDR can indicate that resource availability is sufficient to allow individuals to recuperate energy stores (van Gils et al. 2005). Species reliant on variable food...
sources may also exhibit greater FDR if stopovers align with ephemeral resource peaks (Moore and Simm 1986). Low FDR may indicate poor-quality stopover sites, although this can be mediated by foraging flexibility and the use of social cues (Yong and Moore 2005, Németh and Moore 2007). Low FDR is also associated with individuals nearing their destination (Paxton and Moore 2017). In addition, reduced FDR has been linked to migrant density, as well as the presence of predators or perceived risk, as foraging is disrupted by density-dependent resource competition and risk aversion behaviors (Moore and Yong 1991, Schmaljohann and Dierschke 2005, Cohen et al. 2022). Thus, we may expect different FDRs and stopover durations among species depending on their life-history strategies, foraging niche, susceptibility to risk, and destination. For example, long-distance migrants may experience greater selection for rapid FDR and shorter stopovers than short-distance migrants (Packmor et al. 2020), foraging behavior may influence exposure to risk or the energetic cost of acquiring resources, and diet may affect FDR through resource competition, reliability, and nutritional content (Moore and Simm 1986, Moore and Yong 1991, Hedenström 2008).

Weather events can also influence FDR, especially under a rapidly changing climate. Departure from stopover sites has been linked to temperature, wind, humidity, and precipitation conditions (Dossman et al. 2016, Beauchamp et al. 2020). Weather can have strong impacts on insect activity and abundance (Choi 2008), such that species reliant on insects or unpredictable resources may be highly sensitive to weather disruptions (Ktitorov et al. 2021). Moreover, many songbirds time migration with fluctuations in resource availability, potentially to maximize FDR throughout migration (i.e. green wave hypothesis; La Sorte and Graham 2021, Youngflesh et al. 2021). Seasonal differences in migration destination (e.g., breeding/wintering site) or exposure to severe weather events may influence the presence and strength of associations between environmental conditions, FDR, and stopover duration. For example, many birds employ different migratory strategies during spring and fall, with spring migration often faster and more time constrained (Newton 2008, Horton et al. 2016). However, most studies investigate a single season, which limits our understanding of the effects of environmental conditions on stopover dynamics.

Using banding data from the Iona Island Bird Observatory (IIBO) in southwestern British Columbia, Canada, we assessed spring and fall stopover behaviors among 5 warbler (Parulidae) and 5 sparrow species (Passerellidae) that differ in their migration strategies, diet, and foraging niche. Iona Island is located within the Fraser River Delta, an Important Bird Area along the Pacific Flyway that is recognized as a critical refueling region for migratory birds (Butler et al. 2021). Songbirds were captured in both spring and fall, providing a powerful comparative framework in which to test FDR and stopover dynamic associations among species and seasons. Specifically, we assessed (1) species-specific FDR between seasons, diet guilds (insectivores, omnivores), and migration distances (short, long); (2) season-specific influences of temperature, precipitation, and habitat productivity on FDR; (3) density-dependent effects on refueling performance; and (4) the influence of body mass on departure probability and stopover duration.

We predicted that FDR would be most strongly linked to environmental conditions and density-dependence in insectivores, due to their reliance on more specialized, ephemeral resources than omnivores, and the susceptibility of insect resource pulses to weather events (Moore and Yong 1991, Ktitorov et al. 2021, Cohen et al. 2022). We also expected greater FDR and shorter stopovers during spring compared with fall, corresponding with greater urgency to arrive early at the breeding sites (Briedis et al. 2018). Finally, we predicted initial body condition and mass changes to be more closely linked to stopover duration and departure probability for long- vs. short-distance migrants. Long-distance migrants may be under stronger selection for rapid migration, limiting their capacity to adjust movements in response to prevailing conditions (Packmor et al. 2020). This study will advance our understanding of the ecological processes shaping stopover behaviors in species with different ecological traits.

METHODS

Study Site
From 2010 to 2019, migratory songbird banding was conducted on Iona Island in Richmond, British Columbia, Canada (49.22°N, 123.21°W) on the traditional, unceded territory of the Musqueam (xʷməθkʷəy̓əm) people. Located at the mouth of the Fraser River Delta (Figure 1), Iona Island was originally selected given its significant location along the Pacific Flyway, avian diversity, and proximity to urban centers. The Fraser River Delta is internationally recognized as an Important Bird Area and a site of significance by the Western Hemispheric Shorebird Network, providing staging and wintering grounds for millions of migratory birds annually (Butler et al. 2021). Locally, Iona Island represents a mosaic of brackish wetland, reed beds, and successional deciduous forest patches, surrounded by a larger regional matrix of metropolitan centers and intensive agriculture (Page 2011; Figure 1). Over the study period, average daily temperatures (mean ± SD) during peak songbird migration in spring (May) and fall (September) were 13.3 ± 1.3°C and 15.3 ± 0.8°C, while average total
precipitation was 51.8 ± 33.7 and 72.1 ± 43.1 mm, respectively (Environment and Climate Change Canada).

**Study Species**

We assessed mass gain and stopover behavior for 5 warbler (Parulidae) and 5 sparrow species (Passerellidae; see Table 1 for scientific names for all species). Each species exceeded a minimum threshold of 10 captured individuals per season per year, and at least 20 recaptured birds per species over the study period. The warbler species are primarily foliage-gleaning insectivores during migration, with all but one foraging primarily in the mid- to upper-canopy, while sparrows are omnivorous, ground-foraging species (Table 1). Therefore, comparisons between families represent differences in dietary and foraging guilds, while within-family comparisons can highlight differences between migration strategies. Relative migration distance was reduced to 2 categories, short or medium-long, calculated by taking the great circle distance between the centroid of the breeding and nonbreeding ranges (La Sorte et al. 2013). For Fox Sparrow (*Passerella iliaca*), migration distance was based on the Sooty subspecies (*P. i. unalaschcensis*). Using eBird data (Sullivan et al. 2009), each species was also classified as a breeding or winter resident at Iona Island when the presence was noted on ≥5% of checklists during peak breeding (June) or winter seasons (January), respectively (Table 1). This does not necessarily reflect residence status in the greater surrounding region, but, in combination with migration distance, indicates whether species are close to their destination.

**Bird Banding**

We used 15, 4-panel mist-nets (12-m long, 2.6-m high, 30-mm mesh size) evenly distributed across ~3 ha of forest, shrub, and wetland habitat. In spring, birds were captured daily from April 15 to May 31 (~45 days), and in fall, from late...
August to late October (~60 days). Mist-nets were opened for 7 hr each day, starting half an hour before dawn. For each captured bird, we recorded (1) age and sex based on Pyle (1997), (2) wing length (±0.5 mm), (3) mass (±0.01 g), and (4) fat on a scale from 0 (no fat) to 7 (Ralph et al. 1993). Capture time and date were also recorded. Age was collapsed to hatch-year (HY) and after hatch-year (AHY).

**Body Mass Variables**

For each bird, we estimated lean body mass (LBM; Owen and Moore 2006) by fitting a species-specific regression of body mass on wing length for birds with a fat score of zero:

\[
\text{Lean body mass (LBM)} = \beta_0 + \beta_1 \text{ (wing length)}
\]  

Beta (\(\beta\)) values for each species can be found in Supplementary Material Table A1. The difference between measured and lean body mass at capture as a percentage of lean body mass (hereafter “fuel index”) was calculated to estimate the proportion of mass attributable to fat:

\[
\text{Fuel index (\%) } = \left(\frac{\text{Measured body mass} - \text{Estimated LBM}}{\text{Estimated LBM}}\right) \times 100
\]

To assess stopover mass change, we calculated the difference in measured body mass between the initial (i) and final (f) capture as a proportion of LBM:

\[
\Delta \text{Fuel index (\%)} = \left(\frac{\text{Body mass}_f - \text{Body mass}_i}{\text{Estimated LBM}}\right) \times 100
\]

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\[
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\]

**Environmental Variables**

Daily mean temperature and total precipitation were recorded at the Vancouver International Airport (World Meteorological Organization ID = 71892), 3.9 km south of IIBO. Average daily temperature and precipitation were not highly correlated (spring: \(r = -0.44\); fall: \(r = -0.48\)). However, temperature and date of the first capture were strongly correlated in both seasons (spring: \(r = 0.66\); fall: \(r = -0.72\)), so we used the residuals of a temperature by date regression as the temperature variable, where positive and negative values represented higher and lower than average temperatures for a given day. For habitat productivity, we used the Enhanced Vegetation Index (EVI) from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices dataset (MOD13Q1; Didan 2015). EVI data are estimated at 16-day intervals at a spatial resolution of 250 m² and were extracted using the NASA Earth Data search engine. We assigned each captured bird to a 16-day interval and calculated EVI for that period relative to the annual average EVI.

**STATISTICAL ANALYSIS**

**Fuel Deposition Rates**

For all individuals captured on more than one day, we fit a subset of models to assess FDR for each combination of family and season, as well as migration distance and season (\(n = 8\) models; e.g., warbler-spring, long distance-fall). Individuals recaptured over a period >10 and 14 days for spring and fall, respectively, were removed from FDR analysis to limit the influence of resident birds. These thresholds were based on visually inspecting histograms of the number of days between the first and last capture for each species and removing outliers that represented extended stays. Ultimately, 4.8% and 3.3% of warblers and 24.0% and 28.3% of sparrows in spring and fall, respectively, were removed.
We fit the change in body mass attributable to fat ($\Delta$ fuel index) as the response variable and the observed stopover duration as the primary predictor. Environmental predictors included average daily temperature residuals, daily precipitation, and EVI over the observed stopover period. We also assessed density-dependence by including the number of dietary guild-specific migrants captured during the stopover period as a predictor (Cohen et al. 2022). We included fuel index at initial capture (fuel index) to control for different starting conditions among individuals. All models also included ordinal date of first capture for relative phenology and time of day at last capture, minus those values for first capture. The latter standardizes mass measurements to the same time period at first and last capture to account for diel fluctuations or differences in the amount of foraging time prior to capture (Moore and Yong 1991). Year was fit as a random intercept.

We compared 3 alternate structures for each of the 8 main models, including (1) species as a random intercept and (2) species as both a random intercept and slope to investigate differences in FDR among species. We included sex in the third model (3) for warblers and age for fall migration models only. Sex was only recorded consistently for warblers, as sparrows are monochromatic. Age was most reliable for both warblers and sparrows during fall migration, which is also the season that includes HY birds.

We used a hierarchical Bayesian framework to fit each model in STAN through the R package brms (Bürkner 2017). All predictors were centered and scaled to a mean of zero and a unit standard deviation to allow comparisons among species and seasons. Each model was fit using a skew-normal error distribution. We fit normal priors for the intercept and slopes, a truncated half-Cauchy prior for grouping variables, and an LKJ–Cholesky Covariance prior for correlations among grouping variables (Lewandowski et al. 2009):

\[
\begin{align*}
Y_i & \sim \text{Norm}(\gamma, \sigma) \\
\beta_0 & \sim \text{Norm}(0, 5) \\
\sigma & \sim \text{Cauchy}(0, 2) \\
cor & \sim \text{LKJ}(1)
\end{align*}
\]

Models were fit with 4 Markov chains, each with 3,000 iterations, a burn-in of 1,000, and a thinning rate of 1. We assessed convergence visually using trace plots as well as quantitatively by considering the number of divergent transitions and whether the Gelman–Rubin statistic ($\hat{R}$) was ~1. All models converged with an $\hat{R}$ equal to 1.

We compared the fit of alternate models using leave-one-out (LOO) cross-validation based on the posterior likelihood. LOO information criterion (LOOIC), LOO weights, and the expected log pointwise predictive density (ELPD) for out-of-sample estimations were calculated for each candidate model from 4,000 additional iterations. Models with the lowest LOOIC and highest LOO weight or ELPD were considered the top model (Vehtari et al. 2017).

**Fuel Index and Stopover Duration**

To investigate relationships between daily fuel index and departure probability, we again used birds captured multiple times within a season. Each individual capture event was designated as the last time a bird was captured (1) or not (0) as the response variable in a binomial logistic regression to model departure probability. Fuel index at capture was the primary predictor, while ordinal date and time of capture were included as covariates, year and individual ID as random intercepts, and species as a random intercept and slope to explicitly model differences among species. We also tested an alternate model assessing the influence of average temperature and total precipitation on departure probability. We fit models using the same Bayesian model structure, priors, and model comparison approach as described above.

To estimate stopover duration and assess the association between initial fuel index and the subsequent length of stay, we used all birds captured, whether once or multiple times, except those recaptured >10 days (spring) or 1–4 days (fall) after their initial capture as described earlier. For recaptured birds, we used the fuel index from the first captures only. Individual capture histories denoted whether a bird was captured (1) or not (0) for every day within a banding season where mist-netting took place. We fit Cormack–Jolly–Seber (CJS) models to estimate apparent survival from mark-recapture data (Schaub et al. 2001). Apparent survival probability ($\phi$) is the probability that a marked bird remained at the stopover site from one capture to the next, whereas the capture probability ($P$) is the probability that a marked bird alive after capture at the time $i$ is captured again at $i + 1$ (Lebreton et al. 1992).

We fit CJS models using a Markov Chain Monte Carlo (MCMC) approach with a probit link in the package marked (Laake et al. 2013) and accounted for individual heterogeneity in survival and capture probabilities using individual grouping factors (Gimenez and Choquet 2010). We also included year as a random grouping factor to account for annual variation.

We estimated recapture ($P$) and survival ($\phi$) probabilities using the following equations:

\[
P \sim \beta_0 + \beta_1 \text{ (species) + (1|year)}
\]

\[
\phi \sim \beta_0 + \beta_1 \text{ (fuel index)} + \beta_2 \text{ (ordinal date)} + \beta_3 \text{ (species) + (1|year)}
\]

Thus, we assumed that the probability of recapture was constant within a season but allowed it to vary among seasons.
During model fitting, initial values for $P$ and $\phi$ were estimated with a random Bernoulli process on a subset of the capture histories (Laake et al. 2013). For both $P$ and $\phi$, we fit multivariate normal priors for fixed effects and an inverse gamma distribution for random effect variance components:

$$
\beta_k \sim \text{Norm}(\mu, \sigma) \sim \text{Norm}(0, 0.01 \times (XX)^{-1})
$$

$$
\sigma \sim \text{Inverse Gamma} \ (a, b) \sim \text{Inverse Gamma} \ (2, 0.0001)
$$

Where $XX$ is the covariance matrix. Each model was run with 4 Markov chains of 3,000 iterations and a 1,000 burn-in.

To estimate days until departure, we extracted the mean daily probability of survival ($\phi$) from the posterior probability distribution and used the life-expectancy formula (Seber 1982):

$$
\text{Days until departure} = 1 / \ln(\phi)
$$

(6)

This approach estimates the duration of time spent at the stopover location after initial capture but does not account for days prior to capture. Therefore, we also estimated recruitment probability using a reverse-time CJS model (Pradel 1996, Nichols 2016). Mean estimated recruitment probability ($\Upsilon$) was extracted from the posterior distribution for all species, seasons, and ecological traits among short-distance migrant species (Figure 4).

To estimate days until departure, we extracted the mean daily probability of survival ($\phi$) from the posterior probability distribution and used the life-expectancy formula (Seber 1982):

$$
\text{Stopover duration} = 1 / \ln(\phi) + 1 / \ln(\Upsilon)
$$

(7)

Analyses were conducted using R version 4.1.1 (R Core Team 2021). We report standardized effect sizes and the 93% credible intervals (CIs) to evaluate the level of support for each association. Estimated effect size and 93% CIs were extracted from the posterior distribution for all species individually, as well as averaged among species with similar diets (insectivore, omnivore) and migration distances (short, long) for trait-level comparisons within the migrating community.

RESULTS

From 2010 to 2019, we captured a total of 22,370 warblers and 7,324 sparrows. Of these, 2,375 warblers and 884 sparrows were recaptured within the same season and were used to estimate FDRs (Table 2). Peak warbler (insectivore) migration across years, calculated from the full dataset, was approximately May 7 and September 5, while sparrow (omnivore) migration peaked around April 24 and October 1 (Table 2). In spring, peak migration for long-distance migrants was later (May 10) than short-distance migrants (April 26) but earlier during southward fall migration (long: September 6; short: September 23).

FDRs: Species and Seasonal Differences

FDR varied widely among species, seasons, and ecological traits (Table 2). In spring, all insectivores except Common Yellowthroat exhibited positive FDRs, indicating individuals gained mass during stopover on average (Figure 2A). In fall, only long-distance migrants exhibited a positive FDR: Orange-crowned, Yellow, and Wilson’s warbler (Figure 2B). Omnivores exhibited lower FDRs or a weaker association between stopover days and relative mass gain. In spring, Golden-crowned, Lincoln’s, and, to a lesser extent, Fox sparrows had positive FDRs (Figure 3A). In fall, the long-distance migrant, Lincoln’s Sparrow, had the greatest FDR, whereas the short-distance migrant, Fox Sparrow, had a marginally positive FDR (Figure 3B). On average, FDR was greater for insectivores, long-distance migrants, and during spring migration (Table 2).

Overall, we found weak sex and age effects on FDR, although these results must be interpreted with caution as sex and age classifications were inconsistent among families and seasons (see Methods). During spring migration, male insectivores exhibited greater mass gain than females ($\beta = 0.13$, 93% CI: 0.03–0.23), translating into an average FDR of 1.4% more per day. However, there were no sex differences during fall migration ($\beta = 0.01$, 93% CI: –0.09 to 0.09). During fall migration, age factored into the top model for insectivores (Supplementary Material Table A2), but the association was insignificant ($\beta = 0.05$, 93% CI: –0.07 to 0.18). Finally, capture date had the strongest effect for insectivores during the spring, where later-arriving birds were associated with greater mass gain ($\beta = 0.08$; 93% CI: 0.01–0.15), but was otherwise not influential for omnivores, short-, or long-distance migrants.

FDRs: Environmental and Density-Dependent Effects

The refueling rate was influenced by temperature, precipitation, and habitat productivity (EVI) across species, particularly during spring migration. FDRs of insectivores were greater with above-average temperatures and EVI in both seasons but decreased with greater precipitation during the spring (Figure 4). In contrast, omnivores were generally not influenced by environmental conditions but did suffer reduced refueling rates under heavier precipitation during northward spring migration (Figure 4). For long-distance migrants, FDR was positively associated with average temperatures in the fall, as well as EVI in both seasons, but was negatively associated with precipitation during the spring (Figure 4). We found no consistent associations between refueling rate and environmental conditions among short-distance migrant species (Figure 4).

We found evidence for density-dependent FDR for insectivorous and long-distance migrant species during spring.
Greater migrant density was associated with decreased FDR in the spring ($\beta = -0.11$; 93% CI: $-0.18$ to $-0.04$), but not fall ($\beta = 0.02$; 93% CI: $-0.06$ to 0.10), while density-dependent effects were absent for omnivores (spring: $\beta = 0.17$; 93% CI: $-0.02$ to 0.36; fall: $\beta = 0.10$; 93% CI: $-0.03$ to 0.24). Similarly, refueling rates of long-distance migrants exhibited negative density-dependence in the spring ($\beta = -0.17$; 93% CI: $-0.26$ to $-0.09$) compared with fall ($\beta = 0.03$; 93% CI: $-0.06$ to 0.12), while we did not detect an association in short-distance migrants (spring: $\beta = 0.09$; 93% CI: $-0.03$ to 0.29; fall: $\beta = 0.05$; 93% CI: $-0.02$ to 0.12).

**Fuel Index and Stopover Duration**

For insectivores measured multiple times, fuel index was positively associated with departure probability in both spring ($\beta = 0.51$, 93% CI: 0.14–0.94) and fall ($\beta = 0.38$, 93% CI: 0.02–0.71; Figure 5A, B). In contrast, omnivores did not exhibit associations between fuel index and departure probability during spring ($\beta = 0.14$, 93% CI: $-0.06$ to 0.34) or fall migration ($\beta = 0.26$, 93% CI: $-0.01$ to 0.50; Figure 5C, D). Fuel index was strongly and positively associated with departure probability for long-distance migrants in both seasons (spring: $\beta = 0.55$, 93% CI: 0.28–0.83; fall: $\beta = 0.46$, 93% CI: 0.22–0.64). However, there was no association for short-distance migrants (spring: $\beta = 0.19$, 93% CI: $-0.33$ to 0.73; fall: $\beta = 0.21$, 93% CI: $-0.21$ to 0.60).

Weather influenced departure probability in fall, but not spring (Supplementary Material Table A3). In fall, insectivores were less likely to depart under warmer temperatures ($\beta = -0.16$, 93% CI: $-0.26$ to $-0.05$) and more likely to depart with greater precipitation ($\beta = 0.14$, 93% CI: 0.06–0.37). Omnivores did not respond to temperature...
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Songbird stopover dynamics

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Using all captured birds to estimate stopover duration, 3 general patterns emerged among species: (1) stopover duration was shorter in spring than fall for all species, (2) insectivores tended to exhibit shorter stopovers than omnivores, and (3) long-distance migrants had shorter stopover periods than short-distance migrants (Table 3). Fuel index at initial capture was an important predictor of length of stay, particularly for insectivores and long-distance migrants. During spring, insectivores with greater initial mass attributable to fat departed sooner ($\beta = -0.79$, 93% CI: $-1.22$ to $-0.39$), but there was no evidence for this association in omnivores ($\beta = -0.72$, 93% CI: $-1.50$ to $0.05$). During fall migration, insectivores exhibited a similar association, with heavier-upon-arrival individuals leaving sooner ($\beta = -0.66$, 93% CI: $-1.05$ to $-0.37$). However, omnivores had no clear association between stopover length and mass at capture ($\beta = -0.35$, 93% CI: $-1.03$ to $0.35$).

**DISCUSSION**

We demonstrate that refueling rate and stopover dynamics vary between seasons and among passerine species in a predictable manner based on ecological traits, such as diet and migration distance. FDRs were higher for insectivorous warblers, but across taxa were generally greater during spring migration and for long-distance migrants. Environmental conditions, such as temperature, precipitation, and habitat productivity, also influenced refueling rate, with particularly strong associations for insectivores and long-distance migrants. Similarly, migrant density negatively influenced the refueling rate for insectivores and long-distance migrants during spring migration, highlighting the potential importance of density-dependent competition for time-limited migrants reliant on variable conditions.

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**FIGURE 2.** Species-level slope estimates from the random slope model for warblers during the spring (A) and fall (B). The density plot on the left indicates whether there is a significant association between the number of days between capture and mass gain by whether the thin black bar (93% CI) or thick black bar (83% CI) crosses the dotted zero line. The density curve is the posterior distribution depicting the spread of estimates from 3,000 model iterations, with red (or orange) being a negative estimate and blue a positive estimate. The right panels include the predicted slopes, or FDR, for each species, with the raw data points and the 93% CI of the partial residuals as shaded bands. Individuals with a stopover length of zero (recaptured within a single morning only) are included in the figure to show the full range of values but were not included in estimates of FDR or stopover length to remove the potential influence of transients.

($\beta = 0.02$, 93% CI: $-0.21$ to $0.26$) but were more likely to depart under greater precipitation ($\beta = 0.22$, 93% CI: $0.07$–$0.37$). Long-distance migrants were similarly more likely to depart in response to poor prevailing conditions (temperature: $\beta = -0.25$, 93% CI: $-0.36$ to $-0.13$; precipitation: $\beta = 0.14$, 93% CI: $0.06$–$0.22$), and short-distance migrants under heavier precipitation ($\beta = 0.21$, 93% CI: $0.07$–$0.35$).
resources. Finally, stopover duration and departure probabilities were more closely associated with body condition (fuel index) at first capture and subsequent mass gain than direct environmental effects, providing support for a refueling threshold and time minimization behavior, especially during spring when songbirds are traveling to their breeding site. These results underscore how the use and importance of certain stopover sites vary among species.
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depending on their life-history strategies, with implications for long-distance, migratory insectivores, which may be particularly susceptible to habitat and climate change.

FDRs: Species and Seasonal Comparisons

FDRs varied widely among species, with most falling within the upper range for passerines (about 1–3% day\(^{-1}\); Lindström 2003, Chernetsov 2012), although sparrows were generally on the lower end of the spectrum. These differences may be related to diet or foraging behavior. Warblers are primarily insectivores, whereas sparrows are omnivores and are, therefore, less reliant on insect prey. Beyond resource quality, a higher FDR may reflect the reliance of insectivores on variable resources or an ability to maximize energy gain during ephemeral resource pulses (Moore and Simm 1986). Except for Common Yellowthroat, the insectivorous species we addressed tend to forage in the mid- to upper canopy, compared with the ground-foraging omnivores. This niche separation may produce unmeasured differences between guilds in food availability or quality and perceived risk. Perceived risk can negatively impact FDR as individuals divert time and energy from foraging to territorial or risk avoidance behaviors (Jonker et al. 2010). Iona Island is a popular recreational site and ground-foraging sparrows may be more easily disturbed by passing visitors.

Pronounced differences in FDR were also associated with migration distance. Long-distance migrants had greater FDR than short-distance migrants, particularly in spring. Long-distance migrants incur high energetic costs, promoting greater reliance on refueling stopovers and likely a stronger link between mass gain and stopover dynamics (Newton 2008). Spring migration is often more rapid than fall migration, as early arrival at breeding sites can have pronounced fitness benefits, selecting for rapid refueling to limit stopover duration (Nilsson et al. 2013). As birds approach their destination, FDR may also be expected to lessen, with individuals monitoring prevailing conditions and maximizing fuel loads to prepare for the energetic costs of breeding, decoupling the association between mass gain and stopover length (Hedenström 2008, Paxton and Moore 2017). Short-distance migrants, such as Common Yellowthroat or Song Sparrow, had near-zero FDR during both spring and fall migration, potentially because they were nearer to their breeding and wintering site than long-distance migrants (Table 1).

FDRs: Environmental and Density-Dependent Drivers

During spring, the refueling rates of long-distance, migratory insectivores appeared particularly sensitive to suboptimal environmental conditions, such as cold temperatures and heavy precipitation, which likely influences
food availability, search efficiency, and foraging costs (McNamara et al. 1994). Environmental conditions can strongly impact insect activity and abundance (Choi 2008), such that insectivores may be more at risk from resource disruptions than omnivores, which may be more resilient due to greater dietary flexibility and breadth (Yong and Moore 2005). Insectivores also exhibited greater annual and individual variation in FDR compared with omnivores, potentially matching fluctuations in prevailing conditions among years and arrival dates. Similarly, long-distance migrants may be more likely to arrive in nutritional distress, increasing their susceptibility to poor weather conditions or variable resource availability (Bayly et al. 2021). Short-distance migrants, potentially being less time- or energy-limited, may thus be more resilient to short-term environmental challenges.

Greater habitat productivity was positively associated with spring FDR for insectivores, but not omnivores, potentially driven by a close association between vegetation phenology and insect biomass (Fernández-Tizón et al. 2020). Timing migration to match peaks in habitat productivity may, therefore, be particularly vital for insectivores (Youngflesh et al. 2021), a relationship that is likely more pronounced in the spring (La Sorte and Graham 2021). In spring, stopover site vegetation is in the early stages of foliation, whereas in fall, vegetation cover persists later in the season when most migrants have departed. In fact, insectivores that arrived later in spring gained mass more quickly, suggesting that they may be experiencing more optimal conditions than earlier in the season when resources and prevailing weather may be less reliable. While it is possible that this relationship is driven by a greater abundance of long-distance migrants later in the season, this result provides some support for a potential food availability mechanism, which deserves further study. As shifting phenology and greater annual weather variation is expected under climate change (Haest et al. 2018), associations between FDR and weather have important implications for maintaining energy balances during migration, survival, and reproductive success.

Competition among migrants over limited resources may constrain refueling rates at stopover sites (Moore and Yong 1991, Cohen and Satterfield 2020). We found evidence for density-dependent refueling rates for insectivores and long-distance migrants during spring migration. These results align with studies suggesting that competitive interactions may occur even with relatively abundant resources or low migrant densities (Kelly et al. 2002, Cerasale

### TABLE 3. Spring and fall estimates of stopover duration for the 5 most common warbler and sparrow species at Iona Island Bird Observatory from 2010 to 2019. Mean and standard deviation (SD) values were extracted from a Bayesian posterior distribution representing 3,000 iterations, while LCI and UCI are the upper and lower 93% CIs, respectively.

| Species Code | Migration | Mean ± SD (days) | LCI   | UCI   |
|--------------|-----------|------------------|-------|-------|
| Spring       |           |                  |       |       |
| Insectivores (warblers) | | | | |
| Common Yellowthroat | COYE | Short | 6.71 ± 0.28 | 4.95 | 8.31 |
| Yellow-rumped Warbler | YRWA | Short | 4.26 ± 0.27 | 3.66 | 5.06 |
| Orange-crowned Warbler | OCWA | Long | 3.11 ± 0.27 | 2.67 | 3.55 |
| Wilson’s Warbler | WIWA | Long | 2.76 ± 0.23 | 2.50 | 2.90 |
| Yellow Warbler | YEWA | Long | 3.00 ± 0.36 | 2.40 | 5.27 |
| Omnivores (sparrows) | | | | |
| Fox Sparrow | FOSP | Short | 7.62 ± 0.32 | 5.27 | 11.20 |
| Song Sparrow | SOSP | Short | 10.39 ± 0.28 | 7.86 | 14.24 |
| Lincoln’s Sparrow | LISP | Long | 3.81 ± 0.32 | 2.92 | 4.99 |
| Golden-crowned Sparrow | GCSP | Long | 2.54 ± 0.38 | 1.75 | 3.81 |
| White-crowned Sparrow | WCSP | Long | 2.96 ± 0.44 | 1.80 | 6.18 |
| Fall         |           |                  |       |       |
| Insectivores (warblers) | | | | |
| Common Yellowthroat | COYE | Short | 6.97 ± 0.25 | 5.78 | 7.93 |
| Yellow-rumped Warbler | YRWA | Short | 7.25 ± 0.30 | 5.20 | 9.62 |
| Orange-crowned Warbler | OCWA | Long | 4.12 ± 0.26 | 3.71 | 5.00 |
| Wilson’s Warbler | WIWA | Long | 5.11 ± 0.28 | 4.10 | 6.08 |
| Yellow Warbler | YEWA | Long | 5.14 ± 0.21 | 4.89 | 5.52 |
| Omnivores (sparrows) | | | | |
| Fox Sparrow | FOSP | Short | 8.70 ± 0.14 | 7.26 | 10.56 |
| Song Sparrow | SOSP | Short | 10.24 ± 0.12 | 8.36 | 12.84 |
| Lincoln’s Sparrow | LISP | Long | 4.72 ± 0.15 | 3.06 | 8.53 |
| Golden-crowned Sparrow | GCSP | Long | 8.55 ± 0.17 | 6.50 | 11.50 |
| White-crowned Sparrow | WCSP | Long | 6.03 ± 0.29 | 4.07 | 10.94 |
Insectivores and long-distance migrants may be more affected by density-dependent factors if they are reliant on narrow resource pulses. Greater flexibility in diet and foraging niches (e.g., omnivores) or departure decisions (short-distance migrants) may lessen daily competitive pressures. While we did not test for it here, suboptimal conditions have the potential to both strengthen density-dependent effects or lessen direct resource competition (Rappole and Warner 1976, Jensen et al. 2016). Future research should address interactions between environmental conditions and migratory capacity, and long-term mist-netting data are a valuable resource (Cohen and Satterfield 2020).

**Fuel Index and Stopover Duration**

In line with the time-minimization hypothesis, stopover duration was up to 2 to 4 times shorter in spring compared with fall for several species, likely reflecting the selective advantage of continuing migration and arriving at the breeding site early (Morrison et al. 2019). In addition, long-distance migrants had relatively shorter stopovers than short-distance migrants. Long-distance migrants may be under greater pressure to quickly refuel and continue migration given stronger time limitations and, as a result, potentially less capacity for flexible migratory behaviors (Alerstam et al. 2003, Alerstam 2011). Interestingly, stopover duration of insectivores, but not omnivores, was negatively associated with initial fuel index, suggesting that poor body condition is not associated with increased FDR as expected under the time-minimization hypothesis (Lindström and Alerstam 1992, Alerstam 2011). Instead, insectivores arriving in energetic distress may remain longer to prioritize recuperating energy reserves prior to departure, without necessarily increasing FDR to leave earlier (Bayly et al. 2021, Schmaljohann et al. 2022). Omnivores, on the other hand, are either not remaining to recuperate energy or their fuel loads are not as closely tied to departure decisions.

A positive association between fuel load and departure in insectivores potentially indicates a fuel threshold that dictates departure in insectivorous, but not omnivorous species. Departure probability of insectivore and long-distance migrants was unrelated to weather during spring migration, but, during fall, departure probability increased with colder, wetter conditions. Since the refueling rate was highly responsive to weather, but spring departure probability was not, this suggests that insectivorous, long-distance migrants will continue spring migration when a certain fuel threshold is achieved, regardless of prevailing conditions (i.e. time minimization). Although, we note that we did not address wind dynamics here, which can have pronounced effects on departure decisions (Åkesson and Hedenström 2000). During fall migration, however, weather associations indicated that insectivores are potentially being pushed southward by poor weather conditions (Prytula et al. 2021). Warmer, drier weather may allow individuals to remain farther north, while deteriorating conditions may signal individuals to continue southward migration. The apparent importance of a fuel threshold, particularly during spring migration, further emphasizes the critical nature of high-quality stopover habitats that allow for rapid fuel accumulation.

Banding stations can be powerful tools for studying stopover dynamics, but they are not without limitations. Two subspecies of White-crowned Sparrow, the long-distance migrant Z. l. gambelii and locally breeding Z. l. pugetensis, migrate through the study site (McCallum 2021). Captured birds were inconsistently classified into subspecies, which could explain the unusual variance in FDR and departure probability observed for this species. Furthermore, we removed resident birds from consideration by imposing a length-of-stay threshold. While we believe this was largely successful, we likely could not remove all residents, which may skew results for short-distance migrants in particular and suggest that results are most reliable for long-distance migrants. Finally, while we assumed individuals that were not captured again had continued migration, poor resource availability or transience may cause birds to move beyond the study site but remain within the general area (Schaub et al. 2008, Taylor et al. 2011). We still demonstrated strong associations between refueling rate and stopover dynamics, but future research should use telemetry to better understand how migrating birds use the broader region during stopovers.

**Conclusion**

When comparing among species, ecological traits such as diet and migration distance are strong predictors of refueling rates and set limits on the extent to which extrinsic factors like weather can influence stopover dynamics. Within species, extrinsic factors drive variation in FDR between seasons and among individuals, although the strength of environmental effects on stopover duration and departure probability may be dependent on seasonal destinations and the function of a stopover site (Buler and Moore 2011, Schmaljohann et al. 2022). Ultimately, observed variation in stopover behavior suggests that species may respond to rapidly changing climatic conditions in a predictable manner, conditional on shared ecological traits. While relatively high refueling rates suggest the potential for Iona Island to be a high-quality stopover site, further research is required to address other indices of quality and its importance relative to the surrounding region. Banding stations are valuable for monitoring songbirds long-term. Land managers are encouraged to partner with and support these volunteer-led programs to assess habitat quality and how stopover dynamics might change over time in response to climate shifts, land-use change, and habitat restoration efforts (Dunn 2016).
SUPPLEMENTARY MATERIAL

Supplementary material is available at Ornithology online.

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Data availability: Analyses reported in this article can be reproduced using the data and code provided by de Zwaan et al. (2022a, 2022b).

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