Ornithology
AmericanOrnithology.org

Volume 139, 2022, pp. 1–16
https://doi.org/10.1093/ornithology/ukab083

RESEARCH ARTICLE

Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes

Ana Morales,[1,*] Barbara Frei,[2,3] Greg W. Mitchell,[3] Camille Bégin-Marchand,[3] and Kyle H. Elliott[1]

[1] Department of Natural Resource Sciences, McGill University, Ste. Anne-de-Bellevue, Quebec, Canada
[2] McGill Bird Observatory, Ste. Anne-de-Bellevue, Quebec, Canada
[3] Environment and Climate Change Canada, Ottawa, Ontario, Canada
* Corresponding author: ana.morales@mail.mcgill.ca

Submission Date: May 25, 2021; Editorial Acceptance Date: November 3, 2021; Published January 5, 2022

ABSTRACT

Migration consists of a sequence of small- to large-scale flights often separated by stopovers for refueling. Tradeoffs between minimizing migration time (more flights, shorter stopovers) and maximizing energy gain (fewer flights, longer stopovers) will affect overall migration timing. For example, some individuals make long-term stopovers in high-quality habitat that maximize energy gain (e.g., molt-migration), but movement to those habitats likely costs time. We used radio telemetry and blood plasma metabolite levels to examine physiological and behavioral tradeoffs between molt-migrant (birds molting at the molt stopover; $n = 59$) and post-molt (birds that presumably completed their molt elsewhere; $n = 19$) migrant Swainson's Thrushes (*Catharus ustulatus*) near Montreal, Canada. Molt-migration was a large time investment as the average stopover duration for molt-migrants was of 47 ± 9 days (~13% of the entire annual cycle), almost twice as long as previously assumed from banding records, and far longer than stopovers of post-molting individuals (7 ± 2 days). Daily mortality rate during the molt stopover was similar to the average annual daily mortality rate. Molt-migrants' circadian rhythms closely matched light levels, whereas post-molting birds had irregular rhythms and averaged 1 hr greater activity per day than molt-migrants. Despite being less active, molt-migrants had similar refueling rates based on metabolite profiles. As compared with migrants that completed molt earlier, molt-migrants at this stopover site had slower subsequent migration rates. Thus, birds using long-term stopovers appeared to tradeoff energy (efficient refueling) for time (slower subsequent migration).

Keywords: Catharus ustulatus, circadian rhythm, metabolites, migration rate, molt-migration, radio telemetry, stopover

LAY SUMMARY

- Migratory birds must balance the energy and time costs of molt and migration, and the strategies they employ to overcome this challenge can vary within the same species.
- We captured and tracked molt-migrant (birds molting at the molt stopover) and post-molt-migrant (birds that presumably completed their molt elsewhere before capture) Swainson's Thrushes (*Catharus ustulatus*) at the same stopover site to test the expectation that molting birds remain longer and are less active but have similar refueling rates, as compared to post-molting migrants
- Molting birds were less active and remained six times longer than post-molting migrants while refueling rates did not differ between the two groups.
- Subsequent southward migration rates of molting birds were slower than the post-molting birds.
- Understanding molt-migration at these important stopovers provides insights into why some individuals undergo molt-migration and others do not.

Réduction de l'activité diurne et augmentation de la durée de la halte migratoire chez *Catharus ustulatus* en mue

RÉSUMÉ

La migration consiste en une séquence de vols de petite à grande envergure souvent séparés par des haltes migratoires pour le ravitaillement. Les compromis entre la réduction au minimum du temps de migration (plus de vols, haltes migratoires plus courtes) et la maximisation des gains énergétiques (moins de vols, haltes migratoires plus longues)

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

Copyright © American Ornithological Society 2022. All rights reserved. For permissions, e-mail: journals.permissions@oup.com.

affecteront le moment de la migration en général. Par exemple, certains individus font des haltes migratoires dans un habitat de grande qualité qui maximise les gains énergétiques (p. ex., migration de mue), mais les déplacements vers ces habitats nécessitent du temps. Nous avons utilisé la radiotélémétrie et les niveaux de métabolites dans le plasma sanguin afin d'examiner les compromis physiologiques et comportementaux entre des individus en migration de mue (oiseaux muant à la halte de mue; *n* = 59) et des individus en migration post-mue (oiseaux ayant vraisemblablement complété leur mue ailleurs; *n* = 19) de *Catharus ustulatus* près de Montréal, au Canada. La migration de mue représentait un important investissement en temps, car la durée moyenne des haltes migratoires pour les individus en migration de mue était de 47 ± 9 jours (~13 % du cycle annuel complet), soit presque deux fois plus de temps que ce qui était supposé auparavant à partir des données de baguage, et beaucoup plus de temps que les haltes migratoires des individus en migration post-mue (7 ± 2 jours). Le taux de mortalité quotidien au cours de la halte de mue était similaire au taux de mortalité quotidien moyen annuel. Les rythmes circadiens des individus en migration de mue correspondaient étroitement aux niveaux de lumière, alors que les oiseaux en post-mue avaient des rythmes irréguliers et étaient en moyenne 1 heure plus actifs par jour que les individus en migration de mue. Bien qu'ils aient été moins actifs, les individus en migration de mue avaient des taux de ravitaillement similaires selon les profils des métabolites. Comparés aux individus en migration qui complétaient leur mue plus tôt, les individus en migration de mue sur ce site de halte migratoire avaient des taux de migration subséquents plus lents. Ainsi, les oiseaux utilisant des haltes migratoires à long terme semblaient échanger l'énergie (ravitaillement efficace) contre le temps (migration subséquente plus lente).

Mots-clés: *Catharus ustulatus*, rythme circadien, métabolites, taux de migration, migration de mue, radiotélémétrie, halte migratoire

INTRODUCTION

For migratory birds, seasonal phenology involves tradeoffs in energy investment between breeding efforts, molting, and migration (Lindström et al. 1993, 1994; Cyr et al. 2008; Bridge et al. 2016). After breeding and prior to migration, many birds molt their flight feathers as the structural integrity of the feather is critical for their successful migration thousands of kilometers to their wintering grounds (Swaddle and Witter 1997; Bridge et al. 2016; Tonra and Reudink 2018). However, some bird species have evolved a strategy known as "molt-migration" in which both migration and molt overlap. Molt-migration, an extended stopover during migration where plumage molt occurs, is an example of this type of molt strategy in birds (Pyle et al. 2009; Tonra and Reudink 2018). By completing a partial migration to areas that are productive in late summer, molt-migrants can optimize their energy gain during that period and increase their survival rates (Pyle et al. 2009; Pageau et al. 2020). For instance, in late summer some songbirds in western North America leave their arid breeding grounds and move to the productive monsoon region of northwestern Mexico to molt, before continuing to their primary wintering grounds (Contina et al. 2013; Pageau et al. 2020). While thought to be rarer in eastern North American songbirds, several eastern species do engage in long stopovers during migration to molt their flight feathers (Cherry 1985; Voelker and Rohwer 1998; Leu and Thompson 2002; Morris et al. 2013; Pyle et al. 2018).

Decisions about where and when to molt or migrate are likely driven, in part, by refueling rates at different sites (Guglielmo et al. 2005; Pyle et al. 2009; Seewagen et al. 2013). Selection of stopover sites that allow for high fuel deposition rates (i.e. high-quality sites) is essential for migrating birds (Chernetsov 2006). For molt-migrants, high-quality sites are even more crucial because of the high energetic demands of molt (deGraw et al. 1979; Hemborg and Lundberg 1998; Portugal et al. 2007; Cornelius et al. 2011). Due to high energy needs of growing feathers, molt can inhibit fuel deposition, lowering triglycerides and cholesterol levels, and subsequently increasing glucose levels, due to the catabolism of triglycerides during molt (deGraw et al. 1979; Schaub and Jenni 2000; Podlaszczuk et al. 2017). In contrast, molt-migrants may take advantage of high-quality stopover sites so that refueling rates stay relatively high, despite the molt. For these birds, plasma metabolite profiles should remain similar to those of actively migrating individuals where refueling rates are high during stopovers (Guglielmo et al. 2005). In this sense, they may follow the receding "green wave" southward rather than staying at rapidly deteriorating breeding sites (Bridge et al. 2016).

High refueling rates at molt-migrant stopovers may also be reflected in reduced foraging activity each day. Indeed, diel activity cycles may also play an important role in stopover energetics as migrating birds extend diel activity to increase time available for refueling (Rattenborg et al. 2004; Da Silva et al. 2014). For instance, Morbey et al. (2018) found differences in the timing of diel activity between sexes of two wood-warbler species, with males beginning diel activity earlier, and ending diel activity later than females, potentially explaining why males can have higher refueling rates than females (Seewagen 2013). However, no difference in refueling rates or stopover duration was found between sexes, suggesting that other factors may be at play (Morbey et al. 2018). Molting birds on the other hand may face the choice of maximizing foraging rates to meet the energetic requirements of molt through increased activity rates, or reducing diel activity rates to increase resting rates to expedite the molting period and reduce predation (Pyle

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

et al. 2009; Tonra and Reudink 2018). Therefore, selection of highly productive sites that would allow molt-migrants to achieve lower activity rates and high refueling rates at the same time could be key during this critical period of their life cycle.

Although molt-migrants may achieve higher energy intake rates than birds molting at breeding sites, finding a suitable molting site may take time. For example, molt-migrants may not initiate molt until they find a suitable molting site, and molting sites may not necessarily be directly on the migration route to their wintering grounds (Kjellén 1994; Pyle et al. 2009; Tonra and Reudink 2018). Thus, molt-migrants may face a penalty in terms of time to complete migration (Holmgren and Hedenström's 1995). Indeed, molt-migration is expected to take considerable time, with banding records estimating a molt-migration stopover of ~32 days or 8 times longer than non-molting individuals (Cherry 1985; Junda et al. 2020). It is currently unclear how this penalty will affect the birds on their subsequent migration to their wintering sites and whether molt-migrants will adopt a different migration strategy than birds molting at the breeding sites (or face the same tradeoffs). Furthermore, departure decisions can greatly influence the subsequent migration rates and arrival at wintering grounds for time-constrained migratory birds facing increasingly deteriorating conditions (Dossman et al. 2016). Intrinsic (i.e. fuel stores, sex, and age) and extrinsic (i.e. weather, time of year, migratory barriers) factors can influence timing of departure from stopovers so as to maximize subsequent migration rates (Schaub et al. 2008; Dossman et al. 2016; Schmaljohann and Eikenaar 2017). To make up for lost time spent at the molt stopover, time-constrained molt-migrants may delay departure and wait for favorable weather conditions that will help them achieve faster migration rates than "regular" migrants after departure (Pyle et al. 1993). However, spending time at a deteriorating stopover could be energetically expensive, with birds sometimes spending twice as much energy during a stopover than during a migratory flight (Wikelski et al. 2003). Nonetheless, their knowledge of the molt stopover site may allow them to risk waiting for favorable conditions as opposed to a transient migrant that is not familiar with the area. On the other hand, once they depart, molt-migrants could also have slower subsequent migration rates if they have not yet had sufficient time for the many physiological changes needed for long-distance migration.

Here, we investigate the occurrence of molt-migration in the Swainson's Thrush (*Catharus ustulatus*), an insectivorous Neotropical migrant that undergoes molt-migration in eastern North America (Cherry 1985; Morris et al. 2013; Junda et al. 2020). Molt-migrant Swainson's Thrushes are after-hatch-year individuals that do not molt at their breeding grounds but migrate to another area during late summer, to undertake their post-breeding molt before moving to their wintering grounds in Central and South America. Furthermore, not all individuals of this species seem to undergo molt-migration, presumably molting near their breeding grounds (Cherry 1985; Pyle et al. 2018; Junda et al. 2020). In this study, we compared molt-migrants at a molting stopover site with later arriving migrating individuals that have already completed their molt. The latter may have molted in or near their breeding grounds or at a different stopover location nearby.

We aimed to provide the first detailed information on fall stopover durations for a molt-migrant songbird in Eastern North America and we predicted that molt-migrants would stop over for a significantly longer period of time than post-molt-migrating individuals (Hypothesis 1, Table 1). Furthermore, given that molt-migrations are typically short movements to highly productive regions, we hypothesize that metabolite profiles (i.e. glucose, cholesterol, triglycerides and β-Hydroxybutyrate; a proxy for refueling rates) will be similar between both groups despite the high energy requirements of molt (Hypothesis 2). We also predicted that activity rates as assessed by length of diurnal activity would be lower in molt-migrants (molting birds show high rates of rest presumably to expedite molt and reduce predation risk; (Lind 2001; Portugal et al. 2007; Kiat et al. 2016) despite similar refueling rates (Hypothesis 3). Finally, we predicted that time-constrained molt-migrants will make up for lost time by being selective in their departure decisions and taking the risk of waiting for favorable departure conditions resulting in faster migration rates after departing the molting site (Hypothesis 4). On the other hand, post-molt-migrants, as birds who are actively migrating and whose physiology and circadian rhythms are already altered to optimize migration and minimizing time spend at stopovers, will not risk spending too much time and energy at a stopover while waiting for favorable weather conditions and as such will not be as selective in their departure decisions.

METHODS

Study Area and Long-term Molt-Migrant Data

We worked at the McGill Bird Observatory (MBO) banding station, located at the western tip of the Island of Montreal, in Quebec, Canada (45.43°N, 73.94°W). This area is characterized by a mix of several vegetation types comprising shrubland, mature deciduous forest, hawthorn tracts, sumac stands, and remnants of an apple orchard, and is bordered by mature forest and cash crop agriculture. Research at this site has identified up to 11 species of molt-migrant songbirds that use the site as a molt stopover, including the Swainson's Thrush (Junda et al. 2020).

In addition to the standard monitoring of migratory bird populations, the MBO has collected data on

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

TABLE 1. Hypotheses and predictions that were tested in this study

Hypotheses	Predictions
1. Molt-migrants will require several weeks to replace their feathers and will not migrate until molt is complete or close to complete.	P1. Molt-migrants will stop over longer than post-molt-migrating individuals
2. Molt-migrants take advantage of high-quality stopover sites so that refueling rates are relatively high.	P2a: Despite molt being energetically costly, physiological profiles remain similar to those of actively migrating individuals where refueling rates are high during stopovers. P2b: Alternatively, molt can inhibit fuel deposition, lowering triglycerides and cholesterol and increasing glucose levels due to the catabolism of triglycerides during molt
3. Given the high-quality sites, molt-migrants will be less active than post-molt individuals as they can meet their daily energy needs (assuming energy needs are lower for birds that are not actively migrating) and reduce predation risk without needing to forage throughout the full daylight hours.	P3. Activity rates (length of diurnal activity) will be lower for molting than for post-molt-migrants
4. Molt-migrants will make up for lost time spent at the molt stopover by waiting for favorable weather conditions that will help them achieve faster migration rates than "regular" migrants after departure.	P4a. Molt-migrants will be more selective in their departure decisions, resulting in faster subsequent migration rates than post-molt-migrants P4b. Alternatively, molt-migrants will be less selective in their departure decisions and have slower subsequent migration rates as they have not yet had sufficient time for the physiological changes needed for long-distance migration

molt-migrant songbirds every fall since 2013 (with the exception of 2014) (Junda et al. 2020). Even though Swainson's Thrushes do not typically breed near our site (closest confirmed breeding population recorded 70 km away from the MBO; Robert et al. 2019), a high proportion of molting individuals of the species have been recorded every year since 2013, with numbers varying greatly from year to year (Supplementary Material Table 1). The ratio of molt to post-molt-migrants is conservative as some "post-molt-migrants" may be local molt-migrants that avoid capture during their molting period. Thus, exact molting locations of post-molt-migrant individuals are difficult to determine without the use of proper tools such as stable isotope analyses. Flight feather molt data is collected for every molt-migrant captured at the station by scoring each flight feather (primaries, secondaries, and tertials; methodological details in Newton 1966; Junda et al. 2020). Briefly, each feather is scored as old (0), absent (0.1), or as a percentage of growth in 10% increments from 0.2 to 1 (fully grown). Molt stage was calculated by adding the score of each feather and dividing it by the total number (n = 18) of feathers scored. (We did not use the P10 feather due to its small size making it difficult to score). Using capture–recapture data for birds at different molt stages, we estimated mean flight feather molt rate. Recaptures of birds at 100% molt completion were not included, as we had no means of knowing when the bird had finished molting. However, birds caught at 0% molt stage (all old feathers) were included, assuming they just arrived from their breeding grounds and were likely to start molting within one or two days of arrival.

Stopover Duration

To determine stopover duration, we used the Motus Wildlife Tracking system (Taylor et al. 2017) to monitor the presence and movements of molt-migrant and post-molt Swainson's Thrushes at our site. From July 30 to October 11, 2017, and July 21 to October 17, 2018, we captured, radio-tagged, and monitored the movements of 78 after-hatch-year Swainson's Thrushes. Birds were divided into two groups: molt-migrants (birds that were caught while molting; n = 59) and post-molt-migrants (birds that already completed their molt; n = 19). The birds were captured in mist nets during late summer (July) Monitoring Avian Population and Survivorship (MAPS) sessions and throughout the fall migration monitoring period (August to November 1) at the MBO. All birds captured were aged using molt and skull ossification methods. Standard banding measurements such as weight, fat, and wing chord were taken (Pyle 1997). If the bird was molting, flight feather molt data were noted for each individual following the method previously described. As Swainson's Thrushes do not exhibit sexual dimorphism, birds were sexed by genetic sex determination. Sexing was performed by extracting genomic DNA from 10 to 20 μL of whole blood using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). The polymerase chain reaction (PCR) was performed by following the protocol and PCR cycles from Bioline's MyFi DNA Polymerase kit using the P2 and P8 primers developed by Griffiths et al. (1998). The PCR products were run on 3% agarose gel. All work was completed under animal use protocol 2007–5446 from McGill University, and under federal banding permits

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

10743E, 10743C, and 10743T issued by the Canadian Wildlife Service.

We attached Lotek nanotags (Lotek, Seattle, WA, USA; ANTC-M3-2 and NTQB2-3-2; 1 g) to each bird using a figure eight leg-loop harness made from nylon-elastic thread (Rappole and Tipton 1991). Each of the tags operated on the same frequency of 166.380 MHz and emitted a unique digital code, allowing us to identify each unique individual tagged. In 2017 there was 1 Motus station at MBO and in 2018 2 additional Motus stations were added to the area surrounding our study site. Each Motus station can detect tags on average up to 15 km away in a straight line; however, the detection range for birds at ground level varies greatly depending on vegetation and topography, with detection ranges of ~300 m for ground-foraging species (Crewe et al. 2019). For this reason, we used manual telemetry tracking, in addition to our automated stations, to confirm the presence of tagged birds at our site during stopover. Using a 3-element Yagi and a Lotek receiver SRX 800 M-1, we searched and located tagged individuals every three days, and, if possible, obtained a visual observation and exact GPS coordinates of the observation. If a tagged bird was not being detected by any of the Motus stations, a systematic search was conducted around our study area (out to ~2 km from the banding and tagging site). Based on recapture data at the MBO, it is known that most molt-migrant individuals remain near the capture site throughout their molt. Thus, molt-migrant birds that were not found within the previously defined search area on the days following their capture were assumed to have left our study site to complete their molt elsewhere and are therefore not included in our molting stopover analyses. At the end of our field season, detections were downloaded from each Motus station. The night of migratory departure for each bird was considered to be the last night a bird was detected by a station at our study site, which was confirmed by our manual tracking data the following day. One presumed molt-migrant left the site just 4 days after arriving. This individual was presumed to be a molt-migrant due to the timeframe of its occurrence at the MBO (early August). It had also not started its post-breeding molt yet and it was assumed to have moved to a different molting site. This assumption is supported by a detection on a Motus receiving station 80 km south-west of our study site 2 hr after departing our study site. We removed this individual from analyses.

Daily mortality rate was calculated as number of confirmed deaths/(number of confirmed survivals ×average days molt or post-molt-migrants were present). For post-molt-migrants where no mortalities were recorded, we estimated the mortality rate to be below the rate for one confirmed death. Birds without a confirmed departure were excluded from the mortality rate calculations.

Plasma Metabolites

Plasma metabolite levels were obtained from blood samples. Blood (200 μL) was collected in capillary tubes from the brachial vein of each bird, and used to measure cholesterol, glucose, triglycerides, and β-Hydroxybutyrate levels to assess the nutritional state of the bird. In wild birds, high glucose and triglyceride concentrations in plasma typically represent recent energy intake, whereas high cholesterol and low β-hydroxybutyrate concentrations represent longer-term net energy intake, with β-hydroxybutyrate levels increasing during fasting and mass loss (Alonso-Alvarez and Ferrer 2001; Guglielmo et al. 2005; Morales et al. 2020). Thus, the plasma composition of these 4 different metabolites can be used to determine nutritional state and refueling rates of wild birds. Metabolite levels were tested in situ using CardioChek PA (cholesterol and triglycerides), Bayer Contour (glucose), and Precision Xtra (β-Hydroxybutyrate) point-of-care devices, as validated in 2017 by Morales et al. (2020), except for 2017 where triglycerides were measured from plasma samples using a lab assay kit and ketones were not measured. In 2017, samples were kept in a cooler with ice packs until processed within five hours after sampling. Capillary tubes were spun for 10 min in a hematocrit centrifuge to separate the cells and plasma in the blood. The plasma from each capillary tube was extracted using a Hamilton 25 μL syringe, which was rinsed at least 3 times with MiliQ water before and after each use to prevent contamination between samples. Plasma samples were then frozen −70°C (Celsius) until measured in the laboratory for triglycerides using the Wako LabAssay Triglyceride Kit. The assays were performed following the manufacturer's protocol using a BioTek Epoch 2 Microplate Spectrophotometer. Replicates of the measurements were done and averaged. To compare assay results to point-of-care device values between years, we converted the values using each of the device calibration equations provided by Morales et al. (2020).

We assessed differences in blood metabolites in two ways. First, we used Mann–Whitney tests to assess differences in metabolites (glucose, cholesterol, triglycerides, and β-Hydroxybutyrate) between molt and post-molt-migrants. We then grouped the data for both types of migrants and analyzed it using a generalized additive model (GAM) using the *Mcgv* package in R (Wood 2011). We used calendar date, body mass, and time of day as smooth terms in our model and molt as a parametric term to determine if any of these variables influenced plasma metabolite levels of both molt and post-molt-migrants. We used a GAM, instead of a GLM, to analyze relationships between metabolites and covariates (i.e. body mass or time of day) because we expected non-linear relationships. Metabolite levels were box-cox transformed to meet the normality assumption.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

Activity Budgets

We determined activity budgets from the signal strength patterns of tagged birds throughout their stopover as recorded by our Motus station. From the radio-tagged birds, we selected the molt-migrants (n = 17) and post-molt-migrants (n = 11) of both sexes for which we had clear and near continuous detections from the Motus stations throughout their stopover period in 2017 and 2018 (i.e. those thrushes that were close enough to the towers that signal strength could be continuously recorded most of the time). After plotting signal strength vs. time, we visually determined the time of start and end of diel activity ("Morbey waves") from the signal strength waveform from the port (antennae) with the greatest number of records (Morbey et al. 2018). Departure time was obtained from the last detection of a bird at our main receiver, usually preceded by a quiescence phase, or period of inactivity occurring right before the onset of migratory departure in nocturnally migrating birds (Schofield et al. 2018a, 2018b; Morbey et al. 2020), and often followed by a detection at the next tower in our array a few seconds later (~2 km away). The onset and end of diel activity are characterized by a sudden change in signal strength variability, with periods of inactivity showing constant low signal strength variability while periods of activity showing a sudden increase in signal variability. We modeled activity duration as a function of day length (i.e. the time between civil sunrise and sunset which is also a proxy for calendar date) and molting status, using a linear mixed model with individual as a random factor: activity duration ~ day length + molt + (1|individual). We also modeled migration (yes = 1, no = 0; logit link) as a function of activity pattern using a generalized linear mixed model with a binomial error distribution. For facility, we refer to the start of activity in the morning as "activity onset" and end of activity in the evening as "activity cessation" (Morbey et al. 2018; Schofield et al. 2018b). We considered variability in activity onset and cessation by calculating the standard deviation over three days either across individuals or within individuals using a linear model with variability as the dependent variable and day length and molt as fixed effects.

Departure Decisions and Subsequent Migration Rates

Departure decisions of migrants at stopover sites can be influenced by a variety of intrinsic (age, sex, body condition) and extrinsic (weather conditions, date, migratory barriers) factors that generally minimize the costs of migration by selecting favorable conditions that may improve overall migration rate and survival (Alerstam and Lindström 1990; Pyle et al. 1993; Drake et al. 2014). For instance, migrating birds typically depart with strong tail winds that minimize migration costs, during sudden temperature changes when local food availability is reduced, and once fat reserves are replenished (Richardson 1990; Pyle et al. 1993; Åkesson and Hedenström 2000; Dossman et al. 2016). To assess potential differences in how intrinsic and extrinsic factors affect stopover duration and departure probability in molt-migrants and post-molt birds, we modeled stopover duration using an extended Cox proportional hazard model (Dossman et al. 2016). A higher "risk" is associated with higher probabilities of departure and shorter stopover durations. We included sex as an intrinsic predictor, as sex often influences departure decisions in many migratory birds (Maggini and Bairlein 2012; Morbey et al. 2012), with males often departing earlier than females. We also included average daily residual temperature and hourly wind support as time-varying covariates that can be extrinsic predictors of departure. Daily residual temperature was obtained by fitting a model using the average daily temperatures throughout the year and calculating how much the temperature deviated from the predicted temperature on each date. We did not include absolute temperature, which was strongly correlated with calendar date. Based on foreign detections of birds departing our site, we assumed a south-west direction for all departing birds, and wind support was calculated using the following formula: Wind speed × cos(Wind direction in degrees × π/225). Wind conditions at departure were included in the model as the average conditions for the hour preceding migratory departure of each radio-tagged bird. For days when a bird did not depart, weather conditions were calculated in the same way except that "departure time" was taken as the median-departure hour of all radio-tagged birds (20:00) (Dossman et al. 2016). Calendar date was included as a nuisance variable in all the models. Wind and temperature data for 2017 and 2018 were obtained from Environment Canada's historical climate database. Weather data was specifically collected from the Ste-Anne-de-Bellevue weather station which was located less than one km from our study site. Contrary to some other migration studies, we did not include fat levels or mass in any of our departure models, as we were only able to measure those values at capture and fat levels and mass of molt-migrants likely fluctuated widely over the course of the entire stopover. In other words, fat level or mass at capture for molt-migrants would not influence their departure decisions because most of them typically arrive on-site with almost no fat reserves and stay on-site molting for a significant period of time before starting to build up fat reserves to get ready for migration (Gaddis 2011).

Because most molt-migrants captured at our site do not start migrating until they have completed their molt or at least until they are at an advanced molting stage, we did not include the complete stopover period of each molt-migrant individual in the extended cox model (e.g., favorable weather conditions would not influence departure if the bird is still heavily molting). To accurately assess departure probabilities of molt-migrants, we included only the

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

estimated period of time after each individual had already completed 75% of its molt, which is typically when birds had replaced most of their flight feathers and are likely to be more mobile. This period was obtained using the molting stage of the bird at capture and the 1.9% molt rate from our molt rate estimates to estimate when the bird was at 75% molt completion stage. The resulting "post-molt stopover" would therefore act as our baseline hazard, being more representative of the time when a bird's departure is likely to be influenced by the intrinsic or extrinsic factors that we are investigating.

Our modeling procedure consisted of a series of 4 models. Our first model was our global model, which consisted of intrinsic and extrinsic factors, including sex, residual temperature, wind, and calendar date. Our second model consisted of only intrinsic variables, including sex and calendar date and assumed that stopover decisions were based solely on the sex of the bird. Our third model consisted of only extrinsic variables, including residual temperature, wind, and calendar date and assumed that an individual's stopover decisions were mostly on external factors such as temperature and wind conditions. Lastly, the fourth model was the null, including "calendar date" only. Cox proportional hazards models were performed using the survival package (ver. 3.1-8) in R (ver. 3.6.2; R Core Team 2017). We used Akaike Information Criterion values corrected for sample size (AIC_c) to compare all 4 models. Models were fit separately for molt and post-molt-migrants.

To test whether molt-migration affected subsequent migration rate to the wintering grounds, we assessed differences in migration rates between molt-migrants and post-molt-migrants. For each consecutive detection at a Motus receiving station outside the study site (hereafter "displacements"), we calculated the shortest distance between receiving stations and the time elapsed between both detections, and estimated the movement rate (hereafter "migration rate"). We attributed to each segment a latitude midpoint between both detections. To limit simultaneous detections by receiving stations within the same detection range, we removed displacements <30 km and 30 min apart. We fitted a generalized additive model (GAM) to determine whether migration rate (log) was different between molt-migrant and non-molting birds. Motus is radio telemetry array and the receiving stations are distributed heterogeneously between the breeding and the wintering grounds. There are important variations of the distance between stations, and thus, between detections (a few kilometers to thousands of kilometers), which affect the resulting migration rate between stations (Bégin-Marchand et al. 2020, 2021). The distance of displacements created a bias in the estimation of migration rate. Indeed, detections by receiving stations that are further apart are more likely to include stopover than receiving stations closer (Bégin-Marchand et al. 2021). For this reason, we added this variable to the GAM as covariate, and the latitude midpoint between towers used to derive rate to control for the heterogeneity of the radio telemetry array. Therefore, our model included the molting group (molt-migrant/ post-molt-migrant), the year of capture (fixed effect), both covariates (i.e. the latitude midpoints between detections; displacement's latitude midpoint), and the distance between receiving stations (displacement's distance), and the individual bird as random effect. We tested for correlations between covariates and examined residuals. All statistics were performed in the R statistical environment. We considered statistical significance as $P < 0.05$ and one-tailed P-values were used where we had a priori directional hypotheses.

RESULTS

Long-term Molt-Migrant Data (2012–2018)

Based on MBO's six years of molt-migrant data (no data in 2014), we know that molt-migrant individuals are typically captured when they are molting their first few primaries and are often last recaptured when they have finished molting or are molting their last secondaries (Figure 1). The within-season recapture rate of molting Swainson's Thrush at the site since 2013 was 22% (35 recaptures out of a total of 157 birds), compared with 5% for non-molting migrants (3 recaptures out of a total of 54 birds). Molt-migrants were captured mostly in August, with some early individuals caught as early as July 10 during MAPS banding sessions at the MBO. In comparison, migrants that have already completed their molt were captured in mid to late September, during peak Swainson's Thrush migration (mean peak date = September 19). A summary of molt-migrant Swainson's Thrush captures at the MBO since 2013 is provided in Supplementary Material Table 1. Based on all the recaptures of molt-migrant thrushes at different molt stages since 2013, we estimate an average flight feather molt rate of 1.9% per day for Swainson's Thrushes at this site (Figure 1). This molt rate varied across years from 1.7% to 2.5% per day.

In 2017 and 2018, we radio-tagged 59 molt-migrant thrushes (21 in 2017; 38 in 2018) and 19 post-molt-migrants (3 in 2017; 16 in 2018). Most of the molt-migrants that were tagged were at the earliest stages of molt or had not started molting yet (0–5% molt completion). Four died (3 out of 19 in 2017, 1 out of 34 in 2018; all molt-migrants) and one lost a transmitter (in 2017). Out of the remaining birds, we excluded 6 individuals from our survival calculations (2 in 2017, 4 in 2018) that did not have a confirmed departure and were not detected elsewhere along their migratory route. Therefore, the minimum daily mortality rate was 0.0034 in 2017 and 0.0006 in 2018 for molt-migrants, and below 0.0075 (less than 1 out of 19) for post-molt-migrants. Mortality was due to predation (n = 2; predated remains found) or

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

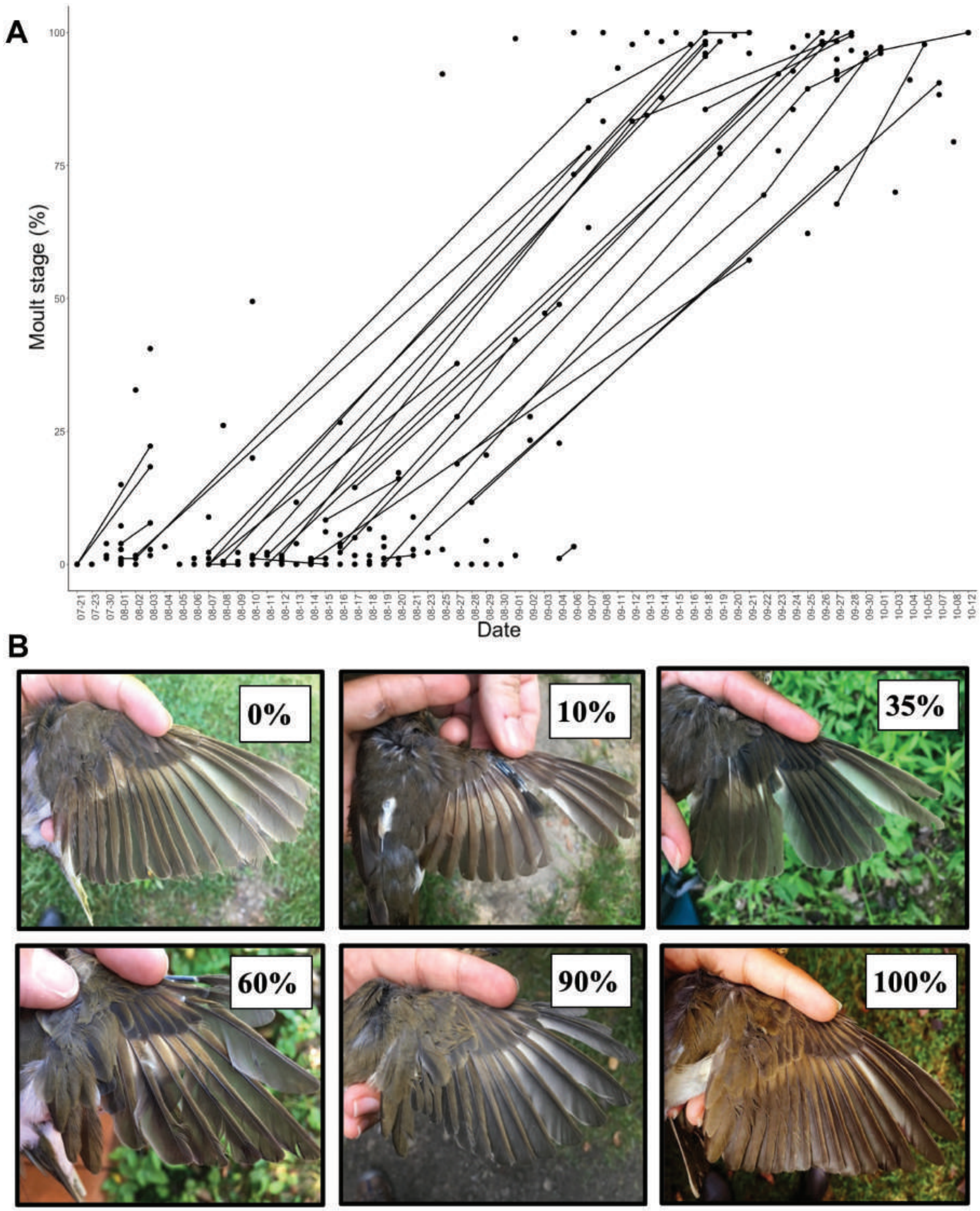

FIGURE 1. (A) Molt stage vs. capture date of molt-migrant Swainson's Thrush captured during fall migration monitoring at the McGill Bird Observatory (MBO) since 2013. Connecting lines represent recaptures of the same individual. Molt rate (slope of connecting lines) represents an average of 1.9% advancement in molt stage per day, allowing researchers to estimate arrival dates of thrushes captured at advanced molting stages. (B) Photos representing some of the different stages of molt at which birds are captured at the MBO.

unknown circumstances (*n* = 2; intact bird found dead). Due to the state of the predated remains found, it is likely that they were predated by a bird of prey, presumably Sharp-shinned (*Accipiter striatus*) or Cooper's Hawk (*A. cooperii*), which are present in high numbers at the MBO during fall migration (Gahbauer et al. 2016). The sex ratio for both molt and post-molt-migrants was of 1:1. 65% of female birds sampled had receding brood patches, all molt-migrants

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

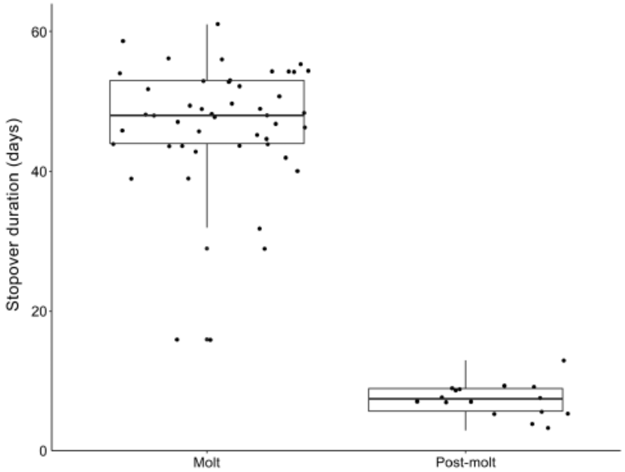

FIGURE 2. Stopover durations of radio-tagged molt-migrant and post-molt Swainson's Thrushes captured at the McGill Bird Observatory (MBO) during the fall migration monitoring periods of 2017 and 2018. Molt-migrant thrushes stopped over at the MBO for a significantly higher amount of time compared to post-molt-migrants.

caught at their earliest stages of molt in August or start of September in 2018. These patches were wrinkled, had no remaining fluid, and had a few or no pin feathers, a characteristic present in incubating females during the last stages of the breeding period (DeSante et al. 2020).

Stopover Duration

Using automated radio telemetry data from tagged thrushes, we determined detailed stopover durations for each bird using their exact departure dates from the site. In 2017, the average stopover since capture for molt-migrants ($n = 13$) was 47 days (range: 43–59 days) and for post-molt-migrants ($n = 2$) was 7 days (range: 5–9 days). In 2018, the average stopover since capture for molt-migrants ($n = 34$) was 46 days (range: 16–61 days) and for post-molt-migrants ($n = 14$) was 7 days (range: 3–13 days) (Figure 2). Based on our estimated molt rate of 1.9%, we determined that on average, molt-migrants departed the site once they have completed 98% of their molt, suggesting that some birds may decide to migrate before fully completing their molt.

Plasma Metabolites

Plasma metabolite levels of molt-migrants did not significantly differ from those of post-molt-migrants (Mann–Whitney test; $P > 0.05$). Rather, time of day explained much of the variation, with triglycerides increasing as birds fed through the day and β-hydroxybutyrate decreasing post-overnight fast. Our GAM models explained much of the variation in all metabolites except glucose (Table 2). Triglyceride levels also declined almost linearly with increasing date until day 255 (September 12) when triglyceride levels were approximately constant. Cholesterol levels followed a parabolic pattern, decreasing with mass until ~31 g, and starting to increase again with higher body masses ($P = 0.02$). Body mass did not differ between molt and post-molt-migrants (see GAM plots in Supplementary Material Figure 1).

Activity Budgets

Thrushes showed classic Morbey waves, with periods of variable signal strength during the day and constant signal strength at night. Approximately 73% of activity onsets and 75% of activity stops could be measured, with the remainder occurring during periods without continuous antennae coverage. Morbey waves closely tracked daylight, with activity onset usually occurring between nautical twilight and sunrise (25 ± 18 min before sunrise), and activity stops usually occurring just after sunset (33 ± 35 min after sunset; Figure 3). Molt-migrants' Morbey waves were more variable at the start of molt and then became consistent relative to daylight (Figure 3), suggesting that molt-migrants were more active at the start of their molt right after arriving to their molt stopover site. Post-molt-migrants' Morbey waves were more variable than those of molt-migrants throughout their stopover, with activity typically extending longer into the night relative to molt-migrants (Figure 3). In the morning, activity patterns of post-molt-migrants started both earlier and later than molt-migrants (Figure 3). Thus, molt status ($t_{20} = -5.62$, $P < 0.0001$) and day length ($t_{124} = 18.3$, $P < 0.0001$) both influenced duration of activity when considered together within a mixed model, with molt-migrants showing decreased activity levels compared to post-molt-migrants ($R^2_m = 0.62$; $R^2_c = 0.79$). There was no association between activity pattern the previous day and probability of migration ($t_{18} = 0.22$, $P = 0.83$); most thrushes appeared to migrate shortly after dark (median = 23 min after civil sunset). All birds for which we had constant detection data with no gaps exhibited a quiescence phase before departure. See Supplementary Materials for more statistics on activity budgets.

Departure Decisions and Subsequent Migration Rates

For molt-migrants the "Null model", which only included calendar date as a nuisance variable, was the top ranked model for explaining departure date (>2.0 AIC from other models) (Table 3). Specifically, as date increases, the probability of departure also increases. For post-molt-migrants, there was no significant difference between all 4 models (<2.0 AIC between all models), and there was no variable that significantly influenced departure probability. After departing our study site, 70% of tagged birds ($n = 54$) were detected along their migratory route by other receivers (>30 km from the tagging location) in the Motus Network (Supplementary Material Figure 2). Mean departure date for all birds was September 24 in 2017 and September 29 in 2018. There was no significant difference in the departure dates between molt-migrants (mean = September 27) and post-molt-migrants (mean = October 1) ($t_{37} = 1.63$, $P = 0.11$). We detected 81

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

TABLE 2. Output parameters of each GAM analysis for every metabolite with calendar date, time of day, mass, and molt status as predictor variables. Asterisks (*) show variables that were significant after a Bonferroni correction for multiple comparisons. Percent of overall variation explained by GAM also shown

	Parametric coefficients			Smooth terms		All	% Explained
	Estimate	SE	*t*-value	edf	*F*	*p*-value	
Glucose							
Molt	3.11	25.7	0.12	–	–	0.90	1.6
Calendar date	–	–	–	1	0.166	0.68	
Time of day	–	–	–	1	0.141	0.29	
Body mass	–	–	–	1	0.000	0.99	
Triglycerides							
Molt	−0.42	0.42	−1.00	–	–	0.31	25.4
Calendar date	–	–	–	4.7	3.180	0.02*	
Time of day	–	–	–	1	6.533	0.01*	
Body mass	–	–	–	1	0.482	0.48	
B-Hydroxybutyrate							
Molt	−0.80	0.47	−1.71	–	–	0.09	19.6
Calendar date	–	–	–	2.1	1.194	0.44	
Time of day	–	–	–	1	5.072	0.02*	
Body mass	–	–	–	1	0.923	0.34	
Cholesterol							
Molt	−0.38	0.43	−0.88	–	–	0.38	19.6
Calendar date	–	–	–	1	0.164	0.69	
Time of day	–	–	–	1	0.222	0.64	
Body mass	–	–	–	2.5	2.993	0.03*	

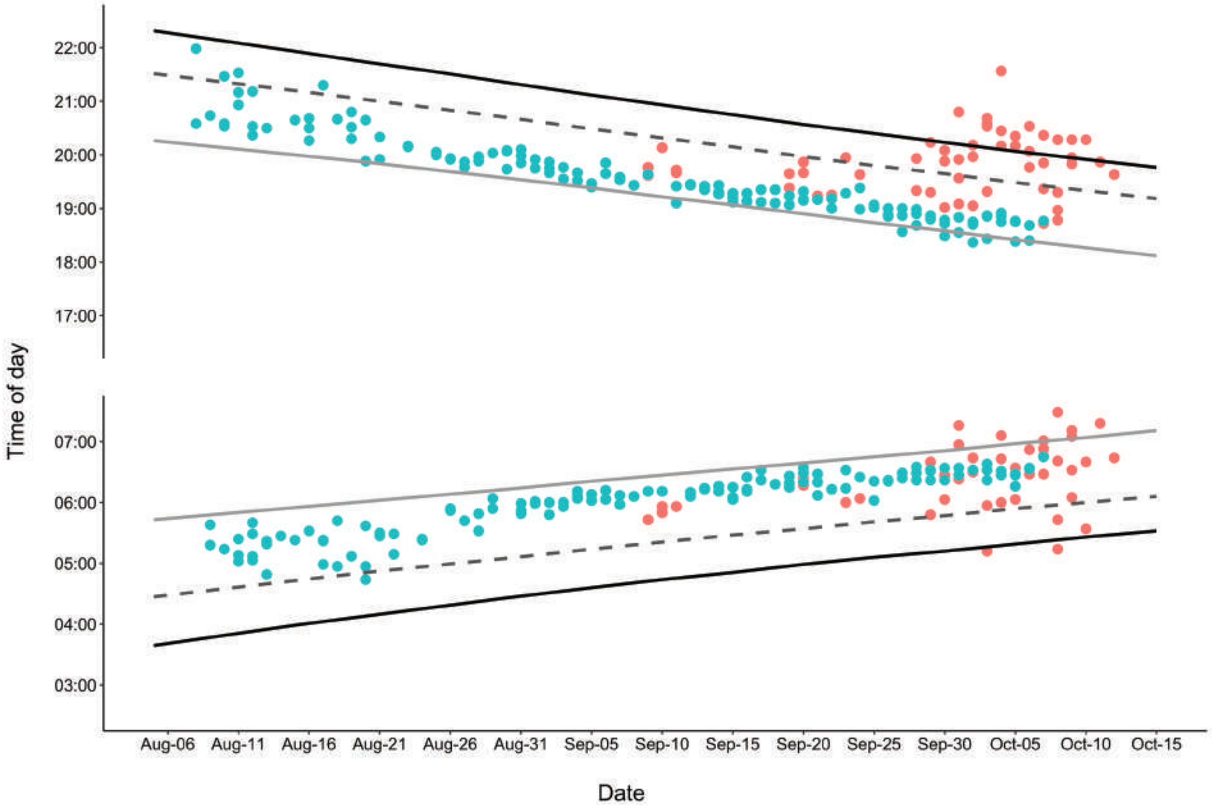

FIGURE 3. Start and end of activity for 17 molt-migrant (blue circles) and 11 post-molt-migrant (red circles) Swainson's Thrushes at the McGill Bird Observatory near Montreal (Quebec, Canada) during the molting stopover and fall migration of 2017 and 2018. Solid dark line represents astronomical twilight, dashed gray line represents nautical twilight, and solid light gray line represents sunrise/sunset in Eastern daylight savings time.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

TABLE 3. AIC model selection results of departure decisions behavior in molt and post-molt-migrant Swainson's Thrushes at the McGill Bird Observatory, near Montreal, Quebec. The top ranked model for molt-migrants was the null, with calendar date as a significant variable affecting the departure probability of a bird in all models. For post-molt-migrants, there was no significant difference between the models and no significant variable that affected departure probability. W_i = AIC weight

Molt Status	Model	Variables	AIC	ΔAIC	w_i
Molt	Null	Calendar date	273.4	0	0.59
	Intrinsic	Sex + calendar date	275.4	2	0.21
	Extrinsic	Residual temperature + wind + calendar date	276.2	2.8	0.14
	Global	Sex + residual temperature + wind + calendar date	278.1	4.7	0.06
Post-Molt	Extrinsic	Residual temperature + wind + calendar date	36.4	0	0.34
	Null	Calendar date	36.5	0.1	0.33
	Global	Sex + residual temperature + wind + calendar date	37.4	1	0.20
	Intrinsic	Sex + calendar date	38.4	2	0.13

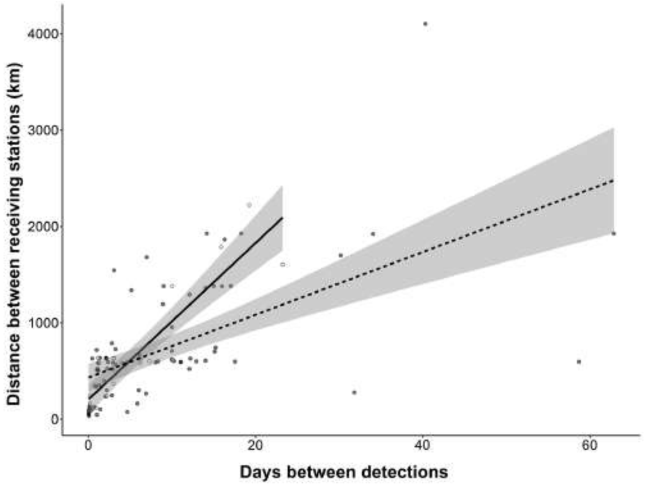

FIGURE 4. Time in days between detections in relation to the distance between the detecting stations for 81 displacements from 41 molt-migrant Swainson's Thrush and 21 displacements from 14 post-molt individuals of the same species tagged at the McGill Bird Observatory near Montreal (Quebec, Canada). The resulting migration rate for each segment is the distance and time elapsed between two different Motus stations. The migration rate of post-molt thrushes was greater than that of molt-migrants.

displacements from 41 molt-migrants and 21 displacements from 14 post-molt-migrants. When controlling for distance between receiving stations and latitude (Supplementary Material Figure 3), molt-migrants migrated slower (mean = 12.33 km hr^{-1}) than post-molt-migrants (mean = 18.13 km hr^{-1}, $\beta = -0.46 \pm 0.27$ [mean ± SE], $t_{120} = 2.02$, $P = 0.045$; model explained 26% of variation in migration rates) (Figure 4). There were no differences in migration rate between years.

DISCUSSION

Our results contribute to growing evidence that molt-migration in Swainson's Thrushes is more common than previously thought and accounts for a significant portion of their annual life cycle. Indeed, our estimate of 47 days stopover is twice the breeding season for a single brood (incubation + nestling = ~24 days; (D.E Mack and Yong, 2020)) and much longer than that of transient post-molt-migrants (~7 days). Molt-migrants also had a relatively low daily mortality rate and daily activity rates despite refueling rates that were similar to post-molt-migrants. Thus, molt-migrants gained energy at a high rate, suggesting that their movement to the berry-rich, productive sub-boreal region in early autumn optimizes energy gain and survival; movement to productive regions is a major pressure behind many molt-migrations (Bridge et al. 2016; Pillar et al. 2016). However, molt-migrants had slow subsequent migration rates. Given that individuals lost time migrating to and setting up home ranges near Montreal, some birds may have lacked the time to fully complete their molt before migrating, reducing flight efficiency and slowing migration rates (Swaddle and Witter 1997). Alternatively, the reduced time spent active each day, perhaps necessary to reduce predation risk on molting birds lacking flight maneuverability, may have reduced fuel deposition and prevented them from achieving migratory preparedness, requiring more subsequent stopovers, and ultimately reducing migration rates. Regardless, birds apparently paid a time penalty (slower subsequent migration rates) for the extensive molt stopover in a region of assumed high productivity.

Stopover Durations and Mortality Rate

Clearly, landscape level movements are important components of migration (Taylor et al. 2011; Wright et al. 2018), and migration is more complex than simple summer-winter models might suggest (Betini et al. 2015). However, few studies have examined stopover duration and molt rates of molt-migrant birds in eastern North America (Cherry 1985; Rohwer et al. 2005; Morris et al. 2013). Based on capture–recapture data of molt-migrant Swainson's Thrushes, Cherry (1985) found a minimum molt stopover and duration of flight feather molt of 32 days, as well as a molt rate of 3.2% day^{-1}. Our estimated molt rate of 1.9%

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

day^{-1} is lower than the one found by Cherry (1985), which matches our longer stopovers and approximate flight feather molt completion of 48 days. Flight feather quality is a direct consequence of conditions during molt, and flight feather quality can impact survivorship and productivity (Murphy et al. 1988; Nilsson Jan-Åke and Svensson Erik 1996; Dawson A et al. 2000). Furthermore, the high proportion of molt vs. post-molt-migrants at the molting stopover site (60–80%), may be indicative of high resource availability during early autumn, as molt-migrants are known to move to areas that maximize their access to resources during molt (Pyle et al. 2009; Bridge et al. 2016). Molt-migration, such as we observed for the Swainson's Thrush, can represent a significant portion of the annual cycle of these migratory songbirds.

Daily mortality rate of molt-migrant Swainson's Thrushes was similar to other published mortality rates for the species. Estimated daily mortality rate for molt-migrants in our study was 0.0032 in 2017 and 0.0006 in 2018. Annual survival rate is between 0.42 and 0.75 across North America (daily mortality rate: 0.0011–0.002), with 0.57 recorded for New Hampshire (daily mortality rate = 0.0015), the closest location to our study site (Nichols et al. 1981; DeSante et al. 1996, 2015; Rosenberg et al. 1999; Mack and Yong 2020; Gardali et al. 2003). As migration is a period when mortality rate is high (Sillett and Holmes 2002; Klaassen et al. 2016), molt-migration may represent an ecological decision to undertake the vulnerable molt in an area of relative safety and to avoid possible deteriorating weather conditions on their breeding grounds.

Molt and Post-Molt-Migrants Differ in Activity Levels, But Not Metabolites, During Stopovers

We provide the first activity budgets of molt and post-molt-migrants. Thrushes showed classic Morbey waveforms, with periods of activity (variable waveforms) during the day and inactivity (constant waveforms) during the night (Morbey et al. 2018; Schofield et al. 2018a). These waveforms closely mirrored daylight trends, with thrushes becoming active shortly after astronomical and nautical twilight when the sky begins to lighten and becoming inactive just after sunset. For molt-migrants, Morbey waveforms were quite variable at the start of their molt, meaning that thrushes were more active during their early molting stages, likely due to being more mobile and less vulnerable to predators. In addition, after arriving to the molt stopover, thrushes may be more active while exploring the area to try to find a suitable molting location within the site that will provide the resources needed for molt and protection from predators (Rivera et al. 1999). A few days after arriving to the molt stopover and starting their molt, the Morbey waveforms of molt-migrants were consistent relative to daylight meaning that they were responding to photoperiod. In contrast, post-molt-migrants had erratic waveforms, especially in the morning when they could be active either before or after typical activity onsets, perhaps due to altered circadian rhythms and sleep schedules in migrants (Rattenborg et al. 2004). Post-molt-migrants were also more active during the early evening, consistent with captive experiments illustrating that migratory birds sleep little (Rattenborg et al. 2004). We suggest lower activity in molt-migrants could be an energy saving mechanism and is consistent with the sedentary, cryptic behavior of molt-migrants avoiding detection by predators during this sensitive stage of their annual cycle (Morris et al. 2013). Also, birds that leave the stopover after completing their molt, may just not be yet in "migratory mode", as opposed as the actively migrating post-molt individuals. Thus, most departure flights may not be "true" migratory flights, possibly explaining why molt-migrants were not selective about weather conditions at departure. However, post-molt-migrants also lacked selectivity towards favorable weather conditions. Thrushes at our study site may be not under enough pressure to select favorable migratory conditions, as they are not faced with a migratory barrier that will require them to undertake a major non-stop flight (Dierschke and Delingat 2001; Deppe et al. 2015; Dossman et al. 2016; Bolus et al. 2017; Pageau et al. 2020). Calendar date predicted departure in all top models other than the null, suggesting that thrushes at our site may be time-constrained and migrate as soon as possible.

The lack of differences in metabolites between the molt and post-molt-migrants suggests that molt-migrants are able to refuel sufficiently during their molt stopover despite their reduced activity rates and their energetically demanding molt. Although migration is energetically demanding with classic changes in metabolite profiles (Guglielmo et al. 2005), molt is also an energetically demanding process requiring important changes in physiology and behavior (Hemborg and Lundberg 1998; Portugal et al. 2007; Cornelius et al. 2011). The decrease in β-Hydroxybutyrate levels with time of day for molt-migrants suggests that they were significantly increasing their energy intake after an overnight fast. Molting birds replace more glucose by β-Hydroxybutyrate, and thus showing a more pronounced response in β-Hydroxybutyrate levels to overnight fasting and subsequent feeding bouts (Jenni-Eiermann and Jenni 1996). Common Snipe (*Gallinago gallinago*) glucose levels increased with molt stage while triglycerides showed a sharp decrease after molt of tertials and rectrices (Podlaszczuk et al. 2017). A similar temporal variation in triglycerides in Swainson's Thrushes could explain the significant decrease in triglycerides in molt-migrants as calendar date progresses. It is also possible that refueling conditions are deteriorating with time.

Molt-Migrants Subsequently Migrated Slower

Molt-migrant Swainson's Thrushes migrated slower than post-molt-migrants. Based on the apparent lack of increased activity in molt-migrants after dusk, the slower

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

migration rates may be a consequence of the additional time needed for molt-migration and of molt-migrants not yet achieving migratory preparedness at time of departure. It is also possible that for molt-migrants, their departure flights were not true migratory flights, but "landscape movements" in preparation for migration and further slowing down their migration rates (Taylor et al. 2011; Schmaljohann and Eikenaar 2017). Alternatively, wing shape and wing-loading affects migration rates in Swainson's Thrushes, and slower migration rates could be due to molt-migrants beginning migration without having fully completed their molt as determined from our estimated molting rates (Swaddle and Witter 1997; Bowlin et al. 2010). A third explanation is that molt-migrants appeared to be active for fewer hours during the day and so may have had lower rates of fueling requiring more subsequent stopovers and resulting in slower migration rates. We do not believe the latter explanation is likely as (1) physiological metabolites, including cholesterol and beta hydroxybutyrate that integrate a signal over days, were similar between the two groups; and (2) the increased activity of post-molt-migrants was primarily after dark when thrushes may have reduced their feeding rates. Rather, the evening activity in post-molt-migrant thrushes may have included supplemental foraging.

Despite the differences in stopover durations between molt and post-molt-migrants, there was no difference in departure dates between the two groups. Furthermore, departure decisions in both groups were independent of weather and sex, suggesting these birds may use different departure cues that we were not able to assess. Alternatively, the stopover site may have been of high enough quality that all individuals were in good condition at departure and relatively insensitive to departure conditions; passerines can be insensitive to wind conditions as they can compensate for unfavorable winds (Alerstam and Lindström 1990; Dierschke and Delingat 2001; Bolus et al. 2017). Refueling rates and fuel stores are also known to impact departure decisions (Schaub et al. 2008; Dossman et al. 2016), plus birds that are not facing an ecological barrier (such as at our site) could be less selective to environmental variables and fuel stores due to the lower risk of overland migration and higher availability of stopover sites (Schaub and Jenni 2000; Schmaljohann and Naef-Daenzer 2011; Bolus et al. 2017).

Conclusions

We provide the most detailed measurements of stopover durations in a molt-migrant songbird to date and clearly show how important molt-migrant stopovers are with respect to the amount of time in the annual cycle they represent. Nonetheless, future research should focus on determining where post-molt and molt-migrants originate, as our study was unable to determine whether post-molt birds are actually molt-migrants that avoided capture. Stable isotope analysis could help answer such questions. Technological advances have allowed researchers to discover molt-migrations of thousands of kilometers in a variety of avian taxa (Harris et al. 2015; Siegel et al. 2016; Gaston et al. 2017; Wright et al. 2018), emphasizing the importance of studying the whole annual cycle of migratory birds for robust conservation and management actions (Marra et al. 2015; Pyle et al. 2018). Technologies such as automated radio telemetry, geolocators, satellite transmitters, and stable isotope analysis have the potential of filling information gaps in a species' annual cycle, including locating molting grounds, as well as the behavior and ecology of these species at these stopover sites (Rubenstein and Hobson 2004; McKinnon et al. 2013; Klaassen et al. 2016; Taylor et al. 2017). Identifying important molting locations and understanding molt-migrant behavior at these sites is key to the conservation of these migratory birds and their habitats.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

ACKNOWLEDGMENTS

We thank A. Zen for her help classifying activity budgets, and J. Head and E. Boulanger for help in the lab. An earlier version of this paper was a chapter within the MSc thesis of A. Morales. We thank R. Titman for his help as committee member, and M. Humphries for his help as external reviewer. S. Duval, G. Gruner and many volunteers helped with banding and tracking at the McGill Bird Observatory. We also thank the City of Montreal for allowing us to install Motus towers and track our birds on their land.

Funding statement: This work was supported by a MITACS scholarship with the Migration Research Foundation and a CREATE-Environmental Innovation scholarship to A.M., as well as from McGill University. Research funding was from Bird Protection Quebec, the Kenneth M Molson Foundation, McGill Bird Observatory, Environment and Climate Change Canada and NSERC.

Ethics statement: This research has followed the guidelines of McGill University's Animal Care Committee (Protocol No. 2007–5446), the Canadian Council of Animal Care (CCAC), as well as federal guidelines by the Canadian Wildlife Service (banding permits: 10743E, 10743C and 10743T). As this was a field study, adult animals were banded, tagged, blood sampled and immediately released by trained personnel. We did not detect any detrimental effects of the tags or blood sampling on the birds. If any bird showed any signs of stress during banding operations they were immediately released without being tagged or blood sampled.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

Author contributions: AM, BF and KE initially conceived the study. AM collected and analyzed the data, with contribution from CB and KE in migration rates and activity budget analyses. GM contributed with substantial equipment needed to carry out the study. AM, BF and KE led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for the publication.

Data repository: Analyses reported in this article can be reproduced using the data provided by Morales et al. (2021)

LITERATURE CITED

Åkesson, S., and A. Hedenström (2000). Wind selectivity of migratory flight departures in birds. Behavioral Ecology and Sociobiology 47:140–144.

Alerstam, T., and Å. Lindström (1990). Optimal bird migration: The relative importance of time, energy, and safety. In Bird Migration (E. Gwinner, Editor). Springer, Berlin Heidelberg, Germany. pp. 331–351.

Alonso-Alvarez, C., and M. Ferrer (2001). A biochemical study of fasting, subfeeding, and recovery processes in Yellow-legged Gulls. Physiological and Biochemical Zoology 74:703–713.

Bégin-Marchand, C., A. Desrochers, P. D. Taylor, J. A. Tremblay, L. Berrigan, B. Frei, A. Morales, and G. W. Mitchell (2021). Spatial structure in migration routes maintained despite regional convergence among eastern populations of Swainson's Thrushes. Movement Ecology 9:23. https://doi.org/10.1186/s40462-021-00263-9

Bégin-Marchand, C., A. Desrochers, J. A. Tremblay, and P. Côté (2020). Comparing fall migration of three Catharus species using a radio-telemetry network. Animal Migration 7:1–8.

Betini, G. S., M. J. Fitzpatrick, and D. R. Norris (2015). Experimental evidence for the effect of habitat loss on the dynamics of migratory networks. Ecology Letters 18:526–534.

Bolus, R. T., R. H. Diehl, F. R. Moore, J. L. Deppe, M. P. Ward, J. Smolinsky, and T. J. Zenzal (2017). Swainson's Thrushes do not show strong wind selectivity prior to crossing the Gulf of Mexico. Scientific Reports 7:14280.

Bowlin, M. S., I.-A. Bisson, J. Shamoun-Baranes, J. D. Reichard, N. Sapir, P. P. Marra, T. H. Kunz, D. S. Wilcove, A. Hedenström, C. G. Guglielmo, et al. (2010). Grand challenges in migration biology. Integrative and Comparative Biology 50:261–279.

Bridge, E. S., J. D. Ross, A. J. Contina, and J. F. Kelly (2016). Do molt-migrant songbirds optimize migration routes based on primary productivity? Behavioral Ecology 27:784–792.

Chernetsov, N. (2006). Habitat selection by nocturnal passerine migrants en route: Mechanisms and results. Journal of Ornithology 147:185–191.

Cherry, J. D. (1985). Early autumn movements and prebasic molt of Swainson's Thrushes. The Wilson Bulletin 97:368–370.

Contina, A., E. S. Bridge, N. E. Seavy, J. M. Duckles, and J. F. Kelly (2013). Using geologgers to investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris*). The Auk 130:265–272.

Cornelius, J. M., N. Perfito, R. Zann, C. W. Breuner, and T. P. Hahn (2011). Physiological trade-offs in self-maintenance: Plumage molt and stress physiology in birds. Journal of Experimental Biology 214:2768–2777.

Crewe, T. L., J. E. Deakin, A. T. Beauchamp, and Y. E. Morbey (2019). Detection range of songbirds using a stopover site by automated radio-telemetry. Journal of Field Ornithology 90:176–189.

Cyr, N., M. Wikelski, and L. M. Romero (2008). Increased energy expenditure but decreased stress responsiveness during molt. Physiological and Biochemical Zoology 81:452–462.

Da Silva, A., J. M. Samplonius, E. Schlicht, M. Valcu, and B. Kempenaers (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. Behavioral Ecology 25:1037–1047.

Dawson A., Hinsley S. A., Ferns P. N., Bonser R. H. C., and Eccleston L. (2000). Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society of London, Series B: Biological Sciences 267:2093–2098.

deGraw, W. A., M. D. Kern, and J. R. King (1979). Seasonal changes in the blood composition of captive and free-living White-crowned Sparrows. Journal of Comparative Physiology 129:151–162.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, et al. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences USA 112:E6331–E6338.

DeSante, D., K. M. Burton, P. Velez, D. Froehlich, D. Kaschube, and S. Albert (2020). MAPS MANUAL: 2020 Protocol. The Institute of Bird Populations, Point Reyes Station, CA, USA.

DeSante, D. F., K. M. Burton, and D. R. O'Grady (1996). The Monitoring Avian Productivity and Survivorship (MAPS) Program fourth and fifth annual report (1993 and 1994). Bird Populations 000:67–120.

DeSante, D. F., D. R. Kaschube, and J. F. Saracco (2015). Vital Rates of North American Landbirds. The Institute for Bird Populations, Petaluma, CA, USA. www.VitalRatesOfNorthAmericanLandbirds.org

Dierschke, V., and J. Delingat (2001). Stopover behaviour and departure decision of Northern Wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535–545.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. Behavioral Ecology 27:567–574.

Drake, A., C. A. Rock, S. P. Quinlan, M. Martin, and D. J. Green (2014). Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechia*. PLoS One 9:e97152.

Gaddis, P. K. (2011). Molt and body condition of Myrtle and Audubon's Warblers during migration-stopover in Portland, Oregon. Northwestern Naturalist 92:107–115.

Gahbauer, M. A., S. Duval, and D. Davey (2016). McGill Bird Observatory Ten-Year Report: 2005-2014. Migration Research Foundation, Ste-Anne-de-Bellevue, QC, Canada.

Gardali, T., D. C. Barton, J. D. White, and G. R. Geupel (2003). Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in coastal California: Annual estimates using capture–recapture analyses. The Auk 120:1188–1194.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

Gaston, A. J., Y. Hashimoto, and L. Wilson (2017). Post-breeding movements of Ancient Murrelet *Synthliboramphus antiquus* family groups, subsequent migration of adults and implications for management. PLoS One 12:e0171726.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson (1998). A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

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

Harris, M. P., S. Wanless, M. Ballesteros, B. Moe, F. Daunt, and K. E. Erikstad (2015). Geolocators reveal an unsuspected moulting area for Isle of May Common Guillemots *Uria aalge*. Bird Study 62:267–270.

Hemborg, C., and A. Lundberg (1998). Costs of overlapping reproduction and moult in passerine birds: An experiment with the pied flycatcher. Behavioral Ecology and Sociobiology 43:19–23.

Holmgren, N., and A. Hedenström (1995). The scheduling of molt in migratory birds. Evolutionary Ecology 9:354–368.

Jenni-Eiermann, S., and L. Jenni (1996). Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. Functional Ecology 10:62–72.

Junda, J. H., S. Duval, and M. A. Gahbauer (2020). Use of discrete molting grounds by migrant passerines undergoing prebasic molt in southern Quebec. The Wilson Journal of Ornithology 132:72–82.

Kiat, Y., I. Izhaki, and N. Sapir (2016). Determinants of wing-feather moult speed in songbirds. Evolutionary Ecology 30:783–795.

Kjellén, N. (1994). Moult in relation to migration in birds—a review. Ornis Svecica 4:1–24.

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Alerstam (2016). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 176–184.

Leu, M., and C. W. Thompson (2002). The potential importance of migratory stopover sites as flight feather molt staging areas: A review for neotropical migrants. Biological Conservation 106:45–56.

Lind, J. (2001). Escape flight in moulting Tree Sparrows (*Passer montanus*). Functional Ecology 15:29–35.

Lindström, Å., S. Daan, and G. H. Visser (1994). The conflict between moult and migratory fat deposition: A photoperiodic experiment with Bluethroats. Animal Behaviour 48:1173–1181.

Lindström, Å., G. H. Visser, and S. Daan (1993). The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66:490–510.

Mack, D. E., and W. Yong (2020). Swainson's Thrush (*Catharus ustulatus*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.swathr.01

Maggini, I., and F. Bairlein (2012). Innate sex differences in the timing of spring migration in a songbird. PLoS One 7:e31271.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury (2013). New discoveries in landbird migration using geolocators, and a flight plan for the future. The Auk 130:211–222.

Morales, A., B. Frei, C. Leung, R. Titman, S. Whelan, Z. M. Benowitz-Fredericks, and K. H. Elliott (2020). Point-of-care blood analyzers measure the nutritional state of eighteen free-living bird species. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 240:110594.

Morales, A., B. Frei, G. W. Mitchell, C. B. Marchand, and K. H. Elliott (2021). Data from: Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. Ornithology 139:ukab083. https://doi.org/10.5061/dryad.nvx0k6dtv

Morbey, Y. E., A. T. Beauchamp, S. J. Bonner, and G. W. Mitchell (2020). Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. Journal of Avian Biology 51. https://doi.org/10.1111/jav.02448

Morbey, Y. E., T. Coppack, and F. Pulido (2012). Adaptive hypotheses for protandry in arrival to breeding areas: a review of models and empirical tests. Journal of Ornithology 153:207–215.

Morbey, Y. E., C. G. Guglielmo, P. D. Taylor, I. Maggini, J. Deakin, S. A. Mackenzie, J. M. Brown, and L. Zhao (2018). Evaluation of sex differences in the stopover behavior and postdeparture movements of wood-warblers. Behavioral Ecology 29:117–127.

Morris, S. R., A. S. Andrijević, R. Sullivan, R. S. Keith, B. S. Keith, and H. D. Sheets (2013). An 18-year study of migration and stopover ecology of Tennessee Warblers in Kalamazoo County, Michigan. The Wilson Journal of Ornithology 125:70–78.

Murphy, M. E., J. R. King, and J. Lu (1988). Malnutrition during the postnuptial molt of White-crowned Sparrows: Feather growth and quality. Canadian Journal of Zoology 66:1403–1413.

Newton, I. (1966). The moult of the Bullfinch *Pyrrhula pyrrhula*. Ibis 108:41–67.

Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Hines (1981). Remarks on the use of mark–recapture methodology in estimating avian population size. In Estimating Numbers of Terrestrial Birds (C. John Ralph, and J. Michael Scott, Editors). Studies in Avian Biology 6:121–136.

Nilsson Jan-Åke, and Svensson Erik (1996). The cost of reproduction: A new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London, Series B: Biological Sciences 263:711–714.

Pageau, C., C. M. Tonra, M. Shaikh, N. J. Flood, and M. W. Reudink (2020). Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. Biology Letters 16:20200155.

Pillar, A. G., P. P. Marra, N. J. Flood, and M. W. Reudink (2016). Moult migration in Bullock's orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. Journal of Ornithology 157:265–275.

Podlaszczuk, P., R. Wlodarczyk, T. Janiszewski, K. Kaczmarek, and P. Minias (2017). When moult overlaps migration: Moult-related changes in plasma biochemistry of migrating common snipe. PeerJ 5:e3057.

Portugal, S. J., J. A. Green, and P. J. Butler (2007). Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): The importance of wing moult. Journal of Experimental Biology 210:1391–1397.

Pyle, P. (1997). Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA, USA.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025

Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers (2009). Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. The Condor 111:583–590.

Pyle, P., N. Nur, R. P. Henderson, and D. F. DeSante (1993). The effects of weather and lunar cycle on nocturnal migration of landbirds at southeast Farallon Island, California. The Condor 95:343–361.

Pyle, P., J. F. Saracco, and D. F. DeSante (2018). Evidence of widespread movements from breeding to molting grounds by North American landbirds. The Auk: Ornithological Advances 135:506–520.

R Core Team (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. The Journal of Field Ornithology 62:335–337.

Rattenborg, N. C., B. H. Mandt, W. H. Obermeyer, P. J. Winsauer, R. Huber, M. Wikelski, and R. M. Benca (2004). Migratory sleeplessness in the White-Crowned Sparrow (*Zonotrichia leucophrys gambelii*). PLoS Biology 2:e212.

Richardson, W. J. (1990). Timing of bird migration in relation to weather: Updated review. In Bird Migration (E. Gwinner, Editor). Springer, Berlin Heidelberg, Germany. pp. 78–101.

Rivera, J. H. V., W. J. McShea, J. H. Rappole, and C. A. Haas (1999). Postbreeding movements and habitat use of adult wood thrushes in northern Virginia. The Auk 116:458–466.

Robert, M., M.-H. Hachey, D. Lepage, and A. R. Couturier (2019). Deuxième atlas des oiseaux nicheurs du Québec méridional. Regroupement QuébecOiseaux, Environment and Climate Change Canada, Bird Studies Canada.

Rohwer, S., L. K. Butler, and D. Froehlich (2005). Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. In Birds of Two Worlds: The Ecology and Evolution of Migratory Birds (R. Greenberg and P. P. Marra, Editors). John Hopkins University Press, Baltimore, MD, USA. pp. 87–105.

Rosenberg, D. K., D. F. Desante, K. S. McKelvey, and J. E. Hines (1999). Monitoring survival rates of Swainson's Thrush *Catharus ustulatus* at multiple spatial scales. Bird Study 46:S198–S208.

Rubenstein, D. R., and K. A. Hobson (2004). From birds to butterflies: Animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Schaub, M., and L. Jenni (2000). Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

Schaub, M., L. Jenni, and F. Bairlein (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657–666.

Schmaljohann, H., and C. Eikenaar (2017). How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. Journal of Comparative Physiology A 203:411–429.

Schmaljohann, H., and B. Naef-Daenzer (2011). Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. Journal of Animal Ecology 80:1115–1122.

Schofield, L. N., J. L. Deppe, R. H. Diehl, M. P. Ward, R. T. Bolus, T. J. Zenzal, J. Smolinsky, and F. R. Moore (2018a). Occurrence of quiescence in free-ranging migratory songbirds. Behavioral Ecology and Sociobiology 72:36.

Schofield, L. N., J. L. Deppe, T. J. Zenzal, M. P. Ward, R. H. Diehl, R. T. Bolus, and F. R. Moore (2018b). Using automated radio telemetry to quantify activity patterns of songbirds during stopover. The Auk: Ornithological Advances 135:949–963.

Seewagen, C. L., C. G. Guglielmo, and Y. E. Morbey (2013). Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. Behavioral Ecology 24:634–642.

Siegel, R. B., R. Taylor, J. F. Saracco, L. Helton, and S. Stock (2016). GPS-tracking reveals non-breeding locations and apparent molt migration of a Black-headed Grosbeak. The Journal of Field Ornithology 87:196–203.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Swaddle, J. P., and M. S. Witter (1997). The effects of molt on the flight performance, body mass, and behavior of European Starlings (*Sturnus vulgaris*): An experimental approach. Canadian Journal of Zoology 75:1135–1146.

Taylor, P., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. Guglielmo, D. Hamilton, R. Holberton, et al. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12:8.

Taylor, P. D., S. A. Mackenzie, B. G. Thurber, A. M. Calvert, A. M. Mills, L. P. McGuire, and C. G. Guglielmo (2011). Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS One 6:e27054.

Tonra, C. M., and M. W. Reudink (2018). Expanding the traditional definition of molt-migration. The Auk: Ornithological Advances 135:1123–1132.

Voelker, G., and S. Rohwer (1998). Contrasts in scheduling of molt and migration in eastern and western warbling-vireos. The Auk 115:142–155.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser (2003). Costs of migration in free-flying songbirds. Nature 423:704.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.

Wright, J. R., L. L. Powell, and C. M. Tonra (2018). Automated telemetry reveals staging behavior in a declining migratory passerine. The Auk: Ornithological Advances 135:461–476.

Downloaded from https://academic.oup.com/auk/article/139/2/ukab083/6498004 by guest on 11 April 2025