



Premigratory ruby-throated hummingbirds, *Archilochus colubris*, exhibit multiple strategies for fuelling migration



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Many avian species fatten to fuel migratory flights. However, the amount of fat deposited prior to departure is variable depending on individual migration strategies. Despite their small size and high mass-specific metabolic rates, migratory hummingbirds at isolated meadows can fatten up to 44% in just 4 days prior to resuming migration, suggesting profound changes in energy acquisition. However, it remains to be seen whether hummingbirds fatten at the breeding grounds prior to initiating migration. Using feeder stations outfitted with radiofrequency identification readers and digital scales, we identified a subset of premigratory ruby-throated hummingbirds that exhibited significant mass gain in the 4 days leading up to migration (pre migratory fattening) and identified others that did not (pre migratory nonfattening). We further assessed foraging behaviour, monitored individual mass throughout the day and calculated rates of overnight mass loss to understand what behavioural variation allowed some premigratory birds to rapidly fatten. Premigratory fattening hummingbirds abandoned foraging restraint during the middle of the day, a behaviour thought to enhance aerial agility, and increased foraging effort during both the middle of the day and the evenings by increasing the duration but not the frequency of feeder visits. Groups did not differ in their morning foraging strategy. Premigratory fattening hummingbirds also lost mass overnight at reduced rates, implying that birds conserved energy to minimize the depletion of existing fat stores, possibly via increased nocturnal torpor use. Fattening hummingbirds used a two-pronged approach of increasing energy intake during specific daily periods and reducing overnight energy expenditure to achieve substantial premigratory mass gain over just 4 days. However, not all hummingbirds adopted this premigratory fuelling strategy; those that did were adults (>1 year old), suggesting that the use of a premigratory fuelling strategy may be age related.

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Migration is an important life history event for many species in which behavioural and physiological changes are necessary to facilitate relatively large-scale movement. Individuals migrating over long distances typically risk mortality and incur significant time and energetic costs (Alerstam, Hedenström, & Åkesson, 2003). While for most organisms seasonal migration offers advantages to fitness, these advantages can only be realized upon the successful completion of migration.

The primary fuel source and energy store for long-distance flights in birds is fat, as it is more energy dense than other fuel types such as proteins and carbohydrates (Jenni & Jenni-Eiermann, 1998; Jenni-Eiermann & Jenni, 1991; Rothe, Biesel, & Nachtigall,

1987; Weber, 2011). The building of large fat stores may be required when birds must traverse substantial ecological barriers where refuelling is impossible (e.g. open bodies of water), and can be beneficial as insurance against unpredictable, unfavourable and inhospitable conditions along the migratory route that limit opportunities for fuelling.

Migrating birds may behave to minimize energy expenditure during migration or time spent on migration, with each strategy requiring distinct fuelling regimes (Alerstam, 1991; Lindstrom & Alerstam, 1992). As carrying large fuel loads can negatively impact aspects of flight performance such as agility and speed (Calder, Calder, & Fraizer, 1990; Pennycuik, 1978) as well as increase flight costs (Calder et al., 1990; Chai, Harrykisson, & Dudley, 1996; Mahalingam & Welch, 2013), birds minimizing energy expenditure should store only enough fat to travel to the next fuelling point (Lindstrom & Alerstam, 1992). Conversely, as most of

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the time spent in migration is spent refuelling to rebuild fat stores at stopovers (Hedenström & Ålerstam, 1997), time-minimizing migrants should store larger fuel loads so that they can embark upon migratory flights with fewer or shorter refuelling stopovers (Gudmundsson, Lindström, & Ålerstam, 1991; Nilsson, Klaassen, Ålerstam, & McPeck, 2013).

Hummingbirds have high mass-specific metabolic rates (Lasiewski, 1963; Suarez, 1992), high thermoregulatory costs due to their small size (Welch & Suarez, 2008), and must sustain high metabolic rates to power hovering and forward flight (Chai, 1997; Chen & Welch, 2014; Clark & Dudley, 2010; Suarez et al., 1990). Given their substantial energetic requirements, it is tempting to assume that hummingbirds would either be incapable of storing large fat reserves to fuel migration or take substantial time to do so. Migrating rufous hummingbirds, *Selasphorus rufus*, refuel over several days (typically <10 days, but up to 21 days) at isolated sub-alpine meadows during their autumnal southward migration. However, most mass gain (up to ca. 44%) occurs within approximately 4 days leading up to the resumption of migration (Carpenter, Hixon, Beuchat, Russell, & Paton, 1993). Similarly, stopover duration for passerines can vary from several days to several weeks during which varying amounts of fuel are deposited (e.g. Chernetsov & Mukhin, 2006; Moore & Kerlinger, 1987; Schaub & Jenni, 2000, 2001); however, the commonly reported fuel deposition rates during stopover do not specify whether mass gain occurs over all stopover days.

Unlike the rufous hummingbird, the ruby-throated hummingbird, which breeds throughout eastern North America, faces a largely continuous and hospitable migratory landscape with the exception of the Gulf of Mexico (La Sorte, Fink, Hochachka, DeLong, & Kelling, 2014). Thus, premigratory fuelling at the breeding grounds prior to autumnal migration may be unnecessary as southbound migrants are travelling into areas with presumably high resource abundance and predictability as a result of longer growing seasons (La Sorte et al., 2014). However, Zenzal and Moore (2016) recently reported highly variable fuel loads among ruby-throated hummingbirds upon arrival at a stopover site and age-related migration where juveniles arrived with smaller fuel loads than adults (Zenzal & Moore, 2016), suggesting that migratory fuelling strategies differ between individuals. This report reflects an emerging broader pattern of potentially age-related interindividual variation in fuelling strategy between migratory birds (e.g. Cherry, 1982; Gannes, 2002; Goymann, Spina, Ferri, & Fusani, 2010; Morris, Holmes, & Richmond, 1996; Woodrey & Moore, 1997; Zenzal & Moore, 2016).

Using artificial feeding stations outfitted with radiofrequency identification (RFID) readers coupled with an electronic balance we monitored ruby-throated hummingbird mass throughout the breeding and premigratory periods to establish whether individuals engaged in substantial premigratory fattening and to characterize potential population level variation in premigratory fuelling strategies.

If, in fact, we observed premigratory fattening in ruby-throated hummingbirds, we could use the same data to better understand the rate at which fuel building occurs and what behavioural changes enabled it. Substantial mass gain can be achieved through behavioural and physiological changes that alter energy intake and expenditure including shifts in foraging behaviour that promote greater food intake (Bairlein, 2004; Scott, Mitchell, & Evans, 1994), or reductions in energy expenditure, such as through torpor, that permit energy conservation (Bartholomew, Howell, & Cade, 1957; Butler & Woakes, 2001; Carpenter & Hixon, 1988; Carpenter et al., 1993; Geiser, 2004; Hiebert, 1990).

Patterns of daily mass change for several species of hummingbirds have been assessed both in the laboratory (Beuchat, Chaplin,

& Morton, 1979) and in the field (Calder et al., 1990) during nonmigratory periods. In these studies, daily mass change resembled a U-shaped pattern where mass was high in the early morning as a result of compensatory feeding after overnight fasting, maintained at a reduced level during the day, and increased in the evening prior to overnight fasting (Beuchat et al., 1979; Calder et al., 1990). It was hypothesized that this pattern of mass change observed in males during the breeding season indicated the prioritization of flight agility for territory defence and courtship displays over energy acquisition during the middle of the day (Calder et al., 1990).

We hypothesized that some premigratory hummingbirds would forgo feeding restraint during the day in order to facilitate accelerated energy storage in preparation for migration, and predicted that these premigratory fattening hummingbirds would therefore exhibit positive linear mass change over the course of a day. We predicted that fattening individuals would increase energy intake throughout the morning and middle of the day by (1) feeding from the feeders more frequently and (2) spending more time feeding from the feeders. We did not expect fattening premigratory hummingbirds to increase their energy consumption during the evenings, as hummingbirds regularly engage in hyperphagia in preparation for overnight fasting. Additionally, we hypothesized that premigratory fattening hummingbirds would increase the use of torpor during the night to conserve energy (Carpenter & Hixon, 1988), and predicted that they would therefore exhibit lower rates of overnight mass loss. To evaluate these hypotheses, we examined foraging behaviour and mass change in a wild population of ruby-throated hummingbirds while taking into account the effects of confounding biotic and abiotic environmental factors, including age, sex, intraspecific competition, temperature and precipitation.

METHODS

Data Collection

Mass and visit data of ruby-throated hummingbirds were collected at six artificial feeding stations on the Koffler Scientific Reserve at Joker's Hill, King City, ON, Canada (44°1'47"N, 79°32'2"W) using the method described in Hou, Verdrame, and Welch (2015). Feeding stations were deployed over ca. 8 ha of open meadows with two ponds, surrounded by mixed forests. Each station was outfitted with a modified Perky-Pet commercial hummingbird feeder (model no. 220, Perky-Pet, Lititz, PA, U.S.A.) supplied with ca. 25% (w/v) sucrose solution, a Denver MAXIMUM X digital scale (model no. MXX-212, Sartorius, Bohemia, NY, U.S.A.) repeatable to 0.01 g, a notebook computer for recording data and a 12 V deep-cycle battery attached to AC power. Five of six stations were constructed using a low-power, low-cost RFID antenna and reader designed by E. Bridge (Bridge & Bonter, 2011), while the remaining station employed a Biomark Reader and racquet antenna (FS2001F-ISO, Biomark, Boise, ID, U.S.A.).

Research protocols were sanctioned by the University of Toronto Laboratory Animal Care Committee (Permits 20008398, 20008930, 20009510, 20010080 and 20010622). The following capture and tagging procedure was conducted under the approval of Environment Canada (Permit 10813 to K.C.W.).

Hummingbird trapping occurred between mid-May and mid-September in 2013 and 2014 beginning at sunrise and ending at 1000 hours for 1–2 days every week. We set up wire-mesh trap door cages at the stations and supplied a Perky-Pet feeder and 25% (w/v) in each. During trapping, feeders with attached antennas were removed from the stations. Each captured hummingbird was sexed, aged (adults: ≥ 1 year old; juveniles: <3 months old; Pyle,

1997) and fitted with a leg band according to standard Bird Banding Laboratory practices.

With the help of an assistant gently restraining the bird, individuals were subcutaneously implanted with a passive integrated transponder (PIT) tag (7 mm UNO PICO ID ISO transponder, ca. 0.026 g) into the upper back between the scapulae (Hou et al., 2015). The site of implantation was topically sterilized using a cotton swab and betadine, and subsequently anaesthetized using a 1% lidocaine solution. The skin of the upper back was lifted using a pair of forceps, and the tag was injected under the skin at a shallow angle using a syringe. The injection site was then sealed with 3M Vetbond Tissue Adhesive. This process took approximately 5 min, with total bird handling time lasting no more than 15 min. All captured individuals were allowed to feed ad libitum from a feeder while being restrained prior to their release. We report no detectable negative effects for the subcutaneous PIT tagging of hummingbirds (see Hou et al., 2015).

Each PIT tag possessed a unique alphanumeric code that individually identified the hummingbird. The detection of a PIT tag at a feeding station triggered the recording of the bird's ID and seven mass readings spaced 0.5 s apart. This was repeated as often as every 5 s for as long as the PIT tag remained within the detection range of the antenna. If no tagged bird was present, a baseline mass record was recorded every 10 min in the same manner as above to allow adjustments for balance drift. Where baseline records were ≥ 0.3 g different from zero, the balance was automatically tared.

Raw mass data collected between May and September of 2013 and 2014 were filtered and culled to remove erroneous and artefact data as described in Hou et al. (2015), and as briefly described here. Single visits by hummingbirds were defined as sequential records occurring within 10 s of each other. We removed erroneous data points for each visit identified as points with Cook's distance values greater than $4/N$ when mass values were regressed against time, or when the rate of mass change between sequential readings was >0.5 g/s. We established sex-specific ranges of biologically realistic mass to further cull erroneous mass readings; mass values, after correcting for balance drift, falling outside the range of minimum recorded mass minus 2 standard deviations and maximum recorded mass plus 2 standard deviations (male: minimum = 2.4–0.6 g, maximum = 4.6 + 0.6 g, $N = 338$; female: minimum = 2.7–0.6 g, maximum = 4.6 + 0.6 g, $N = 409$) were excluded from the data set.

Temperature and precipitation data were collected using a HC-S3 Temperature and Relative Humidity Probe (Campbell Scientific, Edmonton, AB, Canada), and a Tipping Bucket Rain Gauge (model no. 52202-10-L, R. M. Young Company, Traverse City, MI, U.S.A.) at an on-site weather station every 15 min. During periods of local weather station malfunction, we used data collected by the nearest station located at Buttonville Airport ca. 23 km away via a straight-line distance (Toronto Buttonville Municipal Airport, ON, Canada).

Premigratory Status of Hummingbirds

For this analysis, we selected a subset of hummingbirds whose last recorded visit was on or after 1 August of the respective year, as autumnal migration for this species in Ontario, Canada begins in mid-August (Sandilands, 2010). The date of migration was presumed to be the date of the last recorded visit and designated as 'day 0'. Following the finding in Hou et al. (2015) that linear mass gain was observed across the 4 days leading up to the day of migration, we created a subset of records from 0 to 4 days prior to migration for each individual that was redetected in the subsequent year, indicating successful migration to and from the wintering grounds. Those with at least one mass record on at least 4 of 5 days leading up to migration were classified as 'pre migratory';

individuals that lacked sufficient data were classified as 'non-pre migratory' (NP). Additionally, birds for which we had high-resolution data consisting of eight or more mass records per day on at least 4 of the 5 days, irrespective of redetection in the subsequent year, were also classified as 'pre migratory'.

We built a least-squares linear regression of average daily mass as a function of the number of days before migration; individuals whose average daily mass increased significantly across the days leading up to migration were designated as exhibiting pre migratory fattening (PF); those that did not were classified as 'pre migratory nonfattening' (PNF). Both PF and PNF hummingbirds were otherwise designated as NP on all other days. Hummingbirds that were not classified as either PF or PNF were also classified as NP.

All analyses presented in this paper were performed on data collected on or after 1 June 2013 and 2014 in order to exclude patterns that may reflect post migratory recovery in May.

Model Selection Protocol

Unless otherwise stated, we began all model selection by creating a full model. This included the explanatory variables of age, sex, pre migratory status, average temperature, total precipitation and number of unique IDs detected as a proxy for the amount of competition experienced at the feeders. This approximate measure of competition, however, is an underestimate as we cannot be certain that all hummingbirds using the feeders were tagged. We also included three-way interaction terms and all corresponding two-way interaction terms that were deemed biologically relevant (see below).

The best random-effects structure for the model was determined using the corrected Akaike information criterion (AICc; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We subsequently assessed the multicollinearity of the fixed effects using variance inflation factors (VIF), where fixed effects with VIF values greater than 3 (Zuur et al., 2009) were sequentially excluded from the model beginning with the interaction term with the highest VIF value.

We used the all-subset approach to create models with every combination of the explanatory variables listed below. From this, we created a confidence set of models by selecting models with $\Delta\text{AICc} \leq 6$ (Richards, 2008). To avoid the inclusion of overly complex models that offer little improvement in explanatory power, models within this confidence set that were more complex versions of another model with a lower AICc score were excluded (Richards, 2008). The natural averaging method was then used to obtain coefficient estimates upon which we made multimodel inferences for parameters retained within this reduced confidence set of models (Burnham & Anderson, 2002). Below, we present 85% confidence intervals for all model averaged coefficients (Arnold, 2010), as well as the summed Akaike weights (SW) for each parameter (Burnham & Anderson, 2002). Where the exclusion of more complex models from the confidence set left only a single best-fitting model, we present 95% confidence intervals for coefficient estimates. In general, we evaluated the strength of support for coefficient estimates based on their SW (strong: $\text{SW} \geq 0.90$; moderate: $0.70 \leq \text{SW} < 0.90$; some: $0.50 \leq \text{SW} < 0.70$; weak: $\text{SW} < 0.50$). We inferred significance of the parameters based on whether the 85% confidence interval included 0. Where possible, we also included mean marginal and conditional R^2 values for the models within the confidence set (Nakagawa & Schielzeth, 2013).

All analyses were performed using R v.3.2.1 (R Development Core Team, 2015). Linear mixed-effects models and generalized mixed-effects models with a binomial distribution were built using the R package lme4 v.1.1–7 (Bates, Maechler, Bolker, & Walker, 2014). Generalized linear mixed-effects models with a truncated negative binomial distribution were built using R package

glmmADMB v.0.8.1 (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2015). Variance inflation factors were assessed using the *vif.mer* function (Frank, 2011). Marginal and conditional R^2 values were calculated using the method described by Nakagawa and Schielzeth (2013).

Patterns of Daily Mass Change

We assessed whether patterns of daily mass change differed based on the premigratory status of hummingbirds. We selected individuals on days with two or more mass records in seven or more 2 h time bins between 0500 and 2300 hours to ensure that mass records spanned the entirety of a day. For each individual on each day, we built a parabolic regression and a least-squares linear regression of mass versus time. To determine which shape (linear or parabolic) best fitted the data, we assessed the quality of fit of the linear model compared to the parabolic model using AICc and Akaike weights.

Foraging Strategy

To assess the foraging strategy of hummingbirds, we examined the total time they spent at the feeders. In recognizing that the window of time representing the morning and evening periods changed with sunrise and sunset, we also assessed the proportion of available time hummingbirds spent at the feeders. The methods and results of this analysis and an analysis of frequency of visits are presented as [Supplementary Material](#).

We examined the foraging strategy of NP and PNF hummingbirds using a linear mixed-effects model for total time spent at the feeders. Using the same method, we also examined the foraging strategy for PF and the group of 'nonfattening' (NF = NP + PNF) hummingbirds (see [Results](#) for rationale).

Hummingbird visits recorded before 1100 hours, between 1100 and 1500 hours and after 1500 hours were classified as morning, mid-day and evening records, respectively. For each individual hummingbird, on each day, during each time period, we tallied frequency of visits, calculated the proportion of available time spent at the feeders, and totalled the amount of time spent at the feeders, beginning with the date of the first recorded visit and ending with the date of the last recorded visit. Frequency, proportion of time and total time were identified as '0' for time periods during which an individual was not detected. Periods of station malfunction during which all stations failed to detect a hummingbird ID for a period of 4 h or more (excluding overnight hours) were omitted from the data set.

Mean temperature for each morning was calculated as the average temperature beginning 1 h before sunrise, rounded to the nearest 15 min interval, and ending at 1100 hours. Mean temperature for mid-day was calculated as the average temperature between 1100 and 1500 hours, while mean temperature for the evening was calculated as the average temperature between 1500 hours and 1 h after sunset, rounded to the nearest 15 min interval. Temperature values were centred for each analysis. Total precipitation and number of unique IDs detected for each time period were similarly calculated based on the time divisions described above.

Because the data were found to be zero inflated, we built zero-altered models in which zero and nonzero data were first assessed in a binomial model as the presence/absence of hummingbirds at the feeders (see [Supplementary Material](#)), followed by a separate analysis of the nonzero data for frequency of visits (see [Supplementary Material](#)), proportion of available time (see [Supplementary Material](#)) and total time spent at the feeders.

Total Time Spent at Feeding Stations

Linear mixed-effects models were built to assess the total time individual hummingbirds spent at the feeders for the morning, mid-day and evening time periods. Only positive values were used. Total time was log transformed as the data were right skewed. For all models, the best random slope was determined from four options: centred average temperature, total precipitation, number of unique IDs or none. Hummingbird ID nested within year was used as a random intercept.

The following three-way interactions and all corresponding two-way interactions were included in the models: (1) premigratory status, average temperature and total precipitation, (2) premigratory status, sex and total precipitation, (3) premigratory status, sex and average temperature, (4) sex, average temperature and total precipitation, (5) age, average temperature and total precipitation, (6) premigratory status, age and total precipitation, (7) premigratory status, age and average temperature, in addition to a two-way interaction between sex and age.

We first assessed total time spent at the feeders for NP and PNF hummingbirds. The entire season's data for hummingbirds that were identified as PF were omitted from these analyses as changes in foraging effort that facilitated PF could extend beyond the days during which fattening was observed. Additionally, because not all age–sex classes were represented in the group of PNF hummingbirds, the three-way interaction between premigratory status, sex and age was omitted from the models.

We subsequently assessed total time spent at the feeders for NF (see [Results](#) for rationale) and PF hummingbirds. The three- and two-way interactions involving the premigratory status and age were omitted from the models as all PF birds were adults.

We conducted repeated measures analyses using linear mixed-effects models to determine whether total time spent at the feeders differed between the PF and NP states for individuals that were identified as exhibiting premigratory mass gain. Model selection and model averaging were executed as outlined above.

Rate of Overnight Mass Loss

We created a data set of hummingbirds for which the last recorded mass on a given day was matched with the first recorded mass of the subsequent day. To maximize the chances of obtaining true first and last mass records of the day, we only used records occurring as early as 30 min before sunset for last mass records, and as late as 30 min after sunrise for first mass records. Rate of overnight mass change was calculated as the difference between the last mass of the day and the first mass of the subsequent day divided by the difference in time between first and last mass. Masses were size corrected based on folded wing chord length at the time of capture. Wing length is known to change as juvenile hummingbirds undergo their first flight feather moult during winter (Pyle, 1997). For hummingbirds detected in a subsequent year and for which we only had their juvenile wing chord length, we substituted the average adult wing chord length based on our records for the corresponding sex (adult male: 3.96 cm; adult female: 4.45 cm). Positive rates of mass change were excluded from the analysis, representing either measurement error or records that were not true first or last masses.

Average overnight temperature and total overnight precipitation were calculated beginning 30 min before sunset, and ending 30 min after sunrise, for which both were rounded to the nearest 15 min interval. Average overnight temperature and hummingbird last mass were centred.

A linear mixed-effects model was constructed with overnight mass change as a function of sex, age, total overnight precipitation,

centred average overnight temperature, centred hummingbird last mass and premigratory status. The full model included three-way interaction terms for (1) premigratory status, average overnight temperature and last mass, (2) premigratory status, sex and last mass, (3) premigratory status, sex and average temperature, (4) sex, average temperature and last mass, (5) age, average temperature and last mass, (6) sex, age and last mass, and assessed all corresponding two-way interactions. The best random intercept structure was chosen from two options: (1) hummingbird ID nested within year or (2) hummingbird ID. The best random slope was selected from centred last mass, average overnight temperature and total overnight precipitation.

RESULTS

Number of Tagged Hummingbirds

A total of 63 ruby-throated hummingbirds were captured in 2013, of which 59 were tagged (adult females: 28; adult males: 9; juvenile females: 12; juvenile males: 10); three juvenile males and one juvenile female were released without a PIT tag either because an assistant was not available to help with the tag implantation, or it was deemed unsafe for the bird to proceed with tag implantation. In 2014, 52 hummingbirds were captured and tagged (adult females: 21; adult males: 11; juvenile females: 5; juvenile males: 15).

Premigratory Status of Hummingbirds

In August 2013 and 2014, 35 and 26 hummingbirds were detected at the stations, respectively. Of these 61 birds, we identified 17 birds that were redetected in the subsequent year. Of these 17 birds, eight birds for which we had at least one mass record on at least 4 of 5 days leading up to their last day of recorded activity at our feeders, permitting analysis of day to day mass variation over this period, were classified as 'pre migratory'; the remaining nine were classified as 'NP' due to insufficient data. We classified five additional birds for which we had high-resolution data as 'pre migratory', assuming their subsequent absence was due to their departure from the area and not the loss of a tag or their death. These birds, and all other individuals, were categorized as 'NP' on other days (earlier in the season). Excluding individuals that were classified as 'pre migratory' later in the season, the average residency time for NP adult hummingbirds was 36.3 days (minimum = 1 day, maximum = 105 days, $N = 30$) in 2013 and 36.9 days (minimum = 1 day, maximum = 97 days, $N = 28$) in 2014. For NP juvenile hummingbirds, average residency time was 6.4 days (minimum = 1 day, maximum = 18 days, $N = 13$) in 2013 and 10.1 days (minimum = 1 day, maximum = 37 days, $N = 10$) in 2014. These residency times are likely to be underestimates as adult hummingbirds may have been present for some time prior to tagging, and juveniles were tagged only after fledging.

Among the 13 premigratory birds, we noted two distinctively different patterns of mass change over this 5 day premigratory period. Eight birds showed no distinctive differences in mass change compared to other times of the season (i.e. compared to 'NP' birds) and these were classified as PNF (Fig. 1). Average daily mass for PNF birds ranged from 3.02 ± 0.24 g to 3.27 ± 0.22 g over the 4 days prior to migration. Average residency time for PNF adult birds was 57.3 days (minimum = 19 days, maximum = 80 days, $N = 4$) in 2013 and 50.0 days (minimum = 14 days, maximum = 86 days) in 2014. No juvenile hummingbirds were classified as PNF in 2013; however, two PNF juvenile hummingbirds resided for an average of 7.5 days (minimum = 6 days, maximum = 9 days) in 2014.

Five birds (2013: one adult male and two adult females; 2014: three adult females) exhibited a pronounced and sustained

increase in daily average mass beginning 4 days prior to migration (Fig. 2) and were classified as PF. Of these fattening hummingbirds, one adult female exhibited premigratory mass gain in both 2013 and 2014. Average daily mass for PF hummingbirds increased from 3.80 ± 0.18 g 4 days prior to migration to 4.46 ± 0.32 g on the day of migration. Average residency time for PF birds (adults only) in 2013 and 2014 was 91.0 and 91.3 days, respectively (2013: minimum = 50 days, maximum = 113 days; 2014: minimum = 51 days, maximum = 112 days).

Patterns of Daily Mass Change

Patterns of daily mass change on NP bird-days can be characterized as U-shaped, inverse U-shaped, positive linear, negative linear and erratic (Fig. 3), whereas over 75% of PF bird-days can be best characterized by a positive linear pattern of mass change (Fig. 3). Fig. 4 illustrates a shift in the pattern of daily mass change from U-shaped to positive linear as a hummingbird entered the PF state. Patterns of daily mass change could only be confidently identified for 4 PNF bird-days; as a result, these were excluded from the results and no inferences are drawn.

Total Time Spent at the Feeders

Premigratory nonfattening versus nonpre migratory hummingbirds

Table 1 gives all results for the comparison of total time spent at the feeders between PNF and NP hummingbirds.

Premigratory status was not retained as a fixed effect in any of the models within the confidence sets for morning, mid-day and evening periods, suggesting that NP and PNF hummingbirds did not differ in the amount of time spent at the feeders at any point of the day.

Mornings. There was strong support for the negative effect of average temperature and for the positive effect of total precipitation among PNF and NP birds during the morning hours. However, there was some support for the interaction term between average temperature and total precipitation, suggesting that hummingbirds spent more time foraging at the feeders during precipitation events occurring at lower temperatures. Sex and number of unique IDs were also retained in several of the models within the confidence set, but with weak support.

Mid-days. There was strong support for the negative effects of average temperature and total precipitation among PNF and NP birds during the mid-day hours. There was also strong support for age and moderate support for sex and the interaction term between age and sex: juvenile male hummingbirds spent the most time at the feeders, followed by adult females, adult males and lastly juvenile females. The interaction terms between age and average temperature and between average temperature and total precipitation were retained in several of the models within the confidence set with some support.

Evenings. The model selection protocol produced a single best-fitting model for the assessment of total time spent at the feeders by PNF and NP birds in the evenings. Total time spent at the feeders decreased with increasing average temperature, whereas total time increased as the number of unique IDs detected increased.

Premigratory fattening versus nonfattening hummingbirds

As the assessment of total time spent at the feeders revealed no difference between PNF and NP hummingbirds, we grouped PNF birds with NP birds in these subsequent analyses and refer to this group as NF birds. Table 2 shows the results for the following analyses.

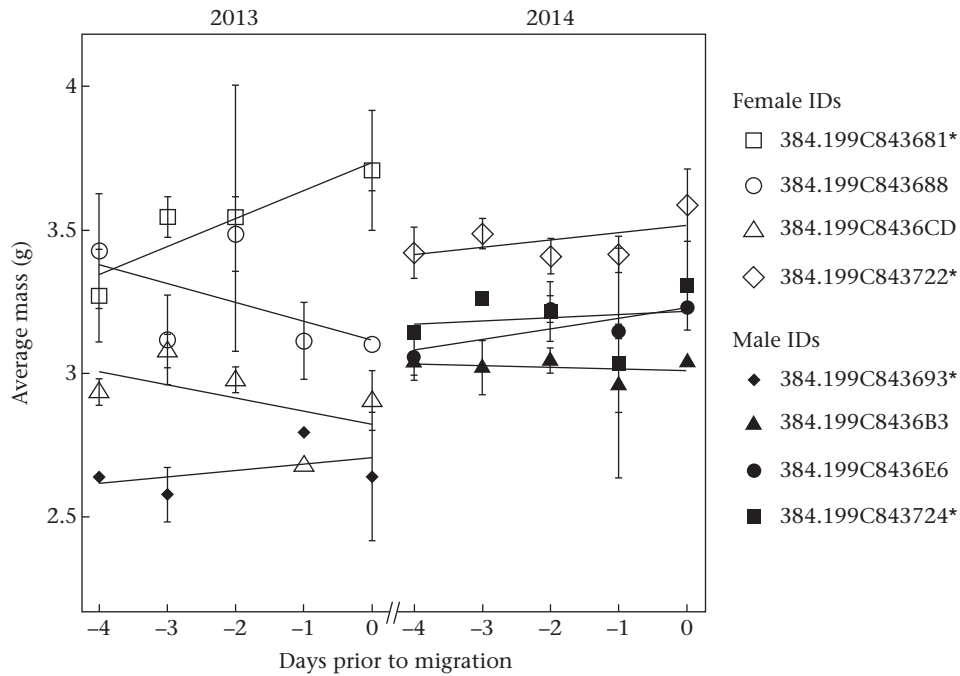


Figure 1. Premigratory nonfattening hummingbirds. Average mass \pm SE of the eight hummingbirds that did not gain mass in the 4 days leading up to the presumed date of migration (day 0) per criteria specified in the Results. Individuals marked with an asterisk were redetected in the subsequent year, indicating successful migration to and from the wintering grounds. Unmarked individuals were those for which we had sufficient data to regress daily average mass against days before migration but they did not exhibit a significant positive linear mass change prior to migration.

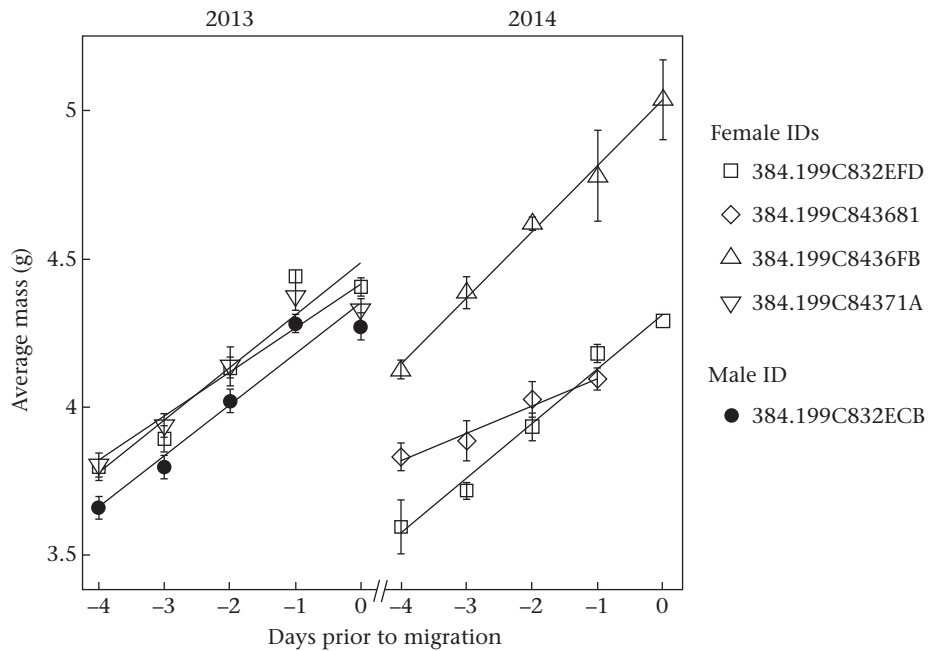


Figure 2. Premigratory fattening hummingbirds. Average mass \pm SE of five adult hummingbirds that exhibited positive linear mass change in the 4 days leading up to the presumed date of migration (day 0). One female (ID: 384.199C832EFD) exhibited positive linear mass change over the 4 days prior to migration in both 2013 and 2014.

Mornings. In the absence of precipitation, premigratory status was not considered an important variable as its SW was 0.71 and its 85% CI included zero. However, there was strong support for the effect of total precipitation and moderate support for the interaction between premigratory status and total precipitation which suggests that PF birds spent less time at the feeders than NF birds as total precipitation increased. Hummingbirds also spent less time at

the feeders as average temperature increased. As the interaction term between average temperature and total precipitation received moderate support, this also suggests that hummingbirds spent more time at the feeders during precipitation events occurring at below average temperature. There was moderate support for the number of unique IDs detected: hummingbirds spent more time at the feeders as the number of unique IDs detected increased. There

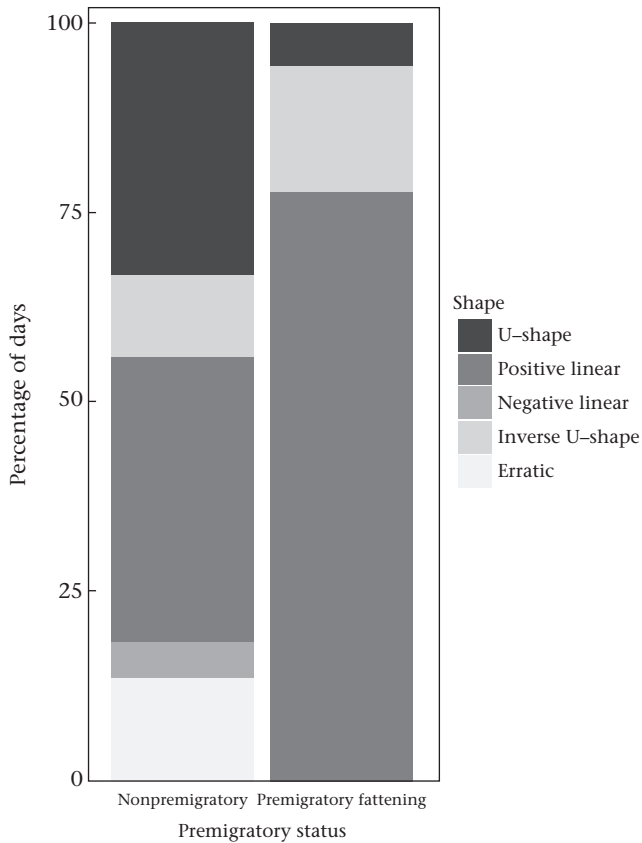


Figure 3. Percentage of days represented by each pattern of daily mass change. We assessed mass change over time for 18 of 24 possible premitigratory fattening days (2013: 3 birds \times 4 premitigratory days; 2014: 3 birds \times 4 premitigratory days). Of these 18 days, 14 were best described by a positive linear pattern, one was best described by a U-shaped pattern and three were best represented by an inverse U-shape. A proper assessment of mass change over time could not be performed for the remaining 6 of 24 days due to insufficient data. Only 4 days were classified as premitigratory nonfattening days; due to the small sample size for this category, we refrain from making any inferences. We classified 327 days representing 28 hummingbirds as nonpremitigratory. Of these, 35 days were best described by an inverse U-shaped pattern, 16 days were best described by a negative linear pattern and 44 days were erratic as both the parabolic and linear adjusted R^2 were negative. Of the remaining 232 days, 109 were best described by a U-shaped pattern and 123 by a positive linear pattern.

was also some support for the effect of sex: males spent less time at the feeders than females. In the repeated measures assessment, premitigratory status was not retained as a fixed effect (Table 3), indicating total time spent at the feeders did not change depending on whether the individual was in the NP or PF state.

Mid-day. Premitigratory status received moderate support in the assessment of total time spent at the feeders during the middle of the day, suggesting that PF hummingbirds spent more time at the feeders than NF birds. We found strong support for the effect of age indicating that juvenile hummingbirds spent less time at the feeders at this time than adults. There was also moderate support for the effect of sex as well as for the interaction term between age and sex suggesting that juvenile males spent the most time at the feeders, followed by adult females, adult males and lastly juvenile females; however, as the 85% CI for sex includes zero, the difference in total time spent at the feeders between adult females and adult males is not substantial. We also found strong support for average temperature and some support for the interaction between age and average temperature suggesting that juveniles spent more time at the feeders than adults as average temperature increased. Premitigratory status was retained as a fixed effect in the repeated

measures analysis with moderate support, suggesting that hummingbirds that exhibited premitigratory mass gain spent significantly more time at the feeders during the mid-day hours in the last several days prior to departure than earlier in the season.

Evenings. Premitigratory status received some support in the assessment of total time spent at the feeders during the evenings suggesting that PF hummingbirds spent more time at the feeders than NF hummingbirds. Average temperature received strong support indicating that hummingbirds spent less time at the feeders as average temperature increased. The number of unique IDs detected received moderate support suggesting that hummingbirds spent more time at the feeders when the number of unique IDs detected increased. Premitigratory status was retained as a fixed effect in the repeated measures analysis with weak support (Table 3), suggesting that hummingbirds that exhibited premitigratory mass gain spent more time at feeders during the evenings just prior to departure than earlier in the season.

Rate of Overnight Mass Loss

The model selection protocol produced a single best-fitting model for the assessment of rates of overnight mass loss (Table 4). Premitigratory status was retained as a fixed effect, indicating that rates of overnight mass loss differed between PF, PNF and NP hummingbirds. NP hummingbirds had the highest rate of overnight mass loss, followed by PNF hummingbirds, while PF birds had the lowest rate of overnight mass loss.

Juvenile hummingbirds had a lower rate of overnight mass loss than adults. The interaction term between age and last mass suggests that juvenile hummingbirds that weighed more at the end of the day had an even lower rate of overnight mass loss. Males had a higher rate of overnight mass loss than females. The interaction term between sex and last mass suggests that males that weighed more at the end of the night had an even greater rate of overnight mass loss.

DISCUSSION

Nonpremitigratory Birds

Patterns of daily mass change provide substantial insight into an individual's daily energy balance. In agreement with our a priori predictions, many NP individuals exhibited a U-shaped pattern of mass variation throughout any given day, as others have observed in other species in both the field and the laboratory (Beuchat et al., 1979; Calder et al., 1990). Mid-day feeding restraint, and a consequent U-shaped pattern of daily mass change, is hypothesized to reflect the prioritization of aerial flight performance over energy acquisition which can be adaptive and beneficial for fitness and survival (Calder et al., 1990). However, it is clear that the expectation that this pattern should be ubiquitous throughout the breeding period is erroneous. Previous studies that have reported the U-shaped pattern of daily mass change either focused on adult males (Calder et al., 1990), which do not participate in chick rearing (Weidensaul, Robinson, Sargent, & Sargent, 2013), or examined mass variation in captive populations with presumably limited opportunities to engage in varied life history phases (Beuchat et al., 1979). We found that daily patterns of mass variation among NP individuals can be characterized by a variety of different shapes (Hou et al., 2015), suggesting that hummingbirds may abandon mid-day prioritization of aerial agility for a number of reasons. For example, daily positive linear mass change during the NP period may indicate egg production in gravid females, whereas inverse U-shaped and negative linear patterns of mass change may indicate

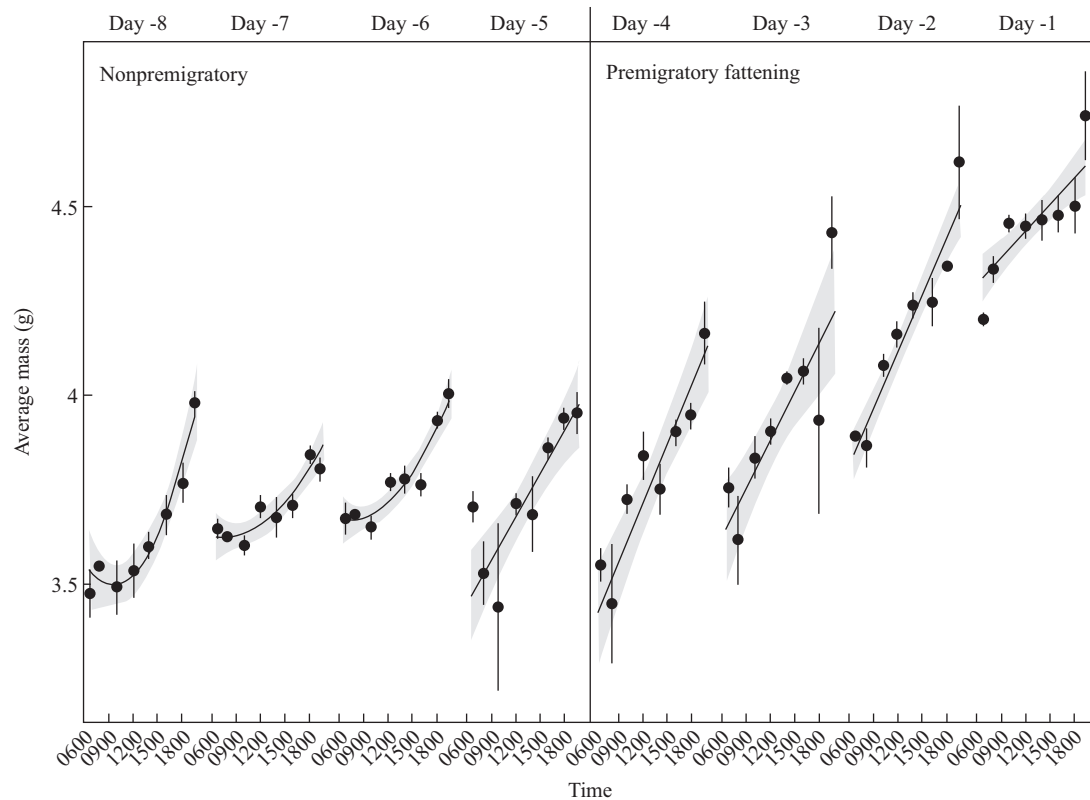


Figure 4. An example graph illustrating the shift from a U-shaped pattern of daily mass change during the nonpre migratory period to a positive linear pattern of daily mass change during the premigratory fattening period by an adult female ruby-throated hummingbird (384.199C832EFD). Shown here are days ranging from –8 days (31 August 2013) to –1 days prior to migration (7 September 2013). U-shaped curves best approximated the pattern of daily mass change for days –8 to –6, as determined by the Akaike weights analysis of a linear versus parabolic regression. Using the same method, we determined that days –5 to –1 were best approximated by a positive linear pattern of mass change. For visual clarity, we plotted average mass \pm SE for each 2 h time bin beginning at 0500 hours and ending at 2300 hours for each day. Lines of best fit were constructed using original mass values and overlaid onto this plot.

egg-laying events, the increased energetic demands of chick provisioning or inadequate energy acquisition leading to a loss of mass. Furthermore, this study could not account for individual body moult status or damage to, loss or wear of flight feathers. Such changes could impact insulation, thermoregulation and flight performance in ways that could alter energetic requirements and cause hummingbirds to adopt patterns of daily mass change different from the expected U-shape.

Premigratory Birds

We identified two distinct patterns of mass change among premigratory individuals: PF individuals which exhibited significant premigratory mass gain and PNF individuals which did not.

Premigratory nonfattening

Hummingbirds that did not exhibit premigratory mass gain may have achieved only moderate fattening, departed from the breeding grounds prior to the initiation of fattening, failed to initiate or complete migration, or failed to visit the feeders often enough to permit sufficient data collection. However, among PNF birds, we identified individuals that were redetected in the subsequent year indicating successful migration to and from the wintering grounds as well as individuals that provided substantial numbers of mass records prior to departure allowing us to conclude that their failure to gain substantial mass was not related to a lack of sufficient data.

We found that PNF hummingbirds visited the feeders more frequently than NP hummingbirds (see [Supplementary Material](#),

[Table S2](#)); however, this did not translate to an increase in time spent at the feeders as total feeder visit duration was similar between the two groups. This may suggest that PNF hummingbirds were attempting to increase foraging effort prior to the initiation of migration, but were prevented from feeding. Although they visited more often, the visits were short, possibly because they were chased away by more dominant individuals. Thus, we conclude that at least some PNF hummingbirds were indeed migrating individuals that avoided substantial premigratory fat deposition, consistent with an energy minimization migratory strategy and the storage of only enough fuel to reach a subsequent refuelling location ([Lindstrom & Alerstam, 1992](#)). Additionally, previous studies have found that substantial fattening occurred near ecological barriers that were significant energetic challenges and precluded foraging ([Caldwell, Odum, & Marshall, 1963](#); [Fransson, Barboutis, Mellroth, & Akriotis, 2008](#); [Odum, Connell, & Stoddard, 1961](#)). Because individuals could not be tracked once they departed, we cannot confirm when or where they subsequently refuelled, or whether they maintained the same fuelling strategy throughout their migratory journey.

Premigratory fattening

In contrast, a different subset of individuals exhibited significant fattening prior to their departure from the breeding grounds. This suggests the use of a time minimization strategy for migration where individuals store substantial fuel loads in order to reduce the amount of time spent refuelling ([Gudmundsson et al., 1991](#); [Hedenström & Alerstam, 1997](#)).

Table 1

Model averaged coefficient estimates, 85% confidence intervals, summed Akaike weights for each parameter and mean marginal and conditional R^2 for the models describing the total time hummingbirds spent at the feeders

'Total time spent at feeders' models fixed effects (random slope random intercept)	Fixed effects estimates	85% CI		Summed Akaike weights	Mean R^2		No. of models in confidence set	No. of individuals	
		Lower	Upper		Marginal	Conditional		NP	PNF
Morning									
Intercept	3.96	3.14	4.77		0.05	0.46	6	♀ _{adu} : 29	♀ _{adu} : 4
Sex (male)	−0.46	−0.85	−0.08	0.41			2	♂ _{adu} : 15	♂ _{adu} : 2
Centred average temperature	−0.07	−0.09	−0.05	1.00			6	♀ _{juv} : 5	♀ _{juv} : 0
Total precipitation	0.14	0.07	0.21	1.00			6	♂ _{juv} : 10	♂ _{juv} : 2
Unique IDs	0.09	0.03	0.15	0.30			2		
Centred average temperature : Total precipitation (Unique IDs Year ID)	−0.04	−0.08	−0.01	0.61			3		
Mid-day									
Intercept	4.08	3.88	4.28		0.03	0.32	10	♀ _{adu} : 29	♀ _{adu} : 4
Sex (male)	−0.25	−0.60	0.09	0.86			6	♂ _{adu} : 12	♂ _{adu} : 2
Age (juvenile)	−1.02	−1.71	−0.33	0.95			8	♀ _{juv} : 6	♀ _{juv} : 0
Centred average temperature	−0.04	−0.06	−0.02	1.00			10	♂ _{juv} : 9	♂ _{juv} : 2
Total precipitation	−0.05	−0.08	−0.01	0.94			8		
Age (juvenile) : Sex (male)	1.61	0.82	2.40	0.86			6		
Age (juvenile) : Centred average temperature	0.11	0.02	0.19	0.64			5		
Centred average temperature : Total precipitation (Unique IDs Year ID)	0.02	0.00	0.03	0.60			4		
Evening									
Intercept	3.76	3.47	4.04		0.02	0.35	1	♀ _{adu} : 31	♀ _{adu} : 4
Centred average temperature	−0.04	−0.06	−0.02	1.00			1	♂ _{adu} : 13	♂ _{adu} : 2
Unique IDs (None Year ID) ^a	0.06	0.03	0.08	1.00			1	♀ _{juv} : 4	♀ _{juv} : 0
								♂ _{juv} : 9	♂ _{juv} : 2

Only premigratory nonfattening birds (PNF) and nonpre migratory birds (NP) were assessed to determine whether total time spent at the feeders differed between the two groups. The number of models used in the natural average method and the number of unique females and males ('♀' and '♂', respectively, with subscripts indicating the age of birds) within each premigratory status classification in the data set used for analyses are also presented.

^a Models with 'none' as the random slope have an intercept-only random effects structure.

In contrast to NP individuals, PF hummingbirds predominantly exhibited a positive linear trend in mass gain throughout the days preceding departure (Fig. 3). This abandonment of mid-day feeding restraint represents a clear shift towards prioritizing energy acquisition and storage throughout the day in support of premigratory fuelling (Fig. 4).

To facilitate PF, and in abandoning mid-day feeding restraint, hummingbirds specifically spent more time at the feeders during the middle of the day in accordance with our prediction; we also found an unexpected increase in the amount of time spent at the feeders during the evenings (after 1500 hours). Since time spent at the feeders increased during the middle of the day and evenings but the frequency of feeder visits did not (see [Supplementary Material, Table S3](#)), it is clear that PF hummingbirds increased foraging effort specifically by engaging in longer feeding bouts at the artificial feeders.

Although we predicted that there would be no change in the evening foraging behaviour of PF hummingbirds, as hummingbirds are expected to maximize energy intake in anticipation of overnight fasting, our findings suggest that PF birds are capable of further increasing energy intake during the evenings. This ability to increase energy intake prior to migration may be facilitated by a change in digestive or metabolic physiology (e.g. late day upregulation of lipogenic enzyme activity; [Ramenofsky, Savard, & Greenwood, 1999](#); [Meier, 1977](#)) or indicate that NF hummingbirds exhibit some degree of feeding restraint during the defined evening periods that is released prior to migration to further facilitate fattening. However, this finding may be an artefact of the arbitrary division between 'mid-day' and 'evening' in this study. Hummingbirds have been observed to exhibit hyperphagia in the evenings to increase energy gain ([Calder et al., 1990](#)); however, hyperphagia may not be protracted across several hours, but rather manifest for a short period of time immediately before nightfall

([Calder et al., 1990](#)). The hours during the early evening period of this study (e.g. 1500–1900 hours) may be time during which hummingbirds continued to exhibit feeding restraint in favour of aerial agility. Further study will be necessary to determine what enables this increase in energy consumption during the evenings.

The total time PF hummingbirds spent at the feeders during the mornings did not differ from that of NF hummingbirds. This may be explained by the energetic requirements of the morning period as the depletion of energy reserves overnight means that hummingbirds must forage in a way that not only satisfies the immediate energetic requirements of continued foraging behaviour in the morning, but also replenishes expended energy reserves. Thus, hummingbirds act to maximize energy intake in the mornings regardless of time in the season. The lack of change in the foraging behaviour of PF hummingbirds in the mornings not only suggests that hummingbirds maximize energy consumption during this time on a daily basis due to the energetic challenge of overnight fasting, but also that the physiological or behavioural upper limit to energy intake during the mornings remains unchanged between the NF and PF states.

We found that PF hummingbirds experienced the lowest rate of overnight mass loss, followed by PNF and NP hummingbirds. For hummingbirds, regulation of overnight energy expenditure is important in preventing a negative energy balance that could be fatal as they do not feed during the overnight hours. Hummingbirds can fuel overnight energy expenditure by catabolizing nectar stored in the crop or accumulated fat ([Powers, 1991](#)). The lower rate of overnight mass loss observed in PF hummingbirds suggests that although these individuals possessed stored energy in excess of that necessary to meet the energetic challenge of overnight fasting, they nevertheless engaged in a nocturnal energy conservation strategy.

Hummingbirds can reduce energy expenditure through the use of torpor in situations when an individual is energetically stressed

Table 2
Model averaged coefficient estimates, 85% confidence intervals, summed Akaike weights for each parameter and mean marginal and conditional R^2 for the models describing the total time hummingbirds spent at the feeders

'Total time spent at feeders' models fixed effects (random slope random intercept)	Fixed effects estimates	85% CI		Summed Akaike weights	Mean R^2		No. of models in confidence set	No. of individuals	
		Lower	Upper		Marginal	Conditional		PNF	PF
Morning									
Intercept	3.82	3.17	4.46		0.05	0.50	10	♀ _{adu} : 32	♂ _{adu} : 4
Premigratory status (PF)	0.41	0.00	0.81	0.71			4	♂ _{adu} : 16	♂ _{adu} : 1
Sex (male)	-0.50	-0.90	-0.11	0.64			5	♀ _{juv} : 5	
Centred average temperature	-0.07	-0.09	-0.05	1.00			10	♂ _{juv} : 11	
Total precipitation	0.11	0.04	0.17	0.95			8		
Unique IDs	0.08	0.04	0.12	0.71			6		
Centred average temperature : Total precipitation	-0.05	-0.08	-0.02	0.71			4		
Premigratory status (PF) : Total precipitation (Unique IDs Year/ID)	-0.33	-0.53	-0.13	0.71			4		
Mid-day									
Intercept	4.19	3.99	4.39		0.03	0.35	15	♀ _{adu} : 32	♀ _{adu} : 4
Premigratory status (PF)	0.51	0.13	0.90	0.71			9	♂ _{adu} : 13	♂ _{adu} : 1
Sex (male)	-0.30	-0.66	0.06	0.86			10	♀ _{juv} : 6	
Age (juvenile)	-1.13	-1.87	-0.39	0.98			14	♂ _{juv} : 10	
Centred average temperature	-0.03	-0.04	-0.01	0.96			13		
Total precipitation	-0.04	-0.07	-0.01	0.66			8		
Age (juvenile) : Sex (male)	1.65	0.81	2.49	0.86			10		
Age (juvenile) : Centred average temperature (Unique IDs Year/ID)	0.11	0.02	0.19	0.64			8		
Evening									
Intercept	3.90	3.49	4.30		0.01	0.43	4	♀ _{adu} : 34	♀ _{adu} : 4
Premigratory status (PF)	0.42	0.01	0.82	0.54			2	♂ _{adu} : 14	♂ _{adu} : 1
Centred average temperature	-0.04	-0.05	-0.02	1.00			4	♀ _{juv} : 4	
Unique IDs (Unique IDs Year/ID)	0.06	0.03	0.09	0.84			2	♂ _{juv} : 10	

The number of models used in the natural average method and the number of unique females and males ('♀' and '♂', respectively, with subscripts indicating the age of birds) within each premigratory status classification (PNF: premigratory nonfattening; PF: premigratory fattening) in the data set used for analyses are also presented.

(Hainsworth, Collins, & Wolf, 1977). However, hummingbirds have also been observed to use torpor in situations when they are not experiencing an energy crisis. It has been postulated that this is beneficial for the conservation of fat stores in preparation for migration, thereby reducing the amount of time needed to achieve adequate fattening prior to migration (Carpenter & Hixon, 1988; Hiebert, 1993). Without direct observation of our hummingbirds during the night, we could not determine for certain whether a hummingbird entered torpor. Still, the comparatively low overnight rate of mass loss observed in PF hummingbirds is consistent with the use of an energy conservation strategy that includes the use of torpor, as has been observed or hypothesized elsewhere (Carpenter & Hixon, 1988; Hiebert, 1993).

Although a reduction in the rate of overnight mass loss can also be explained by the increased insulation that fat provides, a previous study concluded that this explanation would be insufficient in accounting for the observed differences in overnight mass change by fat and lean hummingbirds (Carpenter et al., 1993). Under normothermic conditions, the difference in oxygen consumption by fat and lean hummingbirds was only 1%, whereas in the case of torpor, oxygen consumption by fat hummingbirds exceeded that of lean hummingbirds by 10% (Hiebert, 1989). For fat normothermic hummingbirds, this would mean overnight mass loss would be similar to that of lean normothermic hummingbirds, while for fat torpid hummingbirds, mass loss would be greater than that of lean torpid hummingbirds.

Biotic and abiotic factors

In assessing how PF hummingbirds established a positive energy balance in the wild, our analyses took into account abiotic and biotic variables that could influence behaviour and energetics. Previous studies have found that for small endothermic hummingbirds challenged by low ambient temperatures, increases in foraging frequencies allowed individuals to maintain energy balance (Beuchat et al., 1979; Gass, Romich, & Suarez, 1999).

Precipitation also poses a significant challenge to hummingbirds, as storm events can reduce available foraging time (Gass & Lertzman, 1980). In our study where temperature was retained as a fixed effect, coefficient estimates consistently revealed a negative relationship between temperature and the response variables of frequency, total time and proportion of time spent at the feeders (Tables 1–4 and Supplementary Tables S1–S6). Thus, we found general patterns that match those revealed by other researchers using direct observation techniques (Beuchat et al., 1979; Gass et al., 1999). Where precipitation was retained as a fixed effect, we found that increases in total precipitation led to an increase in total time spent at the feeders during the mornings, which may reflect a greater reliance by hummingbirds on the artificial feeders during inclement weather; however, as the feeders were partially sheltered to limit equipment exposure, this finding may not reflect foraging effort so much as the adoption of preferable microclimates. Interestingly, we found a decrease in time spent at the feeders during the middle of the day and no change in the evenings with increases in total precipitation (Tables 1 and 2). These findings suggest that hummingbirds employ different foraging strategies in response to precipitation events depending on the time of day.

Hummingbird foraging behaviour and energetics can also be influenced by intraspecific competition over resources. We found that in all best-fitting models in which the number of unique IDs detected at the feeding stations was retained as a fixed effect, coefficient estimates consistently revealed a positive relationship with the aforementioned response variables. For dominant individuals that exhibit resource defence at the feeders, greater competitive pressure means an increase in energetically expensive territorial displays and chases. Dominant individuals must therefore increase energy intake in order to meet these energetic demands. Furthermore, it has been observed that when faced with a nectar-robbing intruder, dominant hummingbirds chased away the intruder and subsequently returned to feed at the same site that the intruder robbed; it was hypothesized that dominant hummingbirds

Table 3

Model averaged coefficient estimates, 85% confidence intervals, summed Akaike weights for each parameter and mean marginal and conditional R^2 for repeated measures analyses assessing total time spent at the feeders by hummingbirds exhibiting premigratory mass gain

'Total time spent at feeders' models fixed effects (random slope random intercept)	Fixed effects estimates	85% CI		Summed Akaike weights	Mean R^2		No. of models in confidence set	No. of days	
		Lower	Upper		Marginal	Conditional		NP	PF
Morning									
Intercept	5.39	4.99	5.78		0.11	0.40	1	287	23
Sex (male)	−0.96	−1.21	−0.71	1.00			1		
Centred average temperature (Unique IDs Year ID)	−0.07	−0.10	−0.04	1.00			1		
Mid-day									
Intercept	5.36	4.57	6.15		0.03	0.32	5	276	22
Premigratory status (NP)	−0.52	−0.88	−0.15	0.81			4		
Sex (male)	−0.70	−1.08	−0.32	0.65			3		
Unique IDs (None Year ID) ^a	0.03	0.00	0.07	0.44			2		
Evening									
Intercept	5.47	4.61	6.34		0.01	0.34	5	296	23
Premigratory status (NP)	−0.37	−0.72	−0.02	0.29			2		
Sex (male)	−0.41	−0.70	−0.11	0.63			3		
Centred average temperature	−0.01	−0.04	0.02	0.46			2		
Centred average temperature : Sex (male) (None Year ID) ^a	−0.08	−0.14	−0.02	0.33			1		

We assessed five individuals, and report the number of days for each premigratory status classification (NP: nonpre migratory; PF: premigratory fattening). The number of models used in the natural average method is also presented.

^a Models with 'none' as the random slope have an intercept-only random effects structure.

Table 4

Model averaged coefficient estimates, 85% confidence intervals, summed Akaike weights for each parameter and mean marginal and conditional R^2 for the models describing rate of overnight mass change

'Rate of overnight mass loss' fixed effects (random slope random intercept)	Fixed effects estimates	85% CI		Summed Akaike weights	Mean R^2		No. of models in confidence set	No. of individuals		
		Lower	Upper		Marginal	Conditional		NP	PNF	PF
Intercept	4.71	1.32	8.13		0.51	0.58	1	♀ _{adu} : 23	♀ _{adu} : 2	♀ _{adu} : 4
Premigratory status (PNF)	8.62	2.88	14.31	1.00			1	♂ _{adu} : 7	♂ _{adu} : 1	♂ _{adu} : 1
Premigratory status (NP)	13.49	10.37	16.61	1.00			1	♀ _{juv} : 1	♀ _{juv} : 0	♀ _{juv} : 0
Sex (male)	14.68	12.03	17.32	1.00			1	♂ _{juv} : 5	♂ _{juv} : 1	♂ _{juv} : 0
Age (juvenile)	−13.81	−17.88	−9.63	1.00			1			
Centred last mass	12.37	10.30	14.44	1.00			1			
Sex (male) : Centred last mass	10.56	7.70	13.42	1.00			1			
Age (juvenile) : Centred last mass (Centred average temperature ID)	−13.97	20.62	−7.22	1.00			1			

The number of models used in the natural average method and the number of unique females and males ('♀' and '♂', respectively, with subscripts indicating the age of birds) within each premigratory status classification (NP: nonpre migratory; PNF: premigratory nonfattening; PF: premigratory fattening) in the data set used for analyses are also presented.

did this to further deplete recently robbed resources such that subsequent food loss due to nectar thievery was minimized (Paton & Carpenter, 1984). For nondominant hummingbirds, an increase in the number of competing individuals at the feeders may provide more windows of time in which nectar robbing can occur, as dominant individuals spend more time chasing away other intruders. Furthermore, the fledging and tagging of young partway through the season and their added use of the feeders could also be driving the positive relationship observed between the number of unique individuals detected at the feeders and the aforementioned response variables.

Conclusions

Although previous studies have found that some birds, such as the ruby-throated hummingbird, exhibit substantial fattening once they encounter ecological barriers (Caldwell et al., 1963; Fransson et al., 2008; Odum et al., 1961), we found that a small number of individuals (<5%) exhibited significant fattening at the breeding grounds prior to the initiation of migration where no major ecological barrier exists. While we have found evidence of a substantial

pre migratory fuelling strategy within a population of ruby-throated hummingbirds, a majority of premigratory individuals did not adopt this strategy. Those that did achieved substantial fattening via a two-pronged approach of increasing mid-day and evening foraging effort and reducing overnight energy expenditure.

Although our sample size of PF individuals is small, our study suggests there is age-related variation in premigratory fuelling. This was observed exclusively in adult hummingbirds, suggesting that more experienced birds (particularly females) are more likely to abandon mid-day feeding restraint to prioritize fattening. Significant mass gain and fuel deposition immediately preceding migration could theoretically be used to fuel longer bouts of migratory flights, thereby requiring fewer stopovers; moreover, birds that arrive at stopover sites with larger fuel loads spend less time refuelling (Gudmundsson et al., 1991; Nilsson et al., 2013). As such, birds that engage in premigratory fuelling may be using a migration strategy that approximates time minimization (sensu Alerstam & Lindström, 1990). In contrast, less experienced (juvenile) birds appear more likely to depart the breeding grounds without building substantial fuel stores, perhaps implying the use of a migration strategy akin to energy minimization. However, identifying the

specific use of either migration strategy will require a larger sample size and further analyses of individual departure fuel loads and fuel deposition rates (Alerstam & Lindström, 1990). None the less, our observation of an age-related premigratory fuelling strategy in ruby-throated hummingbirds parallels the finding of age-related migration in ruby-throated hummingbirds at a stopover site by Zenzal and Moore (2016). Their observation that juveniles arrived with smaller fuel loads than adults may be explained, in part, by the absence of a premigratory fuelling strategy observed in juveniles of our current study; however, further study is needed to confirm this hypothesis. Further study is also needed to elucidate what compels an individual to adopt a premigratory fuelling strategy, whether premigratory fuelling directly influences migration strategies, and whether differential body conditions upon arrival at stopover sites can be traced back to premigratory fuelling at the breeding grounds.

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Supplementary Material

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