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Automated tracking of wild hummingbird mass and energetics over multiple time scales using radio frequency identification (RFID) technology

Lily Hou, Michael Verdirame and Kenneth C. Welch Jr

L. Hou, M. Verdirame and K. C. Welch Jr (kwelch@utsc.utoronto.ca), Dept of Biological Sciences, Univ. of Toronto Scarborough, Toronto, ON M1C1A4, Canada. LH and KCWJ also at: Dept of Ecology and Evolutionary Biology, Univ. of Toronto, Toronto, ON, Canada.

We examined the feasibility of automating the collection of hummingbird mass data facilitated by low-cost, low-power radio frequency identification (RFID) technology. In a field study in southern Ontario, wild hummingbirds were captured, subcutaneously implanted with passive integrated transponder (PIT) tags, and released over a three-year period. Tagged hummingbirds were detected at specially designed feeder stations outfitted with low-cost, low-power RFID readers coupled with a perch secured to a digital balance. When tagged birds visited the feeder, transponder detection initiated the recording of the perched hummingbird's mass at regular intervals continuing as long as the bird remained. This permitted a nearly continuous record of mass during each visit. Mass data collected from tagged hummingbirds showed consistent trends at multiple temporal scales: the individual feeder visit, single days, and even whole seasons. These results further confirm that RFID technology is safe for use in the smallest birds. The effective detection range is a function of RFID reader power, antenna, and tag size. Yet, we find that careful arrangement of feeders and detectors allows for reliable detection even when detection range is low. When coupled with additional technologies, such as a precision electronic balance, this approach can yield robust serial measures of physiological parameters such as mass, an indicator of energy balance over time.

The collection of physiological data from wild animals often requires the repeated capture of individuals, which is typically opportunistic and limited by a low probability. Handling can be a physiological stressor to individuals (Cabanac and Aizawa 2000, Remage-Healey and Romero 2001) and can cause persistent changes in behaviour and energy balance, such as learned aversion to traps (Zarnoch and Burkhart 1980), delayed egg-laying (Buttler and Gilcrist 2011), impaired territorial defense (Carpenter et al. 1983), or sustained mass gain (Macleod and Gosler 2006). In a study of wild animals, such changes in behaviour and physiology can bias data. It is therefore necessary to develop alternative methods to collect relevant data from wild animals while minimizing the need for repeated captures.

Physiological studies of free-living animals have been constrained by several logistical limitations. In many cases, recapture rates have been frustratingly low, such as in hummingbirds with recapture rates ranging from 17 to 32% (Calder III et al. 1983, Powers and Nagy 1988, Powers and Conley 1994, Hilton Jr and Miller 2003, Brewer et al. 2011). Moreover, the efficiency of data collection can be limited by the recapture of individuals within and between seasons. Furthermore, the efficacies of certain techniques (e.g. the use of doubly-labelled water) are temporally constrained, requiring recaptures to occur within brief temporal windows (Powers and Nagy 1988, Powers and Conley 1994, Weathers et al. 1996). Even approaches that do not rely on the recapture of individuals have drawbacks. Unique identifiers that are remotely detectable by observers can wear or fall off as birds molt, thus individuals are not easily tracked across seasons. Moreover, the tracking of marked individuals in the field can be both time- and labour-intensive (Carpenter et al. 1991).

More recently, it has become possible to overcome these logistical hurdles and gather both physiological and behavioural data on free-living birds using battery powered transmitters and geolocators, some of which can monitor variables such as heart rate and temperature (Kettlewell et al. 1997), track home range movement (Dunn and Gipson 1977), and migration (Stutchbury et al. 2009). However, such approaches have been limited to use with larger avian species, as the Bird Banding Laboratory (BBL) of the United States Geological Survey only permits the attachment of devices that are 3% or less of a bird's body weight. While dataloggers and transmitters can allow for the collection of spatial, temporal, physiological and behavioural information of individuals (Cooke et al. 2004), these devices rely on an internal battery, and therefore have a limited lifespan.

Unlike other technologies, passive integrated transponder (PIT) tags as small as 5 mm in length show promise as unique identifiers in animals as small as hummingbirds (Brewer et al. 2011). Because PIT tags do not rely on an internal battery, they can potentially provide data collection over the lifetime of a tagged individual (Brewer et al. 2011). To date, RFID technology has been used in many long-term ornithological studies that examine presence–absence, movement, mating, nesting, reproduction, provisioning, foraging, and homing behaviours of birds (reviewed by Bonter and Bridge 2011).

Serial collection of physiological data facilitated by the use of PIT tags has previously been successful in larger avian species, allowing for the collection of visitation and body weight records daily (Boisvert and Sherry 2000, Macleod 2006). However, the feasibility of this approach has not yet been explored for the smallest avian species. Our objective was to determine whether RFID technology could be successfully harnessed to permit the serial collection of hummingbird mass records in the field. The tracking of mass over short time periods in hummingbirds can be a reliable indicator of energetic status (Beuchat et al. 1979, Gass et al. 1999). Hummingbirds exist at the extreme end of the energetic spectrum, where a high mass-specific metabolic rate (Suarez 1992), small size, and highly energetic hovering lifestyle mean changes in energy balance quickly manifest as changes in mass.

We tested the efficacy of the smallest commercially available PIT tag (7 mm) compatible with common readers used in biological research and examined if it could be used to automate the serial monitoring of hummingbird mass. With the hope of reducing overall equipment costs, we tested the use of a low-cost, low-power RFID reader, as the financial burden of commercial RFID technology can be prohibitive (Bonter and Bridge 2011). We predicted that data collected using this approach would have high temporal resolution permitting observations of hummingbird mass change at time scales of seconds to entire seasons. Specifically, this method would permit consistent observations of a) hummingbird mass gain over the course of individual feeding events, b) changes in hummingbird mass over the course of a day from sunrise to sunset (Beuchat et al. 1979, Calder et al. 1990), and c) seasonal changes in hummingbird mass such as exponential mass gain prior to migration (Carpenter et al. 1993). The identification of patterns of mass change similar to those reported in existing literature (Beuchat et al. 1979, Calder et al. 1990, Carpenter et al. 1993) would allow us to conclude that mass variation is reliably measured in the field using this approach, thereby revealing physiologically and ecologically relevant phenomena.

Methods

Study site

The study area, in King City, Ontario, was approximately 8 ha of irregularly shaped land, and centrally located on the Koffler Scientific Reserve (KSR) at Joker's Hill (44°1′47″N, 79°32′2″W). The reserve was surrounded by mixed forests and comprised of open meadows and two ponds.

Automated stations

Six free-standing stations were constructed on the reserve. In addition to the RFID antenna and reader (see below), each station consisted of a Perky-Pet commercial hummingbird feeder (model no. 220, Perky-Pet, Lititz, PA, USA) with five of six 'flowers' sealed so that only one was available to the bird and a Denver MAXX digital scale (model no. MXX-212, Sartorius, Bohemia, NY, USA) onto which a perch was mounted for mass measurements (Fig. 1). Tag detection and mass measurements were recorded to a notebook PC via direct serial communication. All electronic components were housed in weatherproof boxes.

Of the six stations constructed on the reserve, one employed a commercially-available Biomark Reader (FS2001F-ISO, Biomark, Boise, ID, USA) and racquet antenna to detect PIT tags (hereafter referred to as 'station 1'). The remaining five stations were constructed using a low-cost, low-power RFID reader. This involved a custom-made circuit board designed by Eli Bridge (Bridge and Bonter 2011) with programmable poll, pause and data logging times. Upon receipt of tag information from the reader, a custom designed MATLAB script (Mathworks, Natick, MA, USA) queried the digital balance seven consecutive times at 0.5 second intervals. Unique tags were recorded, when in range, as often as every five seconds. This allowed hummingbird mass to be recorded nearly continuously as long as individuals remained within the read range of the antenna. In the absence of a bird, mass readings were automatically obtained every 10 min in a pattern identical to that above. This mass record (referred to as the 'baseline')

Figure 1. Illustration of a perched hummingbird feeding from an artificial feeder with an attached RFID antenna.

permitted us to account for balance drift and triggered automated balance taring when the reported 'empty' mass was more than ± 0.3 g. A 12 V deep-cycle battery attached via a trickle-charger to AC power was used to power the RFID board, antenna, and balance at each station. Notebook computers were attached to AC power. While we had constructed a total of six stations in 2012, a fatal error on one of the electronic balances reduced the number of functional stations to five in 2013.

Except for station 1, we manufactured a low-cost, low-power antenna for use with each low-power reader. The antennas were constructed using 28-gauge copper magnetic wire wound to create a coil of approximately 3.2 cm in diameter, and with an inductance of 1.17 mH corresponding to the frequency of our PIT tags. Each antenna was secured in four spots with small strips of duct tape and coated with silicon glue and clear lacquer. Antennas were then attached to the artificial flower of a Perky-Pet feeder perpendicular to the ground.

Tagging in the field

Hummingbirds were captured, banded and tagged between June and August in 2011 and between mid-May and mid-September in 2012 and 2013 for 1 to 2 d every week. Trapping occurred between sunrise and 10:00h and was suspended during periods of moderate to intense rainfall. During trapping, RFID readers were removed from the stations and replaced with wire-mesh trap-door cages and Perky-Pet artificial feeders supplied with ~25% (w/v) sucrose solution. Hummingbirds were captured at six stations on the reserve. Captured birds were extracted from the cage, placed in a mesh bag and transported to the KSR lab for processing. The age (juvenile: < 3 months old; adult: ≥ 1 yr) and sex of the bird was first determined followed by collection of morphological data and tarsal banding according to standard BBL practices.

We chose to employ the smallest commercially available PIT tag, the 7 mm UNO PICO ID ISO transponder (~0.26 g). Tag implantation was performed in the field using a method similar to that reported by Brewer et al. (2011). With an assistant gently restraining the bird, the bander proceeded to implant the transponder. A cotton swab was used to disinfect and anesthetize the skin on the dorsal surface of the bird between the scapulae with betadine and 1% Lidocane solution, respectively. Using a pair of forceps to lift the skin, the PIT tag was implanted subcutaneously with a syringe at a shallow angle. The injection site was then sealed using 3M Vetbond Tissue Adhesive to promote tag retention. The bird was then allowed to feed freely from a feeder while being held. We passed the bird through an antenna to obtain the unique alphanumeric code of the PIT tag before releasing the bird at the station where it was originally captured. Implantation was typically accomplished in approximately 5 min and total bird handling time was approximately 15 min.

Data and statistical analyses

We identified individual visits to each feeder station by unique hummingbirds as all sequential readings occurring within 10 s of each other. As the response of the electronic balance is not instantaneous, and because hummingbirds could, in some cases, be detected by the RFID reader while not on the perch, it was necessary to filter mass readings associated with each visit. Erroneous or artifact mass readings were filtered by regressing mass versus time within each visit. Readings with Cook's distance values greater than 4/n, where n is the number of points used, or where the calculated rate of change in mass between sequential readings was > 0.5 g s^{-1}, were excluded. Mass values were corrected for balance drift. Corrected mass values that were outside the biologically realistic range (i.e. less than 1.5 g or greater than 10 g) were also excluded. The biologically realistic range of male and female ruby-throated hummingbirds was determined by examining recorded masses of ruby-throated hummingbirds at the time of banding by a fellow hummingbird bander for over 300 males and over 300 females between 2003 and 2012. The threshold values were set at 117% above the maximum recorded mass value and 37% below the minimum recorded mass value such that we are confident that mass values outside this range are highly unlikely.

We analyzed a subset of visits greater than 30 s in length to obtain a net rate of mass change over one visitation, recognizing that this integrated both mass gain via nectar intake and mass loss due to urination. Least-squares linear regressions were developed for each visitation to determine average rate of integrated mass gain.

Daily mass variation of hummingbirds was assessed by selecting individuals on days for which we had more than 50 mass records. We then created two-hour time bins between 05:00 and 22:00 h and selected individuals on days for which we had four or more mass records in at least seven time bins. Masses and times were averaged for each two-hour time bin. A linear least-squares and parabolic model was fitted to these variables for each individual on each day. From this we obtained adjusted R^2 (R^2_{adj}) values and assessed the relative quality of the two models using the Akaike information criterion (AIC).

Pre-migratory mass gain in hummingbirds was examined beginning 14 d prior to the presumed date of migration, identified as the date of last recorded mass. Median mass measurements for each visit obtained between 19:00 and 20:00 h were averaged and modeled exponentially as a function of the number of days before departure using a nonlinear mixed effects model with individual included as a random factor. These same variables were modeled using a least-squares linear mixed effects model. The relative quality of the two models was determined using AIC scores. Percentage mass gain and rate of mass gain for each individual was calculated using the difference in mass between day 0 and day 4, where mass gain appeared to be linear.

All statistical analyses were conducted using R ver. 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria). Linear and nonlinear mixed-effects models were developed using the R packages, lme4 version 1.0-5 (Bates et al. 2013) and nlme ver. 3.1-113 (Pinheiro et al. 2013), respectively. Data are presented as mean ± SEM, except where noted.

Results

We tagged a total of 118 ruby-throated hummingbirds at KSR – 12 of which were tagged during a pilot study in

Table 1. Summary of the annual number of ruby-throated hummingbirds tagged (n) and number of redetections. Age of hummingbirds listed here are at the time of initial capture.

		Redetections		
Initial capture		2011	2012	2013
2011 (n = 12)	9 adult females	6 adult females	4 adult females	1 adult female
	2 adult males	1 adult male		
	1 juvenile male	1 juvenile male		
2012 (n = 50)	31 adult females		29 adult females	7 adult females
	12 adult males		9 adult males	4 adult males
	2 juvenile females		1 juvenile female	1 juvenile male
	5 juvenile males		2 juvenile males	
2013 (n = 56)	25 adult females			17 adult females
	9 adult males			8 adult males
	12 juvenile females			7 juvenile females
	10 juvenile males			6 juvenile males

2011, 50 were from 2012, and 56 were from 2013. Of the 118 birds, 79 were female and 39 were male. By the end of 2013, we redetected ~70% of all tagged hummingbirds (82 individuals) at our stations at least once after initial capture. Annual hummingbird redetections since 2011 have been summarized in Table 1. The return rate in 2012 of individuals originally banded during the pilot study in 2011 was 33% (Table 1), while the return rate in 2013 of individuals originally banded in 2012 was 24% (Table 1). Overall, we redetected 26% of individuals in years subsequent to the initial year of tagging. We recorded in excess of 27 100 separate visits from tagged hummingbirds to five active feeder stations between May and September 2013. Ten hummingbirds were identified as regular visitors, each exceeding 600 recorded visitations at our stations. The most frequent visitor was an adult female with nearly 8000 recorded visitations.

In 2012, three females returned from 2011, but only one fed at the stations regularly throughout the summer – of the

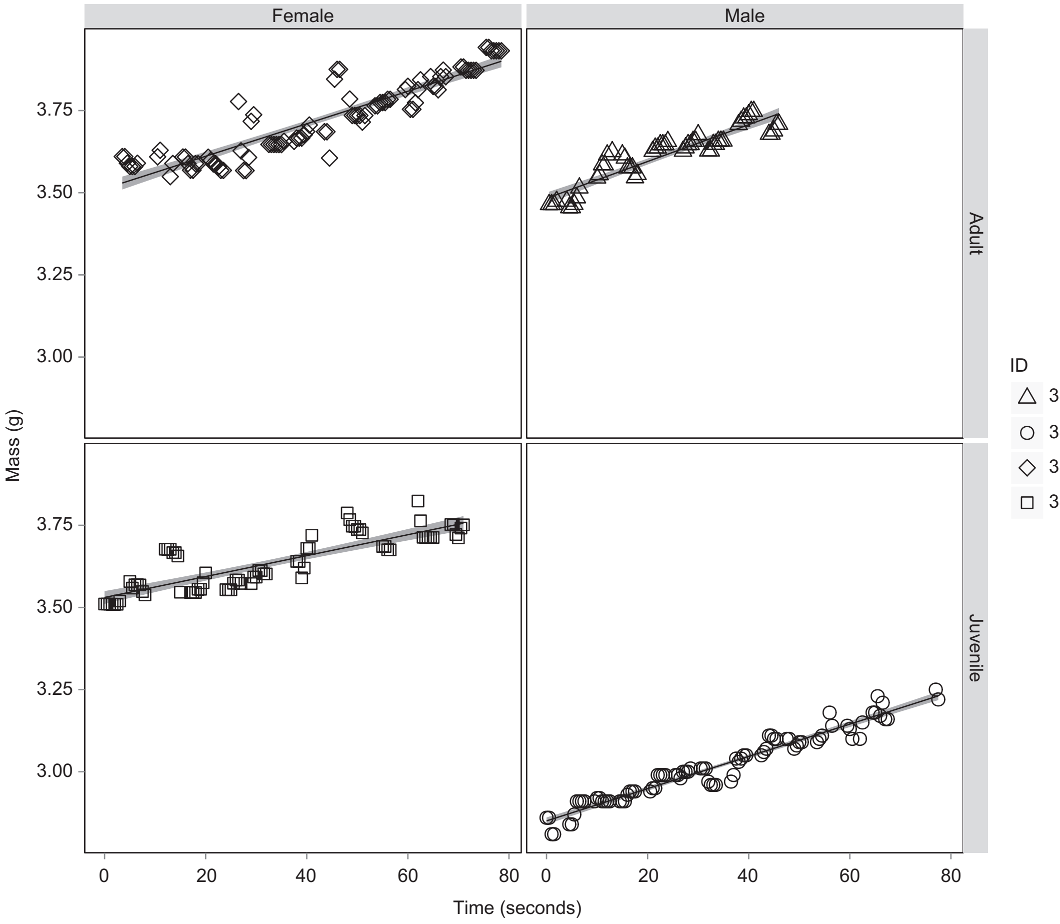

Figure 2. Example visitations illustrating linear mass change of ruby-throated hummingbirds. A linear least squares model with 95% confidence intervals was fitted to each visitation after the removal of influential points.

remaining two females, one was redetected 20–22 May 2012, and the other was redetected on 25 and 27 May 2012.

Patterns of mass change through time

Mass readings consistently exhibited a positive linear relationship with time over the duration of a visitation (Fig. 2). We calculated that hummingbirds gained mass at a median and average rate of 7 ± 0.3 mg s^{-1} (6383 observations, 40 hummingbirds, min = 4 mg s^{-1} and max = 12 mg s^{-1}).

Mass records of 7 hummingbirds for 99 total days (min = 1 d/individual, max = 53 d/individual) were selected, based on the criteria outlined above, to determine the pattern of mass variation in relation to time of day. Parabolic models fit patterns of mass change throughout the day better than linear models for 42 of 99 d, as determined using AIC scores, where mass variation presented as u-shaped curves over time (Fig. 3 and 4A; $0.12 < R^2_{adj} < 0.92$). Inversely parabolic models performed better than linear models in 12 additional analyses (Fig. 4B; $0.06 < R^2_{adj} < 0.87$). For 30 of 99 d, linear models best represented the variation of mass in relation to time (Fig. 4C; $0.05 < R^2_{adj} < 0.70$). The remaining 15 d analyzed produced negative R^2_{adj} values for both linear and parabolic models (Fig. 4D).

For 3 individuals for which large numbers of mass records were available between late August and early September, we observed consistent, predictable patterns of exponential mass gain prior to migration (Fig. 5; Table 2). Average percentage mass gain beginning 4 d prior to migration was calculated to be $23.56 \pm 2.57\%$, at an average rate of 0.23 ± 0.02 g d^{-1}.

Discussion

In our field study, the use of PIT tags and RFID technology allowed the redetection of 70% of tagged individuals, which is much greater than the recapture rates reported previously. A smaller field study by Brewer et al. (2011) using a similar method of PIT tagging in ruby-throated hummingbirds reported redetections after initial capture to be 55.5%, while redetections of hummingbirds in years subsequent to the year of initial tagging were reported to be 26%. These values are comparable to those found in our study. Reasons for failing to redetect individuals after initial tagging may include tag loss, the movement of individuals away from the study location, individuals becoming averse to feeder stations as a result of capture or handling, and death of the individual.

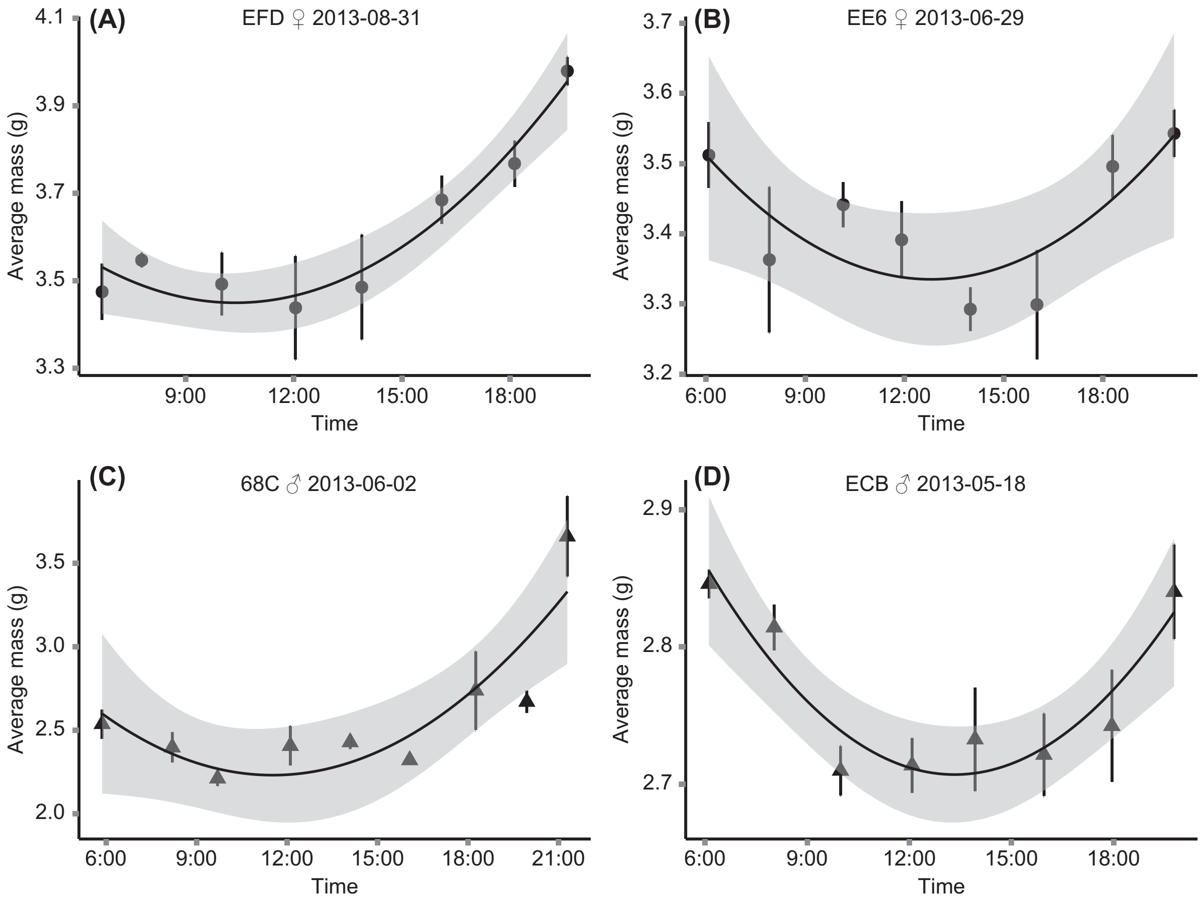

Figure 3. Average mass ± standard error of (A and B) adult females, (C and D) adult males on example days fitted with a parabolic model and 95% confidence intervals. Hummingbird mass variation during the day between sunrise and sunset presents as a u-shaped curve. Mass is higher in the early morning as a result of compensatory feeding after overnight fasting. Mass then decreases and is maintained at a reduced level as the day progresses. Prior to overnight fasting, hummingbirds engage in hyperphagia resulting in mass gain. Hummingbird IDs have been abbreviated to the last three characters.

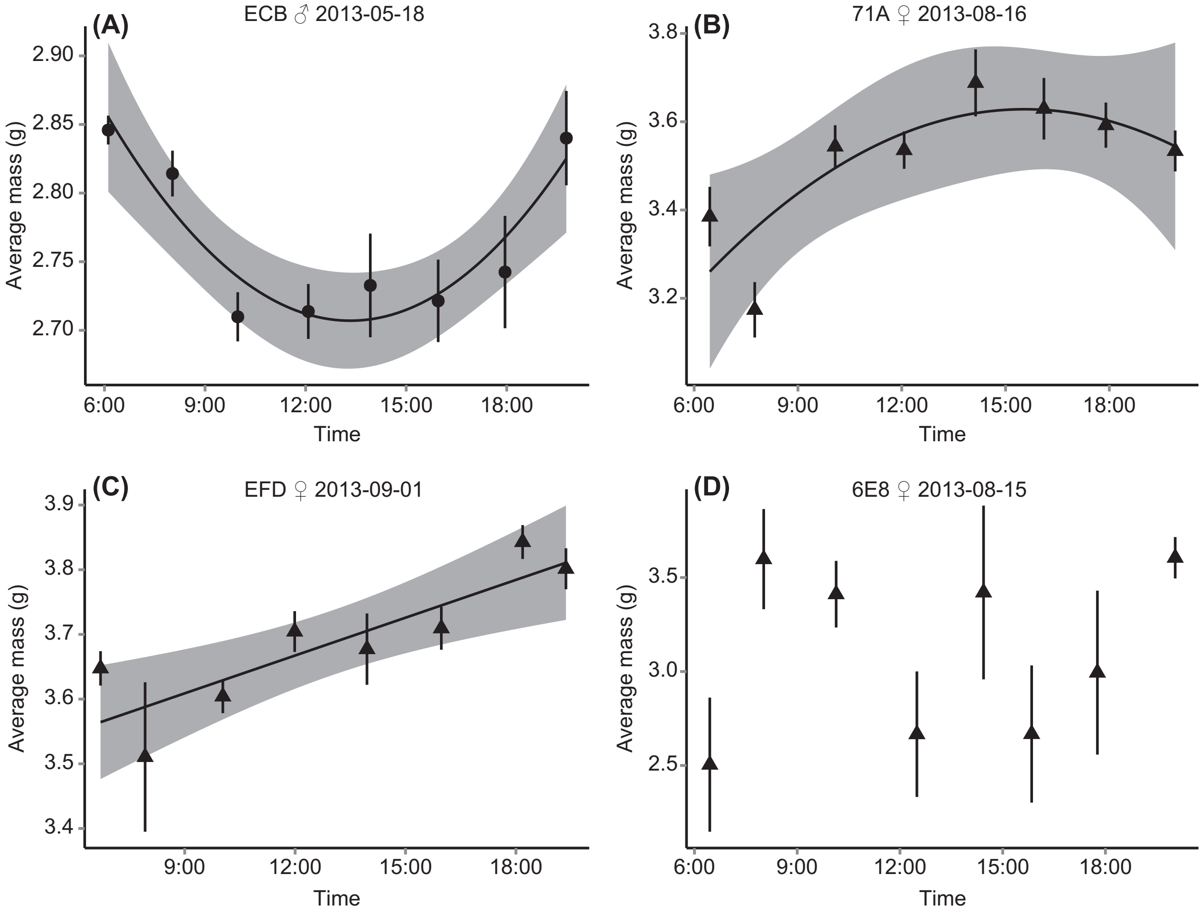

Figure 4. Examples of patterns of daily mass change. Daily mass change in hummingbirds can present as (A) u-shaped curves, (B) inverse u-shaped curves, (C) linear, or (D) erratic.

Hummingbirds tagged early and late in the season may be migrating through the area and thus may not remain at the study site after release. This could explain the redetection of two females in late May 2012 for only two to three days. A 70% redetection rate and the return of individuals in subsequent breeding seasons are evidence for the lack of long-term negative effects and the successful retention of subcutaneously implanted PIT tags.

Analyses of our data produced results consistent with what has been found in other physiological studies of hummingbirds that employ highly labour intensive methods of data collection. Hummingbirds have been found to exhibit feeding restraint during the day to maximize aerial performance and only gained mass at dusk (Calder et al. 1990). For the majority of days examined, patterns of mass versus time of day exhibited either a linear or u-shaped relationship. U-shaped relationships best described data on 42 of 99 d and suggests that our approach generally revealed patterns of mass variation throughout a day that are consistent with laboratory (Beuchat et al. 1979) and smaller field studies (Calder et al. 1990). Where mass data were best described by a linear increase over time, 7 of 30 d were of an adult female between 23 August and 5 September 2013. Because these dates are near the presumed date of migration, we hypothesize that this

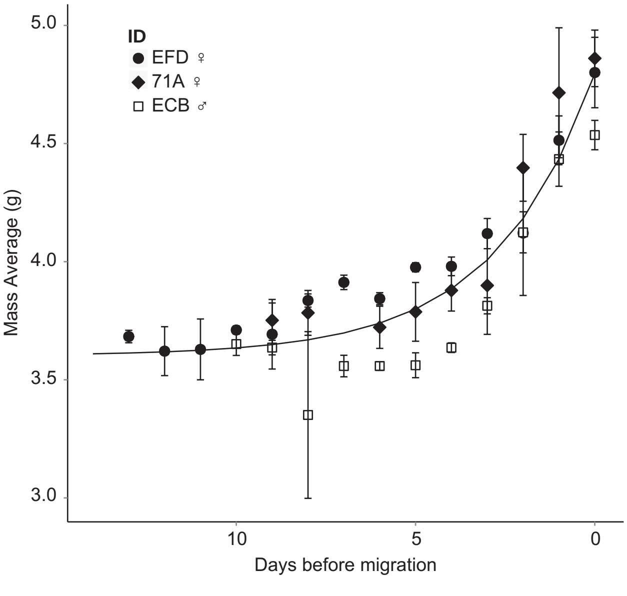

Figure 5. Mass change of three hummingbirds prior to migration. Day zero represents the date of last recorded mass for each individual and is the presumed date of migration. The average of median masses ± standard error between 18:00 and 21:00 h for each individual increases exponentially leading up to migration.

Table 2. Models of pre-migratory mass gain in ruby-throated hummingbirds developed with average body mass between 18:00 and 21:00 h as a function of days before migration with individual as a random factor.

Model	Equation	AIC Score	AIC Weight
Exponential	body mass $= 3.60 + 1.19e^{(-0.36\ [\text{days before migration}])}$	−40.3	1.00
Linear	body mass $= -0.09$[days before migration] $+ 4.41$	13.4	$2.18e^{-12}$

individual may have switched from prioritizing flight maneuverability to mass gain prior to migration. While other patterns of daily mass change were observed, there were no immediately obvious temporal or environmental variables coinciding with the observed variation. With continued data collection, we hope to better analyze this variation. In addition to demonstrating patterns of daily mass change, we were able to identify a pattern of exponential mass gain across multiple days prior to hummingbird migration. Fall migration of hummingbirds typically begins as early as mid-August for males and September for females in Ontario, Canada (Sandilands 2010). Of the ten hummingbirds frequenting our stations, three provided continuous records of mass between late August and early September. Our data show that body mass of these three ruby-throated hummingbirds increased exponentially several days prior to migration and is similar to that found by Carpenter et al. (1993) in rufous hummingbirds. For all other tagged hummingbirds, our records show that the date of last recorded mass was prior to 26 August in 2013. Pre-migratory mass gain was not observed in these individuals suggesting that individuals may move away from the breeding site prior to migration. Such movement has been previously reported by Saunders (1936) who observed the arrival of males after mid-July in New York coinciding with a change in food availability and is suggestive of a switch in breeding habitats.

This automated system eliminates the need for repeated captures, thereby minimizing the disturbance our experiment has on study subjects. In addition to collecting usable physiological data, this technology permits the monitoring of certain life history events such as migratory arrival and departure while requiring minimal labour input (three hours of personnel time per week for the maintenance of six stations). Moreover, the lower power consumption of the low-cost RFID reader at 5 V compared to the Biomark FS2001F-ISO unit at 12 V provides an additional advantage by permitting greater longevity if the unit draws from a battery supply. Commercial RFID readers intended for use in animal studies offer many advantages to the low-power reader used in five of our stations (e.g. superior read range, greater portability or durability). Our intention is not to imply that low-cost readers can replace the need for such specialized equipment in most or all applications. However, this study does demonstrate that lower-cost, low-power readers can be successfully used to monitor hummingbird visits and, when coupled with a balance, individual mass. Equipment cost per station has been summarized in table 3. By substituting the commercial Biomark Reader (model no.: FS2001F-ISO) with a custom RFID circuit board and low-power antenna, we have reduced the equipment cost of a station, which includes a precision electronic balance, from $3680 to $791 CAD. A cost savings of 79% makes this miniaturized design a cost-effective technology for the physiological and ecological study of wild hummingbirds. Ongoing work aims to replace the cumbersome notebook computer used in our setup with smaller, less expensive, and lower power computing circuitry. In doing so, we can further reduce reader station cost and rely exclusively on 12 V battery (coupled with solar) power.

Table 3. Equipment cost for a miniaturized station employing a low-cost, low-power RFID reader and antenna.

Equipment	Cost
Denver MAXX digital scale (model no. MXX-212) with YADAP-RS adapter	$350
Notebook PC	$240
RFID circuit board	$150
Perky-Pet hummingbird feeder (model no. 220)	$20
12 V deep cycle battery	$30
Antenna (28 gauge copper magnetic wire)	$1

While our design employs an antenna with a much smaller read range than that of the Biomark antenna (~1 cm and ~9 cm perpendicular to the plane of the antenna, respectively), the miniaturization of the antenna does not compromise its ability to detect PIT tags that are subcutaneously implanted into hummingbirds. Particularly for small birds, strategic placement of the antenna in relation to food resources can ensure the successful detection of subcutaneous PIT tags. In some instances, such as when multiple birds are competing to feed simultaneously at one feeder, a smaller reading range is desirable for identification accuracy. Though tag migration has been a reported disadvantage of subcutaneous implantation (Bonter and Bridge 2011), in small birds any migration is unlikely to position the tag out of an antenna's detection range. Given the large number of hummingbird redetections within a season, and the redetection of hummingbirds in subsequent breeding seasons, antenna read range and tag migration are not issues of concern.

Implementation of a low-cost, low-power RFID reader in concert with an electronic balance in the field has successfully permitted the automated, serial collection of hummingbird physiological data. The return of tagged hummingbirds in subsequent years and the large quantity of data collected lends support to our hypothesis that ruby-throated hummingbirds are not adversely affected by tagging. Moreover, tagged hummingbirds consistently incorporate nectar from our artificial feeding stations into their diet thereby permitting consistent data collection. As predicted, the regular, repeated recording of mass generated high-resolution data that revealed trends in mass change at time scales of seconds, hours, and days in the wild, demonstrating that this approach can be used to track individual and population-level energetics in even the smallest of avian species.

Given the success of this approach, we contend that the automated and repeated collection of additional types of data from hummingbirds and other small birds is feasible. For example, it may be possible to automate the collection of feather samples for genetic analyses, collect exhaled breath for respirometry (Bartholomew and Lighton 1986), and obtain feather, tissue, or breath samples for isotopic analyses.

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