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Hummingbirds Budget Energy Flexibly in Response to Changing Resources

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Abstract

1. A key component of individual fitness is the ability to manage energy stores in response to variable resource availability, but because directly measuring energy budgets is difficult, daily energy management is rarely measured.

2. Hummingbirds' energy management is relatively simple to model compared to other endotherms because they have high mass-specific metabolic rates and store little fat.

3. We determined which aspects of the hummingbird daily energy budget (i.e. thermoregulation, daytime activity costs, night-time costs) change at the individual level in response to environmental variation.

4. We found that daily energy expenditure varied threefold in two populations of broad-billed hummingbirds (*Cynanthus latirostris*).

5. Our model indicated the energy budget was distributed in the following proportions: daytime activity, 59% (range 22%–84%); thermoregulation, 23% (11%–32%); basal metabolism, 7% (3%–16%); and night-time energy, 17% (6%–37%). Activity costs were higher at the hotter, homogeneous site and during the early-wet season at both sites.

6. Increased daily energy expenditure was related to decreased nectar availability and not significantly related to temperature or bird mass. With climate change, the indirect energetic costs of shifting resources could have greater impacts on endotherm energy budgets than direct costs such as thermoregulation. Increased foraging and activity costs could decrease the energy available to birds for somatic repair and reproduction, potentially causing differential fitness across seasons and sites.

KEYWORDS
activity cost, BMR, *Cynanthus latirostris*, hummingbird, individual energy allocation, static energy budget, thermoregulation, torpor

1 | INTRODUCTION

As resource availability or abiotic conditions change, individuals can adjust how they allocate energy to activities such as foraging, resting and reproduction (Perrigo & Bronson, 1983; Wiersma, Selman, Speakman, & Verhulst, 2004). This behavioural flexibility in energy allocation may be a key factor in determining free-living animals' fitness in changing environmental conditions. One way to assess

the effects of environmental change on behavioural flexibility is to construct individual-level energy budgets, which quantify how animals allocate their energy to different activities. However, models of endotherm energy budgets have largely been conducted in laboratory settings and often do not incorporate individual variability in metabolic rates (Weathers, Buttemer, Hayworth, & Nagy, 1984; Williams & Nagy, 1984). Though these models provide an important starting point for modelling energy budgets, by using mean values they might underestimate the importance of variation in energy budget estimates and, as a result, could yield values similar to those obtained by simply scaling metabolic rates allometrically (Weathers et al., 1984; Williams & Nagy, 1984). Recent studies have begun to incorporate individual variability by using accelerometers or geolocators to build individual dynamic energy budgets (Fort et al., 2013; Shepard, Wilson, Quintana, Gómez Laich, & Forman, 2009). To build generalizable and robust models of animal responses to current and future environmental changes, individual variation and behavioural flexibility inherent in field data as well as real-time environmental changes need to be accounted for when modelling energy budgets. In this study, we assessed which components of the energy budget (thermoregulation, daytime activity, night-time energy expenditure) were most responsive to spatial and temporal variation in environmental conditions in two free-living populations of broad-billed hummingbirds (*Cynanthus latirostris*).

The two currencies of an energy budget are time and energy (measured in intake and expenditure; Pyke, 1984), and these can change in response to environmental conditions, in turn affecting an organism's fitness. Increases in habitat quality result in increases in energy intake and expenditure for a variety of taxa, including both ectotherms (e.g. fish; Auer, Salin, Rudolf, Anderson, & Metcalfe, 2015, and snakes; Beaupre, 1996) and endotherms (mice; Mueller & Diamond, 2001, and voles; Speakman et al., 2003). Such changes in animals' daily energy expenditures are thought to have an energetic ceiling based on environmental conditions (Elliott et al., 2014; Tinbergen & Verhulst, 2001; Welcker et al., 2010). Changes in resource availability and temperature can also cause animals to alter their time–activity budgets (Powers et al., 2017; Powers & McKee, 1994; Tieleman & Williams, 2002). Such changes in environmental conditions and daily energy expenditure (DEE) can impact an organism's fitness and life-history traits. For instance, decreasing resource availability compromises somatic repair and delays egg laying in zebra finches (Wiersma & Verhulst, 2005). Within a species, individuals with higher DEE tend to be larger and have higher growth rates and reproductive output in both ectotherms (snakes; Beaupre, 1996) and endotherms (mice; Mueller & Diamond, 2001). Understanding how much energy gets allocated to different activities and which of these components are flexible and under an animal's control can allow us to model animal responses to environmental variation.

When environmental conditions, such as energy availability or temperature, change, animals are found to either minimize energy loss or maximize energy gain (Hixon & Carpenter, 1988; Hixon, Carpenter, & Paton, 1983; Montgomerie, Eadie, & Harder, 1984;

Pyke, 1984; Tiebout, 1992). Hummingbirds are ideal for evaluating the variability in the use of, and flexibility to switch between, these strategies because they have high mass-specific metabolic rates (Bartholomew & Lighton, 1986; Lasiewski, 1963; Tooze & Gass, 1985; Wolf & Hainsworth, 1977) and, unless migrating, store little fat (Calder, Calder, & Frazier, 1990; Powers, Brown, & Van Hook, 2003). These characteristics ensure that their energy balance can be estimated over very short time-scales, without the confounding effects of large fat stores. Decreasing resource availability or increasing thermoregulatory costs can cause opposite behavioural responses in territorial hummingbirds, of either decreased foraging time to minimize energy loss or increased foraging time to maximize energy gain (Ewald & Carpenter, 1978; Powers et al., 2017; Tiebout, 1991). To minimize energy loss overnight, hummingbirds often use torpor, depending on their endogenous energy stores (Powers et al., 2003), but the effect of torpor on overall daily energy budgets in free-living animals is poorly known (but see Carpenter, 1974; Carpenter & Hixon, 1988).

Our knowledge of hummingbird energy management strategies is based on a handful of studies in which either daily energy use was estimated from doubly labelled water (Powers & Conley, 1994; Powers & Nagy, 1988; Weathers & Stiles, 1989) or the energy budget was constructed from time or energy budgets from controlled metabolic measurements (Hainsworth, 1977; López-Calleja & Bozinovic, 2003; Stiles, 1971; Wolf & Hainsworth, 1971). In these studies, energetic state was estimated using mean values for energy expenditure from controlled measurements, but energetic flexibility over time and how energy expenditure varies under field conditions were not evaluated. We used both doubly labelled water measurements and energy budgets using respirometry measurements made closer to natural conditions to model individual energetic flexibility. We considered a range of environmental conditions by running these models in free-living hummingbirds across two sites and seasons. Since thermoregulatory costs are an important component of the endotherm energy budget, we predicted that hummingbird DEE would be higher when thermoregulatory costs were highest— in conditions with hotter daytime temperatures, cooler night-time temperatures and fewer microhabitat refugia (Wolf, Wooden, & Walsberg, 1996). From past studies of hummingbird energy and time budgets, we hypothesized that night-time torpor use would significantly decrease total DEE (Hainsworth, 1981; Pearson, 1954). In response to decreasing resource availability, we expected that DEE would decrease to minimize energy loss (Ewald & Carpenter, 1978; Hixon & Carpenter, 1988; López-Calleja, Bozinovic, & Martínez del Rio, 1997).

2 | MATERIALS AND METHODS

2.1 | Study sites and species

We studied male broad-billed hummingbirds (2.7–3.6 g) at two sites in Arizona: Harshaw Creek (31°29′N, 110°40′W, alt. 1,370–1,635 m) and Sonoita Creek (31°29′N, 110°51′W, alt. 1,100–1,180 m).
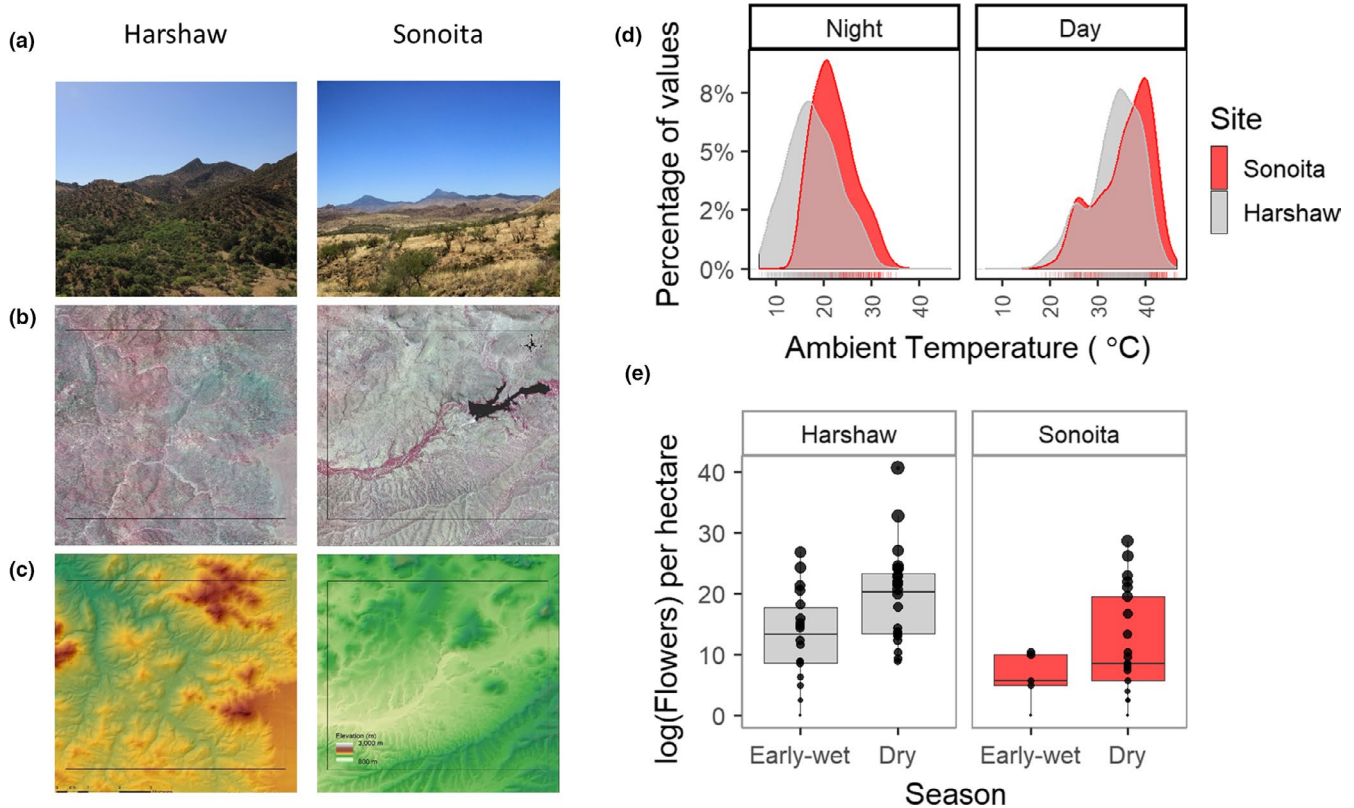
FIGURE 1 (a) Photographs of each site; (b) 1-m resolution National Agriculture Imagery Program infrared images (high vegetation in red, intermediate in green and bare ground in white); (c) elevation (high elevation in red, intermediate in green and low in white); (d) distribution of ambient temperatures facetted by day and night at each site; and (e) flower abundance: the *y*-axis is log (flowers), and points are point-wise non-zero flower totals, scaled per hectare

Harshaw was more diverse in elevation and vegetation structure than Sonoita (Figure 1a–c). We measured only male hummingbirds to minimize the reproductive and nesting trade-offs that could influence the energy budget (hummingbirds are promiscuous breeders). Data were collected in May–July 2013, covering the dry season and early-wet season.

2.2 | Resource availability

To provide an ecological context to the energy budget model, we measured floral resource availability along 1-km transects in each vegetation type within the landscape. The number of transects per vegetation type was based upon the area of the vegetation type, and transects were placed approximately in the centre of the vegetation type (Wallace, Villarreal, & Normal, 2011). Because of the variable terrain at these sites, transects, when possible, used existing trails or were defined based upon walkable topography. We then quantified flower resources on 30-m-radius plots placed between 100 and 250 m apart along each transect. We sampled 67 plots along 11 transects along Harshaw, and 57 plots along 7 transects along Sonoita. Within a plot, we recorded the number and identity of plants with flowers and counted the number of flowers of each hummingbird-visited plant species. We measured nectar volume and concentration using micro-capillaries and a hand-held refractometer for 20 randomly selected

flowers per plant species in a plot. We calculated average energy availability (in kilojoules) for each species by using the following formula (pg. 169, Kearns & Inouye, 1993):

$$C = V * M * 1.3496$$

$$kJ = 4.1814 * C$$

where C = kilocalories per flower; V = volume of nectar (µl); M = molarity; 1.3496 is the number of kilocalories/µl of a 1 M sucrose solution; and 4.1814 is a conversion factor to convert kilocalories to kJ. The nectar availability of a plot was estimated by multiplying the average nectar volume and concentration of a flower by the floral abundance in the plot.

2.3 | Temperature

We measured ambient temperature (T_a) across both sites in order to estimate thermoregulatory costs. We used iButtons (Maxim Integrated, DS1922-L50) and Hobo H8 temperature loggers (Onset Corp.; 13 in Harshaw and 16 in Sonoita) placed inside inverted Styrofoam cups 1 m above the ground to insulate them from solar radiation and wind. T_a was measured every 15 min. We also measured operative temperatures—the temperature as experienced by an object with the approximate surface area of a hummingbird, accounting for the effects of wind and direct sunlight—using hollow

copper sphere thermometers (Walsberg & Weathers, 1986). These sensors were placed at six locations to test whether they were adequately represented by the more extensive T_a measurements. All temperature sensors were calibrated by placing them in a Percival (model I-35LV; Percival Scientific, Inc.) maintained at controlled temperature steps, and checked against a thermometer traceable to the National Institute of Standards and Technology.

2.4 | Energy budget model

We constructed this generalizable energy budget model:

$$DEE = tBMR + tTRE_L + tTRE_H + ACT + TEE$$

where DEE = daily (24-hr) energy expenditure; $tBMR$ = basal metabolic rate, summed over total time spent within the thermoneutral zone (range of temperatures at which endotherms have no thermoregulatory costs); $tTRE_L$ = thermoregulatory costs, summed over total time spent below lower critical temperature; $tTRE_H$ = thermoregulatory costs, summed over total time spent above upper critical temperature during daytime hours; ACT = total daytime activity cost; TEE = total torpid energy expenditure.

In practice, we measured total night-time energy expenditure (NEE), including both normothermic and torpid energy expenditures at night, and so we modelled BMR, TRE_L and TRE_H, and ACT over daytime hours, and added NEE to get DEE:

$$DEE = BMR + TRE_L + TRE_H + ACT + NEE$$

ACT comprises daytime activity costs:

$$ACT = p^* \left[perching\, MR - BMR \right] + h^* \left[hovering\, MR - BMR \right]$$
$$+ f^* \left[flying\, MR - BMR \right]$$

where p = number of hours spent perching; h = number of hours spent hovering; and f = number of hours spent flying. BMR was subtracted from each term since it is included earlier in the DEE equation.

At any given time during daytime hours, energy expenditure comprised one of the following for thermoregulatory costs: BMR, TRE_L or TRE_H, in addition to one of the following ACT components: perching, hovering or flying (i.e. one each of the thermoregulatory in addition to one of the ACT components was always applicable over the 15 daytime hours). All components are reported in joules (J) or kilojoules (kJ), with 1 ml O_2 assumed to be 20.1 J. We collected data on unit costs of BMR, thermoregulation and hovering MR, and on total NEE, and used literature estimates from wind-tunnel studies for flight costs. Night-time energy expenditure includes night-time BMR, thermoregulation and torpid energy expenditure. Reproductive costs for male hummingbirds are confined to courtship behaviour and agonistic costs, and are thus implicitly included in the activity budget. We did not consider migratory or fat storage costs, as our model was for non-migrating hummingbirds that store minimal fat. We used the mean ± 1 SD to model a range of individual variation in each component (see Table 1 for a summary of measures).

2.4.1 | Daily energy expenditure

To test the accuracy of our energy budget model, we collected independent data on DEE using a modified two-sample doubly labelled water (DLW) protocol (Speakman, 1998). Because most hummingbirds are too small to allow multiple blood sample collection in 24 hr, which is the standard protocol, we collected and measured urine samples. We fed the birds a precise dilution of doubly labelled water ($^2HH^{18}O$) in nectar on initial capture, held them for about 45 min to allow ingested isotopes to equilibrate with the body water pool (Figure S1b), and collected a urine sample. We then analysed differences in isotope levels between this initial sample and second urine sample from the same bird caught ~24 hr later to estimate energy expenditure. Further details of our DLW protocol, and verifications of its validity, can be found in Appendix S1.

We constructed a linear mixed-effects model (Gelman & Hill, 2007) to determine the extent to which DEE was related to changes in temperature, bird mass and resource availability in the landscape. It was not possible to collect resource availability data across the landscapes on the same daily resolution as DEE, but we tested the relationship across site and season. We used the 'LME4' package in R (Bates, Mächler, Bolker, & Walker, 2015) to construct these models. A mixed-effects model was useful in this context to model the response (DEE) as a function of both continuous fixed effects (ambient temperature, flower abundance, bird mass) and random effects (season). We ran a full model and then tested simpler models step-wise to reduce the model to its simplest form. In the full model, we included log (flowers), mean and maximum daily ambient temperatures (minimum and maximum temperatures were highly correlated, R^2 = 0.89, and so minimum temperature was left out), and bird capture mass as continuous fixed covariates. We included the site and season together a random covariate, such that the intercept was fixed, and the slope was allowed to vary with the random effect. The simplest model was one without the random effects and was a simple linear model ('LM' function, R Core Team, 2018) with just the fixed effect of log (flowers). The full model was given by:

$$DEE \sim log\,(flowers) + mean\, T_a + maxT_a + bird\, Mass + (1|Site\_season)$$

The simplest model was given by:

$$DEE \sim log\,(flowers)$$

We used AICs to select the best model; the most parsimonious model with the lowest AIC score (by 2 AIC points or more) was considered the best model. Additionally, to quantify how much DEE changed between sites and seasons, we performed unpaired, equal variance t tests.

2.4.2 | Thermoregulatory and basal metabolic costs

For endotherms, thermoregulatory costs and basal metabolism can be estimated by measuring metabolic rates when the adult animal is post-prandial and resting in the dark at different temperatures

TABLE 1 Description of each model parameter, the method used to estimate it, a brief description of the data collected and the way variability in that measure was modelled

Overall model: DEE = Daytime * BMR + Daytime * TRE + ACT + NEE; where TRE = thermoregulatory costs at temperatures measured in the field; ACT = Time_hover * (HMR-BMR) + Time_fly * (FLMR-BMR) + Time_perch * (RMR-BMR)

Category	Measure	Acronym	Method	Raw data	Modelled as	Variability	Source
Daily energy expenditure (DEE)	Daily energy expenditure (DEE)	DEE	Doubly labelled water, field metabolic rate	Individual measurements of DEE	NA	Min, mean, max	This study
Basal metabolic rate (BMR)	Basal metabolic rate (BMR)	BMR	Respirometry: asleep, in the dark, fasting, 35°C		constant daytime cost	Mean ± 1 SD	This study
Thermoregulatory energy expenditure (TRE)	Thermoneutral zone, thermoregulatory costs	TRE_L, TRE_H	Respirometry, controlled conditions	Thermoregulatory MR at 5°C intervals of T_c, from 5 to 35°C; above 35°C modelled from Costa's hummingbird slope	Regression line	Using ambient temperature variability	This study
	Ambient temperatures	T_a	iButtons, operative temperature sensors	Ambient temperatures from across both sites	NA	Random 1 per 15 min; min 4/hr; max 4/hr	This study
Daytime activity energy expenditure (ACT)	ACT = Time_hover * (HMR-BMR) + Time_fly * (FLMR-BMR) + Time_perch * (RMR-BMR)						
	Hovering metabolic rate	HMR	Mask respirometry, free-living birds	Range of HMR measurements (at various Ta's)		Mean ± 1 SD	This study
	Flying metabolic rate	FLMR	From power curves, relatively standard proportion of HMR	Energy expenditure at optimal flight speeds from literature values		Mean ± 1 SD	Clark and Dudley (2010), Powers et al. (2015), Warrick et al. (2012)
	Resting metabolic rate	RMR	From BMR measurements; using relationships from the literature	1.5 * BMR		Mean ± 1 SD	This study
	Night-time energy expenditure	NEE	Respirometry, natural conditions	Whole-night measurements of individual night-time energy expenditure	NA	Min, mean, max	Shankar et al., (2018)
	Activity budget (time hovering: flying:perching)	Hov_fly_per	Literature values, modelled values	Hours spent on each type of activity (hovering, flying, perching)	NA	Modelled a range of time budget scenarios	Bartholomew and Lighton (1986), Lasiewski (1963)

(Scholander, Hock, Walters, Johnson, & Irving, 1950). In the middle range of temperatures—thermoneutral zone—the animal's energy expenditure is only BMR with no thermoregulatory costs. The thermoneutral zone is bounded by the lower and upper critical temperatures, below and above which, respectively, the animal spends energy to maintain body temperature. We measured thermoregulatory costs and BMR at Harshaw in June 2012 in chambers from 5 to 35°C at 5°C intervals at night (rest phase) using open-flow respirometry, following Powers et al. (2003).

Basal MR: We considered the thermoneutral zone for this species to be 32–35°C based on data for broad-billed hummingbirds and several similarly sized hummingbirds (Bucher & Chappell, 1989; Lasiewski, 1963; Lasiewski & Lasiewski, 1967; see Appendix S1). We summed BMR over all daytime hours that had temperatures within the thermoneutral zone. We did not have enough measurements at 35°C to calculate individual variability in BMR at 35°C, but individual variability was similar across all other temperatures measured. To include BMR in the energy budget, we therefore used the mean of our measurements at 35°C but used the standard deviation of our measurements at the closest temperature, 30°C (see Table 1). Time spent thermoregulating will always involve basal metabolic costs, so TRE_L and TRE_H include both BMR and thermoregulatory costs.

TRE_L: We obtained a slope below the lower critical temperature by regressing metabolic rates on chamber temperature: MR_L (J/min) = 19.1 − 0.4 * (T_a), where MR_L is the metabolic rate when T_a < 32°C. TRE_L is MR_L multiplied by 15 to convert it to a per-15-min metabolic rate and then summed over daytime periods for which T_a was < 32°C:

$$TRE_L \ (kJ) = \frac{\sum MR_L * 15}{1000}$$

TRE_H: The only hummingbirds we know of that have been measured above the upper critical temperature are Costa's hummingbirds (*Calypte costae*), which have an upper critical temperature of 35°C (Figure S3). We modified the Costa's regression equation with data from the broad-billed hummingbird. We obtained the y-intercept of the equation by substituting the broad-billed hummingbird's BMR and an ambient temperature of 35°C into the Costa's regression equation: MR_H (J/min) = 4.3 * (T_a) − 145.7, where MR_H is metabolic rate at temperatures above the upper critical temperature. MR_H was converted to TRE_H similar to TRE_L, summed over daytime hours when T_a > 35°C:

$$TRE_H \ (kJ) = \frac{\sum MR_L * 60}{1000}$$

We ran three thermoregulatory scenarios (random, maximum and minimum) per day to calculate a range of thermoregulatory costs given that birds had a choice of various microclimates in their landscape. We obtained the range of temperatures a bird could experience at any given point of time in the field from our T_a sensors. We ran the three scenarios for each daylight hour (15 hr) and added the hourly thermoregulatory costs to get total daytime thermoregulatory costs. In maximum scenario, we used the four temperatures every hour that would cause the bird to maximize thermoregulatory costs (furthest temperatures from thermoneutral). In the minimum scenario, we selected the four temperatures every hour that minimized thermoregulatory costs (closest to thermoneutral). In the random scenario, we assumed that the bird randomly experienced four temperatures per hour, for 15 min each, and we calculated total daytime thermoregulatory costs given these temperatures; this random scenario represented an intermediate thermoregulatory scenario. When ambient temperatures were within the thermoneutral zone, we assumed that there were no thermoregulatory costs and used BMR as the only cost in this component of the budget (and then added on activity costs).

2.4.3 | Activity costs

To estimate total daytime activity costs (ACTs), we multiplied the time spent on each activity by measurements or estimates for the cost of each activity.

Perching: We did not directly measure perching MR for broad-billed hummingbirds; instead, we estimated the relationship between BMR and perching MR from measurements on two Calliope hummingbird individuals (*Selasphorus calliope*), and used BMR measurements of the broad-billed hummingbirds to estimate perching MR (raw data and methods in Appendix S1). We found perching $MR_{Calliope}$ = 5.63 J/min, while $BMR_{Calliope}$ = 3.62 J/min (Lasiewski, 1963). Thus,

$$\text{Perching } MR_{Calliope} \approx 1.55 * BMR_{Calliope}$$

If we assume that the proportional difference between perching MR and BMR in broad-billed hummingbirds is similar to that measured in Calliope hummingbirds, then we can estimate perching MR as:

$$\text{Perching } MR = 1.5 * BMR$$

This correction is similar to the difference between minimum daytime MR and BMR for Anna's hummingbird (*C. anna*) and Costa's hummingbirds reported by Powers (1991). We incorporated individual variability into perching MR by using the estimated range of variation in broad-billed hummingbirds' BMR values and calculating variation in estimated perching MR.

Hovering: Hovering MR has been previously measured in the Harshaw broad-billed hummingbirds (Groom, Toledo, Powers, Tobalske, & Welch, 2018). Thermoregulatory costs were subtracted from the model when the birds were hovering because hovering appears to produce enough heat to substitute for thermoregulation across a wide range of temperatures (see Figure S2). Thus,

$$\text{Hovering } MR = 10.3 * BMR$$

This relationship is consistent with past studies (Bartholomew & Lighton, 1986; Fernandez, Dudley, & Bozinovic, 2011; Welch & Suarez, 2008).

Forward flight: Flying MR was estimated using relationships between BMR and flying MR from other hummingbird species. This relationship is well-established from studies on power curves in hummingbirds (Clark & Dudley, 2010; Powers, Tobalske, Wilson, Woods, & Corder, 2015; Warrick, Hedrick, Fernández, Tobalske, & Biewener, 2012). Assuming that the power curves for broad-billed hummingbirds are similar to those of these other species and that broad-billed hummingbirds will most often fly at their most efficient speed (6–8 m/s), we estimated flying MR to be.

$$Flying\ MR = 0.6 * hovering\ MR,$$

or

$$Flying\ MR = 6.2 * BMR$$

We modelled standard deviation of forward flight MR estimates by using estimates of standard deviation in forward flight MR of Rufous (*S. rufus*; D. R. Powers, unpubl. data) and Calliope (Powers et al., 2015) hummingbirds.

To allow for flexibility in daytime activity costs, we modelled individual variation in both the energy per unit time and the time spent on each activity (hovering, flying or perching). To vary the energy spent per unit time, we used the individual variation in energy expenditure as described for each activity above. To model time per activity, we used behavioural information from the literature, which converged on the following estimates: 15% hovering, 15% flying and 70% perching (15:15:70) (Beuchat, Chaplin, & Morton, 1979; Hainsworth, 1977; López-Calleja & Bozinovic, 2003; Wolf & Hainsworth, 1971; Wolf, Stiles, & Hainsworth, 1976). To reflect behavioural plasticity, we also constructed three other models assuming much lower or much higher hovering and flying time, with hovering: flying: perching being 5:20:75, 25:30:45 and 40:40:20.

2.4.4 | Night-time energy expenditure

Torpor and night-time normothermic MR data on the same populations of broad-billed hummingbirds from a previous study were used to calculate total night-time energy expenditure and model the effects of torpor use on DEE (Shankar, Schroeder, Wethington, Graham, & Powers, 2018). Total NEE was measured using open-flow respirometry (with measurements of oxygen consumption taken every second) under natural temperature and light cycles. Birds experienced a natural photoperiod of 15L:9D hours. In our DEE model, we included minimum and maximum total NEE given maximum torpor use and zero torpor use (night-long normothermia), respectively.

3 | RESULTS

3.1 | Resource availability

There were more flowers and energy (kJ) in plants at Harshaw than Sonoita per transect, both during the dry and early-wet seasons (Figure 1e). Harshaw had an average of 17,147 flowers (range 42–343,434) in the dry and an average of 837 flowers (range 3–7,003) in the early-wet season per hectare. Sonoita had an average of 1,162 (range 3–11,489) in the dry and 32 (range 3–27) per hectare in the early-wet season. Nectar resources (flowering plants and artificial feeders) were always more abundant and clumped at Harshaw than at Sonoita.

3.2 | Temperature

T_a and T_e measurements did not differ at locations where both were measured concurrently; therefore, we used T_a measurements because we had higher coverage across sites. Across both sites, average daytime temperatures were 34.9°C (10–57°C) and average night-time temperatures were 19.8°C (range 0–37°C); Sonoita was warmer and less variable than Harshaw, both during the day and at night (Figure 1d).

3.3 | Energy budget model components

3.3.1 | Daily energy expenditure (DEE)

Daily energy expenditure varied both at the individual and population levels. As measured by the doubly labelled water method, DEE ranged from 12.62 to 39.76 kJ over all sites and seasons. The best model of DEE was the simplest model: DEE ~log (flowers), and we therefore only present this model's results here (for all models, see Table S1). The other factors we considered had no significant effect on DEE in any of the models, except maximum temperature in the temperature-only model. The best model (AIC 172.6) showed that the number of flowers in the landscape had a highly significantly negative effect on DEE (adjusted R^2 = 0.65, $p = 5.6 \times 10^{-8}$). The relationship was given by: DEE ~ 41 − 1.7 * log (flowers).

Within each site, dry season birds had lower DEE than those measured in the early-wet season birds (Harshaw t (19) = −2.35, $p = .03$; Sonoita t (11) = −5.98, $p = <.001$). Mass-related changes in DEE were unlikely, as mass did not vary significantly between sites within a season (dry season t (10) = −0.91, $p = .39$; early-wet season t (20) = −0.66, $p = .51$) or within sites between seasons (Harshaw t (20) = 1.56, $p = .13$; Sonoita t (8) = 1.76, $p = .12$). We captured three individuals both in the dry and in the early-wet seasons at Harshaw and tested whether DEE could change at the individual level within a few weeks. We found that one individual maintained a constant DEE, while two others upregulated theirs (coloured points in Figure 2 for Harshaw).

3.3.2 | Thermoregulatory and basal metabolic costs

We found that the maximum and minimum thermoregulatory cost scenarios accounted for between 5.14 and 6.91 kJ, or a 1.77 kJ variation in the DEE model, causing a difference of 1.36 ± 0.17 kJ (mean ± *SD*) in daytime energy expenditure. The maximum and minimum costs within the randomized models only resulted in an average difference of 0.37 ± 0.05 kJ (mean ± *SD*) in daytime energy expenditure.
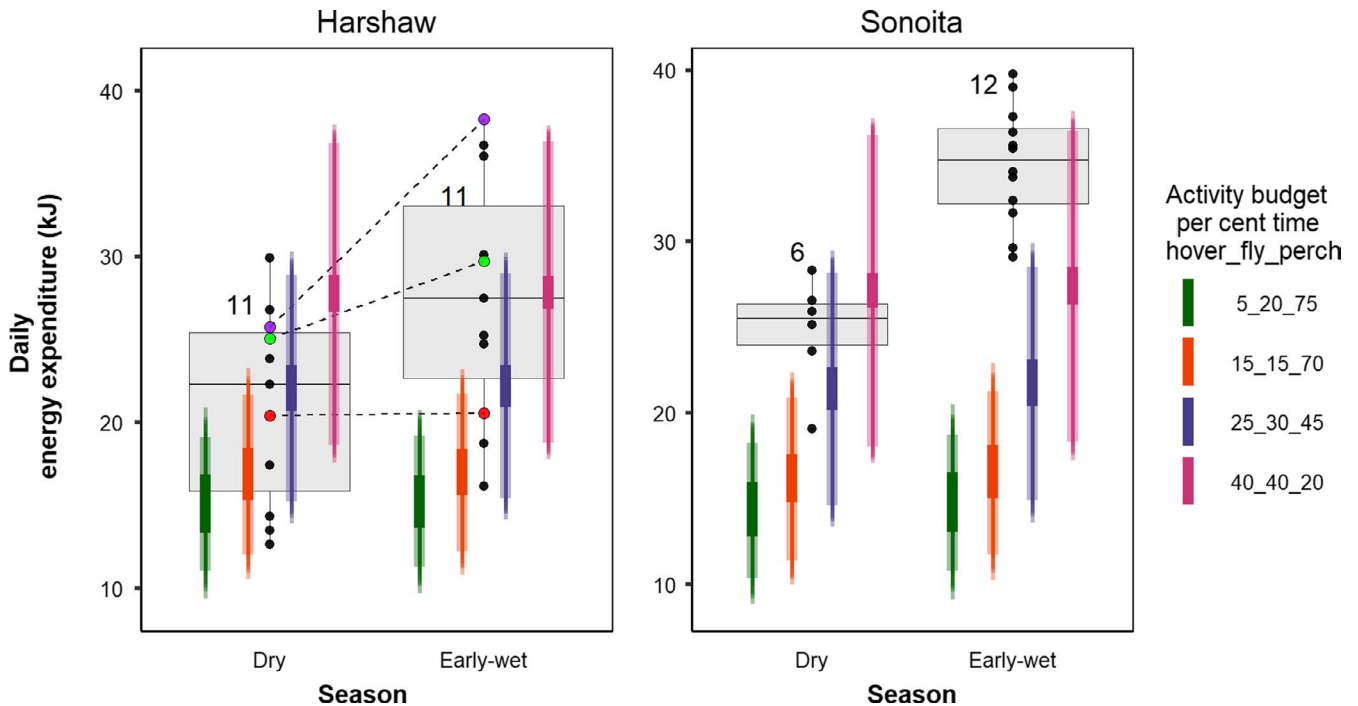
FIGURE 2 DLW and modelled values of DEE for Harshaw and Sonoita. Daily energy expenditure (DEE) from the doubly labelled water (DLW) method in broad-billed hummingbirds at each site–season combination as grey boxplots (median, 25th and 75th quartiles; whiskers are 1.5 * inter-quartile ranges). Points are doubly labelled water measurements of individuals' DEE. Coloured points, connected by dashed lines, are individuals captured both in dry and in early-wet seasons at Harshaw; numbers are sample sizes for that site and season. Coloured line ranges represent energy budget model results. Central darker bars represent models with average activity costs, allowing all other components to vary. Lighter wide bars are models with constant thermoregulatory costs and BMR, and variable activity costs. Thin dark lines are models with all components allowed to vary

We found that for broad-billed hummingbirds, mean BMR = 4.8 J/min; SD = 1.21 J/min.

3.3.3 | Activity costs

We calculated the mean and standard deviation of per-minute costs of each activity type as:

Mean perching MR = 7.19 J/min; SD = 1.21 J/min.

Mean hovering MR = 42.21 J/min; SD = 13.47 J/min.

The flying MR for Rufous and Calliope hummingbirds had standard deviations of 8.04 J/min. We used the relationship flying MR = 0.6 * hovering MR to calculate mean broad-billed hummingbird flying MR, and an SD of 8.04 J/min to model a range of individual variation in forward flight costs:

Mean flying MR = 0.6*42.1 J/min = 25.33 J/min; SD = 8.04 J/min.

Given that hovering costs and flying costs are much higher than perching costs, activity costs were highest when hovering and flying times were assumed to be high (40:40:20 scenario), while the 5:20:75 scenario had the lowest activity cost (Figure 3). Variability in hovering and flying costs had the greatest effect when times spent on these activities were high (Figure 2). Even if time spent hovering versus flying versus perching remains the same, individuals could regulate energy spent within each activity type to change their daily

energy budget (Figure 2). The highest and lowest time budget scenarios resulted in a maximum difference of 27.8 kJ in daytime energy costs, assuming all else was equal. Results of allowing individual variation in the metabolic rate of each type of activity are presented in Table 2.

3.3.4 | Night-time energy expenditure

All birds (7/7) measured in the Harshaw dry season used torpor, with an average night-time energy expenditure of 3.36 kJ (range 2.40–4.91 kJ). Some birds (5/8) at Sonoita used torpor; night-time energy expenditure for the three normothermic birds was an average of 5.75 kJ (range 4.68–6.57 kJ), while for the torpid birds, it was an average of 3.13 kJ (range 1.97–4.24 kJ; Table S2).

3.4 | Energy budget model verification

The energy budget component that was most variable (Figure 2) and caused the greatest change in total DEE (Figure 3) was daytime activity costs. Daily energy costs were influenced largely by changes in daytime activity costs, rather than by daytime thermoregulatory costs, and both these categories caused a higher difference than night-time energy expenditure (Figure 3). We found that daytime activity accounted for an average of 59% (range 22%–84%) of the total energy budget, whereas thermoregulation contributed 23%
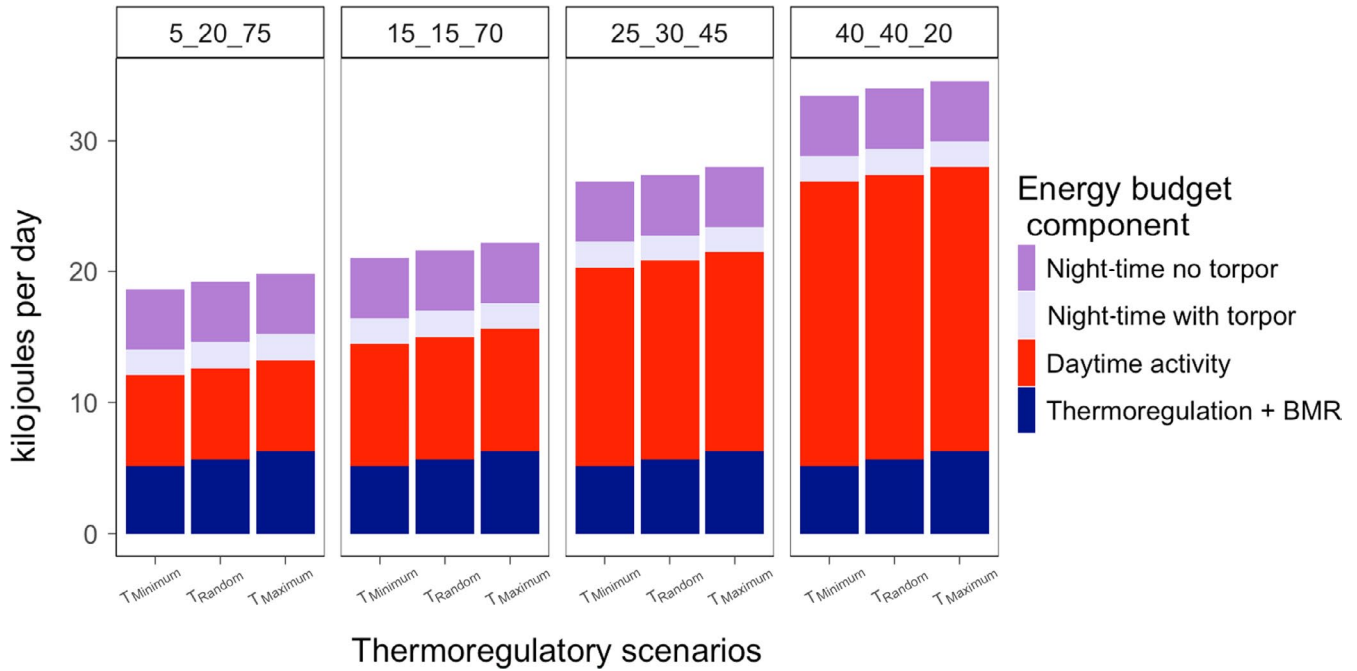
FIGURE 3 Daily energy expenditure for a sample dry season day (2 July 2013) in broad-billed hummingbirds at Sonoita as a stacked bar, coloured by each component of the daily energy budget. $T_{minimum}$, $T_{maximum}$ and T_{random} each refer to a thermoregulatory scenario. The numbers on each facet represent the different activity budget scenarios—percentage of the daytime spent in Hovering_Flying_Perching. Activity values here are mean per activity costs

TABLE 2 Summary of individual-level variability in daytime activity costs (ACTs) alone when per-minute activity costs were varied

| Per-minute activity costs | Total daytime activity cost (ACT; kJ) over all time budget scenarios | | | |
	Minimum	Median	Mean	Maximum
Low activity metabolic rates (high hovering MR, flying MR, perching MR; low BMR)	3.0	6.4	7.1	12.6
Mean activity metabolic rates (mean hovering MR, flying MR, perching MR, BMR)	6.9	12.2	13.3	21.7
High activity metabolic rates (low hovering MR, flying MR, perching MR; high BMR)	10.9	18.0	19.4	30.8

Note: Individual-level variability can contribute a large amount of variation to the overall energy budget.

(11%–32%), basal metabolism 7% (3%–16%) and night-time energy expenditure 17% (6%–37%).

4 | DISCUSSION

Daily energy expenditure (DEE) based on doubly labelled water measurements varied threefold in broad-billed hummingbirds, in response to resource shifts. Our modelling results indicated that daytime activity was the largest and most variable component of DEE and that DEE increased significantly as floral resources decreased. In some cases, our energy budget model based on time–activity

budgets from the literature underestimated DEE compared to the direct doubly labelled water (DLW) measurement; only models with very high activity costs (relative to published time budgets) approached the DEEs from DLW. Changes in DEE and activity budgets appear to occur in parallel with shifts in the abundance and density of flowering plants. With the onset of the rains when resources were more scattered, contrary to our expectation, hummingbirds maximized energy gain and expenditure, even as their mass remained relatively constant, consistent with mass-management strategies in non-migratory birds (Calder et al., 1990). Daily energy expenditure varied both at the population and individual levels, varying within individuals caught in different seasons—indicating rapid individual

responses in daily energy management. By breaking DEE down to its components, and then assessing this daily energy budget in the context of landscape factors, we demonstrate a model evaluating how an organism's energy use patterns can respond to changes in resource availability and abiotic environmental conditions such as temperature.

Daytime activity was a much bigger component (average 59%) of our DEE model, causing more variation (range 22%–84%), than we expected. This result contrasts with previous work in which daytime activity only accounted for relatively small changes (maximum 30%) in time and activity budgets (Wolf & Hainsworth, 1971). Previous energy budgets, estimated either based on captive hummingbirds or based on observations of only territorial hummingbirds in the field, emphasized that hummingbirds spend only about 20%–40% of their daytime hours flying and hovering and about 60%–80% perching (Beuchat et al., 1979; Hixon et al., 1983; Pearson, 1954; Stiles, 1971). Though this budget of 15 hover–15 fly–70 perch fits Harshaw birds well, especially in the dry season (orange lines, Figure 2), it does not fit daily energy budgets at Sonoita, especially during the early-wet season. The only model that fits Sonoita early-wet season birds is one with extremely high activity costs (40 hover–40 fly–20 perch; pink lines in Figure 2). Such high daytime activity has never been recorded in hummingbirds before, to our knowledge, indicating that hummingbirds can employ much higher activity days than previously believed. This variation suggests that hummingbirds' flexible daytime activity budgets could be the primary factor that might facilitate their responses to current and future environmental changes.

While activity seems to be the biggest driver of the hummingbird energy budget, the other components may play a role in fine-tuning the budget. We expected daytime thermoregulatory costs and night-time torpor use to be a greater source of variation than daytime activity in the model, given the range of relatively high (above thermoneutral) daytime and the range of night-time temperatures in our study areas (Figure 1d). Instead, thermoregulation was the second biggest cost, followed by night-time energy expenditure; basal metabolism was both the smallest and least variable component. From a physiological perspective, thermoregulation is determined by environmental temperature, and night-time energy expenditure is capped by energy stores to some extent because hummingbirds do not have any energy intake at night; these components could therefore be more tightly constrained by the environment and relatively less flexible than daytime activity. One possible effect these components could have, which we could not consider in our models, is their interaction with the other components of the model. For instance, thermoregulatory costs are known to influence activity levels in aviary studies. With abundant food availability, high thermoregulatory costs caused birds to minimize energy loss, while low thermoregulatory costs caused them to maximize energy gain (Fernández, López-Calleja, & Bozinovic, 2002; López-Calleja et al., 1997; Sandlin, 2000b, 2000a). When resources are not limiting, hummingbirds could therefore be adjusting their foraging behaviour in response to changes in their thermoregulatory costs, for instance, by perching in the shade when their thermal gradient is unfavourable (Powers

et al., 2017). These scenarios likely more closely mirrored the case in Harshaw and both sites in the dry season, when resources were more abundant, than in Sonoita in the early-wet season, when resources and microclimate variation seemed more limiting.

High variation in DEE and daytime activity costs were significantly related to changes in flower and nectar availability across sites and seasons, more than to temperature changes. Both Harshaw and Sonoita had higher and denser flower resources in the dry than the early-wet season. With the onset of the rains, as resources became scarcer and scattered, hummingbirds increased their DEE at both sites, likely by increasing foraging time. Hummingbirds had lower daytime activity and DEE at Harshaw than at Sonoita, as Harshaw had greater abundance and denser flowering plant distributions. These results indicate that broad-billed hummingbirds might become energy-gain maximizers when resources become less abundant and more scattered (Hixon & Carpenter, 1988; Tiebout, 1992). Daily energy expenditure at Harshaw was always more variable than at Sonoita, indicating that hummingbirds at Harshaw might employ a diversity of ways to use their landscape, while at Sonoita, only a single energy budget model fits the independent DEE measurements, suggesting that they were likely less flexible in their energy budgets.

Three theoretical models have been proposed for the expected relationship between an individual's DEE, its resting metabolic rate and daytime activity (these models are reviewed in Mathot & Dingemanse, 2015; Portugal et al., 2016). The first is the allocation or compensation model (Careau, Thomas, Humphries, & Réale, 2008; Nilsson, 2002; Stearns, 1992), which assumes that DEE is fixed; as resting metabolic rate increases, the energetic costs of activity must decrease. The second is the performance or potentiation model (Careau et al., 2008; Speakman et al., 2003), where higher activity requires higher basal metabolic costs, implying that resting metabolic rate and activity energy are positively correlated. The third is the independent model (Careau & Garland, 2012), where resting metabolic rate is independent of activity costs. We found that DEE varied in hummingbirds across seasons, both at the individual and at the population levels, and we find the allocation model unlikely for hummingbirds though it may hold for other species (Welcker, Speakman, Elliott, Hatch, & Kitaysky, 2014). We cannot directly differentiate between the performance and independent models, but our results hint that hummingbirds might follow the independent model (Koteja, 1991), as the increase in modelled activity costs (Figure 3) is much higher than the measured variation in resting metabolic rates (Speakman, Król, & Johnson, 2004). A review of eleven bird and mammal species found that though resting metabolic rates and DEE were positively correlated, there was no relationship between activity costs and resting metabolic rate among the bird species, supporting the independent model (Portugal et al., 2016).

Broad-billed hummingbirds can greatly upregulate their daily energy expenditure in the span of a few days in response to changing resource availability by increasing the time and energy they spend on daytime activity, and possibly foraging. Hummingbird daily energy budgets therefore seem flexible and adaptable to current changes

in temperature and resource availability. Though this flexibility is already remarkable, it is possible that our data did not reflect the limits of hummingbirds' energetic scope. Additionally, the trade-offs (physiological and/or social) of upregulating daily energy budgets to such an extent are unknown (Wiersma & Verhulst, 2005). It remains to be seen whether activity costs are as flexible in other environmental scenarios such as in the tropics where resource patterns are very different or at high elevations where thermoregulatory costs might dominate the energy budget.

5 | CONCLUSIONS

From our energy budget model, it seems likely that hummingbirds' energy budgets will be more affected by the indirect consequences of climate change—with shifting plant and resource distributions—than by direct changes in thermoregulatory costs (Milne, Cunningham, Lee, & Smit, 2015). Such resource shifts causing hummingbird range expansions are already seen with feeder- and garden-supplemented hummingbirds along the western North America (Greig, Wood, & Bonter, 2017). Measuring individual variation in DEE and metabolic rates can provide a measure of the adaptability and plasticity of metabolic rates and energy budgets within a population (Roche, Careau, & Binning, 2016), providing better insight into which components dominate energy budgets in a given species. Such energy budgets also allow us to determine which components might allow a species the most flexibility in the face of future environmental change. In the case of broad-billed hummingbirds, daytime activity costs seem to be the most flexible component, largely shifting in response to changing floral availability. Behavioural flexibility could even allow them to modulate other, less flexible costs; they could perhaps change their activity and use of microhabitats to moderate thermoregulatory costs (Powers et al., 2017). Our model for an endotherm's daily energy budget can be modified for other species, perhaps even extending to community-level energy budgets, by incorporating individual field measurements of the various components of daily energy budgets.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.