





## RESEARCH ARTICLE

# The allometry of daily energy expenditure in hummingbirds: An energy budget approach

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## Abstract

1. Within-clade allometric relationships represent standard laws of scaling between energy and size, and their outliers provide new avenues for physiological and ecological research. According to the metabolic-level boundaries hypothesis, metabolic rates as a function of mass are expected to scale closer to 0.67 when driven by surface-related processes (e.g. heat or water flux), while volume-related processes (e.g. activity) generate slopes closer to one.
2. In birds, daily energy expenditure (DEE) scales with body mass ( $M$ ) in the relationship  $\log(\text{DEE}) = 2.35 + 0.68 \times \log(M)$ , consistent with surface-level processes driving the relationship. However, taxon-specific patterns differ from the scaling slope of all birds.
3. Hummingbirds have the highest mass-specific metabolic rates among all vertebrates. Previous studies on a few hummingbird species, without accounting for the phylogeny, estimated that the DEE-body mass relationship for hummingbirds was  $\log(\text{DEE}) = 1.72 + 1.21 \times \log(M)$ . In contrast to the theoretical expectations, this slope  $>1$  indicates that larger hummingbirds are less metabolically efficient than smaller hummingbirds.
4. We collected DEE and mass data for 12 hummingbird species, which, combined with published data, represented 17 hummingbird species in eight of nine hummingbird clades over a sixfold size range of body size (2.7–17.5 g).
5. After accounting for phylogenetic relatedness, we found DEE scales with body mass as  $\log(\text{DEE}) = 2.04 + 0.95 \times \log(M)$ . This slope of 0.95 is lower than previously estimated for hummingbirds, but much higher than the slope for all birds (0.68). The high slopes of torpor, hovering and flight potentially explain the high interspecific DEE slope for hummingbirds compared to other endotherms.

## KEYWORDS

birds, body mass, daily energy expenditure, doubly labelled water, field metabolic rate, metabolic-level boundaries hypothesis, scaling, tropics

## 1 | INTRODUCTION

Allometric scaling relationships describe how traits scale with one another (e.g. metabolic rate with body size). These relationships have

intrigued scientists for almost two centuries because of their potential for explaining how metabolic processes constrain the range and proportions of body sizes (Sarrus & Rameaux, 1839). Scaling patterns can be compared among individuals, species or multispecies

clades, which in turn may allow for the identification of outliers that do not follow patterns generated when considering broader taxonomic units (e.g. bird clades that are outliers from the pattern of all birds). Such outlier taxa may have unusual evolutionary constraints to their anatomy or physiology. Investigating how these outlier taxa overcome the limits that constrain other taxa may uncover unique physiological and ecological strategies.

By assessing the allometry of daily energy expenditure (DEE) with mass, we can identify taxa that have three distinct features relative to others in their taxonomic group. First, they sustain unusually high or low metabolic rates; second, they have morphologies and physiological processes that support these unusual metabolic rates; and third, they correspondingly place higher or lower energetic demands on their environment (Brown, Marquet, & Taper, 1993; Koteja, 1991). The form of the allometric relationship between DEE and body mass is:  $DEE = a \times Mass^b$ , or  $\log(DEE) = \log(a) + b \times \log(Mass)$ , in which  $\log(a)$  is the intercept and  $b$  is the slope (we use the latter formula herein). A slope less than one implies that larger individuals spend energy more efficiently per unit of body mass than smaller individuals. Across taxa, the standard interspecies slopes between DEE and mass range from 0.59 for marsupials, 0.66–0.75 for eutherian mammals (Capellini, Venditti, & Barton, 2010), 0.68 for birds (Nagy, 2005) and 0.89 for non-avian reptiles (Nagy, Girard, & Brown, 1999), to 0.92 for lizards (Nagy, 2005). In sum, ectotherms tend to have higher DEE slopes (0.89–0.92) than endothermic birds and mammals (0.68–0.73; Glazier, 2005; McNab, 2002; Nagy, 2005).

According to the metabolic-level boundaries hypothesis, a slope of 0.67 arises from surface-related constraints on fluxes such as loss of heat and water, while a slope close to 1.00 results from mass or volume constraints on energy use or power production, and is observed during high activity and with torpor use (Glazier, 2005, 2008). Given the range of variation across taxa, it is clear that no single universal slope exists (Glazier, 2005; Nagy, 2005; White, Cassey, & Blackburn, 2007). These allometric equations can thus help us investigate taxa that have unique morphology, physiology or ecological characteristics, both by contrasting them against other taxa that follow the standard relationships, and by comparing them with taxa that have similar slopes.

Hummingbirds have long been of interest as outliers in the study of allometry, being extreme in both their small body size and high energy use. While hummingbirds have some of the highest vertebrate metabolic rates, especially while hovering during the day (Hainsworth & Wolf, 1972; Lasiewski, 1963), they also have some of the lowest metabolic rates when they are in the energy-saving state of torpor at night. The metabolic-level boundaries hypothesis proposes that both these extreme metabolic states have high allometric slopes, while intermediate metabolic states have lower allometric slopes (Glazier, 2008, figure 2). There are, however, limited data available on hummingbird DEE across clades with measurements for only six of the c. 340 species across four of the nine hummingbird clades (McGuire et al., 2014). Five of these species measurements were on free-living individuals (Powers & Conley, 1994; Powers & Nagy, 1988; Weathers & Stiles, 1989), while one (on *Patagona gigas* the

giant hummingbird) was from an aviary study (Fernández, Dudley, & Bozinovic, 2011). Including the giant hummingbird aviary measurements, the relationship between DEE and body mass was estimated as  $\log(DEE) = -2.53 + 1.01 \times \log(Mass)$ . However, measurements from aviaries or laboratory studies can underestimate DEE (Stiles, 1971), as they exclude the true costs of foraging and social interactions. In addition, captive-raised birds have a shallower allometric energetic slope than wild birds (McKechnie, Freckleton, & Jetz, 2006), thus confounding the observed patterns. For just the free-living hummingbirds, the relationship is  $\log(DEE) = 1.72 + 1.21 \times \log(Mass)$  (Nagy et al., 1999). A slope of 1.21 implies that larger hummingbirds have higher energetic costs per unit mass than smaller hummingbirds, an unusual pattern for endotherms, which usually better retain heat and have lower mass-specific metabolic rates with increasing body mass across species. A slope less than one implies that larger birds have lower mass-specific metabolic rates, more aligned with patterns in other endotherms. Both the conflicting evidence regarding the scaling of DEE with mass among hummingbirds and their use of extreme metabolic states led us to examine how the scaling of their energy expenditure for different activities (e.g. hovering, flying, torpor) might influence the scaling of their DEE.

We aimed to first estimate the scaling of DEE with body mass for hummingbirds, using new field measurements from more species, and then to determine what aspects of hummingbird physiology and ecology might drive this relationship. We used the doubly labelled water (DLW) technique (Speakman, 1998) to measure DEE for free-living hummingbirds, across 12 species and six temperate and tropical sites. We combined our measures with those from the literature (Fernández et al., 2011; Powers & Conley, 1994; Powers & Nagy, 1988; Weathers & Stiles, 1989) to compare the DEE-mass slopes for 17 species (12 from tropical sites and five from temperate sites) covering eight of the nine hummingbird clades. Given that allometric relationships can be influenced by phylogenetic relatedness (Uyeda, Pennell, Miller, Maia, & McClain, 2017), we evaluated the effects of species relatedness on the allometric relationship. To explore what components of DEE might be driving hummingbirds' DEE allometry, we also assessed the allometric slopes of components of hummingbird daily energy budgets (e.g. hovering, flying, torpor, basal metabolic rate). Our analyses provide a new approach to understanding the allometric scaling of DEE by examining the scaling of various energy budget components. In addition, we broaden the current perspective on how the unique ecology and demanding physiology of hummingbirds set them apart from other endotherms.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and species

We collected DEE and mass data from hummingbirds at six sites—four sites in Arizona, USA and two on the eastern slope of the western Ecuadorian Andes. In Arizona, our sites were Harshaw Creek, Sonoita Creek, the Southwestern Research Station and El Coronado

(three species). In Ecuador, our sites were Maquipucuna and Santa Lucia (nine species). We collected data from May to July, 2013 in Arizona, and from June to August, 2014 and March to July, 2016 in Ecuador.

## 2.2 | Doubly labelled water measurements

We collected data on DEE using DLW. We either followed the standard DLW protocol (Speakman, 1998) by injecting isotopically enriched water (with  $^{18}\text{O}_8$  and  $^2\text{H}_1$ ) into the bird's pectoral muscle (in Ecuador), or used a modified DLW protocol (Shankar, Graham, Canepa, Wethington, & Powers, 2019) by feeding the bird isotopically enriched nectar (in Arizona). Briefly, for the modified protocol we fed the bird a 20% sucrose solution (weight/volume) made with a DLW ( $^2\text{H}_1$  and  $^{18}\text{O}_2$ ) mixture, rather than injecting them with DLW. We determined the exact dose (0.1–0.5 g) by precise mass measurements (nearest 0.001 g) before and after feeding, and calibrated these measurements using a control (see Shankar et al., 2019 for details). In both cases, we collected urine samples both after equilibration (half an hour), and approximately 24 hr after the bird was released. The difference in the concentrations of the isotopes over 24 hr yields an estimate of energy expenditure in the field over that time.

## 2.3 | Literature values

We included data from the four published sources of hummingbird DEE and corresponding masses that we found (Fernández et al., 2011; Powers & Conley, 1994; Powers & Nagy, 1988; Weathers & Stiles, 1989). Wherever possible, we used individual values for DEE. For some of these papers, only species' mean  $\pm$  SD DEE and masses were available; in these cases we used the mean values.

## 2.4 | DEE analyses

To test the DEE–mass relationship while accounting for the lack of independence caused by species relatedness, we ran phylogenetic GLMMs (Pinheiro & Bates, 2000) using the R package MCMCGLMM v. 2.24 (Hadfield, 2010). We incorporated individual-level observations by clustering them within the species-level structure of the phylogeny. Hence, the model estimates both species-specific ('random')

coefficients along with sample-wide 'fixed' effects, for example mass (Gelman, 2005). This package employs a Bayesian approach, by taking an expected prior distribution for the various parameters, fitting a model incorporating the data using a Markov chain Monte Carlo (MCMC) sampler, and returning posterior distributions of parameter estimates. MCMCGLMM explicitly models the phylogenetic relatedness between species as a random variable in the model input. We used the phylogeny generated by McGuire et al. (2014) and pruned it to match our dataset. While most phylogenetic regressions use a Brownian model (BM) of covariance, the DEE–mass relationship in these species might be under strong selection. In that case, an Ornstein–Uhlenbeck (OU) model may more closely approximate the covariance structure of the relationship (Hansen, 1997). Therefore, we first compared a phylogenetic generalized least squares regression (PGLS) model of  $\log(\text{DEE}) \sim \log(\text{Mass})$  with each covariance structure (Felsenstein, 1985; Garland, Harvey, & Ives, 1992), using only the species means for each variable. All logarithms were natural logs. To this end, we used the functions `corMartins` (OU) and `corBrownian` (BM) of the APE package v. 5.1 (Paradis, Claude, & Strimmer, 2004).

The OU model fit the data much better (Table 1), as seen by comparing the PGLS models with the OU structure (AIC = 17.2) and the BM covariance structure (AIC = 38.4). The PGLS model with the OU structure returned a high selection strength  $\alpha = 48.14$ . We therefore transformed the pruned tree with the above  $\alpha$  using the 'rescale' function with the 'OU' option in the 'GEIGER' package (Harmon, Weir, Brock, Glor, & Challenger, 2008). The resulting tree was effectively a star phylogeny with multiple zero-edge lengths, indicating regression residuals were unrelated to the phylogenetic structure. We therefore ran the MCMCGLMM model without accounting for the phylogeny.

We ran the MCMC chain for 5 million iterations, sampling every 1,000 generations, and checked visually for convergence. We used uninformative priors (Hadfield, 2010). The matrix for the variance structure was:

$$R \sim \text{Inv.gamma}(V=1, \text{nu}=0.02),$$

$$G \sim \text{Inv.gamma}(V=1, \text{nu}=0.02),$$

in which the *R*-structure is the covariance matrix of the residuals, *G*-structure is the covariance matrix of random effects in the BM model which included the phylogeny (phylogenetic signal in this models), *V* is the expected covariance structure representing the strength of belief and *nu* is the degree of belief parameter for the inverse Wishart distribution.

**TABLE 1** Results of the phylogenetic generalized least square models of  $\log(\text{DEE}) \sim \log(\text{Mass})$

Tree	Function in APE package	AIC	Log likelihood	Intercept (SE)	t value	p	Corr.	df
1. Brownian motion	corBrownian	38.42	−16.21	2.26 (0.91) 0.91 (0.43)	2.48 2.08	.025 .05	0.87	17
2. Ornstein–Uhlenbeck	corMartins	17.19	−4.59	2.06 (0.32) 0.98 (0.17)	6.45 5.66	0 0	0.97	17

The model is described as:

$$Y \sim \text{Normal}(\mu, \sigma),$$

$$\log(\text{Daily energy expenditure}) = \log(a) + b \times \log(\text{Mass}) + s + u$$

in which  $a$  and  $b$  are the regression coefficients, the  $s$  term accounts for phylogenetic variance using a covariance matrix from the phylogeny and  $u$  accounts for residual variation (i.e. not explained by the other terms in the model).

We also ran a MCMC<sub>GLMM</sub> model including a binary variable representing whether individuals were measured at temperate or tropical sites:

$$\log(\text{DEE}) = \log(a) + b \log(M) \times (\text{Tropical/Temperate}).$$

Finally, there is a large size gap between *P. gigas* (17–20 g) and the next largest species (10 g in this dataset), and allometric analyses of hovering suggest that *P. gigas* might be different from other hummingbirds (Groom, Toledo, Powers, Tobalske, & Welch, 2018). Therefore, to test for its effect on the relationship, we ran the best MCMC<sub>GLMM</sub> model (without the tree) both with and without *P. gigas*. We also ran a traditional linear regression ('lm' in R) using species means, to compare our results with past studies that did not account for phylogenetic relatedness (Nagy et al., 1999).

MCMC<sub>GLMM</sub> results are reported as posterior-mean with credible intervals (CI) and pMCMC. If the reported CIs do not overlap zero, we infer that that variable does influence the structure of the data (e.g. if the post-mean and CI are negative, that variable has a negative effect on the dependent variable and vice versa; Hadfield, 2010). The best model was the most parsimonious model with the lowest DIC value.

## 2.5 | Allometry of DEE components

To determine what factors influence the high allometric DEE slope of hummingbirds, we also assessed the allometry of various

components of DEE. Since the DEE slope is an aggregate of all hummingbird activities over 24 hr, we expect the regression of DEE to emerge from the allometric relationships of its constituent components.

We used published values to assess the allometry of the individual components of hummingbird daily energy budgets. Following previous hummingbird energy budget studies (López-Calleja & Bozinovic, 2003; Shankar et al., 2019; Wolf, Hainsworth, & Gill, 1975), a hummingbird's daily energy costs can be classified as: basal metabolic costs, thermoregulatory costs, hovering, flying, perching and night-time energy expenditure. This energy budget assumes that the individual is a non-reproducing adult. These components add up to DEE as follows (adapted from Shankar et al., 2019):

$$\text{DEE} = \text{BMR} + \text{TRE} + \text{HMR} + \text{FLMR} + \text{PMR} + \text{TMR},$$

where DEE is the daily (24-hr) energy expenditure; BMR is the basal metabolic rate for time spent within the thermoneutral zone (range of temperatures at which endotherms have no thermoregulatory costs), in the dark, and during its inactive phase; TRE are the thermoregulatory costs for time spent at temperatures outside the thermoneutral zone; HMR is the hovering metabolic rate for all time spent hovering; FLMR is the flying metabolic rate for all time spent flying; PMR is the perching metabolic for all time spent perching; TMR is the torpid metabolic rate over time spent in torpor. For constructing an energy budget in practice, BMR would be subtracted from each of the HMR, FLMR and PMR components.

Each component of the daily energy budget has its own allometric scaling with corresponding intercepts and slopes: the intercepts determine the relative contributions of each component to the DEE while the slope determines how they each change with increasing body mass. It is, however, difficult to estimate how much time free-living hummingbirds spend on these different activities and thus to compare the intercepts. Therefore, we focus on how the slopes of the energy budget components, as a function of mass, might contribute to the slope of DEE. The values used for the allometric slope

**TABLE 2** Allometric slopes of energy budget components used

Energy budget component	Lower slope	Higher slope	References
Basal metabolic rate (BMR)	0.45	0.85	Fernández (2010) and Londoño et al., (2014)
Perching metabolic rate (PMR)	0.45	0.85	Fernández (2010) and Londoño et al. (2014)
Thermoregulatory costs (TRE)	0.67		Bennett and Harvey (1987) and Glazier (2018)
Hovering metabolic rate (HMR)	0.76	0.96	Groom et al. (2018)
Flying metabolic rate (FLMR)	0.72	0.90	Bishop and Butler (1995, 2015) and Castro and Myers (1988)
Torpor metabolic rate (TMR)	1.5		Shankar et al. (2018, this study)

of the energy budget components are summarized in Table 2 (see Supporting Information for how these values were obtained).

### 3 | RESULTS

We present four models that represent slightly different ways of estimating the allometric relationship as established in the literature. First, the best MCMC<sub>GLMM</sub> model (DIC = 98.42; no phylogeny) resulted in the following allometric relationship ( $R^2 = .67$ ,  $p\text{MCMC} < 2e-04$ ; Figure 1):

$$\log(\text{DEE}) = 2.04 + 0.96 \times \log(\text{Mass}). \quad (1)$$

Second, *P. gigas* is excluded because it is an outlier in allometric analyses. The model excluding *P. gigas* was (DIC = 98.20;  $R^2 = .65$ ;  $p\text{MCMC} < 2e-04$ ):

$$\log(\text{DEE}) = 2.08 + 0.93 \times \log(\text{Mass}). \quad (2)$$

Third, many studies ignore the individual variation in DEE in allometric estimations. When only species means were modelled with the MCMC<sub>GLMM</sub>, ignoring individual variation, the following relationship was obtained (DIC = 7.56;  $R^2 = .73$ ;  $p\text{MCMC} < 2e-04$ ):

$$\log(\text{DEE}) = 2.16 + 0.94 \times \log(\text{Mass}). \quad (3)$$

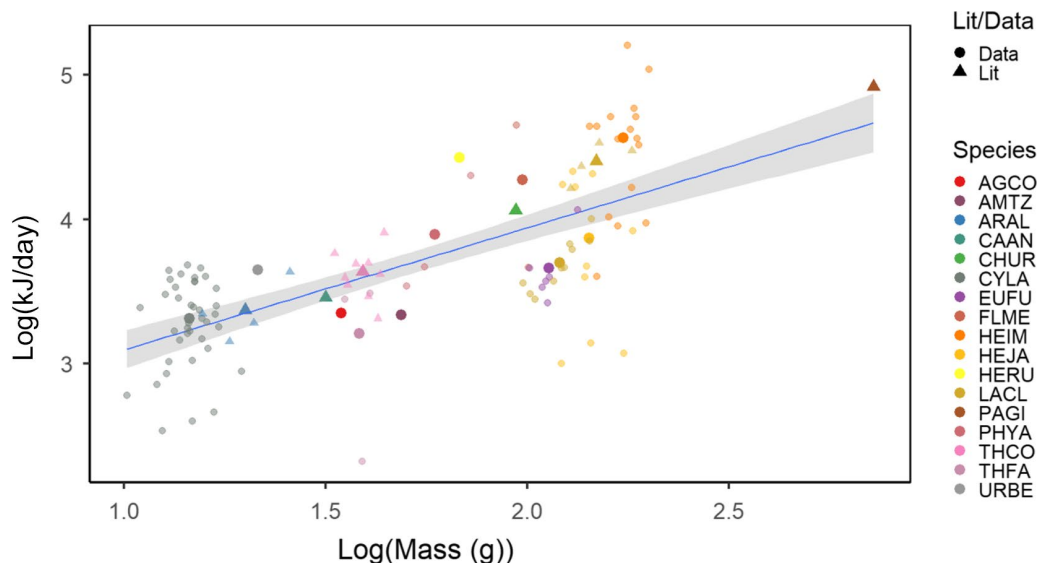
Finally, a traditional linear regression, including all species and individuals (not accounting for phylogeny), yielded the following relationship (with  $R^2 = .66$  and a  $p$ -value of  $4.57e-05$ ):

$$\log(\text{DEE}) = 2.06 + 0.98 \times \log(\text{Mass}). \quad (4)$$

The MCMC<sub>GLMM</sub> model results without the phylogeny and with temperate/tropical as a binary covariate are presented in Table 3. The model including the temperate/tropical covariate (DIC = 100.7) did not perform as well as the model without the temperate/tropical variable, and so was excluded from final analyses (see Supporting Information S1 for details). The DICs of all models present in Table 3 are not directly comparable, because they use slightly different datasets and make different assumptions. The individual-level values (all individuals of all species) of DEE and body mass are given in Table S1.

#### 3.1 | Energy budget components

To combine the slopes of the various energy budget components and compare them to the slope for DEE, we averaged the slopes across the energy budget components. Using the lowest of these estimates to get an estimated slope for DEE (i.e. BMR = 0.45, TRE = 0.67, HMR = 0.76, FLMR = 0.72, PMR = 0.45, TEE = 1.5), we obtain a floor on the aggregate slope of 0.76 ( $SE = 0.18$ ). Using the higher estimates (i.e. BMR = 0.85, TRE = 0.67, HMR = 0.96, FLMR = 0.90, PMR = 0.85, TEE = 1.5), we obtain a ceiling on the aggregate slope of 0.96 ( $SD = 0.12$ ), matching our DEE slope for the best model (0.96). Using the mean set of slopes with the published value for HMR and the higher slopes for all other measures (BMR = 0.85, TRE = 0.67, HMR = 0.76, FLMR = 0.90, PMR = 0.85, TEE = 1.5), we obtain an aggregate slope of 0.92 ( $SD = 0.13$ ), matching our estimate of DEE slope (0.93) excluding *P. gigas*.



**FIGURE 1** A log-log plot (natural logs) of individual and species-level hummingbird daily energy expenditure (kJ) versus mass (g), including values from this study (circles) as well as from the literature (triangles). This regression line corresponds to Equation (1), with the grey denoting 95% confidence intervals. Species means are large points while individual points are smaller. Colours represent species (AGCO = *Agelaiocercus coelestis*; AMTZ = *Amazilia tzacatl*; ARAL = *Archilochus colubris*; CAAN = *Calypte anna*; CHUR = *Chalybura urochysia*; CYLA = *Cyanthus latirostris*; EUFU = *Eugenes fulgens*; FLME = *Florisuga mellivora*; HEIM = *Heliodoxa imperatrix*; HEJA = *Heliodoxa jacula*; HERU = *Heliodoxa rubinoides*; LACL = *Lampornis clemenciae*; PAGI = *Patagona gigas*; PHYA = *Phaethornis yaruqui*; THCO = *Thalurania colombica colombica*; THFA = *Thalurania fannyi*; URBE = *Urosticte benjamini*)

**TABLE 3** Results of the MCMC<sub>GLMM</sub> models with the Brownian motion tree and without a phylogenetic tree. The second model was the best one (DIC value bolded). All the models here used individual values, except the last model which used species means

Model	DIC	G-structure	R-structure	Intercept mean (CI); <i>p</i>	Slope mean (CI); <i>p</i>
Log(DEE) ~ Log(Mass); Brownian motion tree	104.07	0.104 (0.006–0.25)	0.136 (0.100–0.177)	2.18 (1.37–2.94); <2e–04	0.90 (0.50–1.28); <2e–04
Log(DEE) ~ Log(mass); No tree (Ornstein–Uhlenbeck)	<b>98.42</b>	0.06 (0.007–0.13)	0.13 (0.093–0.16)	2.04 (1.35–2.71); <2e–04	0.96 (0.59–1.33); <2e–04
Log(DEE) ~ Log(mass) × Temperate/Tropical; No tree (Ornstein–Uhlenbeck)	100.19	0.06 (0.006–0.14)	0.13 (0.097–0.169)	2.29 (1.24–3.29); .0024	Log(Mass): 0.76 (0.15–1.36); .008 Temp/Trop: –0.44 (–1.89–1.09); .50 Log(Mass): Temp/Trop: 0.31 (–0.58–1.07); .41
Log(DEE) ~ Log(mass); No tree (Ornstein–Uhlenbeck); excluding <i>Patagona gigas</i>	97.94	0.06 (0.007–0.15)	0.13 (0.094–0.17)	2.08 (1.28–2.82); <2e–04	0.93 (0.49–1.35); <2e–04
Log(DEE) ~ Log(mass); No tree; only using species means and not individual values	7.56	0.05 (0.002–0.16)	0.08 (0.01–0.16)	2.16 (1.38–2.92); <2e–04	0.94 (0.56–1.35); 4e–04

## 4 | DISCUSSION

Although hummingbirds are endotherms, their use of extreme metabolic states—torpor and high activity—seems to drive their unusually high allometric slope. Previous analyses implied that larger hummingbirds were much more energetically inefficient than smaller hummingbirds, with the interspecific DEE–mass slope for hummingbirds, estimated at 1.21, compared to the slope of all birds of 0.68 (Nagy et al., 1999). We found that hummingbirds do diverge from the allometric scaling of endotherms, but do not have a DEE–mass slope greater than 1. Instead, DEE scales with body mass as  $\log(\text{DEE}) = 2.04 + 0.96 \times \log(\text{Mass})$ . The slope is even lower:  $\log(\text{DEE}) = 2.09 + 0.93 \times \log(\text{Mass})$ , when we exclude *P. gigas* (mass = 17.45), which is often considered an outlier in hummingbird studies because of its body mass and wing allometry (Groom et al., 2018). However, the slope for hummingbirds is still close to 1, unusually high for endotherms (Glazier, 2014; Nagy, 2005). According to the metabolic-level boundaries hypothesis (Glazier, 2008), allometric slopes approach 1 when energy is expended on volume-related processes (e.g. activity, torpor) than by surface-related fluxes such as those of heat or water. By examining the scaling of the activities in a hummingbirds energy budget we found that this steep slope is likely driven by a combination of their use of torpor (Shankar, Schroeder, Wethington, Graham, & Powers, 2018) and their capacity for high-cost activities (Shankar et al., 2019).

The slopes of metabolic rates plotted as a function of increasing activity levels (e.g. from torpor through thermoregulation to maximal metabolic rate) yield a U-shaped relationship (Glazier, 2010, figure 2). The highest slopes, close to 1, are at either metabolic extreme (torpor and maximal metabolic rate). In contrast, at intermediate metabolic states (thermoregulation, resting metabolic rate), energy is largely spent on surface-related constraints, such as thermoregulation and water loss, and the slope is closer to 0.67 (Glazier, 2005, 2008). At the lower

extreme of metabolic activity, torpor seems to scale with a slope close to 1 across taxa (Glazier, 2008). In hummingbirds, torpor use scales with an even higher slope of 1.5. At the higher extreme, hummingbird forward flight scales with body mass with a slope of 0.72–0.90 (Bishop & Butler, 2015), while hovering scales with slopes between 0.76 and 0.96 (Groom et al., 2018). Together, the high slopes at each extreme of the activity range seem to contribute to hummingbirds' high DEE slope (Table 2).

While BMR is often used in global analyses as a proxy for DEE, few endotherm studies have verified whether their relationship is consistent across taxa (Mathot & Dingemanse, 2015). Individual-level studies indicate that BMR and DEE are often uncorrelated (especially in birds; Koteja, 1991; Portugal et al., 2016; Shankar et al., 2019). Since BMR is measured under often unrealistic controlled conditions, DEE is likely more ecologically relevant and under stronger selection constraints than BMR, because DEE is a more direct measure of how organisms live in their environment (Hudson, Isaac, & Reuman, 2013). Considering the influence of activity levels on the allometry of DEE in hummingbirds, DEE seems a more ecologically relevant measure than BMR for comparing species (see Halsey, Matthews, Rezende, Chauvaud, & Robson, 2015 for ectotherm comparisons). With our approach assessing the scaling of multiple energy budget components, rather than just BMR, we can better understand the factors contributing to the scaling of DEE, and why it might not match the scaling of BMR alone. This approach can be further expanded to include a better assessment of the intercept of DEE, by incorporating time-activity budgets. By including the time (not just energy per unit time) spent on each component by species across a range of body masses, the relative contributions of the energy budget components to DEE could be estimated. Hummingbirds often spend many hours at night in torpor (0–8 hr; Shankar et al., 2018) and can spend a large but also highly variable proportion of their day on hovering and flying (10%–75%; Shankar et al., 2019). However, very limited data



are available on field time budgets to carry out a robust allometric analysis incorporating time-activity budgets.

Similar to previous studies across all birds, phylogeny did not significantly influence the allometric relationship among hummingbirds. The lack of a phylogenetic effect indicates that the hummingbird DEE–mass relationship is driven more by strong selection than by phylogenetic conservatism (Nagy, 2005). Unlike other studies on avian BMR, we did not find a difference in DEE between temperate and tropical hummingbirds (Londoño, Chappell, Castañeda, Jankowski, & Robinson, 2014); however, this result may be caused by small sample sizes. Additionally, high allometric slopes mean that large hummingbirds (e.g. 10 g, 20 g) have similar mass-specific DEE to smaller (c. 3 g) hummingbirds. Compared with other endotherms, for which larger animals are more energy-efficient per unit mass, large hummingbirds are relatively inefficient, perhaps explaining why there is only one large hummingbird (*P. gigas*), while other species range from 1.5 to c. 10 g. Thus, the multiple physiological adaptations necessary to persist in their niche, as integrated by the allometry of DEE with body mass, likely prevent the evolution of massive hummingbirds.

## 5 | CONCLUSIONS

By analysing the relative scaling of all the components of the daily energy budget, we can achieve a more comprehensive assessment of what determines the scaling of DEE across species of different body masses. This approach can be used to relate morphological and physiological features to interspecific allometric trends. For example, in hummingbirds the ability to use torpor, and unique wing morphology and biomechanics associated with hovering flight results in high allometric slopes. Hence, the unusual physiology and ecology of hummingbirds seem to drive them to their unique place in pushing the energetic limits for what an endotherm can achieve.

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## AUTHORS' CONTRIBUTIONS

C.H.G., D.R.P. and A.S. were involved with study conception and design; A.S. and D.R.P. collected the data; A.S. and L.M.D. performed the analyses; A.S. drafted the manuscript; C.H.G., L.M.D. and D.R.P. provided major comments and revisions. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

The dataset supporting this article is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.905qfttgm> (Shankar, Powers, Dávalos, & Graham, 2020). Code used to run analyses (R Core Team, 2018) are available through github ([https://github.com/nushiamme/Hummingbird\\_allometry](https://github.com/nushiamme/Hummingbird_allometry)) and through Zenodo at: <https://doi.org/10.5281/zenodo.3604303> (Shankar, 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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