FOCUSED COLLECTION

Widespread Torpor Use in Hummingbirds from the Thermally Stable Lowland Tropics*

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ABSTRACT

Torpor, the temporary reduction of metabolic rate and body temperature, is a common energy-saving strategy in endotherms. Because of their small body size and energetically demanding life histories, hummingbirds have proven useful for understanding when and why endotherms use torpor. Previous studies of torpor in hummingbirds have been largely limited to tropical montane species or long-distance migrants that regularly experience challenging thermal conditions. Comparatively little is known, however, about the use of torpor in hummingbirds of the lowland tropics, where relatively high and stable year-round temperatures may at least partially negate the need for torpor. To fill this knowledge gap, we tested for the occurrence of torpor in tropical lowland hummingbirds ($n = 37$ individuals of six species) from central Panama. In controlled experimental conditions simulating the local temperature regime, all six species used torpor to varying degrees and entered torpor at high ambient temperatures (i.e., ≥28°C), indicating that hummingbirds from the thermally stable lowland tropics regularly use torpor. Torpor reduced overnight mass loss, with individuals that spent more time in torpor losing less body mass during temperature experiments. Body mass was the best predictor of torpor depth and duration among and within species—smaller species and individuals tended to use torpor more frequently and enter deeper torpor. Average mass loss in our experiments (~8%–10%) was greater than that reported in studies of hummingbirds from higher elevation sites (~4%). We therefore posit that the energetic benefits accrued from torpor may be limited by relatively high nighttime temperatures in the lowland tropics, although further studies are needed to test this hypothesis.

Keywords: body size, energy savings, environmental temperature, heterothermy, metabolic rate, thermoregulation, Trochilidae.

Introduction

Endothermic animals rely on endogenous metabolic heat production to regulate internal body temperatures (McNab 2002; Townsend et al. 2008). Obtaining energy sufficient to meet these metabolic costs is a fundamental challenge (Koteja 2004) that can be mitigated with increased energy consumption (Cottle and Carlson 1954; Hart 1962), behavioral modifications (Grubb 1978), or reduction in energetic demand. Adaptive fluctuations in body temperature (T_b) can result in substantial energetic savings for endotherms (McKechnie and Lovegrove 2002; Lovegrove 2012; Boyles et al. 2013), and one common strategy is torpor—a controlled reduction in metabolic rate and T_b that reduces energy expenditure (Wang and Wolowyk 1988; Ruf and Geiser 2015).

Hummingbirds (family Trochilidae) are well suited for exploring when and why endotherms use torpor. Because of their small body sizes and use of hovering flight, hummingbirds have some of the highest surface-area-to-volume ratios (Krüger et al. 1982) and mass-specific metabolic rates of any vertebrate (Suarez 1992). Small body size coupled with dependence on nectar, a spatiotemporally variable food resource, places hummingbirds regularly at risk of energetic deficit (Schleucher 2004),

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and many species undergo torpor frequently (Hainsworth and Wolf 1970; Krüger et al. 1982; Shankar et al. 2020; Spence and Tingley 2021). Previous studies have found that torpor use results in substantial energetic savings for most species (Shankar et al. 2020). Furthermore, body mass is an important predictor of torpor use both within and among hummingbird species (reviewed in Spence and Tingley 2021), with smaller individuals and species generally using torpor more frequently and entering deeper torpor (i.e., exhibiting greater reductions in T_b).

Current understanding of hummingbird torpor use, however, has focused on north-temperate migrants (e.g., Carpenter and Hixon 1988; Hiebert 1993; Spence and Tingley 2021) or tropical montane species (e.g., Wolf et al. 2020), which regularly face cold temperatures and/or the energetic costs of migration. The lowland Neotropics are a center of global hummingbird diversity (McGuire et al. 2014), but we know relatively less about torpor use in species that occur in these relatively warm (i.e., ≥20°C) and stable thermal environments (but see Krüger et al. 1982; Bech et al. 1997; Shankar et al. 2020). High, stable air temperature (T_a) may reduce torpor efficiency because hummingbirds can drop T_b only as low as the local minimum T_a. Counterintuitively, then, warmer nights experienced by lowland tropical hummingbirds may reduce energetic savings by limiting their ability to reduce T_b, compared with montane hummingbirds that can maximize their energetic savings in response to colder temperatures. Because lowland tropical hummingbirds may be expected to use torpor less frequently or under different circumstances than north-temperate or tropical montane species, this knowledge gap may bias our understanding of torpor use in hummingbirds and small vertebrates in general.

Here, we report data on torpor use in six lowland tropical hummingbird species in central Panama. We used these data to address the following questions: (1) do lowland tropical hummingbirds regularly use torpor under ecologically relevant temperature conditions, (2) does torpor reduce overnight mass loss among hummingbirds, (3) does physiological condition (i.e., body mass, body condition, fat stores) influence patterns of torpor use within species, and (4) does body mass influence patterns of torpor use among species?

Material and Methods

Bird Capture and Handling

We conducted fieldwork in and around the town of Gamboa in central Panama (09°07′N, 79°42′W; elevation 50 m asl) from February to April 2015. This region is characterized by seasonal rainfall, with the dry season typically lasting from January to May and the rainy season lasting from June to December. To control for potential seasonal variation in torpor use (Geiser and Baudinette 1987; Hiebert 1993), we restricted sampling to the dry season. To capture birds, we first deployed feeders (~1.5 m high) containing a 20% sucrose solution at five sampling locations in urban areas or successional forest (fig. A1). After a 3-wk period of acclimation to the feeders, hummingbirds were captured in mist nets (12 m × 2.6 m; 36-mm mesh) as late in the afternoon as possible (i.e., 1700–1800 hours) to minimize the handling time and the potential impacts of food restriction on torpor use. We acknowledge that capturing hummingbirds between 1700 and 1800 hours may have restricted them from natural hyperphagia (i.e., intensified foraging) that some species exhibit before sunset (Powers et al. 2003) and could potentially influence patterns of torpor use. By catching birds as close to sunset as possible, however, we were able to minimize the impacts of food restriction while simultaneously capturing the natural variation in energy state among individuals with different amounts of nectar in their crops.

Upon capture, birds were placed in cloth bags and transported to the laboratory, where we weighed them with a digital scale (American Weigh Scales AWS-201, 200 ± 0.01 g) and used surgical scissors to clip a unique combination of tail feathers on each individual to facilitate identification. Additionally, we assessed physiological condition based on external morphology of the pectoralis muscle using a four-point categorical scale (described in Bolton et al. 2008) and fat score based on furcular fat deposits using a five-point categorical scale (Helms and Drury 1960; reviewed in Brown 1996). We used temperature-sensitive PIT tags (13 mm × 2 mm; BioTherm13, Biomark) to measure torpor in hummingbirds. The PIT tags were too large for cloacal insertion (e.g., Pollock et al. 2021), so we attached them with adhesive glue to the pectoralis muscles of focal individuals (the tag reader was able to monitor only one bird per experiment) to measure skin temperature (T_{skin}) as a proxy for T_b. We used the same minimal amount of glue (one or two drops) on all individuals of all species to reduce the glue's potential impact on T_{skin} measurements and facilitate comparison of T_{skin} measurements across individuals and species. We acknowledge that T_{skin} measurements only approximate actual T_b values, yet T_{skin} is often closely correlated with T_b (McCafferty et al. 2015), particularly in small animals, and can therefore yield insight into patterns of thermoregulation and torpor use.

Temperature Experiments and Thermal Ramping Protocols

We conducted temperature experiments overnight (from 1800 to 0500 hours) and measured one ($n = 7$ experiments) or two ($n = 15$ experiments) birds per experiment. Following PIT tag attachment, at 1800 hours on the day of capture, the focal individuals were placed in respirometry chambers (see "Respirometry System and Metabolic Measurements" for details) situated inside a temperature cabinet (PTC-1, Sable Systems) controlled by a Peltier device (PELT-5, Sable Systems). All birds were awake and active at this time, and we allowed them 1–3 h to acclimate to chambers at $T_a = 30°C$ (i.e., some individuals exhibited periodic activity in the initial acclimation phase and took longer to become quiescent) before initiating the temperature experiment. Throughout the experiments, T_a of both the temperature cabinet and the individual chambers was measured continuously and precisely regulated using thermistor probes (SEN-TH, Sable Systems; ±0.2°C accuracy). We monitored behavior and activity levels throughout experiments using infrared cameras (WCM-6LNV, Sabrent) to confirm that focal individuals were indeed quiescent. Focal individuals were exposed to a thermal ramping protocol (sensu Mitchell and Hoffmann 2010) designed to approximate the nocturnal temperature conditions experienced at the study site, where minimum T_a averages ~24.5°C during the sampling period of February to April (fig. A2; temperature data from https://biogeodb.stri.si.edu/physical_monitoring/research/panamacanalauthority). Specifically, starting at $T_a = 30°C$, we lowered T_a in successive 3°C increments, maintaining birds at a given T_a for at least 1 h each (2 h total) until 24°C was reached. Thereafter, we maintained chamber T_a at 24°C throughout the duration of the experiment. Between 0500 and 0600 hours on the morning following the temperature experiment, we increased T_a back to 30°C and let birds rewarm at this T_a for approximately 1 hr. All birds rewarmed successfully and became active following the 1-h rewarming period, which terminated just before or during the sunrise of the following day (0600–0630 hours). Following rewarming, we removed birds from metabolic chambers, detached their PIT tags by using a cotton swab dipped in alcohol to dissolve the adhesive, and reweighed them. We then provided sugar water, placed birds in cloth bird bags, transported them to the site of capture, and released them.

Respirometry System and Metabolic Measurements

We used push-mode flow-through respirometry (Withers 2001; Lighton and Halsey 2011) to measure gas exchange and quantify metabolic responses to T_a. We pumped ambient air (AIR-8000, Top Fin) through a column of Drierite to remove water and into a mass-flow controller (Flowbar-8, Sable Systems), which divided the air into three separate streams—two to animal chambers and one to an empty baseline chamber. The Flowbar-8 regulated flow rates to each chamber at 250–300 mL min^{-1}. Chambers (1.97 L) were made of Plexiglas, equipped with a rubber gasket, and sealed with binder clips (ACCO Brands) to prevent leakage. Each chamber contained a wire-mesh floor for birds to perch on, and a 1-cm layer of mineral oil covered the bottom of each chamber to trap feces and absorb fecal water (Muñoz-Garcia and Williams 2007). Chamber excurrent air was subsampled manually at 100–150 mL min^{-1} with barrel syringes and put into a humidity meter (RH-300, Sable Systems) that measured H_2O content, followed by a dual CO_2/O_2 analyzer (FoxBox, Sable Systems) that measured CO_2 content and O_2 content. During each experiment, flow rate, T_a, and percent CO_2 were measured for all individuals in each chamber in real time at 1-s intervals using the program Expedata (Sable Systems). To measure T_{skin} of the single focal individual in each experiment that had been affixed with a temperature-sensitive PIT tag, we placed a PIT tag antenna (HPR Plus reader, Biomark) inside the temperature cabinet, which collected T_{skin} data for the tagged focal individual at 1-min intervals throughout the experiment. We synced the PIT tag reader with Expedata before each experiment to ensure that T_{skin} measurements corresponded temporally with metabolic measurements. To calculate metabolic rate, we converted raw percent CO_2 data to $\dot{V}_{CO_2}$ (rate of CO_2 production; mL CO_2 min^{-1}), assuming a respiratory quotient of 0.75 (Powers 1991) and using the following equation (Lighton 2018):

$$\dot{V}_{CO_2} = \frac{FR \times (F_eCO_2 - F_iCO_2) - F_eCO_2 \times \dot{V}_{O_2}}{1 - F_eCO_2},$$

where FR is the flow rate of the animal chamber (mL min^{-1} STPD), F_iCO_2 is the incurrent fractional CO_2 concentration (0.0005), F_eCO_2 is the excurrent fractional CO_2 concentration, and $\dot{V}_{O_2}$ is the rate of O_2 consumption (mL O_2 min^{-1}). We switched between focal individuals every 15 min, sampling each bird for a cumulative hour over the 2 h at a given T_a. We switched from animal chambers to an empty baseline chamber for 5 min every 30 min (i.e., 15 AC1, 15 AC2, 5 BL) to control for drift in the O_2 analyzer (Lighton and Halsey 2011). To determine the relationship between $\dot{V}_{CO_2}$, T_{skin}, and T_a, the most stable 5-min averages of $\dot{V}_{CO_2}$, T_{skin}, and T_a during each 15-min sampling interval were obtained throughout the entire experiment for each focal individual. To estimate lower critical temperature, we used the R package segmented (Muggeo 2008) to identify inflection points in the relationship between $\dot{V}_{CO_2}$ and T_a (following Pollock et al. 2019).

Statistical Analyses

Do Lowland Tropical Hummingbirds Use Torpor? We measured thermoregulatory responses to T_a in 37 individuals of six hummingbird species (tables 1, A1; fig. A4). We defined torpor as a reduction of metabolic rate of ≥25% of normothermic resting metabolic rate at the same T_a, following Geiser (2021). To estimate depth and duration of torpor for each individual, we used minimum T_{skin} and proportion of time spent in torpor, respectively. Minimum T_b is a commonly used proxy for depth of torpor in endotherms, as greater reductions to T_b are indicative of deeper torpor (Willis et al. 2006; Vuarin et al. 2013).

Proportion of time spent in torpor. To control for variation in experiment length (mean length ± SD = 516 ± 80.5 min), we used the proportion of time spent in torpor rather than the absolute duration of torpor as an index of duration of torpor, which was calculated as follows:

$$\frac{\text{total time spent in torpor}}{\text{total experiment time}}.$$

The total experiment time refers to the cumulative amount of time from when an individual became quiescent and its gas traces stabilized to the end of the temperature experiment. The total time in torpor refers to the cumulative amount of time that an individual spent in torpor during the total experiment time. Experiment times varied considerably (range: 335–670 min; mean ± SD = 507 ± 79.8 min) owing to variation in individual behavior (i.e., certain individuals took longer to come to rest inside the respirometry chambers) and respirometry system stabilization time (i.e., certain experiments required more time for the O_2 meter to stabilize and span). By using a proportional metric of time spent in torpor, we were able to control for this variation and compare patterns of torpor use across individuals and species.

Minimum T_{skin}. Because we were able to PIT tag only one bird per experiment, T_{skin} data were available for only ~55% (20 of 37) of focal individuals (table A1). Therefore, we explored the feasibility of using minimum $\dot{V}_{CO_2}$ (the minimum rate of CO_2 production) as a substitute for minimum T_{skin} by testing the

Table 1: Sample sizes of focal species and physiological trait data from torpor experiments

Focal species	n	M_b	Resting $\dot{V}_{CO_2}$	LCT	Normothermic T_{skin}	Minimum T_{skin}	Proportional mass loss	Proportion of time spent in torpor	Frequency
White-necked jacobin (*Florisuga mellivora*)	16	6.59 ± .81	.45 ± .08	28.25 ± 1.76	37.3 ± .8	29.7 ± 4.7	.08 ± .03	.38 ± .31	12/16
Blue-chested hummingbird (*Amazilia amabilis*)[a]	9	3.51 ± .57	.27 ± .06	28.74 ± 1.85	35.8 ± .7	25.5 ± .5	.10 ± .02	.57 ± .28	9/9
Rufous-tailed hummingbird (*Amazilia tzacatl*)[a]	9	4.69 ± .46	.36 ± .06	28.94 ± 1.57	36.2 ± 1.0	27.4 ± 3.5	.09 ± .04	.56 ± .34	8/9
Violet-bellied hummingbird (*Juliamyia julie*)[a]	1	3.23	.21	29	35.6	24.4	.09	.76	1/1
Black-throated mango (*Anthracothorax nigricollis*)	1	5.84	.51	29	38.3	24.7	.09	.25	1/1
Long-billed hermit (*Phaethornis longirostris*)[a]	1	5.58	.33	30	37.3	27.9	NA	.58	1/1
Total	37								

Note. Included are mean body mass (M_b; g) ± SD, normothermic CO_2 production (resting $\dot{V}_{CO_2}$; mL min^{-1}) ± SD, lower critical temperature (LCT; °C) ± SD, normothermic skin temperature (T_{skin};°C) ± SD, minimum skin temperature (T_{skin}; °C) ± SD, proportional mass loss (mean ± SD), the proportion of time spent in torpor (mean ± SD), and the proportion of individuals that used torpor (frequency sensu Shankar et al. 2020).

[a] First record of torpor use.

relationship between the two variables. A univariate linear regression showed a very strong correlation between the two variables ($F_{1,18} = 97.89$, $R^2 = 0.84$, $P < 0.0001$; fig. A3), confirming that minimum $\dot{\mathrm{V}}\mathrm{CO}_2$ was a reliable proxy for minimum T_{skin} with regard to torpor depth. The model equation is represented below, where m is the slope of the line and b is the y-intercept:

$$T_{\mathrm{skin}} = m \times \text{minimum } \dot{\mathrm{V}}\mathrm{CO}_2 + b. \tag{1}$$

Does Torpor Reduce Overnight Mass Loss? To determine whether torpor reduced overnight mass loss, we calculated the percentage of mass that was lost by each individual during the experiment (ΔM_{b}: (M_{b} capture $-$ M_{b} release)/M_{b} capture) as a proxy for energy expenditure (following Bech et al. 1997; Wolf et al. 2020). Although mass loss is an integrated measure of energy expenditure that includes both fecal loss and water loss, it has been used to broadly explore patterns of torpor use and nighttime energy expenditure in higher-elevation hummingbirds in particular (i.e., Bech et al. 1997; Wolf et al. 2020), and we therefore employed this metric to directly compare mass loss in the lowland hummingbirds we sampled with that from higher-elevation species. We then tested for an association between an individual's ΔM_{b} and its proportion of time spent in torpor. To do so, we constructed a generalized linear mixed model including ΔM_{b} as a fixed effect and individual ID as a random effect. Because the response variable was a proportion bounded by 0 and 1, we employed a beta regression with a logit link function using the R package glmmTMB (Brooks et al. 2017). We report the Z and P values, β estimates, and 95% confidence intervals from the model below, where ID is the unique identification number assigned to each hummingbird caught and tagged:

$$\begin{aligned}&\text{proportional mass loss } (\Delta M_{\mathrm{b}})\\&\quad = \text{proportion of time spent in torpor} + (1|\mathrm{ID}).\end{aligned} \tag{2}$$

Does Individual Condition Influence Patterns of Torpor Use? To explore the influences of physiological condition (i.e., body mass, body condition, fat stores) on torpor use among individuals, we constructed generalized linear mixed models for both torpor depth (i.e., minimum $\dot{\mathrm{V}}\mathrm{CO}_2$) and duration (i.e., proportion of time spent in torpor). Each additive model included body mass, fat score, and condition score as fixed effects and individual ID as a random effect. For torpor depth, we ran a linear regression with a Gaussian error distribution, whereas we ran a beta regression with a logit link function for torpor duration given that it was a proportional response variable. We report the Z and P values, β estimates, and 95% confidence intervals from the models below, where ID is the unique identification number assigned to each hummingbird caught and tagged:

$$\begin{aligned}&\text{torpor depth (minimum } \dot{\mathrm{V}}\mathrm{CO}_2) = \text{body mass} + \text{body condition}\\&\qquad + \text{fat stores} + (1|\mathrm{ID}),\end{aligned} \tag{3}$$

$$\begin{aligned}&\text{torpor duration (proportion of time spent in torpor)}\\&\quad = \text{body mass} + \text{body condition} + \text{fat stores} + (1|\mathrm{ID}).\end{aligned} \tag{4}$$

Does Body Mass Influence Patterns of Torpor Use among Species? To explore the influence of body mass on patterns of torpor use among species, we tested for associations between species' mean body mass and torpor use. We conducted univariate linear regressions between body mass and torpor depth and between body mass and torpor duration. For torpor depth, we ran a linear regression with a Gaussian error distribution, whereas for torpor duration, we ran a beta regression with a logit link function. We report Z and P values from each model below:

$$\text{torpor depth (minimum } \dot{\mathrm{V}}\mathrm{CO}_2) = m \times \text{body mass} + b, \tag{5}$$

$$\begin{aligned}&\text{torpor duration (proportion of time spent in torpor)}\\&\quad = m \times \text{body mass} + b.\end{aligned} \tag{6}$$

Correcting for Phylogeny

To control for the potential influence of species' phylogenetic relationships on torpor use, we used phylogenetic generalized least squares implemented in the package caper (Orme et al. 2013). We found no evidence of phylogenetic signal in the residuals of any of our regressions (all $\lambda = 0$), so we present results from ordinary least squares regressions below.

Results

Do Lowland Tropical Hummingbirds Use Torpor?

Species varied substantially in mean body mass (range: 3.23–6.59 g) and resting $\dot{\mathrm{V}}\mathrm{CO}_2$ (range: 0.21–0.51 mL min^{-1}; table 1). Normothermic T_{skin} was less variable across the focal species (range: 35.6°C–38.3°C; table 1). All six species and 32 of 37 (~86%) individuals sampled entered torpor during our temperature experiments, and we report the first records of torpor use in four hummingbird species (table 1). The lower critical temperatures of the thermoneutral zone for all species (range: 28.25°C–30°C; table 1; fig. A5) exceeded minimum nighttime temperatures (e.g., ≥24°C–25°C) at the study site (fig. A2), indicating that hummingbirds routinely experienced nonthermoneutral conditions. Four white-necked jacobins (WNJA; *Florisuga mellivora*) and one rufous-tailed hummingbird (RTAH; *Amazilia tzacatl*) defended normothermic T_{b} throughout the duration of temperature experiments and did not enter torpor (fig. A4). The mean proportion of time spent in torpor varied substantially among focal individuals (table A1) and species (blue-chested hummingbird [BCHH]: range = 0.1–1.0; RTAH: range = 0.0–1.0; WNJA: range = 0.0–0.93; table 1).

Does Torpor Reduce Overnight Mass Loss?

Individuals that spent more time in torpor lost significantly less body mass ($\beta = -0.52$ [95% CI $= -0.34$ to -0.69], $Z = -2.98$, $P = 0.003$; fig. 1). This indicates that higher frequency of torpor may act to conserve energy and reduce mass loss.

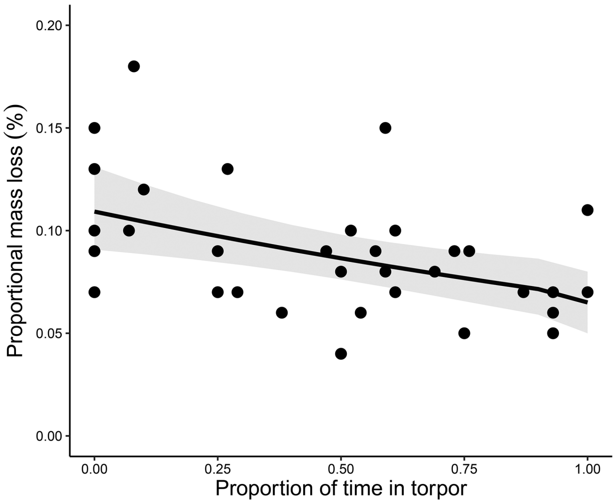

Figure 1. Relationship between torpor duration (i.e., proportion of time spent in torpor) and proportional mass loss (percent change) in hummingbirds ($n = 6$ species, 37 individuals) of central Panama. The line shows the predicted values from the beta regression model (shading indicates 95% confidence intervals), with raw data shown by circles.

Does Individual Condition Influence Patterns of Torpor Use within Species?

Body mass was the only significant predictor of variation in both duration of torpor (table 2) and depth of torpor (table 3). Larger individuals spent significantly less time in torpor than smaller individuals ($\beta = -0.71$ [95% CI $= -0.53$ to 0.89], $Z = -3.99$, $P < 0.0001$; fig. 2*A*). Similarly, larger individuals exhibited shallower depth of torpor compared with smaller individuals ($\beta = 0.31$ [95% CI $=$ 0.24 to 0.37], $Z = 4.46$, $P < 0.0001$; fig. 2*B*).

Does Body Mass Influence Patterns of Torpor Use among Species?

Body mass influenced patterns of torpor use among species. Larger-bodied species spent significantly less time in torpor than smaller-bodied species ($\beta = 0.03$ [95% CI $=$ 0.003 to 0.05], $Z = 2.19$, $P = 0.03$; fig. 3*A*) and entered into significantly shallower torpor than smaller-bodied species ($\beta = -0.43$ [95% CI $= -0.58$ to -0.28], $Z = -2.92$, $P = 0.004$; fig. 3*B*).

Table 2: Outputs from generalized linear mixed model testing for predictors of variation in torpor duration (i.e., proportion of time spent in torpor)

Model term	β (95% CI)	Z	P
M_b	**−.56 (−.76 to −.36)**	**−2.80**	**.005**
Body condition	−.56 (−1.15 to .03)	−.95	.34
Fat stores	−.19 (−.54 to .16)	−.54	.59

Note. Model terms include body mass (M_b), body condition, and fat stores. β estimates, confidence intervals (CIs), Z values, and P values are presented, with significant terms indicated in bold.

Table 3: Outputs from generalized linear mixed model testing for predictors of variation in torpor depth (i.e., minimum rate of CO_2 production − minimum $\dot{V}_{CO_2}$)

Model term	β (95%CI)	Z	P
M_b	**.29 (.21 to .37)**	**3.66**	**.0002**
Body condition	.07 (−.08 to .23)	−.01	.99
Fat stores	.002 (−.21 to .22)	−.45	.65

Note. Model terms include body mass (M_b), body condition, and fat stores. β estimates, 95% confidence intervals (CIs), Z values, and P values of the model are presented, with significant terms indicated in bold.

Discussion

Do Lowland Tropical Hummingbirds Use Torpor?

We provide new evidence that hummingbirds of the lowland tropics routinely use torpor under ecologically relevant temperature conditions. Nearly 90% (32 of 37) of all individuals used torpor, and hummingbirds entered torpor at higher T_a (i.e., ≥28°C) than the minimum nighttime T_a at our site (i.e., ≥24°C). We also documented, to our knowledge, the first records of torpor use in four hummingbird species (table 1). We sampled hummingbirds during the middle to late dry season, a period of high food availability when the peak flowering of hummingbird food plants occurs (Stiles 1980; Wright and Calderón 1995). Furthermore, our study took place at lower elevation (50 m asl) and at higher nighttime T_a than the few previous studies of tropical resident hummingbirds from nonmontane sites (i.e., Bech et al. 1997: 700 m asl; Shankar et al. 2020: >1,275 m asl). Whereas hummingbirds are expected to use torpor in extreme environments (e.g., Wolf et al. 2020), our findings indicate that routine torpor may also be a common strategy under comparatively moderate temperature regimes. Our results are consistent with recent findings that hummingbirds exist along a routine-to-emergency heterothermic spectrum, whereby smaller species almost universally employ torpor and larger species use torpor more facultatively (Spence and Tingley 2021; Shankar et al. 2022).

Does Torpor Reduce Overnight Mass Loss?

Proportional mass loss decreased with increasing time in torpor for WNJA, RTAH, and BCHH (table 2), confirming that torpor reduced mass loss and functioned as an energy-savings mechanism for these species. Although some proportion of total mass loss may be attributable to the excretion of urine and feces, measurements of mass loss are still a useful proxy for assessing changes in energy balance and have been employed to assess torpor in studies of other hummingbird species, facilitating direct comparison with our findings. The pattern of reduced mass loss with increasing torpor is consistent with that of studies of high-elevation (3,800 m asl) hummingbirds from Peru (Wolf et al. 2020) and lowland (700 m asl) hummingbirds from Brazil (Bech et al. 1997).

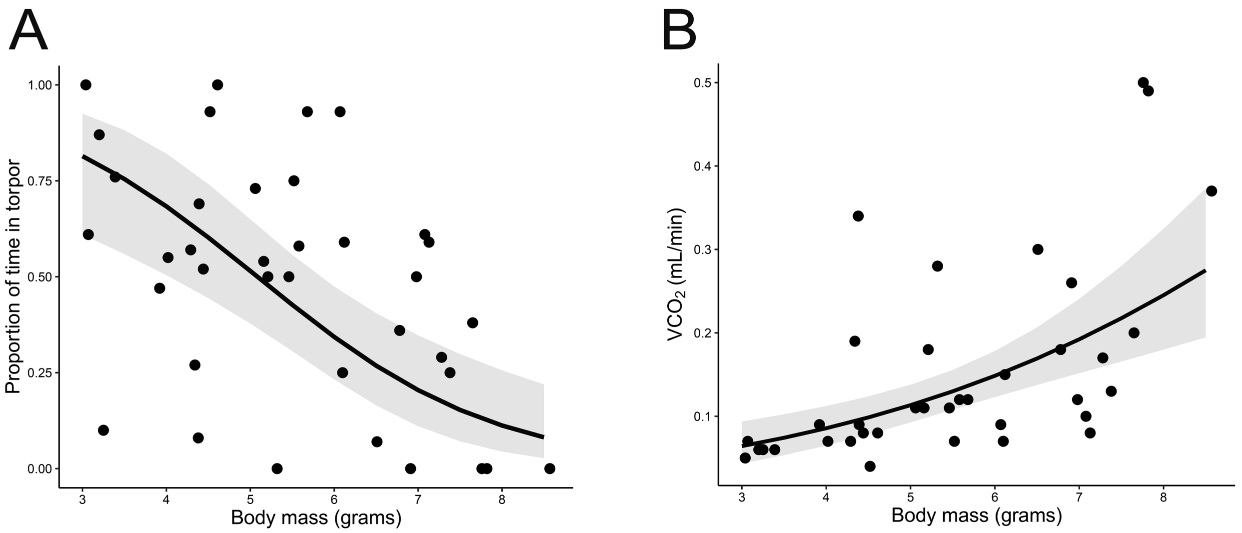

Figure 2. Relationships between body mass and torpor duration (i.e., proportion of time spent in torpor; *A*) and between body mass and torpor depth (i.e., mean minimum rate of CO_2 production [$\dot{V}CO_2$]; *B*) in hummingbirds ($n = 6$ species, 37 individuals) of central Panama. The lines show the predicted values from the respective regression models (shading indicates 95% confidence intervals), with raw data shown by circles. Lower values of minimum $\dot{V}CO_2$ indicate greater depth of torpor.

However, hummingbirds in our study lost more than double the mass on average (~8%–10%) than hummingbirds in either of the previous two studies (~4%), despite experiencing the warmest nighttime temperatures. This is likely because higher-elevation hummingbirds are able to reduce T_b much lower in colder T_a, thereby entering deeper torpor and losing less mass (Wolf et al. 2020). In contrast, the benefits of torpor could be constrained in lowland species by warmer nighttime T_a, which consequently could impede the ability of hummingbirds to reduce T_b and gain energy savings (Song et al. 1997; Reher and Dausmann 2021). If correct, this hypothesis would suggest that lowland hummingbirds in particular may be susceptible to possible energetic or fitness consequences associated with increasing nighttime temperatures (Shankar et al. 2020).

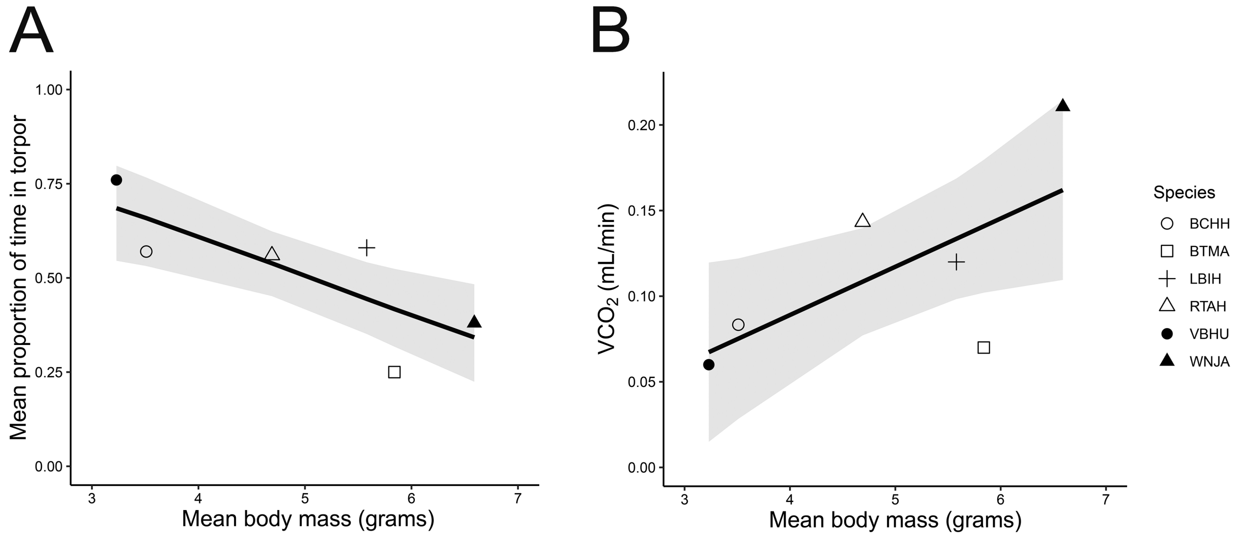

Figure 3. Interspecific relationships between body mass and torpor duration (i.e., proportion of time spent in torpor; *A*) and between body mass and torpor depth (i.e., mean minimum rate of CO_2 production [$\dot{V}CO_2$]; *B*) in hummingbirds ($n = 6$ species, 37 individuals) of central Panama. The lines show the predicted values from the respective regression models (shading indicates 95% confidence intervals). Lower values of minimum $\dot{V}CO_2$ indicate greater depth of torpor. BCHH = blue-chested hummingbird; BTMA = black-throated mango; LBIH = long-billed hermit; RTAH = rufous-tailed hummingbird; VBHU = violet-bellied hummingbird; WNJA = white-necked jacobin.

The Importance of Body Mass as a Predictor of Torpor

Body mass was the most important predictor of both torpor depth and torpor duration. Larger-bodied species and individuals tended to use torpor less frequently and went into shallower torpor than smaller-bodied species and individuals. In contrast, we did not find any influence of fat stores or body condition on torpor use, as has been documented in migratory hummingbirds (e.g., Hiebert 1993). This was likely because our focal species store minimal fat and do not have to undergo energetically intensive life history events such as migration. Our results are consistent with both historical and recent empirical studies that have documented the influence of body mass on patterns of torpor use in both birds and mammals (Carpenter and Hixon 1988; Hiebert 1993; Geiser 1998; Powers et al. 2003; Czenze and Dunbar 2020; Shankar et al. 2020). Moreover, a review by Ruf and Geiser (2015) found that body mass was strongly associated with minimum T_b, minimum metabolic rate, and the use of torpor across endotherms. Finally, the three heaviest individuals of the largest-bodied focal species (WNJA) did not enter torpor, further suggesting that having a larger body mass reduces the need to employ torpor (Spence and Tingley 2021). We speculate that body mass (and, indirectly, torpor use) could be related to territoriality and the ability to monopolize food resources, as WNJA is the behaviorally dominant species at our study site (H. S. Pollock and D. Lamont, personal observations). For example, several studies have found that larger or more territorial hummingbird species forego torpor entirely or use shallower/less frequent torpor bouts than smaller, subordinate species (Powers et al. 2003; Shankar et al. 2020). The species we sampled had a relatively narrow range of body sizes (i.e., ~3–6.5 g; table 1), however, and we did not perform quantitative behavioral observations at feeders. Therefore, additional sampling from other assemblages and larger-bodied hummingbird species in particular is needed to establish the generality of our results. Nevertheless, our results are consistent with a recent meta-analysis indicating that larger hummingbirds are physiologically more flexible and can facultatively respond to changing environmental conditions (Spence and Tingley 2021). Overall, our data support the growing realization that torpor appears to be a near-universal trait in hummingbirds (Spence and Tingley 2021; Shankar et al. 2022), even in species that inhabit relatively thermally stable climates such as the lowland tropics.

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