Extreme and variable torpor among high-elevation Andean hummingbird species

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Abstract

Torpor is thought to be particularly important for small endotherms occupying cold environments and with limited fat reserves to fuel metabolism, yet among birds deep torpor is both rare and variable in extent. We investigated torpor in hummingbirds at ~3,800 m a.s.l. in the tropical Andes by monitoring body temperature (T_b) in 26 individuals of six species held captive overnight and experiencing natural air temperature (T_a) patterns. All species used pronounced torpor, with one *Metallura phoebe* reaching a minimum T_b of 3.26 °C, the lowest yet reported for any bird or non-hibernating mammal. The extent and duration of torpor varied among species, with overnight body mass (M_b) loss negatively correlated with both minimum T_b and bout duration. We found a significant phylogenetic signal for minimum T_b and overnight M_b loss, consistent with evolutionarily conserved thermoregulatory traits. Our findings suggest deep torpor is routine for high Andean hummingbirds, but evolved species differences affect its depth.

Keywords

body temperature; evolution; heterothermy; hypometabolism; thermoregulation; Trochilidae

Introduction

Hummingbirds (Apodiformes: Trochilidae) occupy elevations up to ~5,000 m a.s.l. in the Andes Mountains, providing one of the most spectacular examples of avian adaptation to extreme environments. The challenges of living in these cold, wet and hypoxic environments are compounded by hummingbirds being among the smallest of endotherms and possessing the highest mass-specific metabolic rates of any vertebrates [1-3]. Pronounced thermoregulatory costs are combined with very high costs of hovering flight at high elevations [4, 5] and a diet of flower nectar requiring daily intake rates sometimes exceeding hummingbirds' own body masses (M_b) [6, 7]. These energetic challenges have focused long-standing interest on physiological and behavioural processes that facilitate hummingbird occupancy of high elevations [8-10]. The major hummingbird clades vary in the extent to which they have occupied montane and cold regions [11, 12], but the basis for these evolutionarily conserved environmental niches is not fully understood.

A suite of physiological and behavioral adaptations facilitates hummingbird occupation of high elevations. In addition to roosting in thermally-buffered caves and bouts of intense feeding before dark to maximize fat reserves for overnight metabolism, hummingbirds in the high Andes are thought to make extensive use of nocturnal torpor [8, 13]. Torpor, or daily heterothermy, is characterized by facultative hypometabolism and reductions of body temperature (T_b), typically by 10-30 °C below normothermic values that, unlike hibernation, are restricted to a single circadian cycle [14, 15]. Torpor is widespread among hummingbirds [13, 16-19], with variation in frequency or depth attributed to factors including nutritional status [20], migratory status [21], weather [19], typical thermal environment [18], seasonal acclimatization [22] and foraging behaviour [23]. However, the role of phylogenetic structure as a source of interspecific variation in setpoint T_b and related variables among co-occurring species has received little attention.

We investigated torpor in six hummingbird species experiencing natural cycles of air temperature (T_a) at 3,800 m a.s.l. in the Peruvian Andes, with the goal of quantifying interspecific variation among free-ranging populations with different evolutionary histories. We tested four predictions: first, all species in a high-elevation community routinely use torpor at night, with torpid T_b closely approaching T_a; second, overnight M_b

losses are directly related to torpor bout duration, with longer bouts associated with smaller overnight M_b losses [24]; third, variation in torpor T_b and overnight M_b loss is at least partly explained by phylogeny; and fourth, lower T_b and longer torpor bouts characterize species in the 'coquette' clade [11], a group particularly diverse and abundant in high-elevation, cold habitats.

Methods

Detailed methods are presented in the Supplementary Material. In brief, we caught hummingbirds representing six species (Figure 1) between 7 and 18 March 2015 at Bosque Japani, Peru (~3,800 m a.s.l.; S11° 39’ 41” W76° 26’ 48”). Night length this time of year (around the autumnal equinox) was ~12 hours. After capture in mist-nets, birds were temporarily held in tents adapted as aviaries. Food was withheld from 30 min before dark, at which time birds were transferred into individual roosting enclosures for overnight measurements of cloacal T_b using 36-gauge Teflon-coated thermocouples, inserted 1-2 cm and secured to retrices using small pieces of laboratory tape. Total M_b loss was taken as the difference between evening and morning measurements and bout duration as the period with $T_b < 30$ °C, a value often, albeit somewhat arbitrarily, used in studies of avian heterothermy [e.g., 25, 26].

We analysed effects of bout duration on minimum T_b and M_b loss using generalized linear multilevel models (GLMMs) using the *brms* [27, 28] and *stan* [29] packages in R [30]. We estimated phylogenetic signal by calculating Pagel’s λ and Bloomberg’s K and quantified phylogenetic signal from GLMMs by estimating the proportion of total variance attributed to phylogeny or species random effects. In addition, we visualized minimum T_b and overnight M_b loss across the phylogeny of our study species using a published hummingbird phylogeny [11] and the contMap() function in the R package *phytools* [31]. Detailed analytical methods and comparisons of alternative statistical models are provided in the Supplementary Materials.

Results

All six species and 24 of 26 individual hummingbirds entered torpor, but bout duration and minimum T_b varied within and among species (Figure 1,2). Normothermic T_b in individuals that remained normothermic for part or all of a night varied from 35.8 °C in *P. gigas* to 37.0 °C in *A. cupripennis* (Figure 1). Night-time T_a minima remained between 2.4 °C and 5.9 °C throughout the study.

The gradient between minimum T_b and T_a varied among species; for instance, *Colibri coruscans* appeared to defend a setpoint of ~ 8 °C, whereas *Metallura phoebe* thermoconformed over the entire T_a range (Figure 2). The mean minimum T_b of *M. phoebe* was 5.13 ± 1.18 °C, with individual minima on the coldest nights of 3.80 °C and 3.26 °C. Moreover, *M. phoebe* was the only species with no indication of defending a T_b setpoint, maintaining $T_b – T_a$ gradients of just 0.87 ± 0.53 °C (Figure 2). The T_b of *Oreotrochilus melanogaster* tracked T_a closely at T_a > 3.7 °C but increased to 2 – 4 °C above T_a at lower T_a values (Figure 2). Maximum cooling rates during torpor entry were ~0.6 °C min^{-1} in four species and peak rewarming rates ranged from ~1 °C min^{-1} in *P. gigas* to ~1.5 °C min^{-1} in *A. cupripennis* (Figure 1). Hummingbirds generally rewarmed while T_a was low and stable, but in a few instances "hitch-hiked" increasing T_a and thereafter warmed endogenously (e.g., Figure 2 – *P. gigas*).

Bout duration varied from 2.3 h in one *P. gigas* to 12.9 h in a *M. phoebe* (Figure 2) with species means of 5.7 - 10.6 h (Figure 1). In all models, minimum T_b and overnight mass loss were negatively related with bout duration (Table 1, Figure 2). Among models of minimum T_b, but not models of overnight M_b loss, incorporating a species random effect, phylogenetic random effect or both improved fit compared to models with no random effect (Table 1).

Phylogenetic signal was greater for minimum T_b (Pagel's λ = 0.620 [95% highest posterior density [HPD] 0.074 – 0.998]; Bloomberg's K = 1.643, p = 0.007) than overnight M_b loss (Pagel's λ = 0.562 [95% HPD 0.055 – 0.999]; Bloomberg's K = 1.223, p = 0.048). Phylogenetic signal was important for all GLMMs with phylogenetic random effects, and 95% HPD did not overlap zero (Table 1). Species random effects were also important, with 95% HPD not overlapping zero (Table 1). Furthermore, both phylogeny and species explained a considerable proportion of total variation when included in models (Tables 1, S1 and S2).

Discussion

Frequent use of torpor and accompanying low T_b values support our prediction that heterothermy is a routine component of thermoregulation in high-elevation hummingbirds. Although torpor use is responsive to proximate organismal and environmental variables [18-23], the significant phylogenetic signal in minimum T_b and overnight M_b loss reveals that phylogenetically-conserved evolution explains significant portions of variation in torpor performance among our study species. In particular, the tendency for lower T_b and longer torpor bouts among species in the coquette clade (*O. melanogaster, P. caroli, M. phoebe*), together with traits such as hemoglobin oxygen-binding affinity [10], may help to explain the over-representation of this clade in high-elevation Andean assemblages.

The minimum torpor T_b of *O. melanogaster* and *M. phoebe* during torpor are the lowest yet documented in hummingbirds; Calder and Booser [19] recorded a temperature of 6.5 °C in an artificial egg under an incubating female *Selasphorus platycercus* at 2,900 m a.s.l., and Carpenter [13] documented cloacal T_b of ~6.5 °C (5.0 °C in one individual) in *O. estella*. In the present study, *M. phoebe* showed no evidence of maintaining a setpoint T_b at even the lowest T_a encountered (Figure 2), raising the possibility that it may reach even lower T_b during colder conditions.

The minimum T_b values of 3.3 °C and 3.8 °C in two *M. phoebe* individuals are, to the best of our knowledge, the lowest yet recorded among birds. In free-ranging common poorwills (*Phalaenoptilus nuttallii*), minimum T_b = 4.3 °C was inferred from a skin temperature (T_{skin}) datum of 2.8 °C [25], with similar values reported more recently [32]. Moreover, the T_b minima for *M. phoebe* appears to be the lowest reported for any avian or mammalian daily heterotherm, with T_b < 5 °C otherwise restricted to hibernators [15].

Hummingbirds rewarmed from deep torpor surprisingly rapidly, with the maximum observed rate for *P gigas* equivalent to 168 % of the value reported under laboratory conditions [33]. Observed maximum rates for the smaller species were equivalent to 163-194 % of allometrically expected values [34], consistent with hummingbirds' metabolic rates while rewarming approaching those during hovering flight [35]. Rapid rewarming may maximize time spent in deep torpor before commencing foraging [24].

Our data supported the prediction that energy expenditure is directly related to time spent torpid, with overnight M_b loss negatively related to bout duration. Similar findings were reported for three Brazilian lowland species [18]. Rates of overnight M_b loss for our study species were comparable to those reported by Bech et al. [18], despite the much colder environment of the present study. Both hummingbird communities achieved similar overnight energy savings despite differences in T_b and T_a of ~ 20 °C, likely reflecting greater costs of rewarming under colder conditions.

The relationship between torpor bout duration and minimum T_b we observed likely reflects how costs of rewarming constrain overall energy savings. The negative, approximately linear effect of torpor depth on rewarming costs [34] combined with the non-linear, Arrhenius effect on metabolic rate while thermoconforming [36], leads to the prediction that energy savings are maximised when bout duration increases with decreasing torpor T_b. Our results are consistent with recent findings that bout duration is the primary determinant of energy savings during overnight torpor in hummingbirds [24].

Individuals in our study fasted for just 30 min before dark but entered torpor routinely, suggesting that torpor use is less tightly coupled to individuals' energy reserves as often reported for hummingbirds in other environments [18, 22, 37]. However, several authors have documented intense feeding immediately before dark [38, 39] and the extent to which torpor in high Andean hummingbirds is a routine component of thermoregulation or an "emergency" response (e.g., [20]) requires further investigation.

In conclusion, we found that tropical hummingbird species living at elevations approaching 4,000 m a.s.l. have evolved pronounced, but variable, capacities for torpor, with minimum T_b rivalling that of temperate- and boreal-latitude mammalian hibernators. Although avian hibernation (i.e., multi-day torpor) has been reported only in one caprimulgid [32, 40], the depth of overnight torpor we document here raises the possibility that some high-elevation hummingbirds may hibernate during periods of inclement weather. Regardless, the energy savings associated with pronounced torpor are one of the major reasons why these tiny birds can persist in these harsh, physiologically challenging environments. Our finding that phylogenetic relationships are linked to torpor energy savings among co-occurring species suggests that differential evolutionary colonization of mountains [11, 12] may have resulted from deeply conserved physiological differences among hummingbird clades.

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Data accessibility

Data are available from the Dryad Digital Repository at: https://datadryad.org/stash/dataset/doi:10.5061/dryad.vx0k6djp6

Author contributions

BOW and CCW designed the research. BOW, CJS, ABJ and CCW collected the data, which were analysed by AEM, CJS and ZJC. AEM led the writing of the manuscript; CJS, ZJC, BOW, ABJ and CCW contributed. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests

We declare no competing interests.

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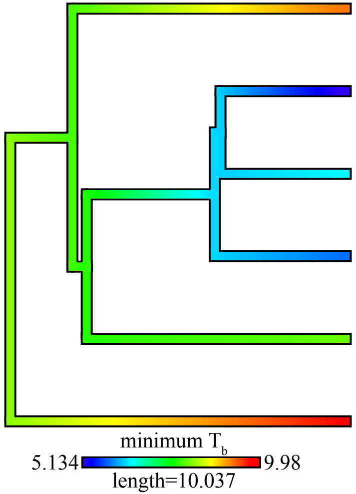
Table 1. Comparison of generalized linear multilevel models of minimum body temperature (T_b) and percent overnight body mass (M_b) loss. Models varied in whether they incorporated species, phylogenetic, both or no random effects. Estimated effect sizes and 95% highest posterior density (HPD) are provided. Oroportion of variance explained and 95% HPD are indicated for models with species and phylogenetic random effects. Model fit was assessed using leave-one-out cross-validation (LOOIC). The difference between each model and the best-fit model is shown as Δelpd (expected log predictive density) with standard error (se). The structure of the full models are: *Min* T_b *~ bout duration + species + phylogeny* and M_b *loss ~ bout duration + species + phylogeny.*

Response	Fixed effect	Random effects		% variance explained		Δelpd (se)
	Bout duration	Species	Phylogeny	Species	Phylogeny	
Min. T_b	-0.60 (-0.80, -0.40)	1.54 (0.08, 4.75)	0.39 (0.02, 1.29)	0.51 (0.004, 0.95)	0.12 (0.0002, 0.57)	0
Min. T_b	-0.58 (-0.78, -0.38)	–	0.47 (0.15, 1.24)	–	0.15 (0.01, 0.53)	-0.1 (0.3)
Min. T_b	-0.60 (-0.80, -0.41)	1.78 (0.65, 4.24)	–	0.63 (0.21, 0.94)	–	-0.1 (0.3)
Min. T_b	-0.66 (-0.85, -0.47)	–	–	–	–	-7.1 (3.5)
M_b loss	-0.64 (-0.96, -0.32)	–	–	–	–	0
M_b loss	-0.60 (-0.97, -0.23)	1.18 (0.04, 3.85)	–	0.19 (0.0002, 0.69)	–	-1.0 (1.9)
M_b loss	-0.57 (-0.95, -0.19)	–	0.32 (0.01, 1.05)	–	0.03 (0.00002, 0.15)	-1.1 (2.1)
M_b loss	-0.56 (-0.96, -0.14)	1.32 (0.05, 4.60)	0.36 (0.01, 1.27)	0.21 (0.0003, 0.78)	0.03 (0.00002, 0.21)	-1.6 (2.6)

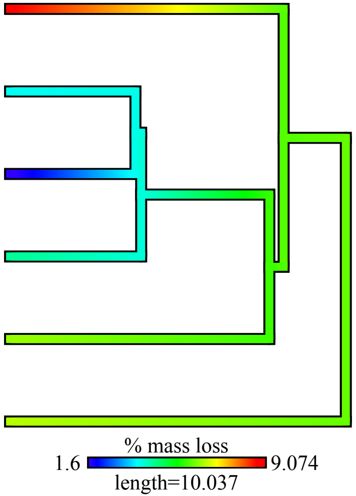
Figure legends

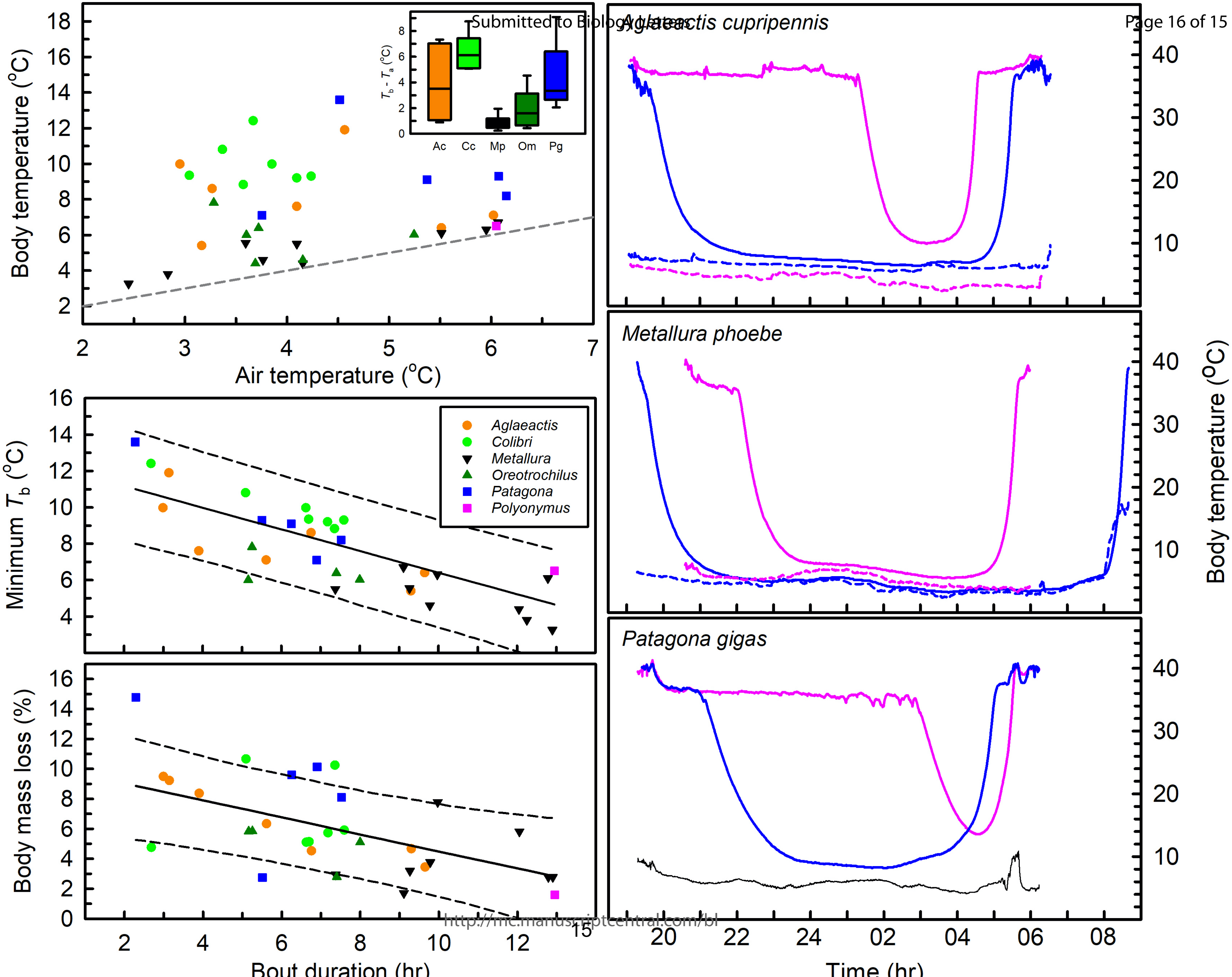
Figure 1. Torpor-related parameters for hummingbirds at ~ 3,800 m a.s.l. in the Peruvian Andes: normothermic body temperature (Norm. T_b), maximum cooling rate during torpor entry, minimum torpor body temperature (Min. T_b), bout duration and maximum rewarming rate during arousal. Values are means ± standard deviations, with sample sizes in parentheses. Phylogenetic reconstructions of minimum T_b and overnight body mass loss are at left and right, respectively. Superscripts: a = fewer data because some individuals entered torpor immediately after thermocouple insertion, and dislodged thermocouple upon rewarming; b = did not rewarm until placed in sun.

Figure 2. Relationships between torpor variables among six species of hummingbirds at 3,800 m a.s.l in the Peruvian Andes (left panels), and traces of body temperature (T_b) illustrating individual variation in bout duration (right panels). Minimum body temperatures (T_b) varied among species (left top panel; dashed line indicates equality) and the gradient between minimum T_b and T_a (inset) varied significantly. Minimum T_b (left centre panel) and overnight body mass loss (left bottom panel) were significantly related to bout duration, defined as the period with T_b < 30 °C. Solid lines are best-fit models (Table 1), and dashed lines 95% highest posterior density intervals. In the right panels, the solid pink and blue lines show T_b during the shortest and longest bouts, respectively, for each species. Dashed lines show corresponding T_a (both *P. gigas* traces obtained on the same night).



Species	Body mass (g)	Norm. T_b (°C)	Cooling (°C min^{-1})	Min. T_b (°C)	Duration (hr)	Warming (°C min^{-1})	Mass loss (%)
Giant Hummingbird *Patagona gigas* (4)	24.23 ±1.63(5)	35.79 ±1.40(6)	0.56 ±0.19(5)	9.46 ±2.47(5)	5.7 ±2.05(5)	1.03 ±0.27(5)	9.07 ±4.33(5)
Black Metaltail *Metallura phoebe* (5)	6.03 ±0.37(9)	36.47 ±0.59(4[a])	0.83 ±0.23(9)	5.13 ±1.18(8)	10.61 ±1.95(9)	1.42 ±0.23(8)	3.84 ±1.98(8)
Bronze-tailed Comet *Polyonymus caroli* (1)	4.87(1)	–	0.72(1)	6.50(1)	12.95[b](1)	–	1.6(1)
Black-breasted Hillstar *Oreotrochilus melanogaster* (4)	7.34 ±0.29(6)	35.91 ±0.52(3[a])	0.62 ±0.10(5)	5.87 ±1.25(5)	6.45 ±1.46(4)	1.48 ±0.24(5)	4.48 ±1.54(5)
Shining Sunbeam *Aglaeactis cupripennis* (7)	7.23 ±0.40(16)	36.95 ±0.79(8)	0.64 ±0.11(7)	8.14 ±2.22(7)	5.91 ±2.78(7)	1.51 ±0.15(7)	6.58 ±2.46(7)
Sparkling Violetear *Colibri coruscans* (5)	8.78 ±0.94(8)	36.94 ±0.77(7)	0.56 ±0.05(7)	9.98 ±1.25(7)	6.18 ±1.74(7)	1.21 ±0.12(7)	6.79 ±2.53(7)




Body temperature (°C)
Air temperature (°C)
$T_b - T_a$ (°C)
Ac
Cc
Mp
Om
Pg
Aglaeactis cupripennis
Metallura phoebe
Patagona gigas
Minimum T_b (°C)
Aglaeactis
Colibri
Metallura
Oreotrochilus
Patagona
Polyonymus
Body mass loss (%)
Bout duration (hr)
Time (hr)