EnergyBudget

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Using published and unpublished data from Dr. Don Powers' earlier work, I construct here a preliminary energy budget for a North American species, the Broad-billed hummingbird (BBLH; *Cynanthus latirostris*).

1. Basal Metabolic Rate

Basal metabolic rate is the minimum metabolic rate required for survival. It includes basic body upkeep, and does not include thermoregulation, digestive costs, or any activity costs. The basal metabolic rate measurements here are based on a regression of metabolic rates measured under basal metabolic conditions over a range of temperatures (in the dark, fasted, during the sleep phase; measured during summer 2012).

Mean BMR_{BBLH} = 0.2385 mL/min (4.8 J/min; 0.0799W; where MR of 1 ml/min = 20.1 Joules/min. 1 Watt is 1 Joule/second)

The assumptions of these measurements are:
- 32°C is the lower critical temperature for the Broad-billed hummingbird, and represents the lowest temperature for measurement of the basal metabolic rate. A lower critical temperature of 32°C is consistent with measurements for a number of other hummingbirds (Lasiewski 1963, Lasiewski & Lasiewski 1967, Hiebert 1990, Lopez-Calleja & Bozinovic 1995) and data on Costa's Hummingbirds (*Calypte costae*) and broad-tailed hummingbirds (*Selasphorus platycercus*; unpublished, Donald R. Powers).
- Basal metabolism is assumed as a continuous cost for 24 hours except when birds use torpor. If torpor is used then BMR is a continuous cost for 24 hours, excluding the hours spent in torpor. Torpor was used for a maximum of four hours at the Sonoita Creek site where these Broad-billed hummingbirds were studied.

2. Thermoregulation

The thermoneutral zone (TNZ) is the optimum range of ambient temperatures over which there are no regulatory changes in metabolic heat production or evaporative heat loss (Kingma et al. 2012). Thermoregulatory costs are calculated separately below and above the TNZ, as the slopes are different and asymmetric for these two regions, as seen in Figure 1. I thus retain separate equations for the two even though the TNZ of small hummingbirds appears so small that the lower and upper critical temperatures are essentially identical Lasiewski (1963).

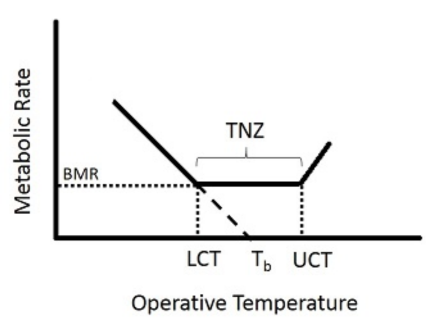

Figure 1: The thermoneutral zone (TNZ). T_b = Body temperature; LCT = Lower critical temperature; UCT = Upper critical temperature; BMR = Basal metabolic rate

A. Below the TNZ (Operative temperature T_e < 32°C)

First, hourly averages for metabolic rate across a range of temperatures below the TNZ were measured. By regressing metabolic rate on temperature below the lower critical temperature, we get this equation:

MR_L (mL O_2/min) = 0.9530 - 0.0223*(T_e) **-Equation 1a**

Here, MR_L is metabolic rate when $T_e < 32°C$. I then calculate TRE_L, which is the sum of the hourly averages of MR_L for all hours where mean T_e < lower critical temperature. Pure thermoregulatory costs below the lower critical temperature can be calculated by subtracting BMR from the result of equation 1a, but for simplicity of calculation, TRE_L includes both basal metabolic costs and thermoregulatory costs.

TRE_L (kJ) = $\Sigma(MR_L * 60)$ **- Equation 1b**

Thus, TRE_L is the total daily energy spent on thermoregulation and basal metabolism below the TNZ. Torpor was assumed to be zero because birds rarely entered torpor in Sonoita Creek.

B. Above the TNZ ($T_e > 35°C$)

Lasiewski's (1963) data suggests that the upper critical temperature for small hummingbirds is ~35-37 °C. The only data I know of for metabolic rate above the upper critical temperature in small hummingbirds are Powers' unpublished data on Costa's. These data also show an upper critical temperature of 35°C. The slope of the relationship below was based on unpublished measurements of Costa's Hummingbird (*Calypte costae*), a similarly sized species. The Y intercept of this equation was obtained by substituting the Broad-billed hummingbird's BMR and an operative temperature of 35°C into the Costa's regression equation.

MR_H (mL O_2/min) = 0.214 (T_e) - 7.2515 **- Equation 2a**

Where MR_H is metabolic rate at temperatures above upper critical temperature. Pure thermoregulatory costs above the upper critical temperature can be calculated by subtracting BMR from the result of equation 2a. Again, for simplicity of calculation the result of equation 2a is the combined cost of BMR and thermoregulation.

TRE_H (kJ) = $\Sigma(MR_H * 60)$ **- Equation 2b**

TRE_H is calculated as the sum of hourly averages for all hours where mean T_e > upper critical temperature, again assuming no torpor use.

3. Activity Costs

A. Resting (perching)

Little data are available for how much resting metabolic rate (RMR) is elevated above BMR in hummingbirds. An Aschoff & Pohl study (1970) reported data for several bird species suggesting RMR = 1.25 x BMR. The Aschoff & Pohl correction has often been used to estimate RMR but might underestimate true resting costs because the measurements upon which it is based were typically made on birds resting in the dark. This would eliminate any costs associated with response to light or surrounding events. Further, Aschoff & Pohl fasted birds so the cost of specific dynamic action (i.e. the cost of digestion; SDA) is also not included. Two years ago Powers made RMR measurements on Calliope hummingbirds (*Selasphorus calliope*; ~2.4 g) on a perch in an illuminated chamber. After subtracting thermoregulatory costs $RMR_{Calliope}$ = 0.2835 mL O_2/min. $BMR_{Calliope}$ = 0.1843 mL O_2/min (Lasiewski 1963). Thus,

$RMR_{Calliope}$ = 1.54 x BMR

This is likely to more accurately reflect the metabolic rate of a perching hummingbird in the wild. Thus, I can estimate RMR as:

RMR = 1.5 x BMR **- Equation 3**

This is a fair relationship to use for broad- billed hummingbirds, as Calliope and Broad-billed hummingbirds are behaviorally similar and perch in similar environments.Thus,

RMR_{BBLH} = 0.3578 ml/min (7.1908J/min; 0.1198W)

B. Hovering

Powers has measured hovering metabolic rates (HMR) in Broad-billed hummingbirds. Mean HMR_{BBLH} = 2.1 mL O_2/min, with values ranging from 0.764 to 5.771 ml O_2/min.

Going from these values and from past studies (Fernandez et al. 2011),

HMR_{BBLH} = 10.3 x BMR

C. Forward flight

No measurements have been made on the metabolic cost of forward flight (FLMR) in Broad-billed hummingbirds. Assuming that hummingbirds fly most often at their most efficient speed (6-8 m/s), FLMR can be estimated using data from other hummingbird species. These relationships are well-established from studies on power curves in hummingbirds (Tobalske et al. 2003, 2010).

$FLMR_{Calliope}$ = 0.53 x HMR

$FLMR_{Rufous}$ = 0.49 x HMR

Thus, I can estimate FLMR for Broad-billed hummingbirds to be:

FLMR = 0.5 x HMR **- Equation 4**

$FLMR_{BBLH}$ = 0.5*2.1 ml/min = 1.05 ml/min (21.11 J/min; 0.3518W)

D. Total activity costs

ACT = (($Time_{RMR}$ * (RMR - BMR)) + ($Time_{HMR}$ * (HMR - BMR) + ($Time_{FLMR}$ * (FLMR - BMR) **- Equation 5**

4. Nighttime Metabolic Rate

There is a large amount of individual and daily variation in the frequency and duration of torpor use. For the sake of modeling DEE I assume that either torpor is not used at all, or if torpor is used, it is used to the full extent observed at the site. By doing so I can create upper and lower energetic boundaries based on whether or not torpor was used.

A. No torpor

Nighttime metabolic rate (NMR) will be BMR plus the cost of thermoregulation below the lower critical temperatures. Thus, NMR for normothermic hummingbirds can be calculated using equation 1a.

B. Torpor

For birds that used torpor maximally last summer:

Nighttime energy expenditure (NEE) = 2 kJ

Note: This value can change slightly as I refine the calculations. Even so, this is such a small component of DEE that small changes to this value will have little impact on model results.

5. DEE Model

DEE = BMR + (TRE_L + TRE_H) + ACT + NEE

Where:
DEE = Daily energy expenditure
BMR = Basal metabolic rate for time spent within the TNZ
TRE_L = Metabolic rate below lower critical temperature (including thermoregulation and BMR)
TRE_H = Metabolic rate above higher critical temperature (including thermoregulation and BMR)
ACT = Activity costs (from above)
NEE = Nighttime energy expenditure
Note: If no torpor is used then NEE = 0, and NEE is included in TRE_L. If the species had a broader TNZ, BMR for time spent in the TNZ would be included as an additional term (thermoregultory costs would be 0).

Model test using Sonoita Creek *C. latirostris* values

Here, assuming:

1. 70% of the daytime was spent perching and 30% flying. Flying was 50% hovering and 50% forward flight [**add citations**].
2. No torpor (this is realistic for SC).
3. Respiratory quotient (RQ) = 0.85 (for conversion of oxygen consumption to CO_2 production)
4. 14/10 photoperiod.

Results:

```
## DEE = BMR + (TRE_L + TRE_H) + ACT + NEE

## Basal metabolic rate for time spent within the TNZ in 14 daytime hours (5am-7pm)
bmr <- 14.3

## TRE_H from SC 14-hour temperature data and broad-bill equation
tre_h <- 135.8

## TRE_L from SC 14-hour temperature data and broad-bill equation
tre_l <-121.3

## Total energy spent on BMR + thermoregulation in 14 daytime hours
tre_total <- tre_h + tre_l + bmr

## Nighttime energy expenditure in ml O2/h from broad-bill data, 10 hour night (7pm-5am)
nee <- 218.9

## Metabolic rates in ml O2/h
bmr <- 0.2385*60
rmr <- 1.5*bmr
hmr <- 10.3*bmr
flmr <- 0.5*hmr

## Total energy spent on daytime activities in ml O2/h.
## Assuming ACT = 70% resting + 15% hovering + 15% flying; 14 daylight hours
ACT <- (0.7*14*(rmr-bmr)) + (0.15*14*(hmr-bmr)) + (0.15*14*(flmr-bmr))

## Model estimate in ml O2 per 24h
DEE_model <- ACT + nee + tre_total

## To get a per hour CO2 estimate, multiply by RQ (0.85) and divide by 24
DEE_model_hr <- DEE_model*0.85/24
```

Mean Measured DEE (DLW) = 51.3 ± 6.6 mL CO_2/h (range 39.5-58.6)

Model Estimate = 34.1631 CO_2/h

The model estimate is 16% lower than the measured value but is within the range of measured values (albeit at the low end). I am very encouraged by this considering that this model is likely biased low since costs of molt and reproduction are not specifically considered.