



Bachelor Thesis

Torpor dynamics in a suite of lowland Neotropical nectarivorous birds

Daniel Lamont || September 2016



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Preface

When I went to Panama in 2014 to conduct a five and a half month internship at the Smithsonian Tropical Research Institute, I was very excited. It was the first time in my life that I would be spending such a long time in another country. It was also then that I encountered a hummingbird for the first time in my life. I was putting up poles to use in a small inventory plot in the forest. The poles had pink fluorescent flagging tape on them, which obviously stood out from the forest background. It was then that I heard a buzzing sound hovering around me, which startled me a lot because I thought it was a giant wasp or beetle. I was jumping around to avoid whatever was flying around my head, until I saw it was a tiny bird that was trying to determine if the flagging tape was a flower it could feed from. I had never heard or seen a hummingbird in my life, so I became excited, but in a matter of seconds it was gone. The same scenario happened multiple times during my internship, it wasn't until the fifth time it happened that I stopped being startled from the buzzing sound around my head. Over the five and a half months that I spent in Panama, I saw a lot of different hummingbirds, most of them near the place I lived in Gamboa.

It was also in Gamboa that I met my current external advisor, Henry Pollock. He was working on his PhD research on Neo-tropical bird thermal physiology. It wasn't long before we became friends and I started to learn about birds and how to handle them. I asked Henry if he had a project that I could do with him for my thesis. He proposed several possible research endeavors that we could conduct, with one of the possibilities being an extension of his PhD research. Using respirometry (measuring the gas exchange of animals), he had found that a lot of hummingbirds showed variation in physiological responses to ambient temperature, even within the same species. Some individuals actively thermoregulated and defended body temperature by increasing their metabolic rate in response to low ambient temperatures, whereas others lowered their body temperatures and metabolic rates (i.e. went into torpor) to cope with low ambient temperatures. We decided to measure torpor in a suite of Neotropical nectarivorous species to explore the factors that could be influencing the observed intra- and interspecific variation in torpor that Henry had documented. So we decided that this topic would be a good research for my thesis; Thermoregulatory flexibility in a suite of lowland Neotropical nectarivorous birds.

We made preparations to conduct the research in the dry period in Panama the following year. I spent three months catching and processing hummingbirds. I learned how to catch birds with mist-nets, handle birds and assess their condition and use a respirometry system.

I also learned that conducting scientific research is not a straightforward affair, and that it takes a lot of effort, patience and a positive mindset.

I would like to thank a few people who have mentored me, helped me or influenced me to be able to work on hummingbirds and finish my thesis. First of all I would like to thank Henry Pollock. Without his tireless work over the last year, many Skype meetings and mentoring this would have never happened. I would also like to thank Jos Wintermans, Peter van der Meer and Erika Duijl for their advice and guidance. Furthermore I would like to thank Jeffrey D. Brawn who facilitated the project and provided me with all the respirometry and field equipment that I needed, and also Zac Cheviron who advised me on the statistical analyses. And finally I would like to thank Mies van Aar, Marcus Smeekes, Dara Wilson and all the other people who kept me company and supported me during the making of this project.

Abstract

Maintaining energy balance is a challenge shared by all animals which has resulted in an enormous variety of strategies for maintaining this vital balance. One of these is torpor, a mechanism that slows down basic metabolic rate (BMR) which results in a low expenditure of energy otherwise used to maintain homeostasis. Torpor is often seen as an emergency response used by animals when food resources and/or ambient temperatures are low.

However recent evidence suggest that torpor use in birds is a common energy-saving strategy that is not necessarily reserved for energetic emergencies, but a more dynamic response to ambient temperatures that involves flexible adjustments to environmental factors. To determine the underlying physiological factor that affect torpor dynamics (depth and frequency of torpor). I measured the metabolic response of six hummingbirds and one tanager (Red-Legged Honeycreeper – *Cyanerpes cyaneus*) to gradual reduction of ambient temperature, mimicking nighttime temperatures using flow-through respirometry. There were substantial variation in torpor use both within and between species, suggesting that torpor is a flexible trait that depends on a combination of an individual's current energetic state/physiological state and environmental conditions. Birds were using torpor as an energy –savings mechanism, having substantial lower metabolic rates during exposure to low ambient temperatures than individuals that defended body temperature. Torpor was used as an energy-savings mechanism, resulting in lower BMR, and less loss of M_b (body mass) in birds that used torpor more frequently as opposed to individuals that defended body temperature. Interspecifically M_b is a predictor for torpor patterns. The smaller species used torpor more frequently and went into a lower depth of torpor than larger species. Intraspecifically, M_b is a predictor for frequency of torpor in both *F. mellivora* and *A. amabilis* but insignificant for *A. tzacatl*. M_b is a predictor for depth of torpor for only *F.mellivora* and not for *A. tzacatl*, *A. amabilis* or *C.cyaneus*. Physiological condition (expressed as fat content and condition of the pectoral muscle) is not a predictor in this research. Although more accurate and precise measurements may show a significant relationship. The large difference in responds of the *C. cyaneus* compared to the hummingbird species may be due to its relative large M_b and/or different diet. Torpor patterns are influenced due to M_b , but other factors are likely also involved with fat, physiological condition and diet being the most probable.

Chapter 1 **Introduction**

Endothermic animals require high levels of endogenous metabolic heat production to maintain internal body temperatures (McNab 2002, Townsend et al. 2008) and therefore obtaining enough energy to offset these thermoregulatory costs is a fundamental challenge (Koteja 2004). A common energy-saving mechanism in certain groups of endotherms is torpor – a decrease in body temperature (T_b) that reduces the temperature gradient between T_b and ambient temperature (T_a), subsequently reducing heat loss and the energetic costs of thermoregulation (Wang & Wolowyk 1988). Organisms in environments that are thermally challenging or where food availability is low may be especially prone to incurring energy deficits, potentially resulting in serious fitness consequences (Koteja 2004). Therefore, torpor has traditionally been described as an ‘emergency’ response to energetic stressors like limited food resources and low ambient temperatures (Hainsworth et al. 1977).

Consistent with this idea, among birds, the main predictors of torpor use are body size, diet, and predictability of food resources (Schleucher 2004), all of which influence energy budgets. For example, species with small body sizes have high mass-specific metabolic rates (Lasiewski & Dawson 1967, McKechnie & Wolf 2004) and surface area to volume (SA:V) ratios (Kruger et al. 1982), increasing heat loss to the environment and as a result, energy expenditure. Additionally, food resources with low nutrient quality or variable availability may result in difficulty obtaining enough food to balance energy budgets (Schleucher 2004). Indeed, the bird species that have been documented to use torpor are generally small and specialize on nectar, fruit, or aerial insects, all of which are spatiotemporally variable (Schleucher 2004). Most physiological traits are flexible, however, and recent evidence suggests that torpor use in birds is a common energy-saving strategy and not necessarily reserved for energetic emergencies (McKechnie & Lovegrove 2002, Schleucher 2004). For example, in hummingbirds, the depth and duration of torpor can vary considerably both intra- and inter-specifically (Bech et al. 1997), and torpor occurs even in the absence of food shortage or low ambient temperatures (Carpenter & Hixon 1988). Taken together, these results suggest that torpor use is a flexible, continuously variable trait that depends not only on current environmental conditions (both abiotic and biotic) but also on an individual's physiological condition (Shiple et al. 2015). Within species, individuals with small body sizes have high mass-specific metabolic rates (Lasiewski & Dawson 1967, McKechnie & Wolf 2004) and surface area to volume (SA:V) ratios (Kruger et al. 1982) and therefore may be forced to rely on torpor more than larger individuals (Geiser 1998).

Physiological factors, such as an individual's fat reserves body condition and/or nutritional state) may also influence the dynamics of torpor use in birds (Hainsworth et al. 1977, Carpenter

& Hixon 1988, Hiebert 1993). However, the association between an individual's physiological condition and its patterns of torpor use is not well understood.

In this thesis, I used flow-through respirometry to measure thermoregulatory responses to ambient temperature in a suite of lowland Neotropical nectarivorous bird species and characterize the factors underlying variation in the duration and depth of torpor to determine whether or not torpor was a binary, 'emergency' response to energy shortages or alternatively a flexible, continuously variable trait that also depends on an individual's current physiological condition.

In my thesis, I address the following three questions: (1) Does an individual bird that uses a higher frequency of torpor, lose less body mass than birds that use a lower frequency of torpor? (2) Is body size a predictor of interspecific variation in torpor patterns? (3) Within species, how does an individual's physiological condition influence torpor patterns?

Chapter 2 **Materials and Methods**

To answer the research questions, I conducted a temperature experiment with a flow-through respirometry system. With this system I was able to measure the intake of O₂ and the CO₂ and H₂O production (metabolism) of the birds during the experiment. With this data I was able to determine the effects of M_b, fat score and the state of the pectoral muscle (in this thesis expressed as body condition) on the torpor patterns of each bird.

2.1 Capture and processing protocols

Field work was conducted in and around the town of Gamboa, Panama (09°07' N, 79°42' W) from February–April 2015 (Annex 1). Sites of capture were chosen based on accessibility, proximity to the lab, and preliminary observations of hummingbirds.

To minimize the difference between the acquired stress I standardized the handling of each individual as much as possible. But despite this measure, differences in stress levels are unavoidable. As each individual bird responses differently to stress (Cockrem, 2007), it is impossible to exclude this as a variable.

Between 16:00–17:00 in the afternoon, hummingbirds were attracted to feeders (~1.5 m high) containing a 20% sugar water solution and subsequently captured in mist-nets (12 x 2.6m; 36-mm mesh). Upon capture focal individuals were placed in a cloth bags and transported to the laboratory where they were weighed with a digital scale (American Weigh Scales model AWS-201, 200±0.01g) and clipped with a unique tail feather combination to facilitate identification. Additionally, physiological condition was assessed based on external morphology of the pectoralis muscle using a four-point categorical scale (described in Bolton, Monaghan & Houston 2008) and fat score was assessed based on a five-point categorical scale (Helms & Drury 1960, reviewed in Brown 1996). This was done by checking the furcular fat deposits between the collar bones (wishbone) (See Annex 5 Data per individual bird). Molt, sex and breeding condition (as indicated by brood patch/cloacal protuberance) were also determined whenever possible. Before each temperature experiment, a temperature-sensitive PIT-tag (13mm x 2.2mm: model Biothermo13, Biomark, Inc.) was attached to the pectoralis muscle of one focal individual with adhesive glue to measure skin temperature (T_{skin}) as a proxy for body temperature (T_b). Although T_{skin} measurements only approximate actual T_b values, Bech et al. (1997) found differences of only 0.2–0.3 °C between T_b and T_{skin} using a similar methodology (thermocouples were placed subcutaneously) and therefore, T_{skin} can yield insight into patterns of T_b regulation and the relationship between T_b and T_a in the context of torpor.

2.2 Temperature experiment

Temperature experiments were conducted overnight (from 18:00–6:00) with two focal birds measured per experiment. Following PIT-tag attachment, at 18:00 of the day of capture, focal individuals were placed in respirometry chambers (see ‘Respirometry system’ below for details) situated inside a temperature cabinet (PTC-1, Sable Systems, Inc.) controlled by a Peltier device (PELT-5, Sable Systems, Inc.). Throughout experiments, T_a of both the temperature cabinet and individual chambers was measured continuously and precisely regulated using thermistor probes (model SEN-TH, Sable Systems, Inc. ± 0.2 °C accuracy). Behavior and activity levels of focal individuals were monitored throughout experiments using infrared cameras (model WCM-6LNV, Sabrent, Inc.) to ensure that birds were at rest. After 3 hours of acclimation to the metabolic chambers at a T_a of 30 °C (within the thermoneutral zone of most bird species; H. Pollock, unpublished data) the temperature experiment was initiated. Focal individuals were exposed to a thermal ramping protocol (Mitchell & Hoffmann 2010) designed to approximate the ambient nighttime temperature conditions experienced at the field site (H. Pollock, unpublished data) – T_a was lowered at a rate of approximately 2 °C h⁻¹ to 24 °C and maintained at this temperature throughout the night. At 6:00 on the morning following the temperature experiment, focal birds were removed from the metabolic chambers, re-weighed, and fed with sugar water before being released at the site of capture.

Chapter 2.3 Respirometry system

A flow-through respirometry system (Withers 2001, Lighton & Halsey 2011; Annex 2) was used to measure physiological responses to ambient temperature and torpor dynamics of the focal species. (Annex 5). Air was pumped with an aquarium pump (model AIR-8000, Top Fin) through a column of Drierite to remove water and into a mass-flow controller (Flowbar-8; Sable Systems, Inc.), which divided the air into three separate streams – one for each animal chamber and one for an empty baseline chamber. Chambers (1.97 L) were made of Plexiglas, equipped with a rubber gasket and sealed with binder clips (ACCO Brands Corporation) 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-García & Williams 2007). A PIT-Tag antenna (HPR Plus Reader, Biomark, Inc.) was placed in the main chamber to collect T_{skin} data. Flow rates ranged from 250–300 mL min⁻¹ for hummingbird species and 300–350 mL min⁻¹ for the tanager species (Red-legged honeycreeper – *Cyanerpes cyaneus*) due to its larger body size. Excurrent air was subsampled manually at 100–150 mL min⁻¹ through barrel syringes into a humidity meter (RH-300, Sable Systems, Inc.) that measured H₂O content, followed by a dual CO₂–O₂ analyzer (Foxbox, Sable

Systems, Inc.) that measured CO₂ content and O₂ content. The following sampling set-up was repeated throughout the entire experiment: animal chamber 1 (15 minutes), animal chamber 2 (15 minutes), baseline (5 minutes).

During each experiment, flow rate, T_a, and CO₂ were measured in each chamber in real-time at one-second intervals using the program Expedata (Sable Systems Inc.). T_b was also measured at one-minute intervals using a PIT-tag reader (HPR Plus reader, Biomark, Inc.), which was synced with Expedata before each experiment to ensure that T_b measurements corresponded temporally with metabolic measurements. The %CO₂ data was then converted to $\dot{V}CO_2$ (rate of CO₂ production measured in mL CO₂ min⁻¹) using the following equation:

$$\dot{V}CO_2 = (FR \cdot (FeCO_2 - FiCO_2) - FeCO_2 \cdot \dot{V}O_2) \div (1 - FeCO_2) \quad (\text{Eqn } 1)$$

Where FR was the flow rate of the animal chamber (mL min⁻¹ STPD), FiCO₂ was the incurrent fractional CO₂ concentration (0.0004), FeCO₂ was the excurrent fractional CO₂ concentration and $\dot{V}O_2$ was the rate of O₂ consumption in mL O₂ min⁻¹. A coefficient of 25.0 Joules mL⁻¹ CO₂ (Warthog Systems, www.warthog.ucr.edu) was used to convert $\dot{V}CO_2$ to metabolic rate (watts). To determine the relationship between $\dot{V}CO_2$, T_b and T_a, 5-minute averages of $\dot{V}CO_2$, T_b and T_a were obtained throughout the entire experiment for each focal individual.

2.4 Estimating patterns of variation in torpor

To investigate patterns of variation in torpor both within and between species, both frequency and depth of torpor were estimated for each focal individual. Two criteria were used to define torpor: focal individuals had to have 1) become hypothermic (T_b ≤ 38 °C; (Schleucher 2004) and 2) exhibited a rate of decrease in T_b (ΔT_b) of ≥ 0.5 °C min⁻¹.

Frequency of torpor: To estimate the total duration of torpor used by focal individuals while controlling for variation in duration of the temperature experiments, an index of frequency of torpor was calculated for each focal individual as follows:

$$\text{Frequency of torpor} = \text{Total time spent in torpor} \div \text{total experiment time (Eqn 2)}$$

Depth of torpor: Minimum body temperature ($T_b \text{ min}$) was used as a proxy for depth of torpor (under the assumption that greater reductions in T_b are indicative of deeper torpor). However, because T_b data was only available for 23/41 (56%) focal individuals, a linear regression between $T_b \text{ min}$ and $\dot{V}\text{CO}_2 \text{ min}$ (the minimum rate of CO_2 production) was conducted to investigate the feasibility of using $\dot{V}\text{CO}_2 \text{ min}$ as a substitute for $T_b \text{ min}$. There was a very strong correlation ($F_{1,21} = 148.30$, $R^2 = 0.89$, $p < 0.0001$; Fig. 1a) indicating that $\dot{V}\text{CO}_2 \text{ min}$ was a reliable proxy for $T_b \text{ min}$. Due to the allometric relationship between M_b and metabolic rate (Lasiewski & Dawson 1967, McKechnie & Wolf 2004), the relationship between mass-specific $\dot{V}\text{CO}_2 \text{ min}$ ($\dot{V}\text{CO}_2 \text{ min} \div M_b$; units = $\text{mL min}^{-1} \text{g}^{-1}$) and $T_b \text{ min}$ was also investigated, and there was a moderately strong correlation ($F_{1,21} = 21.52$, $R^2 = 0.48$, $p < 0.0001$; Fig. 1b) between mass-specific $\dot{V}\text{CO}_2 \text{ min}$ and $T_b \text{ min}$. However, because the relationship between $\dot{V}\text{CO}_2 \text{ min}$ and $T_b \text{ min}$ was stronger, $\dot{V}\text{CO}_2 \text{ min}$ was used in subsequent analyses as the metric for depth of torpor.

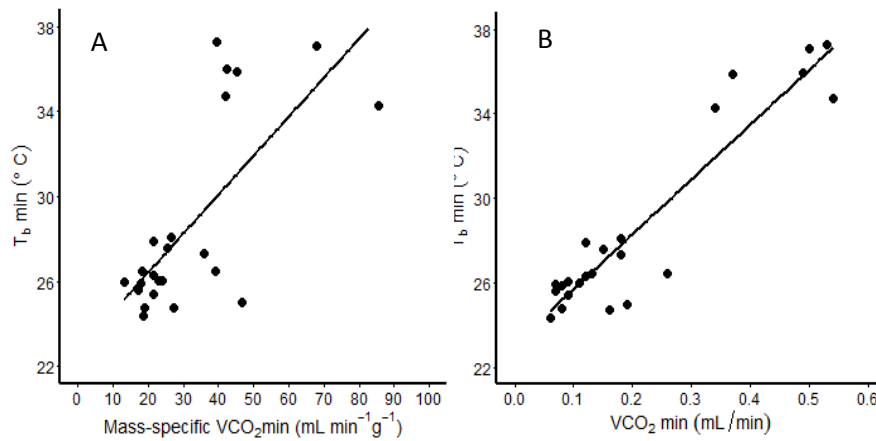


Figure 1 – Relationship between minimum body temperature ($T_b \text{ min}$) and a) minimum rate of CO_2 production ($\dot{V}\text{CO}_2 \text{ min}$) and b) mass-specific $\dot{V}\text{CO}_2 \text{ min}$ in the focal species.

2.5 Statistical analyses

To determine if torpor was an energy-savings mechanism the percentage of mass that was lost by each individual during the experiment (ΔM_b : $(M_{b \text{ capture}} - M_{b \text{ release}}) \div M_{b \text{ capture}}$) was used as a proxy for energy expenditure (following Hainsworth et al. 1977, Carpenter & Hixon 1988). A bivariate linear regression was conducted for each species to test if intraspecifically, there was a relationship between an individual's frequency of torpor and ΔM_b . This analysis was restricted to the three species (White-necked Jacobin (*Florisuga mellivora*), Rufous-tailed Hummingbird (*Amazilia tzacatl*) and the Blue-chested Hummingbird (*Amazilia amabilis*) that had a sample size of $n \geq 1$. To determine the influence of interspecific variation in body size on patterns of torpor use, the mean frequency of torpor and mean depth of torpor was calculated for each species. Then, bivariate linear regressions were conducted to determine the relationship

between mean M_b and I) mean frequency of torpor per species and II) mean depth of torpor per species.

To determine the influence of an individual's physiological condition on patterns of torpor use in all individuals, associations between three indices of physiological condition (M_b , fat score, and body condition; see Section 2.1) and a) frequency of torpor and b) depth of torpor were quantified. For M_b , a bivariate linear regression was conducted and for fat score and body condition, generalized linear models with Poisson error distributions were conducted.

Chapter 3 Results

Thermoregulatory responses to ambient temperature were measured in 41 individuals of six hummingbird species (family Trochilidae) and one tanager species (family Thraupidae) (Annex 3). Torpor patterns varied widely among the seven focal species that were sampled. None of the individuals of the tanager species entered torpor (0/4 individuals – *C. cyaneus*). In contrast, the proportion of individuals in the six hummingbird species that entered torpor ranged from 81% (13/16 individuals – *F. mellivora*) to 100% (9/9 individuals – *A. amabilis*). Among hummingbird species the mean frequency of torpor use also varied, ranging from 0.29 (*A. nigricollis*) to 0.61 (*A. amabilis*; range = 0.30-1.0) (see figure 2).

3.1 Do individual bird that use a higher frequency of torpor loose less body mass then birds that use a lower frequency of torpor ?

Individual birds that showed a higher frequency of torpor during the night, lost significantly less M_b than individuals that used no torpor or a lower frequency – there was a significant negative relationship between frequency of torpor and ΔM_b for individuals of all three hummingbird species with sample size of $n \geq 1$ (*F. mellivora*: $F_{1,13} = 8.84$, $R^2 = 0.36$, $p = 0.01$; *A. tzacatl*:

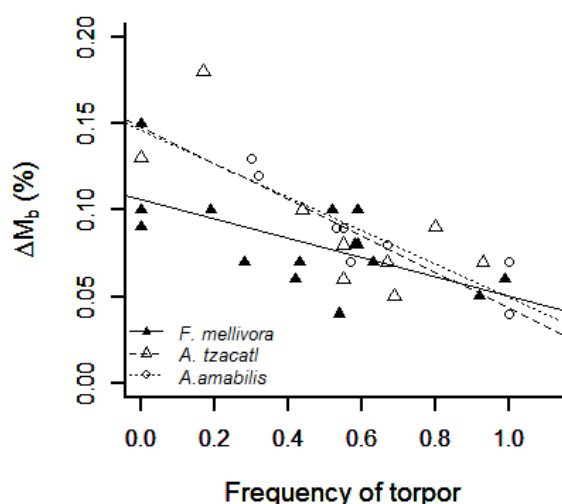


Figure 2 – Relationship between frequency of torpor use and mass loss (ΔM_b – % change) in the three most commonly sampled hummingbird species.

3.2 Is body size a predictor of interspecific variation torpor patterns?

3.2 a) Frequency of torpor

Interspecifically, there was a strong negative relationship between mean M_b and frequency of torpor ($F_{1,5} = 51.63$, $R^2 = 0.89$, $p = 0.001$; Fig. 3) – larger species tended to use torpor less frequently than smaller species.

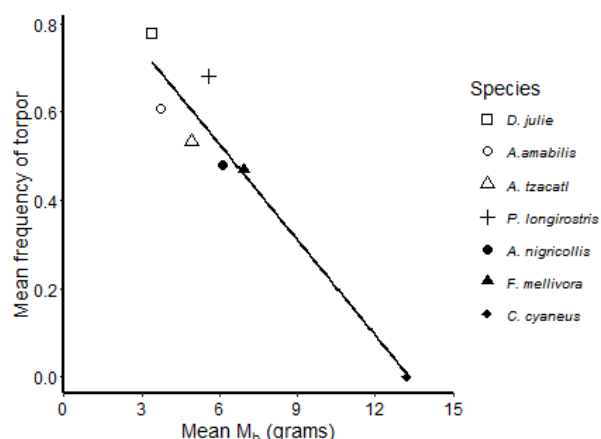


Figure 3 – Relationship between mean M_b and mean frequency of torpor in the focal species.

3.2 b) Depth of torpor

Interspecifically, there was a very strong negative relationship between mean M_b and depth of torpor ($F_{1,5} = 277.50$, $R^2 = 0.98$, $p < 0.001$; Fig. 4.) – larger species tended to go into shallower torpor than smaller species.

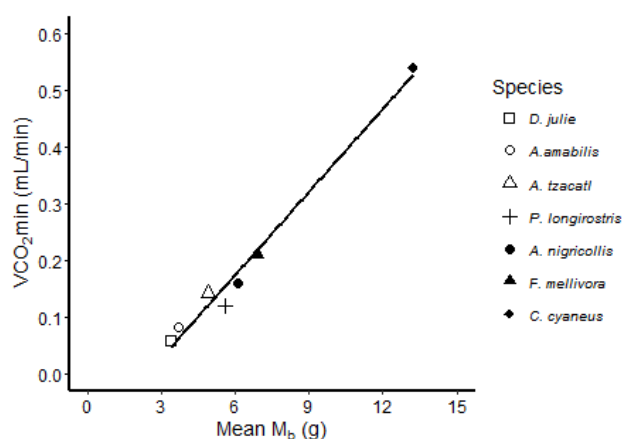


Figure 4 – Relationship between mean M_b and mean depth of torpor (as indicated by $\dot{V}CO_2min$) in the focal species. Lower values of $\dot{V}CO_2min$ indicate greater depth of torpor.

3.3 How does an individual's physiological condition influence torpor patterns?

3.3 a) Frequency of torpor with body mass

Intraspecifically, frequency of torpor decreased with increasing M_b – larger individuals tended to use torpor less frequently than smaller individuals (Fig. 5). However, this relationship was only significant for *F. mellivora* ($F_{1,14} = 15.45$, $R^2 = 0.49$, $p = 0.002$) but not for *A. amabilis* ($F_{1,7} = 1.93$, $R^2 = 0.10$, $p = 0.21$) or *A. tzacatl* ($F_{1,7} = 0.01$, $R^2 = 0.001$, $p = 0.93$).

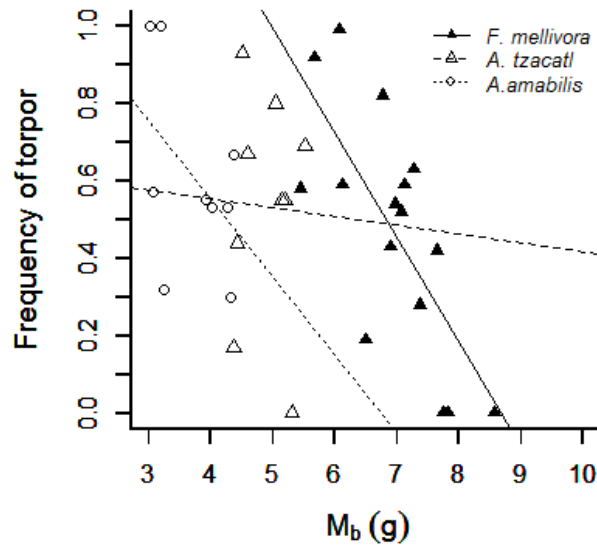


Figure 5 – Relationship between M_b and frequency of torpor in the three most commonly sampled hummingbird species.

3.3 b) Frequency of torpor with fat score and body condition

Neither fat (GLM: $z = -0.88$, $p = 0.38$; Fig. 7a) nor body condition (GLM: $z = -0.91$, $p = 0.37$; Fig. 7b) was a significant predictor of variation in frequency of torpor, although there was a trend of decreasing frequency of torpor with increasing fat score and body condition.

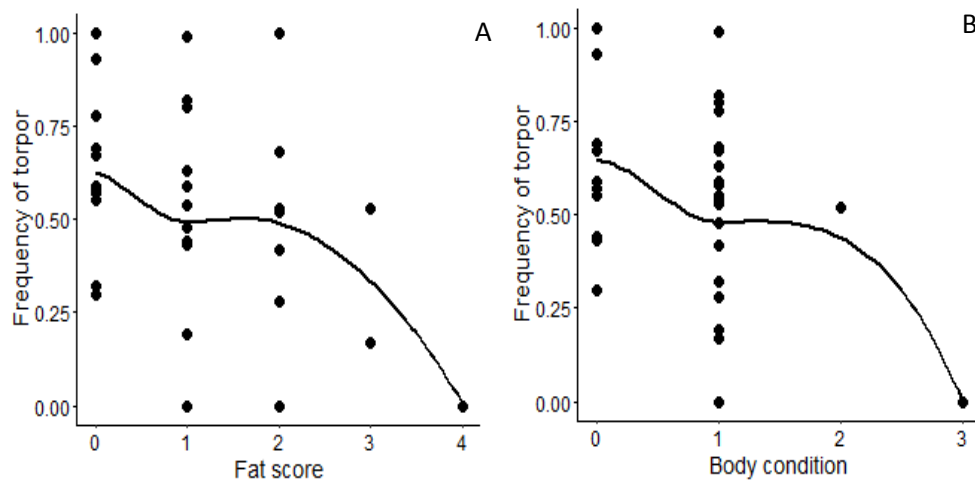


Figure 6 – Relationship between frequency of torpor and a) fat score and b) body condition in focal individuals. Regression lines in each panel indicate loess fit.

3.3 c) Depth of torpor with body mass

Intraspecifically, there was a trend of increasing depth of torpor with decreasing body mass – smaller individuals tended to go into deeper torpor than larger individuals (Fig. 6). However, this trend was only significant for *F. mellivora* ($F_{1,14} = 7.87$, $R^2 = 0.31$, $p = 0.01$) and not for *A. tzacatl* ($F_{1,7} = 0.002$, $R^2 = 0.003$, $p = 0.96$) or *A. amabilis* ($F_{1,7} = 3.74$, $R^2 = 0.26$, $p = 0.09$).

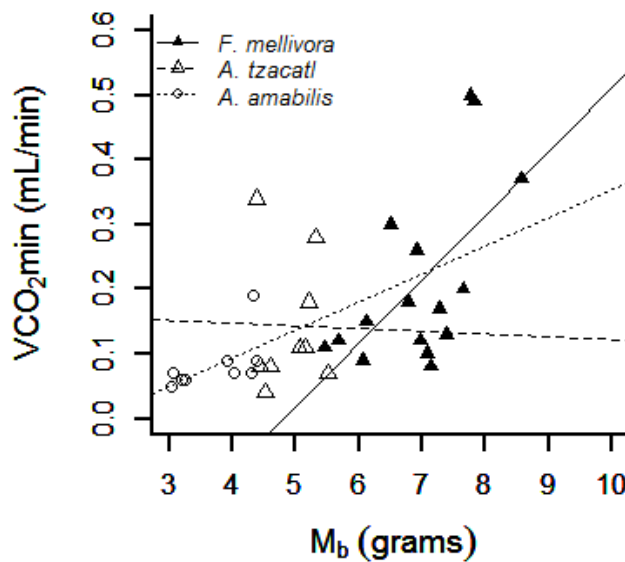


Figure 7 – Relationship between M_b and the depth of torpor (as indicated by $\dot{V}CO_2min$) in three most commonly sampled hummingbird species.

3.3 d) Depth of torpor with fat score and body condition

Neither fat (GLM: $z = 0.75$, $p = 0.45$; Fig. 8a) nor body condition (GLM: $z = 0.65$, $p = 0.52$; Fig. 8b) was a significant predictor of variation in depth of torpor, although there was a trend of decreasing depth of torpor with increasing fat score and body condition.

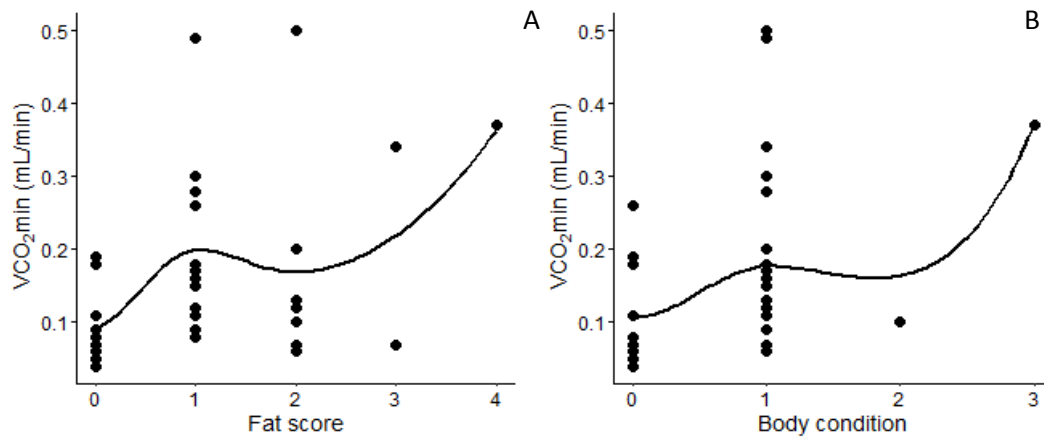


Figure 8 – Relationship between depth of torpor and a) fat score and b) body condition in focal individuals. Lower $\dot{V}\text{CO}_2$ min represents greater depth of torpor. Regression lines in each panel indicate loess fit.

Chapter 4 Discussion

4.1 Do individual birds that use torpor loose less body mass then birds that use a lower frequency of torpor

Within species, individuals that exhibited higher frequency of torpor lost less body mass, indicating that torpor functions as an energy-savings mechanism (Hainsworth et al.1977, Kruger et al. 1982, and Wang & Wolowyk 1988). However, there was substantial intraspecific variation in both depth and frequency of torpor, suggesting that torpor may not be an emergency response solely to energy shortages (as proposed in Hainsworth et al. 1977), but rather a dynamic process that likely depends on an individual's energetic state and exhibits continuous variation (as suggested by McKechnie & Lovegrove 2002 and Schleucher 2004).

4.2 Patterns of interspecific variation in torpor

Frequency and depth of torpor varied between species and M_b was an important predictor of interspecific variation in torpor. Mean frequency of torpor increased with decreasing body mass, indicating that smaller species need to employ torpor more often to maintain energy balance. Similarly, mean depth of torpor increased with decreasing body mass, indicating that smaller species enter into deeper torpor than larger species. These results are consistent with the idea that torpor is probably used more frequently by small birds due to their higher SA:V ratios and mass-specific metabolic rates. (Geiser 1998). Thus a small bird will try to loose less heat to its environment by reducing the T_b-T_a gradient more compared to a relative larger bird which has a relative lower SA: V ratio due to its larger size, resulting in less heat loss per mass unit.

Kruger et al. 1982 found no relation between M_b and torpor, stating that all the hummingbirds measured went into torpor and dropped their metabolic rate to the same level regardless of their M_b . This is in contrast with my results for *F. mellivora*, which had individuals that did not enter torpor at all (fig 2). In figure 7, it is shown that depth of torpor (a proxy of metabolic rate) is correlated with M_b , showing that a lower M_b can result in a lower drop in metabolic rate than birds with a relative higher M_b . Perhaps this is due to a larger bird needing more energy (thus higher metabolic rate) to maintain body functions during torpor compared to a smaller bird which would need less energy to maintain its body functions during torpor.

The only focal species that did not enter into torpor was the tanager species, *C. cyaneus*. There are several possible explanations for why *C. cyaneus*, which is also a small nectarivore, did not use torpor at all. First, *C. cyaneus* (order Passeriformes) is phylogenetically distant

from the hummingbirds (order Apodiformes). Although it is not clear in what extend phylogeny relates to the occurrence of torpor in the avian class, there is a general view that members of the “ancestral” orders undergo torpor more than members of younger taxa. (Schleucher, 2004). However, Geiser (1998), suggests that M_b and diet, rather than phylogeny *per se*, are the primary determinants of torpor use in birds. *C. cyaneus* is also nearly twice (~ 13 g) as large as the next closest focal species (*F. mellivora*: ~7 g) and also has a less specialised diet than hummingbirds - only a small part of its diet consists of nectar and the largest part of fruit and arthropods (Snow & Snow 1971). Because *C. cyaneus* differs from hummingbirds with respect phylogeny, body size and diet, it is unclear why they did not use torpor. Future studies that incorporate a more diverse complement of species with a broader range of body sizes and diets will be necessary to address this question.

4.3 The influence of physiological condition on patterns of torpor use

The wide range of intraspecific variation in torpor that was found within the focal species suggests that torpor is a flexible trait that depends on an individual's current energetic state, which may be a function of its physiological condition. It seems that M_b does influence torpor patterns, most likely due to larger individuals having a higher SA: V ratio and lower mass-specific metabolic rates (as was found with the interspecific patterns), but larger individuals also contain more energy reserves and so are probably more able to maintain their energy balance than smaller individuals. This could result in less use of torpor, and shallower torpor when used.

Two common indicators of an individual's current energetic state are its fat reserves and its body condition. Body condition (i.e. pectoral muscles) and fat are good indicators for a bird's energetic state. Muscles store energy in the form of glycogen, which can be used by the muscle cells for fuel, indicating that the more muscles a bird has, the larger its energy reserves are. Fat content also says a great deal about the energetic state of a bird. Fat, also called adipose tissue has as its main purpose to store energy for later use. Thus a larger fat content would mean that a bird has more energy reserves. Both fat reserves and body condition have previously been found to be important determinants of torpor (Hainsworth et al. 1977, Carpenter & Hixon 1988, Hiebert 1993).

There was a trend of decreasing frequency of torpor and reduced depth of torpor with increasing fat score and better body condition, although this trend was not significant. It was most likely not significant due to the coarse measurements used for both fat (5-point categorical scale), and body condition (4-point categorical scale). Most individuals that were measured had poor/fair body condition and low fat reserves, and this lack of variation probably

explains why neither trait was a significant predictor of variation in depth or frequency of torpor. However, the fact that there were consistent trends of decreasing torpor frequency and shallower torpor depth with increasing body condition and fat reserves suggests that an individual's physiological condition may play an important role in determining its patterns of torpor use. Future research should employ a more precise measurement method to quantify fat score and body condition to determine the relationship between an individual's physiological condition and its patterns of torpor use.

4.4 The benefits and disadvantages of torpor

Within the hummingbird species, the largest species (*F. mellivora* and *A. tzacatl*) were the only ones that had individuals that did not go into torpor. Secondly, within species, the largest were the ones that were using torpor less or going into shallower torpor. So, it is clear from the data that using torpor saves energy, thus why would any bird not choose to go into torpor? First, when a bird is torpid it will not respond to external stimuli. (Schleucher, 2004) This combined with the process of arousal that can take a long time, during which the bird is susceptible for predators (Csada & Brigham, 1994). Another advantage of not using torpor could be a competitive advantage. During observations of hummingbirds near the feeders, it was mostly the *F. mellivora* and occasionally the *A. tzacatl* that were dominating the feeders. Due to the feeders presenting a consistent source of food, the dominant individuals are able to feed whenever they want, gaining enough energy to perhaps forgo torpor during the night. Secondly, if an individual forgoes torpor, it can wake up earlier and get to the feeder, or the most nutrient flowers, to replenish their energy reserves before individuals that used torpor. Thus, although it costs more energy to forgo torpor it could give individuals a competitive advantage, particularly the larger individuals who can endure more energy loss over the night due to their size.

4.5 Conclusion

Within the three most abundant sample species, the birds that showed a higher frequency of torpor lost less body mass (i.e. energy) than individuals with a lower frequency of torpor. Torpor functions as a flexible energy savings mechanism which depends on an individual's energetic state and exhibits continuous variation in hummingbirds.

Interspecific M_b influences torpor patterns, species with a high M_b went less often in torpor and had shallower torpor compared to species with a low M_b . Suggesting that smaller hummingbird species use torpor more frequently to maintain their energy balance than larger species.

Physiological conditions seem to influence torpor patterns. There was a trend of decreasing use of torpor in individuals with a higher fat content, higher M_b and a better body condition, although none of the trends were significant enough.

Torpor is an amazing tool used by endotherms to adjust to rapid daily changes in ambient temperature, especially in the smallest of animals that lack the capacity for long term energy storage. An obvious question that arises is; what are the consequences of climate change for small 'sensitive' endotherms that use torpor? There is some information on the possible effects of climate change on mammalian endotherm that use torpor. But almost no data on the possible effects of climate change on (tropical) hummingbirds. Torpor is undoubtedly an important survival mechanism used by these birds, especially in changing climates, thus torpor will be a very important mechanism to study when trying to answer this question.

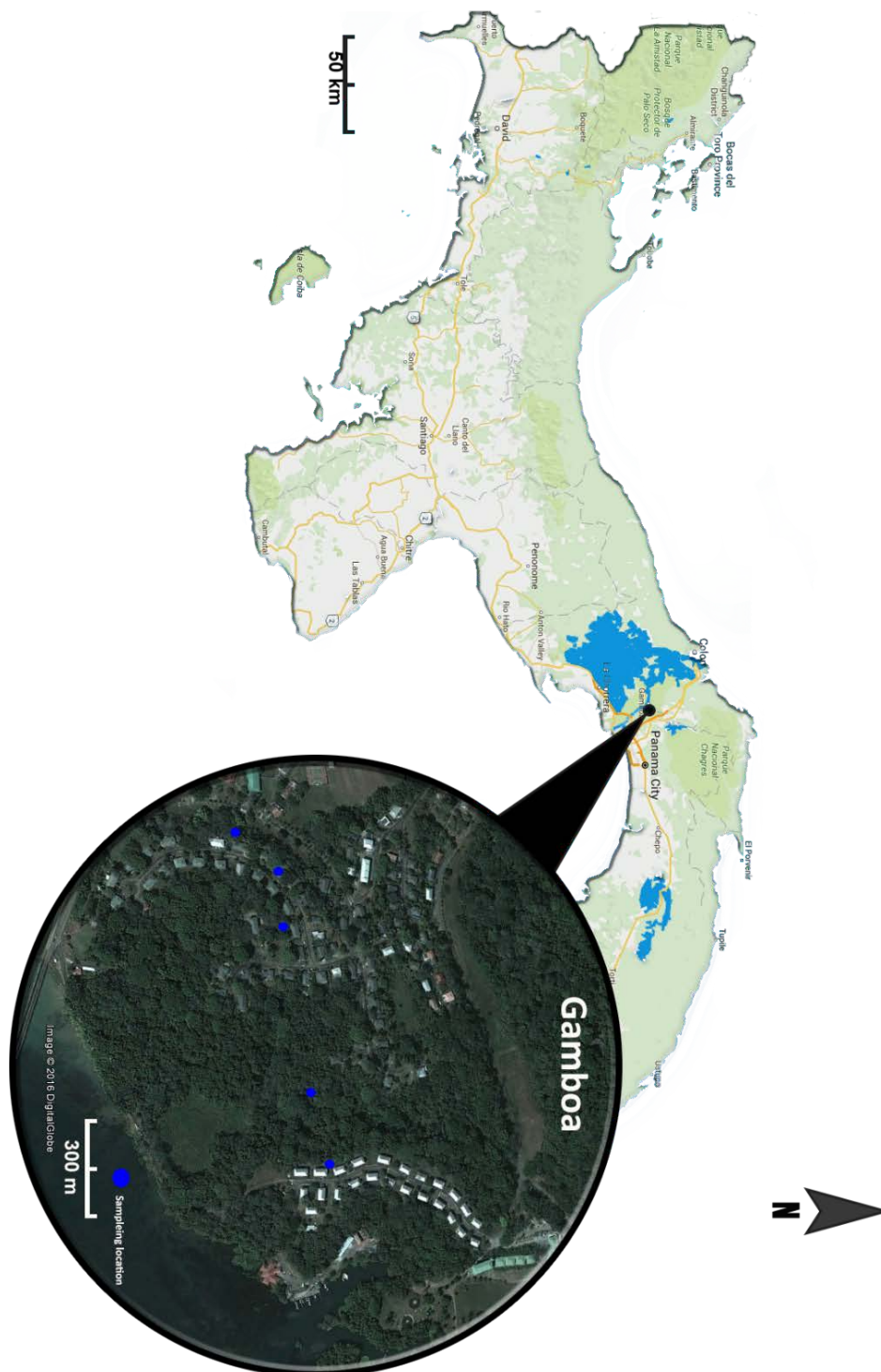
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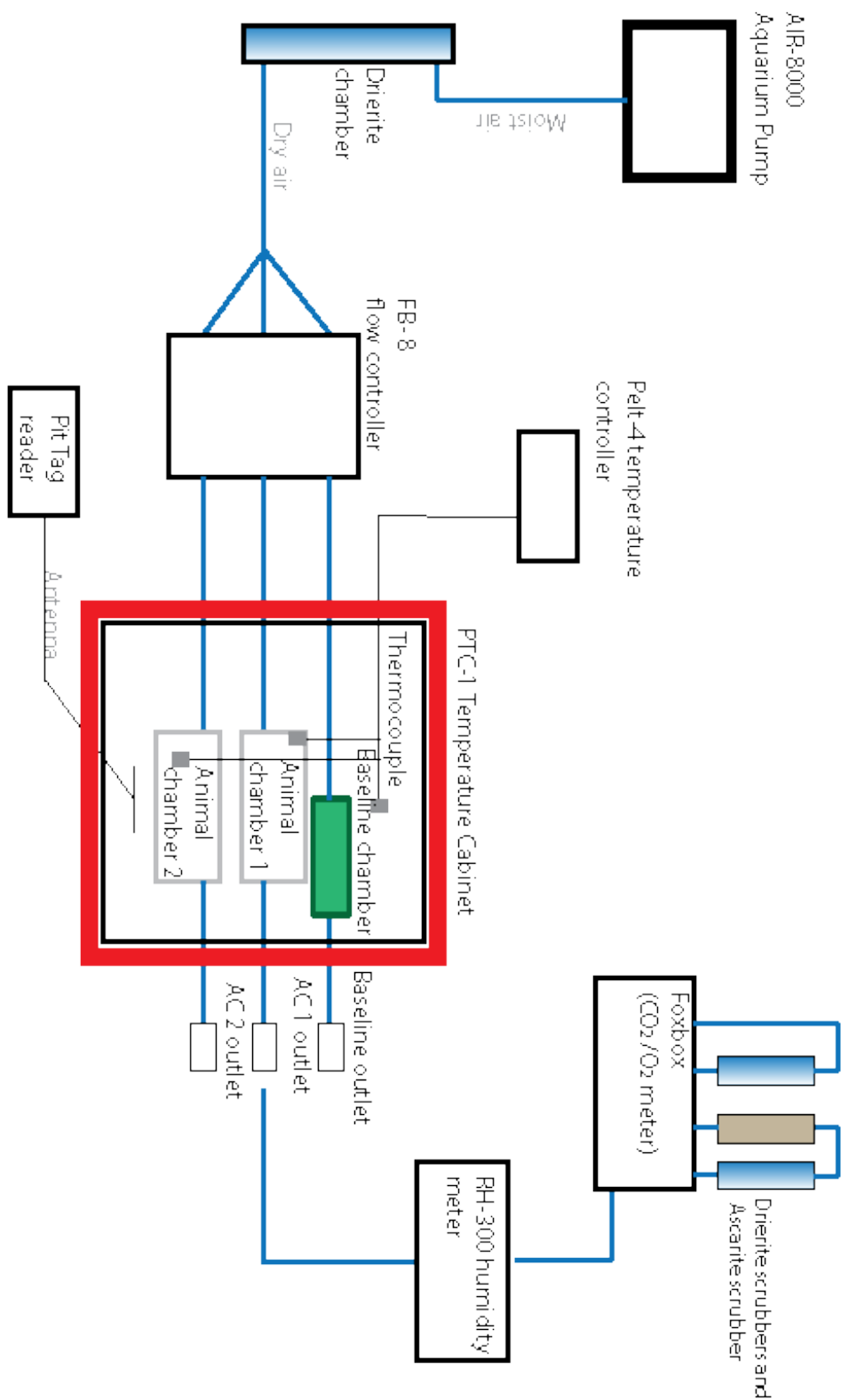
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Annex 1 Location of research

Map of Panama denoting the geographic location of the research (Gamboa) with an inset of the sampling locations.



Annex 2 Schematic of respirometry system



Annex 3 Equipment summary

List of all the equipment used during the research, including quantity and costs.

Equipment	Qty.	Unit cost (\$)	Total cost (\$)
<i>Capturing and housing</i>			
Perky-Pet® hummingbird feeders (model 203CPBN)	6	10.00	60.00
Mist-net (12x2.6m: 36-mm mesh)	6	75.00	450.00
Mist-net poles (1.5" diameter x 10' PVC pipe)	9	5.00	45.00
Digital pocket scale (American Weigh Scales, model AWS-201,200±0.01 g)	1	30.00	30.00
Cloth bird bags (Avian Research Supplies, 10" x 12")	8	3.00	24.00
<i>Respirometry system</i>			
PIT-Tags (Biomark, Inc. model Biothermo13 tag, 13mm x 2.2 mm)	15	5.00	75.00
PIT-Tag antenna (HPR Plus Reader, Biomark, Inc.)	1	2,500.00	2,500.00
PTC-1 temperature cabinet (Sable Systems, Inc.)	1	1,530.00	1,530.00
Pelt-4 temperature controller (Sable Systems, Inc.)	1	2,865.00	2,865.00
Thermistor probe (Sable Systems, Inc. model SEN-TH)	3	55.00	165.00
Infrared camera (Sabrent, Inc. model WCM-6LNV)	2	10.00	20.00
Aquarium pump (Top Fin, model AIR-8000)	1	40.00	40.00
Mass-flow controller (Sable Systems, Inc. Flowbar-8 mass-flow controller)	1	5,700.00	5,700.00
Respirometry chambers (Custom-built Plexiglas, 1.97 L)	2	100.00	200.00
Binder clips (ACCO Brands Corporation)	20	0.25	5.00
Humidity meter (Sable Systems, Inc. model RH-300)	1	2,700.00	2,700.00
CO ₂ -O ₂ Analyzer (Sable Systems, Inc. FoxBox model)	1	12,300.00	12,300.00
Indicating Drierite (W.A. Hammond Drierite Co.; size 8 mesh)	4	75.00	300.00
Ascarite (Thomas Scientific, size 20-30 mesh)	1	270.00	270.00
Total			29,279.00
<i>Software</i>			
Expedata (Sable Systems, Inc.)			
R development Core Team (2015) R: A Language and environment for statistical computing Version 3.2.2.			
Microsoft Excel 2013			
Microsoft Access 2010			
BioTerm PIT-Tag reader software (Biomark, Inc.)			

Annex 4 Focal species

Focal species and associated physiological data, including mean M_b , M_b range (the range of body masses of the individuals of each focal species), mean basal metabolic rate, torpor range (the range of torpor frequencies used by individuals of each focal species), the proportion of

Common name	Scientific name	<i>n</i>	Mean M_b (g±sd)	M_b range	Mean BMR (Watts±sd)	Torpor range	Proportion of individuals using torpor (%)	Fat range (0-4)	Pectoral muscle (0-3)
Black-throated Mango	<i>Anthracothorax nigricollis</i>	1	5.84	–	0.20	0.29	1/1 (100%)	1	1
Blue-chested Hummingbird	<i>Amazilia amabilis</i>	9	3.51±0.57	2.88–4.21	0.10±0.01	0.30–1.0	9/9 (100%)	0,2,3	0,1
Long-billed Hermit	<i>Phaethornis longirostris</i>	1	5.58	–	0.14	0.68	1/1 (100%)	2	1
Red-legged Honeycreeper	<i>Cyanerpes cyaneus</i>	4	12.74±0.84	11.54–13.44	0.22	0.00	0/4 (0%)	1,2	1,2
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	9	4.69±0.46	3.98–5.38	0.12±0.03	0.00–0.93	8/9 (89%)	0,1,3	0,1
Violet-bellied Hummingbird	<i>Damophila julie</i>	1	3.23	–	0.07	0.78	1/1 (100%)	0	1
White-necked Jacobin	<i>Florisuga mellivora</i>	16	6.59±0.81	5.24–8.19	0.16±0.03	0.00–0.99	3/16 (19%)	0,1,2,4	0,1,2,3
Total	<i>n</i> = 7 species	41							

individuals of each focal species that used torpor, fat range and the condition shown as “Pectoral muscle”.

Fat range is divided in classes 0 till 4, representing the furcular fat deposits.

0 = no fat, 1 = trace fat, 2 = layer of fat, 3 = half amount, - and 4 = full amount of fat.

Pectoral muscle is divided in classes 0 till 3, representing the condition.

0 = poor, 1 = fair, 2 = good, 3 = very good.

Annex 5 Data per individual bird

Physiological and torpor data is shown here per individual bird, including date of capture/experiment, bird ID and temperature data for the individuals that had a PIT-tag attached. All M_b data is expressed in grams, duration in minutes and temperature data in degree Celsius.

Date	Species	ID	Age	Sex	Condition	Fat	Molt	Mb_capture	Mb_release	Deltamb	Meanmb	Longest_bout	Duration_torpor	Total_time	Freq_torpor	N_bouts	Tbmin	Tbmax	Tbmean	Tbrange
13-4-2015	Black-throated Mango	BTMA_R1	a	f	1	1	0,5	6,1	5,57	0,09	5,84	148,8	148,8	509,4	0,29	1				
20-4-2015	Blue-chested Hummingbird	BCHB_L3	a	f	0	0	0	3,04	2,71	0,11	2,88	335,4	335,4	335,4	1	1				
22-3-2015	Blue-chested Hummingbird	BCHB_R3	a	f	0	0	0	3,07	2,87	0,07	2,97	225	225	393	0,57	1				
20-3-2015	Blue-chested Hummingbird	BCHB_L4	j	f	0	2	0,5	3,2	2,99	0,07	3,1	547,8	547,8	547,8	1	1				
20-4-2015	Blue-chested Hummingbird	BCHB_L2	a	f	1	0	0	3,25	2,86	0,12	3,06	115	164	518,4	0,32	2	24,37	34,3	29,54	9,93
3-4-2015	Blue-chested Hummingbird	BCHB_L3	a	f	1	0	1	3,92	3,57	0,09	3,75	268,2	268,2	489	0,55	1	26,06	35,88	31,57	9,82
13-2-2015	Blue-chested Hummingbird	BCHB_R1	a	f	1	2	1	4,02			4,02	223,2	223,2	417,6	0,53	1				
14-2-2015	Blue-chested Hummingbird	BCHB_R1-L4	a	f	1	3	1	4,29	3,92	0,09	4,11	228	320	604	0,53	2	25,6	35,6	30,83	10
20-3-2015	Blue-chested Hummingbird	BCHB_L1	i	f	0	0	0,5	4,34	3,79	0,13	4,07	153,6	153,6	516,6	0,3	1	25	35,81	32,95	10,81
21-2-2015	Blue-chested Hummingbird	BCHB_R1.2	a	m	1	0	3	4,39	4,02	0,08	4,21	342,6	342,6	513,6	0,67	1	34,26	37,48	36,18	3,22
22-3-2015	Long-billed Hermit	LTHE_L1L2	a	u	1	2	0	5,58			5,58	452,4	452,4	661,2	0,68	1	25,4	37,64	31,11	12,24
15-4-2015	Red-legged Honeycreeper	RLHC_R2	a	f	1	2	1	11,94	11,14	0,07	11,54	0	0	600	0	0	24,77	35,16	30,46	10,39
19-4-2015	Red-legged Honeycreeper	RLHC_R1	a	f	2	1	0,5	13,36	12,26	0,08	12,81	0	0	600	0	0				
9-3-2015	Red-legged Honeycreeper	RLHC_noid	a	f	1	1	0,5	13,73	12,61	0,08	13,17	0	0	604	0	0	25,88	34,1	30,43	8,22
13-4-2015	Red-legged Honeycreeper	RLHC_R3	a	f	1	2	0,5	13,84	13,03	0,06	13,44	0	0	590,4	0	0	26,01	35,05	30,39	9,04
15-4-2015	Rufous-tailed Hummingbird	RTHB_L1	a	m	1	3	1	4,38	3,57	0,18	3,98	74	74	435	0,17	1				
15-4-2015	Rufous-tailed Hummingbird	RTHB_L2	a	u	0	1	0	4,44	4	0,1	4,22	216	268	613,2	0,44	2	27,33	36,58	33,62	9,25
13-3-2015	Rufous-tailed Hummingbird	RTHB_R3	a	u	0	0	1	4,52	4,19	0,07	4,36	467,4	467,4	502,8	0,93	1				
15-3-2015	Rufous-tailed Hummingbird	RTHB_L3	a	u	0	0	0	4,61	4,28	0,07	4,45	280	280	420	0,67	1				
13-3-2015	Rufous-tailed Hummingbird	RTHB_R4.2	a	u	1	1	0,5	5,06	4,61	0,09	4,84	295,2	295,2	369,6	0,8	1	25,96	37,95	30,91	11,99
13-2-2015	Rufous-tailed Hummingbird	RTHB_R1	a	u	0	0	1	5,16	4,85	0,06	5,01	267	267	487,2	0,55	1	27,9	37,3	32,33	9,4
9-4-2015	Rufous-tailed Hummingbird	RTHB_R2	j	u	0	0	3	5,21	4,81	0,08	5,01	266,4	266,4	482,4	0,55	1	26,3	38,33	31,25	12,03
16-4-2015	Rufous-tailed Hummingbird	RTHB_R4	a	u	1	1	0	5,32	4,63	0,13	4,98	0	0	502,8	0	0				
9-4-2015	Rufous-tailed Hummingbird	RTHB_L1.2	j	u	0	0	2,5	5,52	5,23	0,05	5,38	366,6	375,6	547,2	0,69	2				
6-4-2015	Violet-bellied Hummingbird	VBHB_R1	a	m	1	0	0,5	3,39	3,07	0,09	3,23	489,6	489,6	624	0,78	1	24,73	39	34,35	14,27
7-3-2015	White-necked Jacobin	WNJA_L3.2	a	f	1	0	0	5,46	5,02	0,08	5,24	278,4	278,4	480	0,58	1	27,6	38,16	31,91	10,56
17-2-2015	White-necked Jacobin	WNJA_R4.2	i	m	1	2	0	5,8	5,41	0,07	5,61						28,11	36,39	32,58	8,28
15-3-2015	White-necked Jacobin	WNJA_R1.2	a	f	1	1	0	6,07	5,71	0,06	5,89	436,2	436,2	441,6	0,99	1	26,46	36,4	32,5	9,94
2-3-2015	White-necked Jacobin	WNJA_R3R2	i	f	1	1	1	6,12	5,61	0,08	5,87	351,6	351,6	597	0,59	1				
5-3-2015	White-necked Jacobin	WNJA_R1	a	m	1	1	0	6,51	5,86	0,1	6,19	96	96	498,6	0,19	1				
3-4-2015	White-necked Jacobin	WNJA_L1	a	m	1	1	0	6,78			6,78	503,4	503,4	614,4	0,82	1				
1-4-2015	White-necked Jacobin	WNJA_L1.2	j	f	0	1	0	6,91	6,4	0,07	6,66	180	211	489,6	0,43	2				
5-3-2015	White-necked Jacobin	WNJA_R4	a	m	1	1	0,5	6,98	6,69	0,04	6,84	253,8	253,8	469,8	0,54	1	26,46	37,16	33,82	10,7
17-2-2015	White-necked Jacobin	WNJA_L3.2	a	f	2	2	0	7,08	6,38	0,1	6,73	351,6	351,6	670,2	0,52	1				
6-4-2015	White-necked Jacobin	WNJA_R1L4	a	f	0	0	0	7,13	6,03	0,15	6,58	288	288	488,4	0,59	2				
1-4-2015	White-necked Jacobin	WNJA_R3L3	a	m	1	1	0,5	7,28	6,79	0,07	7,04	257,4	305,7	483	0,63	2	37,06	38,84	38,19	1,78
21-2-2015	White-necked Jacobin	WNJA_L4	a	f	1	2	0,5	7,38	6,87	0,07	7,13	180	180	642	0,28	1				
26-2-2015	White-necked Jacobin	WNJA_L4.2	a	m	1	2	0	7,65	7,16	0,06	7,41	227,4	227,4	543,6	0,42	1	35,96	37,02	36,36	1,06
23-2-2015	White-necked Jacobin	WNJA_R4L4	a	m	1	2	1	7,76	6,96	0,1	7,36	0	0	483	0	0	34,7	37,32	35,93	2,62
14-2-2015	White-necked Jacobin	WNJA_L3	a	m	1	1	0,5	7,82	6,66	0,15	7,24	0	0	435,6	0	0				
19-4-2015	White-necked Jacobin	WNJA_L5R5	a	m	3	4	1,5	8,57	7,81	0,09	8,19	0	0	493,2	0	0	37,29	38,3	37,74	1,01

Fat range is divided in classes 0 till 4, representing the furcular fat deposits. 0 = no fat, 1 = trace fat, 2 = layer of fat, 3 = half amount,- and 4 = full amount of fat. Pectoral muscle is divided in classes 0 till 3, representing the condition. 0 = poor, 1 = fair, 2 = good, 3 = very good.

Age is divided in j = Juvenile, I = immature and a = adult.