

1 **Running head**

2 *A bird torpor spectrum*

3 **Title**

4 Facultative variation across a shallow to deep torpor spectrum in hummingbirds

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13

14 **Abstract**

15 Many small endotherms use torpor, saving energy by a controlled reduction of their body
16 temperature and metabolic rate. Some species (e.g. arctic ground squirrels, hummingbirds) enter
17 deep torpor, dropping their body temperatures by 23-37 °C, while others can only enter shallow
18 torpor (e.g., pigeons, 3-10 °C reductions). However, deep torpor in mammals can increase predation
19 risk (unless animals are in burrows or caves), inhibit immune function, and result in sleep
20 deprivation, so even for species that can enter deep torpor, facultative shallow torpor might help
21 balance energy savings with these potential costs. Deep torpor occurs in three avian orders.
22 Although the literature hints that some bird species can use both shallow and deep torpor, little
23 empirical evidence of such an avian torpor spectrum exists. We infrared imaged three hummingbird
24 species that are known to use deep torpor, under natural temperature and light cycles, to test if they
25 were also capable of shallow torpor. All three species used both deep and shallow torpor, often on
26 the same night. Depending on the species, they used shallow torpor for 5-35% of the night. The
27 presence of a bird torpor spectrum indicates a capacity for fine-scale physiological and genetic
28 regulation of avian torpid metabolism.

29 **Key words:** body temperature, torpor, metabolism, hypothermia, avian, mammals

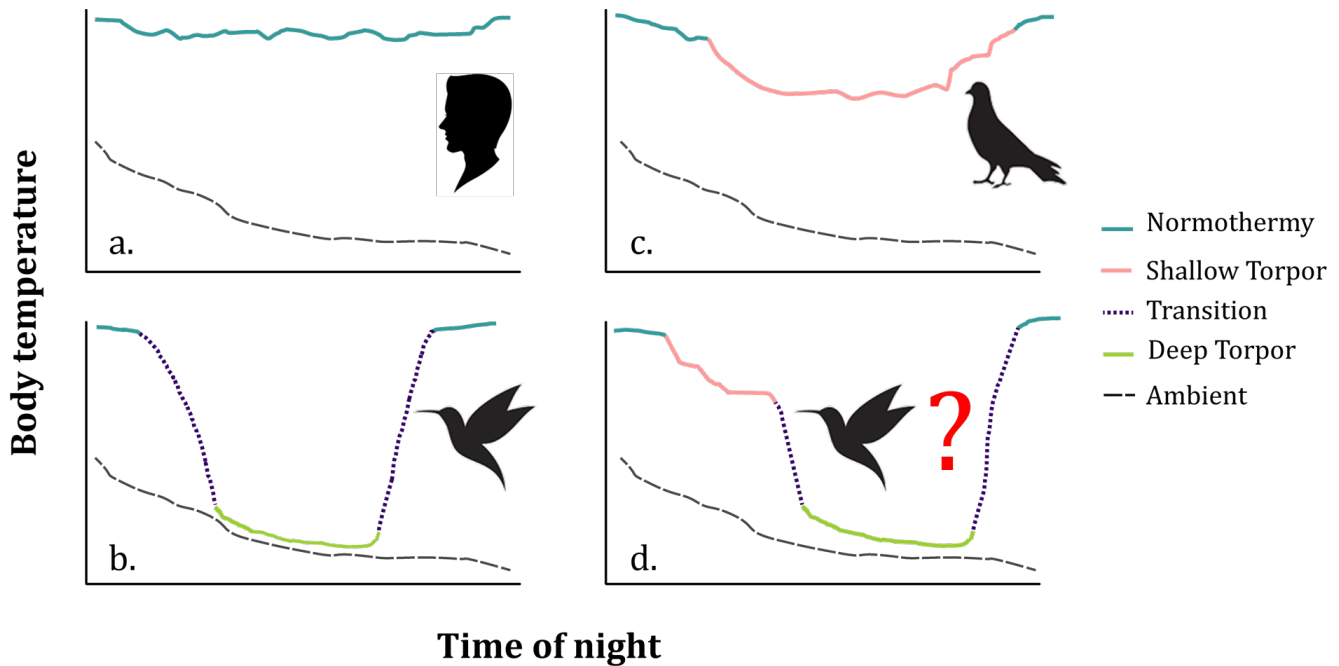
30 Introduction

31 Torpor is an energy saving strategy documented in over 200 species of birds and mammals
32 [1]. Torpid animals save energy by lowering their metabolic rate and body temperature as their
33 environment gets colder. Much of the relatively recent work on the metabolic torpor spectrum has
34 focused on mammals [1–3]. A flexible physiological continuum from shallow to deep torpor seems
35 to exist in mammals, given energetic, neurological (EEG), transcriptomic, and ecological data, as
36 found in several ground squirrel species, marmots, and kangaroo rats [4–11]. Some bird species
37 are known to use shallow torpor at night, while others regularly use deep torpor [1]. Though avian
38 shallow torpor and deep torpor have separately received research attention [12–16], the
39 differences and potential trade-offs between these states in birds are poorly studied relative to
40 mammals. There are some hints in the literature that such a torpor spectrum exists in birds under
41 specific conditions [in mousebirds, 17]. Though birds constitute 65% of extant endotherms, the
42 data on avian heterothermy are sparse compared to mammalian data [18,19], as are data on this
43 avian torpor spectrum. Exploring the range, variability, and flexibility of avian torpor can help
44 elucidate behavioural and physiological mechanisms underlying thermoregulation, energy
45 regulation and torpor use across vertebrates, and move us closer to understanding the evolution
46 of homeothermy vs. heterothermy.

47 Heterothermic animals are often described as having species-specific minimum torpid
48 body temperatures [between -2 and 29.6 °C, 1,20–23]. Depending on their minimum torpid body
49 temperatures, some birds only use a ‘shallow’ form of torpor (e.g. pigeons, body temperature 28 –
50 36 °C; Figure 1c), while others use ‘deep’ torpor, in which body temperature is low (e.g.
51 hummingbirds, 3 – 18 °C; Figure 1b). Of the 42 bird species reported to use daily torpor, only
52 hummingbirds (*Trochilidae*), nightjars (*Caprimulgidae*), and one mousebird (*Coliidae*) species

53 have minimum body temperatures colder than 20 °C; the rest use a relatively shallow form of
54 torpor [1].

55 Deep torpor likely reflects a trade-off between its benefits—an average of 60% energy
56 savings relative to basal metabolic rates [24,25]—and potential costs such as susceptibility to
57 predation, inability to rewarm, immune suppression, and sleep deprivation [3,26–30]. Given these
58 trade-offs, it might be beneficial for birds that use the deepest possible form of torpor to
59 sometimes use a shallower form, to allow moderate energy savings while minimizing some of the
60 potential costs of deep torpor [31]. Yet in contrast to mammals, birds that are known to use deep
61 torpor do not seem to use a shallower version of torpor by regulating their body temperatures
62 above this minimum [1,5,15,20,32–34]. One mousebird species has been described to use both
63 shallow and deep torpor when starved over several days, with their depth of torpor deepening as
64 their energy stores were depleted [35,36]. However, mousebirds are thought to have diverged
65 early in the avian phylogeny and their unusual combination (among birds) of low-quality plant
66 diet with a relatively small body size makes them physiologically distinct in other ways. It is also
67 possible that they display a form of ‘proto-torpor’ without the standard entry and rewarming
68 patterns of other avian lineages [36–38]. The rarity of shallow torpor in birds that use deep
69 torpor, and vice versa, would imply that shallow and deep torpor are mutually exclusive and
70 relatively inflexible states. The possible existence of a torpor continuum has been hinted at in the
71 literature [20], but evidence supporting or disproving its existence is scarce.



72

73 **Figure 1:** A schematic depiction of body temperature (coloured lines) relative to ambient
74 temperature (black dashed line) at night, in sleep, shallow torpor, and deep torpor. a. A
75 normothermic individual, with minimal circadian reductions in nighttime body temperature (e.g.
76 humans). b. An individual starts the night normothermic, then transitions into deep torpor, where
77 body temperature drops with ambient temperature, minimizing the difference between minimum
78 body temperature and ambient temperature (e.g. hummingbirds). c. An individual starts the night
79 normothermic, then transitions into 'shallow' torpor, potentially because the species has a very
80 high minimum body temperature of only 4-5 °C below normothermic levels (e.g. some pigeon
81 species). d. An individual uses a combination of normothermy, shallow, and deep torpor, at times
82 regulating its body temperature above its minimum torpid body temperature – here we
83 investigate the presence of such a torpor spectrum in hummingbirds.

84 Hummingbirds have long been known to use deep torpor to save energy overnight, with
85 minimum body temperatures varying from 3-22 °C [21,25,39,40]. One past study reported a

86 shallower form of torpor in hummingbirds, but its experimental conditions may have prevented
87 deep torpor: those birds were maintained at warm temperatures, were not free-living, and were
88 frequently disturbed at night [41]. If hummingbirds can use both shallow and deep torpor, they
89 are facultatively controlling their body temperature and metabolism over a broad range of torpid
90 temperatures, despite much lower ambient temperatures. This flexibility in body temperatures is
91 almost never described in birds, but such a capacity could contribute to hummingbirds' ability to
92 thrive under diverse and variable environmental conditions, from deserts to tropical forests and
93 from sea level to the high Andes, despite their small body size and extreme metabolic demands.
94 Previous work suggested that some larger hummingbird species had more variable metabolic
95 rates than smaller hummingbirds [24,39], and our preliminary data from sites in the high
96 Ecuadorian Andes has also suggested that some hummingbird species there might be using a
97 range of shallow and deep torpor (Shankar et al., unpub).

98 Here we test whether hummingbirds are capable of shallow torpor by recording nighttime
99 surface temperatures in three species sympatric at sites in Arizona (USA) where nighttime
100 temperatures are cold enough to allow deep torpor. We know from previous work that all three
101 species use deep torpor [16,24]. We hypothesized that these hummingbirds might facultatively
102 use shallow torpor to balance the energy savings and physiological costs of deep torpor.
103 Hummingbirds appear to delay torpor until they have reached some minimum threshold of energy
104 stores [16,25,42]. We therefore expected birds to use shallow torpor in one of two ways: either
105 exclusively with normothermy (Figure 1c), or before entering deep torpor, as a strategy to delay
106 the onset and potential costs of deep torpor (Figure 1d). Given that hummingbirds seem to reach a
107 minimum energetic threshold before entering deep torpor [16], we expected that once a bird
108 entered deep torpor, it would stay in deep torpor for the remainder of that night, and then rewarm

109 to normothermy before flying off, rather than using shallow torpor after deep torpor. We use
110 thermal imaging to study hummingbird torpor under near-natural conditions. This study design
111 allows us to assess torpor use under natural light and temperature cues, as well as near-natural
112 energy stores. If hummingbirds can use shallow as well as deep torpor, it would imply that they
113 are able to regulate their metabolism and body temperature dynamically and with great flexibility.
114 Such physiological control in torpor would in turn imply that a broad and perhaps continuous
115 avian metabolic torpor spectrum exists, much like in mammals.

116 **Methods**

117 *Study sites and species*

118 We studied males of three hummingbird species at the Southwestern Research Station
119 (SWRS) in the Chiracahua mountains of Arizona (Lat: 31.9, Long: -109.2): the blue-throated
120 mountain-gem (*Lampornis clemenciae*; 8.4g, n = 14), Rivoli's hummingbird (*Eugenes fulgens*; 7.6g,
121 n =12) and the black-chinned hummingbird (*Archilocus alexandri*; 2.9g, n = 7). Two blue-throated
122 mountain-gem individuals had some bill corrugation and were likely late-stage juveniles. Within
123 this hummingbird community, both the black-chinned and Rivoli's hummingbirds are subordinate
124 to blue-throated mountain-gems (i.e., with less exclusive access to floral resources) [16,43]. We
125 collected data between June 10 – 19, 2017 and May 20 – June 7, 2018.

126 *Thermal imaging—nighttime surface temperatures*

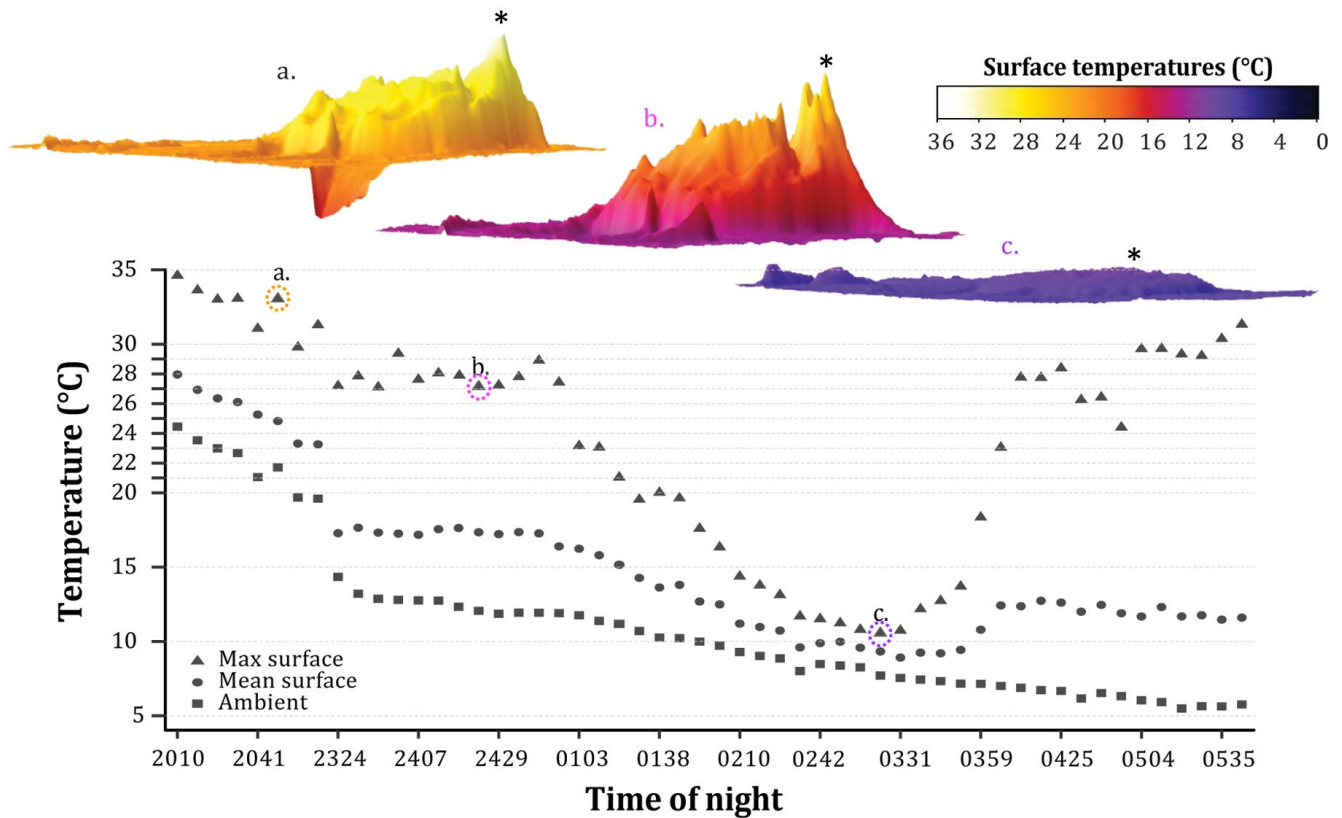
127 We captured hummingbirds using modified Hall traps at hummingbird feeders [44] within
128 1.5 hours before sunset, to allow them to store energy naturally through the day, but also
129 acclimate to our experimental setup. Most birds were already banded (this is a long-term bird
130 monitoring site), but un-banded birds were marked with a small dot of non-toxic paint on the

131 forehead. We recorded capture mass, allowed the birds to feed *ad libitum*, and weighed them again
132 for mass after feeding. They were then placed outdoors (individually) in five-sided acrylic
133 chambers (either 18x17x22 cm or 46x23x46 cm), exposed to natural light and temperatures. The
134 front face of the chamber was covered by a clear plastic sheet to prevent the bird escaping. This
135 sheet caused the thermal reading of the bird's surface temperatures to be up to 2 °C cooler than
136 direct bird readings, so once the bird was observed to settle down, the plastic sheet was removed.
137 We placed a wire grill at the base of the chamber to encourage birds to perch with their sagittal
138 plane facing the camera, usually ensuring that recordings included a direct view of the bird's eye.
139 Recordings without this view were excluded from analyses.

140 Bird eye surface temperatures seem to closely reflect internal physiological state (e.g. body
141 condition), from recent work in blue tits [45]. Hummingbirds have low feather density around the
142 eye, so skin eye temperature patterns should closely reflect the patterns of core body
143 temperature, minimizing the confounding effects of feather insulation, unlike in larger animals for
144 which skin and core temperatures might vary because of reduced peripheral blood flow in torpor
145 [15,46–49]. The traditional rules of endotherm thermoneutrality and body temperature do not
146 seem to apply in hummingbirds because of their small size and status as 'micro-endotherms'; they
147 do not seem to maintain steady-state thermal equilibrium as a result [50]. . Powers et al. [51] used
148 thermal imaging to measure heat dissipation areas in hovering hummingbirds during the day in
149 three species. They found that across all three species, eye surface temperature remained
150 relatively constant across a range of ambient temperatures, with an intercept of 32–33 °C [Figure
151 2 in 51]. Although this is lower than core body temperature, it is consistent with what is observed
152 in individuals from these same species that are clearly normothermic. This supports our
153 measurements of 32 °C being a common resting normothermic body temperature. A recent study

154 of hummingbird body temperature in torpor across six species showed that many individuals
155 maintained normothermy at body (cloacal) temperatures below 40 °C [39]. Additionally, there
156 seems to be high concordance between eye surface temperatures and metabolic rates as measured
157 in ruby-throated hummingbirds (Erich Eberts, unpub.).

158 We used a FLIR SC6701 infrared video camera (640 × 480 pixel resolution, sampling at
159 300 Hz; accurate to 1 °C at measured temperatures) to record surface temperatures of
160 hummingbirds. We assumed emissivity was 0.95 across all surfaces of the hummingbird [47,52].
161 We monitored birds continuously through the night, and sampled surface temperatures by
162 recording 10 seconds of 30Hz video approximately every 10 minutes, using ResearchIR (FLIR,
163 Inc.). From one frame per recording, a region including the bird and a slight buffer to include
164 ambient temperatures was marked as a region of interest and exported to csv files for analysis in
165 R [v.3.5.1; 53]. From each exported region of interest, we extracted maximum surface temperature
166 (in Celsius) and mean surface temperature of the bird, as well as minimum temperature (our
167 proxy for ambient temperature). We verified that maximum surface temperatures corresponded
168 with maximum eye surface temperatures, and validated outliers in temperature measurements to
169 ensure that they were reliable measurements. We also exported entire single-frame images from
170 selected recordings and used ImageJ (NIH) to construct 3D images to assess how surface
171 temperatures changed over the entire surface of the bird.



172

173 **Figure 2:** A Rivoli's hummingbird using all four metabolic states (normothermy, shallow torpor,
174 transition and deep torpor). Top: 3D plots of the surface temperature of the bird in normothermy,
175 shallow torpor, and deep torpor, aligned with the tail-beak axis along the x-axis. Asterisks indicate
176 the location of the eye. See Supplementary Video SV1 for perspective on the 3D plots. a.
177 Normothermic: surface temperatures peak at 35 °C near the eye; mean surface temperature is 25
178 °C. b. Shallow: surface temperatures peak around the eye at 27 °C, followed by a drop in
179 temperature and steady, much lower, surface temperatures over the rest of the body (17 °C), and
180 then a steady drop towards the tail. c. Torpor: The entire surface of the bird is cold, peaking
181 around the eye at 11 °C.

182 *Ambient temperature*

183 We used minimum temperatures from thermal image regions of interest as an estimate of
184 ambient temperatures, verifying that these closely matched independent ambient temperature
185 measurements from iButtons (Maxim Integrated DS1921) or thermocouples (Cu-Cn type-T,
186 recorded on a TC-1000; Sable Systems). The FLIR camera was factory calibrated and verified by
187 imaging a surface of a known temperature. Thermocouples and iButtons were calibrated by using
188 a Percival (model I-35LV, Percival Scientific, Inc.) at controlled temperature steps, and checked
189 against a thermometer traceable to the National Institute of Standards and Technology.

190 *Thermal categories*

191 We assigned bird surface temperature measurements at each time point to one of four
192 categories: normothermy, shallow torpor, transition to and from deep torpor, or deep torpor. We
193 defined these categories using individually assigned thresholds for each bird. We used eye surface
194 temperatures of the bird once it had settled, but its eyes were still open, to define resting
195 normothermic temperatures. Once the eyes were closed, we considered the bird asleep [54]. If eye
196 surface temperatures dropped more than 2 °C below these resting temperatures, we classified the
197 birds into one of the other three categories based on 1. rate of temperature change (stable, slow
198 change, rapid change), and 2. magnitude of decrease of eye surface temperature below
199 normothermic temperature, and above ambient temperature.

200 Birds were considered in shallow torpor if they dropped more than 2 °C but less than 20 °C
201 below their resting temperature (but were still above ambient temperature), and maintained that
202 temperature for more than 10 minutes (stable temperatures). Measurements were assigned to the
203 transition category if they dropped or increased rapidly between normothermy and deep torpor,

204 or between shallow and deep torpor (i.e. transitions were defined by rapid, large temperature
205 changes; average rate of change \pm s.e. of 0.45 ± 0.06 °C/min, up to 3 °C/min; see Figure S2 for
206 details). Birds were considered to be in deep torpor if eye surface temperature was close to
207 ambient temperature, or if it was maintained below 20 °C without dropping any lower (stable, low
208 temperatures), for an extended period [highest reported hummingbird torpid body temperature is
209 22 °C, 21,55].

210 *Surface temperatures models*

211 Normothermy, shallow torpor and deep torpor could be distinguished by the relationship
212 between surface (response) and ambient (predictor) temperature. While a normothermic
213 homeotherm can maintain a relatively stable body or surface temperature over a large range of
214 ambient temperatures, in deep torpor the body and surface temperatures become a positive
215 function of ambient temperature. Therefore, we would expect deep torpor to have a steep slope
216 and a very low intercept. If shallow torpor exists, then the slopes for normothermy and shallow
217 torpor should be similar and low, while their intercepts should vary (shallow torpor lower than
218 normothermy). Additionally, we expected species to use these torpor categories differently, and
219 expected mass to negatively influence torpor use [birds with greater energy stores should use
220 torpor less, 16].

221 To estimate regression equations of surface temperature as a function of ambient
222 temperature for each of the four thermal categories (normothermy, shallow torpor, transition,
223 deep torpor) we used linear mixed effects models [56] using the 'nlme' package in R [57]. A mixed
224 effects model is appropriate because the response (surface) can be modelled as a function of
225 various data types; in this case both continuous fixed effects (ambient temperature, thermal

226 categories, mass, species, and year), as well as random effects (categories nested within
227 individuals) and an autocorrelation term were incorporated. To first test the effect of ambient
228 temperature on surface temperature, we ran a simple linear model of surface temperature (T_s) as
229 a function of ambient temperature (T_a). This model only explained 15% of the variation in surface
230 temperatures, and we therefore ran an 'lme' linear mixed effects model of surface temperature as
231 a function of ambient temperature. We included mass as a continuous fixed covariate; thermal
232 category (normothermy, shallow torpor, etc.), species, and year as discrete fixed covariates, and
233 categories within individuals as a random covariate. We included interaction terms between
234 category and both ambient temperature and species. We also included an autocorrelation term
235 ('CorAR1'; see Supplement 1 for model details):

$$236 \quad T_s \sim T_a * Category + Species * Category + Capture\ mass + Year + \left(1 \middle| \frac{Individual}{Category}\right) + CorAR1$$

237 *Frequency of thermal category use*

238 To estimate the proportion of time that each species spent in each of the four categories,
239 we calculated the proportion of the night spent in each thermal category for every individual. We
240 then modelled the percentage of the night spent in each category per species. We ran thermal
241 category and species as interacting terms because we expected them to have interactive effects.

242 The model was:

$$243 \quad \textit{Category frequency} \sim \textit{Category} * \textit{Species}$$

244 We ran a generalized linear model, fitting a negative binomial distribution to the data [58].

245 We first ran Poisson and quasipoisson models, but both were overdispersed (see Supplement 1

246 and Table S1). We therefore fit a negative binomial which was much better fit than the others
247 (Table S2). We used the 'glm.nb' function in the MASS package in R to run this model [53,58,59].

248 **Results**

249 *Ambient temperatures*

250 Ambient temperatures usually declined steadily over the course of the night (1930h and
251 550h, e.g. in Figure 2). In 2017, temperatures were an average \pm s.d. of 13 ± 4.6 °C (range 3 to 23
252 °C), and in 2018 they were 11 ± 5.7 °C (range -1 to 24 °C). Most nights ranged between 5 – 20 °C
253 (mean 12 °C), except for one particularly cold night with ambient temperatures between -1 and 14
254 °C (May 20, 2018), and one especially warm night (June 5, 2018) during which ambient
255 temperatures ranged between 15 – 25 °C.

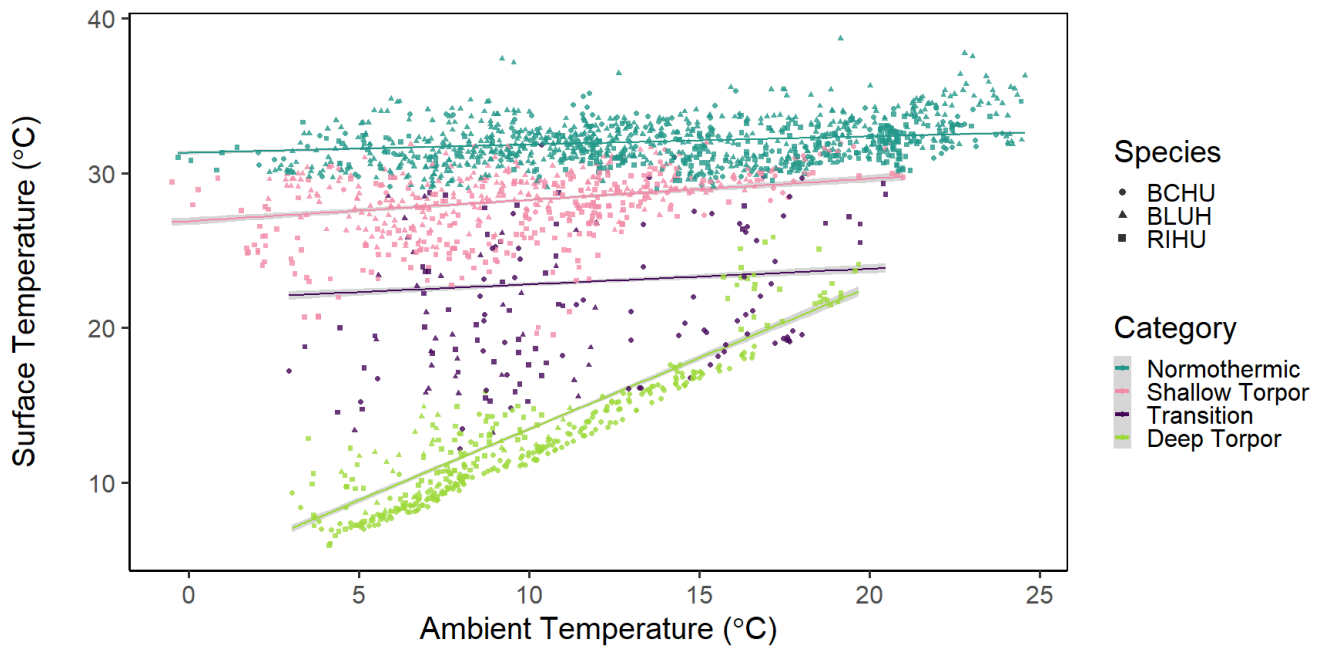
256 *Nighttime surface temperatures*

257 The surface temperatures of normothermic birds and birds in shallow torpor peaked near
258 the eye and decreased from the eye towards the tail (Figures 2 and 3). Birds in deep torpor were
259 evenly cold. Nighttime eye surface temperature varied overall between 5.9-38 °C (Supplement 2).
260 Active birds at the beginning of the night had normothermic temperatures ranging between 31-38
261 °C. This wide range included birds that were hovering and birds at rest. When they settled down,
262 normothermic temperatures usually stabilized (when the bird was resting with eyes open) at 31
263 °C, so we usually considered minimum normothermic resting surface temperatures to be around
264 31 °C. In some cases, birds stabilized at 29 °C, at both the start and end of the night, with minimal
265 fluctuation; in these cases we set the resting normothermic threshold to be 29 °C. Maximum eye
266 surface temperatures ranged from 29-38 °C in normothermy, to 19.5–29 °C in shallow torpor, and
267 5.9–24.1 °C in deep torpor. Categories varied slightly across individuals because we assigned

268 category thresholds per bird based on its surface temperature patterns relative to resting and
269 ambient temperatures, and based on the rate of temperature change.

270 *Surface temperature model results*

271 The full model for surface temperature (where the slopes and intercepts vary by category
272 and species) allowed us to identify and quantify the various thermal categories, including shallow
273 torpor (Figure 3, Table S3 and Table S4). Mass did not seem to have a large effect surface
274 temperature given the other factors, but year did.



275

276 **Figure 3:** Predicted model fit from the linear mixed effects model of maximum surface
277 temperatures (eye temperatures) as a function of ambient temperatures, coloured by category. As
278 we predicted, deep torpor had a steep slope and low intercept, while shallow torpor and
279 normothermy had similar low slopes and high intercepts (see Tables S3 and S4 for regression
280 coefficients).

281 The normothermic and shallow torpor categories had similar, very low, slopes (0.11), while
282 the normothermy intercept was about 4 °C higher than the shallow torpor intercept. A 4 °C drop
283 from normothermy has previously been categorized as being a form of torpor [1]. In contrast with
284 these thermoregulating states, hummingbirds largely thermoconform in deep torpor (down to the
285 ambient temperatures we measured them at, which were all above their minimum body
286 temperatures in deep torpor). In deep torpor, their surface temperatures closely tied to ambient
287 temperature (slope of 0.85) and a low intercept about 20 °C lower than the normothermy intercept).
288 The transition category is a non-equilibrial physiological state, with an intermediate intercept 17 °C
289 lower than normothermy.

290 *Frequency of thermal category use*

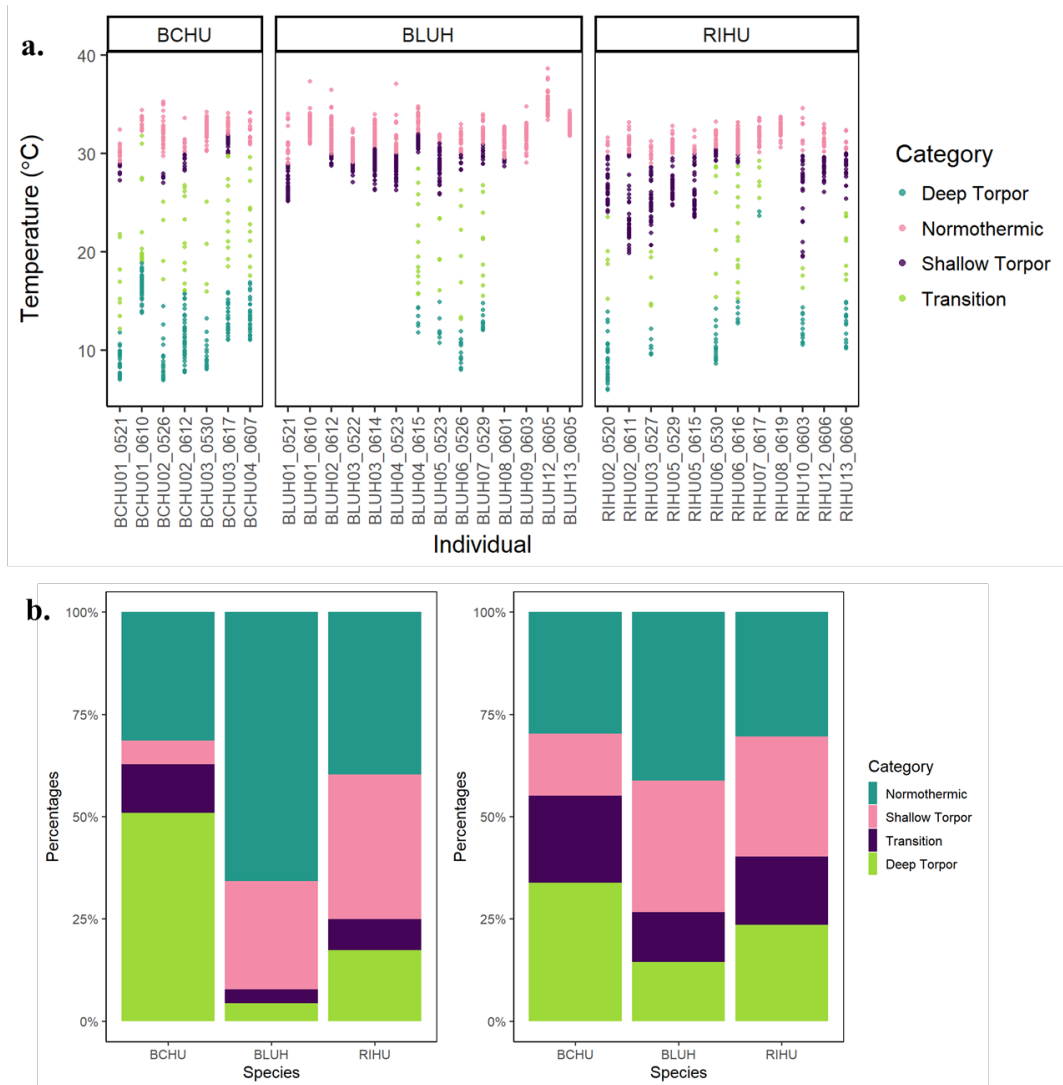
291 Shallow torpor was used by all species, but at varying frequencies (Figure 4, Figure S1). Of
292 the 33 individuals we studied, all 33 were normothermic for part of the night; 24 used shallow
293 torpor for part of the night; 17 transitioned between deep torpor and normothermy, and 17 used
294 deep torpor (Figure 4a).

295 All seven black-chinned hummingbirds (BCHU) used deep torpor, for an average of 49% of
296 the night, while only three of these individuals used shallow torpor, for an average of 5% per
297 night. BCHU spent 34% of the night on average in normothermy, and 12% in transition. The 14
298 blue-throated mountain-gems (BLUH) remained largely normothermic (67% of the total
299 nighttime), and used shallow torpor an average of 25% of the night, with four individuals
300 remaining normothermic all night, 10 individuals using shallow torpor for at least some time and
301 only four using deep torpor (4% of the night), with 3% of the night spent on transitioning on
302 average. The 12 Rivoli's hummingbirds (RIHU) were the most variable in their use of the various
303 metabolic states, with 10 individuals using shallow torpor (33% of total nighttime), six individuals
304 using all four categories, four using normothermy and shallow torpor, one individual remaining
305 normothermic all night, and one individual using all categories except shallow torpor. The RIHU
306 individuals spent an average of 43% of the night in normothermy, 8% in transition, and 17% in
307 deep torpor.

308 The model of thermal category frequency across species showed that there were overall
309 clear differences in the thermal categories across all species. There were also species-specific
310 differences in the use of normothermy, shallow torpor, deep torpor and the transition categories

311 (Figure 4b and Table S3). The model resulted in estimates that were more evenly distributed than
312 the raw data (the two panels on Figure 4b), but the differences between species were still clear.

313 The two blue-throated mountain-gems that we studied on an especially warm night
314 maintained high surface temperatures all night (33-35 °C). The two blue-throated mountain-gem
315 individuals that could have been late-stage juveniles appeared to behave similarly to adults: one
316 used all four categories, and the other used only normothermy and shallow torpor. Contrary to
317 our expectations, several Rivoli's hummingbirds and a few blue-throated mountain-gems used
318 shallow torpor for 1-2 hours after coming out of deep torpor, while the black-chinned
319 hummingbirds never used shallow torpor after deep torpor.



320

321 **Figure 4: a.** Distribution of values recorded per category (colours), per individual. BCHU = black-
 322 chinned hummingbird; BLUH = blue-throated mountain-gem; RIHU = Rivoli's hummingbird. **b.**
 323 The relative percentages of time a species spent over all nights studied (1900h-0559h) in each of
 324 the four categories: normothermic, shallow torpor, transition, torpor. BCHU = black-chinned
 325 hummingbird; BLUH = blue-throated mountain-gem; RIHU = Rivoli's hummingbird. Left:
 326 Percentages calculated using raw data. Right: Model estimates from the glm model (Category
 327 frequency ~ Category*Species - 1), of the relative time per category per species, presented as
 328 percentages.

329 Discussion

330 We describe and quantify the novel use of shallow torpor in birds that are known to use
331 deep torpor. Similar to mammals, and in contrast with previous studies that either describe birds
332 as using shallow torpor or deep torpor, hummingbirds appear capable of using both.
333 Hummingbirds in shallow torpor appear to thermoregulate to maintain surface temperatures
334 below normothermy. In contrast, hummingbirds in deep torpor largely thermoconform to ambient
335 temperatures. The intermediate shallow state could serve to balance nighttime energy savings
336 with the potential ecological and physiological costs of deep torpor. Reflecting what previous
337 studies have found [16], birds with larger energy stores seem to have greater flexibility in
338 avoiding deep torpor. The two larger species in our study used normothermy and shallow torpor
339 for a greater proportion of the night than the smaller species. Our minimally invasive study design
340 allowed us to thermally image hummingbirds under near-natural temperature cycles, without
341 disturbing or touching the birds through the night, and allowed us to discover a new level of
342 flexibility in hummingbirds' management of their nighttime energetic needs.

343 All three species used all metabolic categories, but unequally. Rivoli's hummingbirds used
344 shallow torpor the most, followed by blue-throated mountain-gems. The small black-chinned
345 hummingbirds used shallow torpor the least. It therefore appears that black-chinned
346 hummingbirds, the smallest of the three study species, might have the least flexibility in managing
347 their nighttime energy budget, while blue-throated mountain-gems, the large territorial species,
348 have the most flexibility. Individuals of the two larger species appeared to have more flexibility in
349 regulating their nighttime body temperature, commonly using shallow torpor or a combination of
350 shallow and deep torpor. The more limited use of deep torpor in these two species is consistent
351 with previous findings that these species tend to avoid deep torpor [16,24].

352 Our results support the argument that there must be either physiological or ecological
353 costs of deep torpor [1], because hummingbirds that are clearly capable of using deep torpor
354 sometimes use shallow torpor or avoid torpor altogether. Using shallow torpor rather than deep
355 torpor could be especially beneficial in three scenarios. First, deep torpor in mammals (especially
356 hibernation) is usually considered helpful in avoiding predation because torpid animals are less
357 conspicuous to predators; but these animals are usually hidden in hibernacula or dens [1,60].
358 Torpid birds in trees, in contrast, might be more conspicuous, making shallow torpor more
359 efficient than deep torpor in allowing them to respond to potential predators [30]. Hummingbirds
360 in shallow torpor could afford quicker rewarming times (< 5 minutes), and quicker responses to
361 predators or other external stimuli, relative to deep torpor for which rewarming to normothermy
362 takes an average of 20-30 minutes [24,61]. Second, at least in mammals, the physiological costs of
363 torpor include rewarming costs, immune suppression [27,28], increased oxidative stress [62], and
364 potential sleep deprivation [3,63]. There are hints that daily heterothermic mammals (Djungarian
365 hamsters, *Phodopus sungorus*; 26g) enter a euthermic state after torpor to recover from sleep
366 deprivation [26,63]. Shallow torpor would allow higher levels of metabolic function than deep
367 torpor, perhaps facilitating some of the restorative functions of sleep, immunity, and lowered
368 oxidative stress. Though avian sleep has been studied to some extent [13], little is known about
369 the physiological basis for torpor vs. sleep in birds. Third, for nesting birds that need to keep their
370 nest warm, shallow torpor could help balance the birds' need to maintain energy balance with the
371 need to supply heat to their eggs or chicks. Nesting hummingbirds have been found to generally
372 avoid torpor (with exceptions when energy stores seemed to be low); but the use of shallow
373 torpor by nesting birds has not been evaluated [64–66]. If deep torpor had no ecological or
374 physiological consequences, hummingbirds would likely maximize torpor use, or remain in deep

375 torpor for the duration of the night after entering torpor. Instead, some individuals used shallow
376 torpor not just before a deep torpor bout as we predicted, but after emerging from a deep torpor
377 bout, indicating that they may be trying to save energy but also balance these energy savings with
378 the potential costs of deep torpor.

379 Here we identified four metabolic categories in hummingbirds: two thermoregulatory
380 categories—normothermy and shallow torpor; a thermoconforming category—deep torpor; and
381 the transition between deep torpor and the other categories. In normothermy and shallow torpor
382 the animal actively thermoregulates to maintain a constant body temperature across a range of
383 ambient temperatures. Based on the similar surface temperature slopes of normothermy and
384 shallow torpor (Figure 3), and the rapid transitions between normothermy and shallow torpor
385 that we often observed, these two states seem metabolically continuous in hummingbirds [67].
386 Shallow torpor, as defined here, could potentially be a metabolically inhibited form of
387 normothermic sleep, but it is unclear whether the shallow torpor and deep torpor we report are
388 on a similar metabolic spectrum, and we were unable to definitely distinguish sleep using only
389 body temperature measurements. Multiple lines of evidence, especially in ground squirrels and
390 pocket mice, from electroencephalograms (EEGs), measurements of brain temperature, and
391 metabolic rates indicate that mammals slow their metabolism continuously down from sleep into
392 torpor, and regulate their body temperatures variably above minimum body temperature
393 [1,5,11,31,68]. Thus, though sleep and torpor appear to be on a continuous spectrum in mammals,
394 we are yet to confirm if they are on a continuum in birds.

395 Given that hummingbirds can regulate between shallow and deep torpor, the biological
396 relevance of minimum body temperature measurements must be assessed. Recent work with

397 high-elevation Andean hummingbirds found that minimum torpid body temperature showed a
398 phylogenetic signal, indicating that minimum torpid body temperature, at least at very cold sites,
399 is evolutionarily conserved [39]. Shallow torpor can occur either because a bird's minimum
400 possible torpid body temperature is relatively high (i.e., it does not have the capacity for deeper
401 torpor), or when a bird regulates at a high, sub-normothermic, body temperature despite its
402 minimum torpid body temperature being much lower (e.g. 15 °C, indicating that it is capable of
403 deep torpor; Figure 1c). These two shallow torpor scenarios are indistinguishable (as in Figure 1c)
404 unless the species' "true" minimum body temperature is known. If a bird regulates at a body
405 temperature above its minimum, even though ambient temperatures were lower, these
406 measurements might appear to be minimum body temperature measurements although they are
407 not. In Rivoli's hummingbirds, for instance, we found that eye surface temperatures went as low as
408 5.9 °C. However, Rivoli's individuals in the laboratory were previously reported to regulate their
409 minimum body temperature at 12 °C despite ambient temperatures going lower [14]. Such a large
410 disparity in birds in deep torpor is unlikely to be due to differences between core and skin
411 temperatures, and could either indicate intra-specific differences in minimum body temperature,
412 or that the birds in the previous study were using a shallower form of torpor. This disparity could
413 also be caused by birds reducing their blood circulation around the eye during torpor, but such
414 regional variation seems unlikely given the small size of hummingbirds and the even distribution
415 of low surface temperatures we observed in torpid birds. Minimum body temperature may
416 therefore be lower than has been reported in some species. Currently minimum body temperature
417 across all hummingbirds is thought to vary from 3–22 °C [39,40,55]. But if some of the
418 hummingbirds measured were using shallow rather than their deepest possible torpor, the range
419 of hummingbirds' true minimum body temperatures would be narrower or lower. Additionally,

420 torpor studies in hummingbirds are often conducted in laboratory conditions, which could alter
421 torpor responses [1,20].

422 We propose three reasons for why this form of shallow torpor in birds has so rarely been
423 detected [35]. First, small drops in oxygen consumption or body temperature might have been
424 overlooked. Second, most studies of bird torpor are either done under controlled laboratory
425 conditions, or involve handling the birds many times at night to record body temperature. Birds in
426 captivity are often overweight and have to be starved to enter torpor [69]. Laboratory torpor
427 studies conducted at controlled temperature steps might have pre-empted the use of shallow
428 torpor, because shallow torpor is presumably a fine-scale response to energetic state and
429 environmental conditions, and controlled temperature steps or repeated handling might not elicit
430 the same physiological responses as natural decreases in nighttime temperature would [70].
431 Third, birds in laboratory settings are known to show altered torpor use relative to free birds:
432 free-living animals often use torpor more frequently, and drop to a lower body temperature in
433 torpor than laboratory animals [reviewed in 1,20,71]. Taken together, under relatively predictable
434 natural temperature patterns, hummingbirds might be able to use intermediate torpor states
435 more often, while in the laboratory, low temperatures, the factor most often tested, might cause
436 the bird to either stay awake or drop into deep torpor if energetically necessary.

437 At the whole-animal level, the next step in understanding avian torpor would be to
438 combine respirometry, thermal measurements and measurements of breathing or heart rates
439 while keeping in mind the possible existence of shallow torpor. These measures have been found
440 to sometimes be uncoupled in torpor [72,73], and therefore studying whether they vary together
441 in shallow torpor would be the first step in identifying the physiological differences between
442 sleep, shallow torpor and deep torpor. A promising future avenue for research would be to

443 investigate which metabolic and genetic pathways shut down at different temperatures in
444 hummingbird torpor. It remains to be seen if other hummingbird and bird species that use deep
445 torpor are also capable of shallower torpor, or if such control over their torpid metabolism is
446 unique to these two hummingbird clades. Our data indicate that these hummingbird species in a
447 temperate environment with cold ambient temperatures often use shallow torpor; it is therefore
448 possible that tropical species at sites with high ambient temperatures might be doing the same.

449 **Author contributions**

450 AS, DRP, CHG and INHC were involved in study conception, design and obtaining funding.
451 AS, INHC, ST and DRP collected data; AS analysed the data and wrote the manuscript, CHG and
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467 **Data and Code accessibility**

468 The R scripts used to run the analyses are available on Github:

469 <https://github.com/nushiamme/TorporShallowDeep>. The data associated with this manuscript
470 are available as supplementary data files.

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