Temperature-dependent use of daily torpor attenuates the energetic consequences of habitat selection for a widespread bat

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Summary

1. Many animals employ heterothermy to conserve energy during periods of inactivity, stress, or low resource availability. Unlike homeotherms, these heterotherms have some flexibility in body temperature. Unlike poikilotherms, heterotherms can maintain body temperatures independently from their

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environments. Heterotherms should thus exhibit fundamentally different responses to suboptimal environmental temperatures than either homeotherms or poikilotherms.

2. In a species of heterothermic bat (*Myotis thysanodes*), we studied how daily torpor and roost selection could mitigate the energetic consequences of variation in ambient temperature. We then (1) quantified the relationship between ambient temperature and torpor use, (2) simulated daily energy expenditure over a range of roost temperatures, and (3) quantified the influence of roost temperature on roost selection.

3. Bats did not select roosts with specific thermal characteristics, nor did ambient temperature alter patterns of roost selection. This was likely because bats could modulate use of torpor to maintain a consistent level of energy expenditure over the course of a day, irrespective of ambient temperature.

4. Thermoregulatory processes in heterotherms differ from that of homeotherms and poikilotherms, including through behaviours as universal as habitat selection. Unlike homeotherms, bats face little pressure to select warm habitats to avoid heat loss during periods of inactivity—bats can use daily torpor to fully offset any increases in energy expenditure from maintaining homeothermy at colder temperatures.

Key-words Bayesian hierarchical models, climate change, daily torpor, fringed myotis (*Myotis thysanodes*), heterothermy, temporal heterothermy, VHF telemetry

1. Introduction

48   The thermal environments in which organisms live strongly influence metabolic rates

49   (Huey and Stevenson 1979, Brown et al. 2004, Pörtner and Farrell 2008). Among

50   homeotherms—which regulate body temperature internally within a narrow range to

51   optimize physiological processes—metabolic heat production is tightly regulated in

52   response to variation in temperature in the surrounding environment (i.e., ambient

53   temperature; Lowell and Spiegelman 2000). Controlling body temperature thus requires

54   increased energy expenditure by homeotherms when ambient temperatures depart from

55   the thermoneutral zone (i.e., the range of ambient temperatures in which homeotherms

56   can regulate body temperature with minimal metabolic effort; McNab 2002). Because

57   survival and reproduction require that energy intake equal or exceed energy

58   expenditure, operating in ambient temperatures outside the thermoneutral zone can

59   reduce fitness over time (Angilletta et al. 2010, Boyles et al. 2011).

60   Although the influence of ambient temperature on metabolism in homeotherms

61   is understood relatively well, many animals are heterotherms that can temporarily or

62   partially enter poikilothermy (in which body temperature tracks ambient temperature;

63   Withers et al. 2016). Heterothermy is common among mammals and birds (Geiser,

64   2004; Geiser & Ruf, 1995; McKechnie & Mzilikazi, 2011; Ruf & Geiser, 2015) and

65   can reduce energy expenditure during both hot and cold periods (Körtner & Geiser

66   2008, Stawski and Geiser 2012, Boyles et al. 2016, Nowack et al. 2017, Reher &

67   Dausmann 2021). As ambient temperatures depart the thermoneutral zone,

68   heterotherms can relax internal controls on metabolism; this physiological response

69   allows body temperature to track ambient temperature and reduce or altogether

70   eliminate the increased energetic costs of maintaining stable body temperatures outside

71   the thermoneutral zone (Levesque et al. 2016). Heterotherms often achieve this by

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72   entering daily torpor, a short-term hypometabolic state of inactivity in which animals

73   allow body temperature to track ambient temperature (Ruf and Geiser 2015).

74   The influence of ambient temperature on daily torpor use (and therefore energy

75   expenditure) by heterotherms is dynamic. Heterotherms use daily torpor more as

76   ambient temperatures decrease below the thermoneutral zone (Chruszcz & Barclay,

77   2002; Geiser & Broome, 1993; Geiser & Kenagy, 1988; Rambaldini & Brigham, 2008;

78   Solick & Barclay, 2006), but it is unclear how this tendency influences cumulative

79   energy expenditure over periods of time covering sequential bouts of homeothermy and

80   torpor. For a given period of time, total energy expenditure for heterotherms depends

81   on (1) the duration and frequency of bouts of torpor during that time frame, (2) ambient

82   temperatures during that time frame, and (3) the difference in metabolic rates between

83   torpor and homeothermy at a given ambient temperature. Energy expenditure might

84   increase as ambient temperatures fall below the thermoneutral zone: even though

85   heterotherms save energy by using torpor, such energy savings could be exceeded by

86   the increased energetic costs of maintaining homeothermy in colder ambient

87   temperatures (Fig. 1B). In this scenario, periodic bouts of torpor dampen but do not

88   completely offset increases in energy expenditure during periods of homeothermy at

89   cold ambient temperatures. Alternatively, it is possible that energy expenditure by

90   heterotherms is stable through a wide range of ambient temperatures because energy

91   savings from using progressively more torpor at progressively colder ambient

92   temperatures closely matches increases in energy expenditure from maintaining

93   homeothermy at colder ambient temperatures (Fig. 1C). Finally, as ambient

94   temperatures decline, the energetic savings from torpor could more than offset the

95   increased energy expenditure necessary to maintain homeothermy (Fig. 1D).

96   Such relationships between ambient temperature and energy expenditure have

97   cascading repercussions for other aspects of an animal's life. For example, animals

98   seeking to avoid fitness costs from extreme ambient temperatures often move to areas

99   of the landscape with more suitable ambient temperatures (Kearney et al. 2009, Sunday

100   et al. 2014). Animals thus often select habitats that help them maintain body

101   temperatures near optimal levels (Huey 1991, Melin et al. 2014, Freitas et al. 2016). At

102   ambient temperatures below the thermoneutral zone, homeotherms select areas of the

103   landscape where they can reduce heat loss (Courbin et al. 2017, Matthews et al. 2019)

104   or increase heat gain from the environment (Poole et al. 2016, O'Keefe and Loeb 2017).

105   At ambient temperatures that exceed the thermoneutral zone, homeotherms select areas

106   of the landscape where they can increase heat loss (McCann et al. 2016, Sarmento et al.

107   2019) or reduce heat gain from the environment (Hovick et al. 2014, Alston et al. 2020).

108   Because it allows animals some control over their thermal environments, ecologists and

109   evolutionary biologists have long been interested in such temperature-dependent habitat

110   selection by which individuals can expand the range of climatic conditions that they

111   can tolerate (Huey 1991, Morris 2011).

112   Temperature-driven habitat selection is less understood for heterotherms than

113   for homeotherms, but patterns of temperature-driven habitat selection are likely to be

114   different between animals that use these two metabolic pathways. Homeotherms have

115   relatively fixed relationships between ambient temperature and metabolic rate, and thus

116   often consistently select habitats to maintain optimal body temperatures with little

117   metabolic effort (e.g., Poole et al. 2016, Courbin et al. 2017, Sarmento et al. 2019). In

118   contrast, looser relationships between ambient temperature and metabolic rate for

119   heterotherms may allow heterotherms to select habitats with less regard to ambient

120   temperature, or even to prefer habitats that might be colder than ideal for homeotherms.

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121   For example, heterothermic Australian owlet-nightjars (*Aegotheles cristatus*)

122   preferentially roost in colder, less thermally stable tree cavities, whereas homeothermic

123   cavity-nesting birds typically select warmer, more thermally stable tree cavities

124   (Doucette et al. 2011). Empirical data on habitat selection by heterotherms is rare,

125   however, particularly for free-ranging animals.

126   Uncertainty surrounding the form and strength of relationships between ambient

127   temperature and energy expenditure limit our understanding of temperature-driven

128   habitat selection by heterotherms. For an animal attempting to minimize energy

129   expenditure during periods of inactivity, each of the hypothetical relationships between

130   energy expenditure and ambient temperature in Fig. 1 would result in a different pattern

131   of habitat selection. A heterotherm exhibiting the relationship shown by the red (B) line

132   in Fig. 1 should select warm microhabitats to save energy, similar to homeotherms. A

133   heterotherm exhibiting the relationship shown by the grey (C) line in Fig. 1 should not

134   select microhabitats based on their thermal characteristics. This pattern of habitat

135   selection would also diverge from the pattern followed by homeotherms. A heterotherm

136   exhibiting the relationship shown by the blue (D) line in Fig. 1 should select cool

137   microhabitats to save energy, opposite of the pattern followed by homeotherms.

138   Empirical tests of the influence of ambient temperature on energy expenditure are thus

139   needed to understand how ambient temperature drives habitat selection for

140   heterotherms.

141   We sought to understand how ambient temperature influences energy

142   expenditure, and how energy expenditure in turn influences habitat selection, in a bat

143   that is widely distributed throughout western North America (fringed myotis, *Myotis*

144   *thysanodes*). Like other bats inhabiting temperate latitudes, fringed myotis are

145   heterotherms that are believed to select diurnal roosts to minimize energy expenditure

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146   during diurnal periods of inactivity (Sedgeley 2001, Willis and Brigham 2005,

147   Ruczyński 2006). At temperate latitudes, temperature within roosts can vary

148   substantially throughout the day and year, and ambient temperature influences the

149   amount of time bats spend in torpor each day. Like other heterotherms, bats spend more

150   time in torpor when it is cold than when it is hot (Chruszcz and Barclay 2002, Solick

151   and Barclay 2006, Rambaldini and Brigham 2008). We hypothesized that differences

152   in energy expenditure at roosts of varying temperatures drive patterns of roost selection

153   (i.e., bats select roosts that minimize energy expenditure). Specifically, we weighed

154   evidence for four competing sets of predictions (Fig. 2).

155   *Prediction Set 1*: Bats select warm roosts regardless of ambient temperature. In this

156   scenario, energy expenditure during the day should be higher in cool roosts than in

157   warm roosts (Fig. 2.1A) because the energetic benefits from being warmer when bats

158   are maintaining homeothermy outweigh the energetic costs of spending less time in

159   torpor. If this is the case, bats should select roosts that are warmer compared to available

160   structures on the landscape (Fig. 2.1B); this pattern of selection should be consistent

161   regardless of ambient temperature during the day (Fig. 2.1C).

162   *Prediction Set 2*: Bats select cool roosts regardless of ambient temperature. In this

163   scenario, energy expenditure during the day should be higher in warm roosts than in

164   cool roosts (Fig. 2.2A) because the energetic benefits from spending more time in torpor

165   outweigh the energetic costs of being colder when bats are maintaining homeothermy.

166   If this is the case, bats should select roosts that are cooler compared to available

167   structures on the landscape (Fig. 2.2B); this pattern of selection should be consistent

168   regardless of ambient temperature during the day (Fig. 2.2C).

169   *Prediction Set 3*: Bats do not alter roost selection as ambient temperatures change. In

170   this scenario, energy expenditure during the day is roughly equal across roosts of all

171   temperatures (Fig. 2.3A). This could occur if bats modulate use of torpor such that roost

172   temperatures over the course of a day have little influence on overall energy

173   expenditure. In this case, bats should select roosts that are similar in temperature to

174   available structures on the landscape (Fig. 2.3B), and this pattern of selection should be

175   consistent regardless of ambient temperature during the day (Fig. 2.3C).

176   *Prediction Set 4*: Bats select cool roosts on cool days and warm roosts on warm days

177   (shifting roost selection). In this scenario, energy expenditure is lower in cool roosts

178   than in warm roosts on cool days, lower in warm roosts than in cool roosts on warm

179   days, and consistently higher in roosts at intermediate ambient temperatures (Fig.

180   2.4A). This may arise because of threshold effects from a non-linear relationship

181   between ambient temperature and torpor use. Namely, a threshold may exist above

182   which homeothermy requires relatively little energy even as bats spend little time in

183   torpor, but below which bats save a substantial amount of energy by using torpor. Near

184   the threshold, however, bats may use relatively little torpor even as maintaining

185   homeothermy is relatively energetically costly. In this case, bats should select roosts

186   that are roughly the same temperature on average as available structures on the

187   landscape (though the distribution may be bimodal; Fig. 2.4B), and temperatures in

188   roosts should be positively correlated with ambient temperature (Fig. 2.4C).

189

2. Materials and methods

2.1 Study Area and Species

192   We conducted our study during the summers of 2017 and 2018 on Jewel Cave

193   National Monument (43˚ 45' N, 103˚ 45' W) and surrounding areas of Black Hills

194   National Forest in South Dakota, USA. Our study area is described in Alston,

195   Abernethy, Keinath, & Goheen (2019). Mean monthly summer high temperatures

196   range between 22 – 27˚C and mean monthly summer precipitation ranges between 60

197   – 80 mm (Western Regional Climate Center 2018). Open ponderosa pine (*Pinus*

198   *ponderosa*) forests dominate, with Rocky Mountain juniper (*Juniperus scopulorum*)

199   and quaking aspen (*Populus tremuloides*) occurring locally. Forests are actively

200   managed to prevent wildfire, and those managed by the US Forest Service and private

201   landowners also undergo intensive logging. Forests form a mosaic with northern

202   mixed-grass prairie where a large stand-replacing fire occurred in in 2000. A large

203   system of caves and several smaller caves lie underground, and the landscape exhibits

204   substantial topographic relief in the form of intersecting canyon systems and rock

205   outcrops.

206   Fringed myotis roost in caves, mines, rock crevices, tree cavities, and under

207   the sloughing bark of dead trees, and forage in forest canopy and riparian areas

208   (O'Farrell and Studier 1980). We chose to focus on males because sex ratios of bats in

209   the Black Hills are heavily (>90%) male-biased (a common pattern in high-elevation

210   areas; Barclay, 1991; Cryan, Bogan, & Altenbach, 2000; Senior, Butlin, &

211   Altringham, 2005), because male *M. thysanodes* usually roost solitarily (O'Farrell and

212   Studier 1980), and because male bats maintain consistent patterns of torpor use

213   throughout the reproductive season (unlike females, which alter patterns of torpor use

214   at different stages of reproduction; Chruszcz & Barclay, 2002; Dzal & Brigham,

215   2013; Johnson & Lacki, 2014).

216

217   **2.2 Capture and VHF Telemetry**

218   We used mist nets to capture bats over permanent and semi-permanent water sources

219   (e.g., springs, stock tanks, and stock ponds). From June through August of 2017 and

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220 2018, we netted 20 and 49 nights, respectively, at 15 water sources. We opened mist

221 nets at civil sunset and closed them after five hours or during inclement weather.

222   We affixed temperature-sensitive VHF transmitters (LB-2XT model .28/.33 g

223 – Holohil Systems Ltd., Carp, ON, Canada) between the scapulae of adult male

224 fringed myotis with latex surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal,

225 QC, Canada). The transmitters measure and transmit data on skin temperature—an

226 accurate proxy for body temperature—of bats, enabling researchers to delineate bouts

227 of torpor (Barclay et al. 1996, Chruszcz and Barclay 2002, Stawski and Geiser 2010).

228 All transmitters weighed <5% of the mass of the bat (Aldridge and Brigham 1988).

229 We tracked bats to roosts each day transmitters were active, and installed VHF data

230 loggers (SRX800-D1 – Lotek Wireless Inc., Newmarket, ON, Canada) that collected

231 and recorded data transmitted by the VHF transmitters. All protocols were approved

232 by the University of Wyoming and National Park Service Animal Care and Use

233 Committees and met guidelines approved by the American Society of Mammalogists

234 for research on wild mammals (Sikes and the Animal Care and Use Committee of the

235 American Society of Mammalogists 2016).

236

237 **2.3 Energetic Modelling**

238 To quantify torpor use, we delineated bouts of torpor from data logger readings that

239 captured full days (i.e., from roost entry in the morning to roost exit in the evening) of

240 skin temperature data from individual bats. This was a fraction of total days in which

241 we located roosts, because bats typically were not located until after they entered roosts.

242 We defined torpor as beginning when skin temperature dropped below the lowest skin

243 temperature of bats maintaining homeothermy during a day and ending when skin

244 temperature began a steep rise that led to bats re-entering homeothermy or leaving a

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245   roost (as recommended by Barclay, Lausen, & Hollis, 2001; Fig. A1). Because fat

246   reserves and body mass can substantially alter the amount of time spent in torpor

247   (Wojciechowski et al. 2007, Stawski and Geiser 2010, Vuarin et al. 2013), we also

248   controlled for the body mass of each individual at time of capture on torpor duration.

249   We then used the modelling software 'Stan' (Carpenter et al. 2017) via the R package

250   'brms' (Bürkner 2017) to build a linear Bayesian hierarchical model to quantify the

251   influence of ambient temperature and body mass on torpor duration while accounting

252   for non-independence among data points collected from the same individual. The model

253   included 3 chains run for 13,000 iterations (1,000 iterations of warm-up and 12,000

254   iterations of sampling). We assessed chain convergence using the Gelman-Rubin

255   diagnostic ($\hat{R}$) and precision of parameter estimation using effective sample size. $\hat{R} <$

256   1.01 and effective sample sizes > 10,000 represent acceptable convergence and

257   parameter precision (Gelman et al. 2013, Kruschke 2015). We used leave-one-out cross

258   validation to check model fit using the R packages 'loo' (Vehtari et al. 2017) and

259   'bayesplot' (Gabry et al. 2019) to visually assess the cross-validated probability integral

260   transform.

261   To quantify energy expenditure in bats, we combined published estimates of

262   metabolic rates of fringed myotis as a function of temperature (Studier and O'Farrell

263   1976) and the linear model of the influence of ambient temperature on torpor use to

264   simulate the influence of roost temperature on energy expenditure. Specifically, we

265   simulated minute-by-minute energy expenditure by bats in each used roost between

266   0445 hrs and 2100 hrs (typical entry and exit times for bats in our study) on each day

267   over the duration of our study period. We modeled torpor use as a function of decision

268   rules that reflect torpor use observed over the course of our study (raw data presented

269   in Table A1). Specifically, we assumed that bats entered torpor immediately upon

270 entering roosts, exited torpor after an interval determined by roost temperature, and

271 remained in homeothermy for the rest of the time spent in the roost except for a shorter

272 bout of torpor in the evening. We further assumed that bats would use 86.9% of the

273 duration of daily torpor in the morning and 13.1% in the afternoon unless the afternoon

274 bout of torpor would be less than 30 minutes in duration, in which case 100% of the

275 day's torpor would occur in the morning period. We also assumed that the mean

276 duration of torpor that we observed would be used in the baseline "average" roost, with

277 the duration of torpor in warmer and cooler roosts determined by the slope of the

278 modeled relationship between ambient temperature and torpor use described in the

279 above paragraph. To account for uncertainty in our estimate of the slope of the

280 relationship between ambient temperature and daily torpor use, for each roost on each

281 day we randomly drew a different slope estimate for this relationship from the posterior

282 distribution of slope estimates from the model described in the prior paragraph.

283

284 **2.4 Roost Characterization**

285 To characterize rock roost structures, we collected data for 31 roosts and 62

286 randomly sampled available (i.e., unused by bats in our study) roosts. Hereafter, we

287 distinguish between 'used roosts' and available but unused 'available roosts'; we use

288 the term 'roost structure' when we refer to both used and available roosts

289 simultaneously. We identified available rock roosts in two ways: at each used roost,

290 we 1) located the nearest rock crevice large enough to hold a bat, and 2) generated a

291 paired point in a random cardinal direction a random distance between 100 – 300 m

292 away, then located the nearest rock crevice large enough to hold a bat.

293 To characterize tree roost structures, we collected data for 9 used roosts and 36

294 randomly sampled available roosts. We identified available tree roosts in two ways: at

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295   each used roost, we 1) located the nearest snag and selected the nearest cavity large

296   enough to hold a bat, and 2) generated a paired point in a randomly determined

297   distance between 100 – 300 m away, in a randomly-determined (cardinal) direction,

298   then located the nearest tree cavity large enough to hold a bat. For each available

299   point, we placed data loggers in two locations: one in a cavity in the trunk and one

300   underneath sloughing bark. We defined available roost trees as any dead tree with a

301   visible defect (e.g., sloughing bark or cavities) sufficiently large to hold a bat. This

302   description fit every tree in which we found a bat roosting.

303   In Summer 2018, we monitored temperatures within both used and available

304   roosts using data loggers (Model MX2201; Onset Computer Corporation, Bourne,

305   MA, USA). The first data loggers were deployed on 17 July 2018, and the last data

306   logger was removed on 8 October 2018. This period of time includes the full range of

307   daily high temperatures occurring during the active season for bats at our study site.

308   During data logger deployment and opportunistically thereafter, we checked roost

309   structures for the presence of bats. We sometimes found bats in used roosts, but we

310   never found bats in available roosts. When we found bats in used roosts, we waited to

311   deploy data loggers until there was no bat within the roost.

312   To quantify the thermal characteristics of each roost structure, we calculated the

313   mean temperature within each roost structure for periods between 0445 and 2100 hrs,

314   which corresponds with the period in which a bat is likely to be within a roost (Table

315   A1). To control for potential confounding variables, we also calculated the timing of

316   the peak temperature in all roost structures (because if two roost structures have the

317   same mean temperature but peak in temperature at different times, the roost structure

318   with the later peak will have cooler temperatures in the morning when bats use torpor

319   most), and the standard deviation of temperature during the day (because stability in

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320   roost temperature can be an important factor in roost selection; Sedgeley, 2001). To

321   quantify the timing of the daily temperature peak, we located the peak temperature in

322   each roost structure for each day and calculated the mean time of day at which this

323   occurred over our study period. To quantify thermal stability in roost structures, we

324   calculated the standard deviation of temperatures between 0445 and 2100 hrs in each

325   roost structure for each day and calculated the mean daily standard deviation over our

326   study period. To ensure consistency, we only calculated these values for the period

327   between July 28 and September 31 (a period in which all data loggers were actively

328   logging temperatures, and in which average daily high temperatures correspond with

329   the range a bat might be exposed to during the active season in our study area).

330   We used the R statistical software environment (R Core Team 2020) to quantify

331   differences between used and available roosts. To determine whether bats select cooler

332   roosts than those available, we used the modelling software 'Stan' (Carpenter et al.

333   2017) via the R package 'brms' (Bürkner 2017) to build a binomial-family Bayesian

334   model to quantify the influence of mean temperature within roost structures, the timing

335   of daily peaks in temperature within roost structures, and the standard deviation of

336   temperatures within roost structures on roost selection. The model included 3 chains

337   run for 13,000 iterations (1,000 iterations of warm-up and 12,000 iterations of

338   sampling). We assessed chain convergence using $\hat{R}$ and precision of parameter

339   estimation using effective sample size. We checked predictive performance with

340   receiver operating curve analysis using the R package 'pROC' (Robin et al. 2011) and

341   used the R package 'bayesplot' (Gabry et al. 2019) to visually assess binned residual

342   plots.

343

344   **3. Results**

345   We tracked 46 bats to 107 roosts (93 in rocks and 14 in trees) and collected 27 full days

346   of skin temperature data from 7 bats. Data from 16 data loggers within roost structures

347   (3 used rock, 12 available rock, 1 available tree) could not be collected because they

348   were not relocated or were dislodged from roost structures. We thus excluded these data

349   from analyses, leaving a total of 122 (78 rock, 44 tree) data loggers that collected data

350   on temperatures within roost structures.

351   Use of torpor stabilized daily energy expenditure across the range of roost

352   temperatures observed during our telemetry study. In our model of the effect of ambient

353   temperature on daily torpor duration, 95% credible intervals for the effect of mean

354   ambient temperature over the course of the day on daily torpor duration did not cross 0

355   (parameter estimate: -37.4 min; 95% credible intervals: -64.0 – -12.6 min), indicating

356   that bats spent ca. 37 minutes less in torpor per day for each additional 1˚C in daily

357   mean ambient temperature between 0445 hrs and 2100 hrs (Fig. 3). Assessment of the

358   cross-validated probability integral transform indicated that model fit was adequate.

359   When incorporated into our simulation of bat energy expenditure over the course of a

360   typical day, this estimate of the relationship between ambient temperature and torpor

361   use led to similar estimates of energy expenditure across temperatures within used

362   roosts (Fig. 4; blue points). Daily energy expenditure was roughly equivalent in all

363   roosts. Our estimates for energy expenditure using observed bat behaviour were always

364   substantially lower and substantially less variable than our estimates for energy

365   expenditure if bats had remained in homeothermy all day (Fig. 4; red points). Bats that

366   remain in homeothermy would expend substantially more energy in cool roosts than in

367   warm roosts.

368   Overall, temperatures in both rock and tree roost structures were similar, though

369   roost structures in trees were slightly cooler and less stable than roost structures in

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370   rocks. During the day, rock crevices averaged 20.1°C (range: 16.5° – 24.2°C) while tree

371   roost structures averaged 18.8°C (range: 16.1° – 25.5°C). Daily maximum temperatures

372   within rock crevices averaged 26.1°C (range: 17.9° – 40.8°C), while daily maximum

373   temperatures within tree roost structures averaged 28.3°C (range: 21.0° – 52.1°C).

374   Temperatures within rock crevices peaked at 1441 hrs on average (range = 1005 – 1742

375   hrs), while temperatures within tree roost structures peaked at 1357 hrs on average

376   (range = 1056 – 1659 hrs). Ambient temperature strongly influenced temperatures

377   within roost structures. Temperatures within rock crevices at each hour (in °C) followed

378   the equation $7.67 + 0.73*$ambient temperature ($R^2 = 0.54$), while temperatures within

379   tree roost structures at each hour followed the equation $1.63 + 1.00*$ambient

380   temperature ($R^2 = 0.63$). We pooled rock and tree roost structures in roost selection

381   analyses, but we report descriptive statistics for each type of roost structure in Appendix

382   1.

383   Despite substantial variation in temperatures among roost structures, we found

384   little evidence that the thermal characteristics of used roosts differed from those of

385   available roosts (Fig. 5). In our model of roost selection, 95% credible intervals for the

386   effect of mean ambient temperature over the course of the day on roost selection did

387   not cross 0 (parameter estimate: 0.30; 95% credible intervals: 0.04 – 0.58), indicating

388   that bats were more likely to roost in warm roost structures than cool ones. However,

389   predictive performance was poor (AUC: 0.650), and overall, used roosts (20.1°C) had

390   similar mean temperatures as available roosts (19.4°C; Fig. 5A). Bats also did not

391   differentiate between roost structures with temperatures peaking late in the day versus

392   roost structures with temperatures peaking early in the day (Fig 5B). In our model of

393   roost selection, 95% credible intervals for the effect of the timing of daily peaks in

394   temperature on roost selection crossed 0 (parameter estimate: -0.10; 95% credible

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395   intervals: -0.34 – 0.14). Overall, used roosts (1408 hrs) had similar timing of peak

396   temperature as available roosts (1434 hrs). Bats also did not differentiate between roosts

397   with stable temperatures and those with more variable temperatures (Fig. 5C). In our

398   model of roost selection, 95% credible intervals for the effect of standard deviation in

399   roost temperature over the course of the day on roost selection crossed 0 (parameter

400   estimate: -0.20; 95% credible intervals: -0.47 – 0.06) Overall, there was no difference

401   in the standard deviation of temperatures of used roosts (7.0˚C) and available roosts

402   (7.0˚C). Finally, there was also no relationship between ambient temperature on a given

403   day and mean temperatures within roosts used on that day ($R^2 = 0.03$; $p = 0.132$; Fig.

404   6).

405

4. Discussion

407   The thermal environments in which animals operate strongly influence physiological

408   processes, and can thereby pose substantial challenges to animals living in variable

409   environments. How animals overcome these challenges is a central question in animal

410   ecology. Attempts to address this question have focused largely on poikilotherms and

411   homeotherms. Because heterotherms are neither as strongly tied to narrow ranges of

412   body temperature as homeotherms nor as subject to ambient temperatures as

413   poikilotherms, heterotherms are likely to respond to heat and cold fundamentally

414   differently than either homeotherms or poikilotherms.

415   We sought to better understand how variation in ambient temperature influences

416   use of daily torpor and habitat selection for heterotherms, using a species of bat as a

417   model system. Simulations of energy expenditure at varying roost temperature

418   indicated that bats can modulate use of torpor to maintain a consistent level of energy

419   expenditure over the course of a day over a wide range of thermal conditions within

17

420   roosts. As a result, roost selection was not driven by temperatures within roosts. Our

421   results provide evidence for Prediction Set 3 (no selection) in our introduction (Fig. 2).

422   The energetic savings associated with torpor—particularly at cooler

423   temperatures—likely result in habitat selection that differs substantially from habitat

424   selection by homeotherms. For example, we showed that use of daily torpor can reduce

425   the energetic costs of inhabiting roosts that are colder than optimal for homeotherms. If

426   bats were strict homeotherms, the energetic costs of inhabiting cool roosts would have

427   been substantially higher (Fig. 4), which would likely result in bats selecting warm

428   roosts. In contrast, heterothermic bats face little pressure to select warm habitats, even

429   on relatively cool days.

430   Individual traits (e.g., sex, age, and reproductive condition) can alter the

431   energetic costs and benefits of using torpor for heterotherms, thereby driving the extent

432   to which habitat selection might follow the pattern demonstrated in this study. For

433   example, roost selection by bats varies by sex, age, and reproductive condition (Elmore

434   et al. 2004, Hein et al. 2008). While male bats in our study did not select roosts with

435   specific thermal characteristics, female bats seem to use less torpor and prefer warmer

436   roosts than males while pregnant or raising young, and females typically aggregate in

437   social maternity colonies rather than roosting solitarily (Hamilton and Barclay 1994,

438   Kerth et al. 2001, Ruczyński 2006). Compared to males, then, roost selection by females

439   will likely be governed more strongly by thermal characteristics (though social

440   thermoregulation via huddling can influence thermal conditions within roosts more than

441   a roost's physical and environmental characteristics; Pretzlaff, Kerth, & Dausmann,

442   2010; Willis & Brigham, 2007). Further research on the roles of sex, age, and

443   reproductive condition on torpor use in heterotherms (and thus habitat selection by

444   heterotherms) is likely to reveal important context for our findings.

445   Climate warming increases energy expenditure for many animals, including

446   both poikilotherms (Pörtner and Knust 2007, Dillon et al. 2010) and homeotherms

447   (Humphries et al. 2002, Şekercioğlu et al. 2012, Albright et al. 2017). However, the

448   degree to which climate warming will impact heterotherms is poorly understood,

449   largely due to a lack of data on relationships between ambient temperature, torpor use,

450   and thermolability that is needed to accurately model the influence of ambient

451   temperature on heterotherm metabolism (Levesque et al. 2016). Our results indicate

452   that temperature-dependent use of torpor may stabilize energy expenditure, and thus

453   buffer against the energetic costs associated with variable ambient temperatures.

454   However, most of the energetic savings derived from heterothermy arise during periods

455   of cold. Increased temperatures due to climate change may thus reduce the relative

456   energetic benefits of heterothermy compared to homeothermy, as homeotherms

457   experience fewer and milder periods of cold.

458   In conclusion, we showed that a heterothermic bat selected neither warm nor

459   cool roosts, because bats can modulate torpor use to stabilize energy expenditure over

460   the course of a day. Unlike homeotherms, bats face little pressure to select warm

461   habitats to avoid heat loss during periods of inactivity—when maintaining a high, stable

462   body temperature becomes energetically costly, bats can enter torpor to reduce energy

463   expenditure. Although such fine-tuning of torpor use to stabilize daily energy

464   expenditure is intuitive, it has not been demonstrated in previous studies to the best of

465   our knowledge. Furthermore, our study provides evidence that the thermoregulatory

466   behaviours of heterotherms are likely to diverge in meaningful ways from those of

467   homeotherms, including in behaviours as basic and pervasive as habitat selection.

468

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484

Data Accessibility

486   Data and code used in analyses for this paper will be archived on *Zenodo* upon

487   acceptance of this manuscript.

488

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Figures

Fig. 1. Heuristic diagram outlining the potential energetic benefits for an individual of using periodic bouts of daily torpor rather than remaining in homeothermy at temperatures below the thermoneutral zone. Each hypothetical relationship would result in different patterns of habitat selection for animals seeking to minimize energy expenditure during periods of inactivity. The black (A) line represents energy expenditure over a unit of time while maintaining homeothermy 100% of the time. The red (B), grey (C), and blue (D) lines indicate energy expenditure over the same unit of time while using some amount of torpor. For all three relationships, torpor provides energy savings (i.e., the difference between the black and other lines), and these savings are more pronounced at colder ambient temperatures. (B) For heterotherms that use at least some torpor, energy expenditure *increases* at colder ambient temperatures because while some energy is saved from employing torpor, maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *warm* microhabitats to reduce energy use. (C) For heterotherms that use at least some torpor, energy expenditure *is stable* across a wide range of ambient temperatures because the energy saved from employing torpor matches (and thus offsets) the increase in energy expended to maintain homeothermy at colder temperatures. A heterotherm exhibiting this relationship would not benefit from seeking either warm or cool microhabitats. (D) For heterotherms that use at least some torpor, energy expenditure *decreases* at colder ambient temperatures because relatively more energy is saved from employing torpor even as maintaining homeothermy at colder ambient temperatures is relatively more costly than at warmer temperatures. A heterotherm exhibiting this relationship would seek *cool* microhabitats to reduce energy use.

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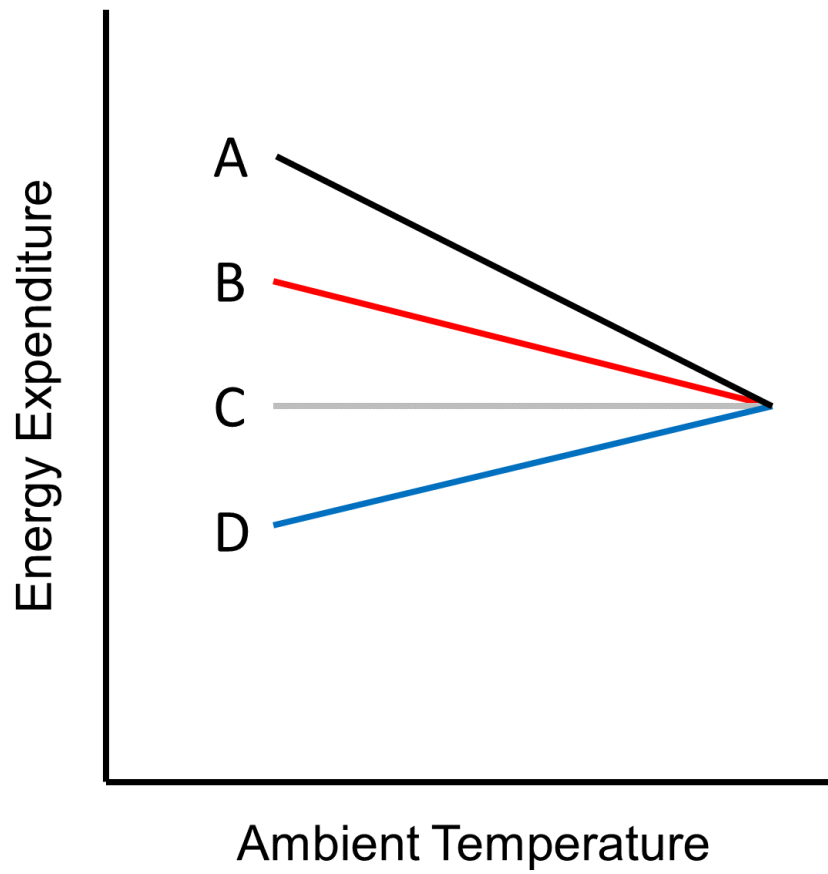
737

738   **Fig. 2.** Four competing sets of predictions of roost selection by a heterothermic bat. Each column represents one of four sets of predictions, and

739   each row represents a statistical relationship consistent with the predictions. In column 1, energy expenditure over the course of a day is higher

740   in cool roosts than in warm roosts (1A). In response, bats select warm roosts to minimize energy expenditure during the day (1B). In this

741   scenario, there should be no directional relationship between ambient temperature and roost temperature (i.e., bats always select warm roosts

742   regardless of ambient temperature; 1C). In column 2, energy expenditure over the course of a day is higher in warm roosts than in cool roosts

743   (2A). In response, bats select cool roosts to minimize energy expenditure during the day (2B). In this scenario, there should be no directional

744   relationship between ambient temperature and roost temperature (i.e., bats always select cool roosts regardless of ambient temperature; 2C). In

745   column 3, energy expenditure over the course of a day is constant across roosts of all temperatures (because bats can adaptively use torpor so

746   that roost temperatures over the course of a day have little influence on overall energy expenditure; 3A). Because energy expenditure is

747   consistent across roosts of all temperatures, bats do not select roosts due to roost temperature (3B). In this scenario, there is no relationship

748   between ambient temperature and roost temperature (i.e., bats never select roosts due to temperatures within roosts, regardless of ambient

749   temperature; 3C). In column 4, energy expenditure peaks at intermediate roost temperatures where bats use relatively little torpor but the costs of

750   maintaining homeothermy are relatively high (4A). In response, bats select cool roosts on cool days and warm roosts on warm days (4B) because

751   torpor saves more energy in cool roosts than in warm roosts. In this scenario, the relationship between ambient temperature and roost

752   temperature should be positive (i.e., bats select warmer roosts on warmer days; 4C).

1 | Selection for warm roosts   2 | Selection for cool roosts   3 | No roost selection   4 | Shifting roost selection

753
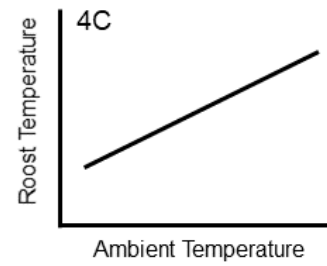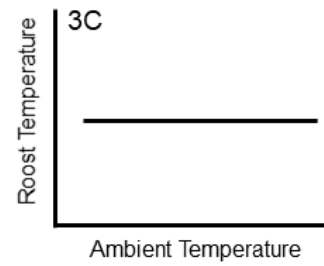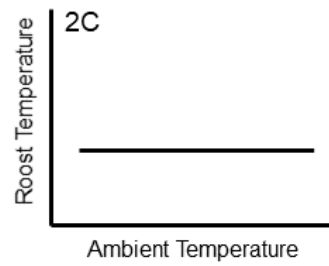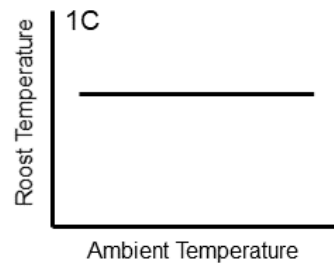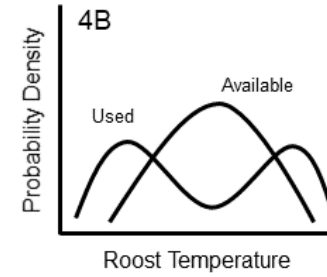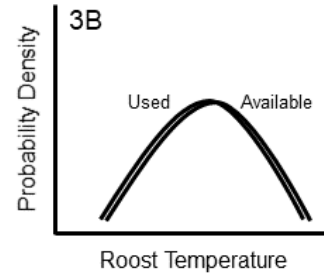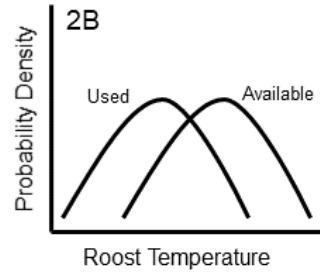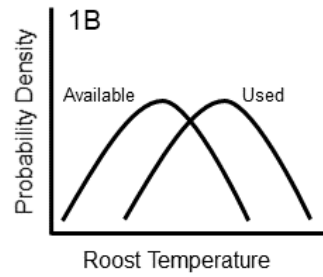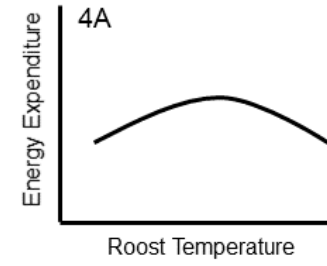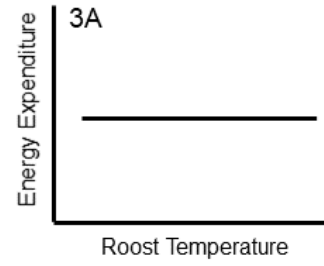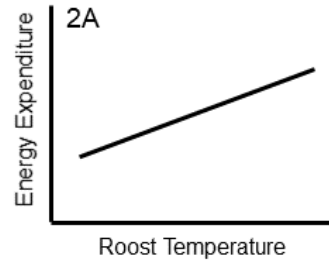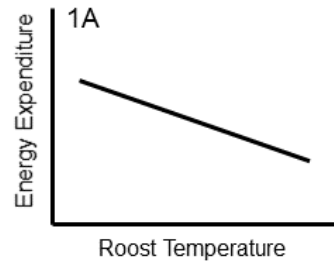
754   **Fig. 3**. Scatter plot illustrating the conditional effect of daily mean ambient

755   temperature on the total duration of bouts of torpor during the day. Each point is

756   based on observed data and represents one day. The line represents the regression line

757   for this relationship and the grey band represents 95% credible intervals around this

758   line. Credible intervals for this conditional effect did not cross zero (parameter

759   estimate: -37.4 min; 95% credible intervals: -64.0 – -12.6 min), indicating that bats

760   spent ca. 37 minutes less in torpor per day for each additional 1˚C in daily mean

761   ambient temperature between 0445 hrs and 2100 hrs.
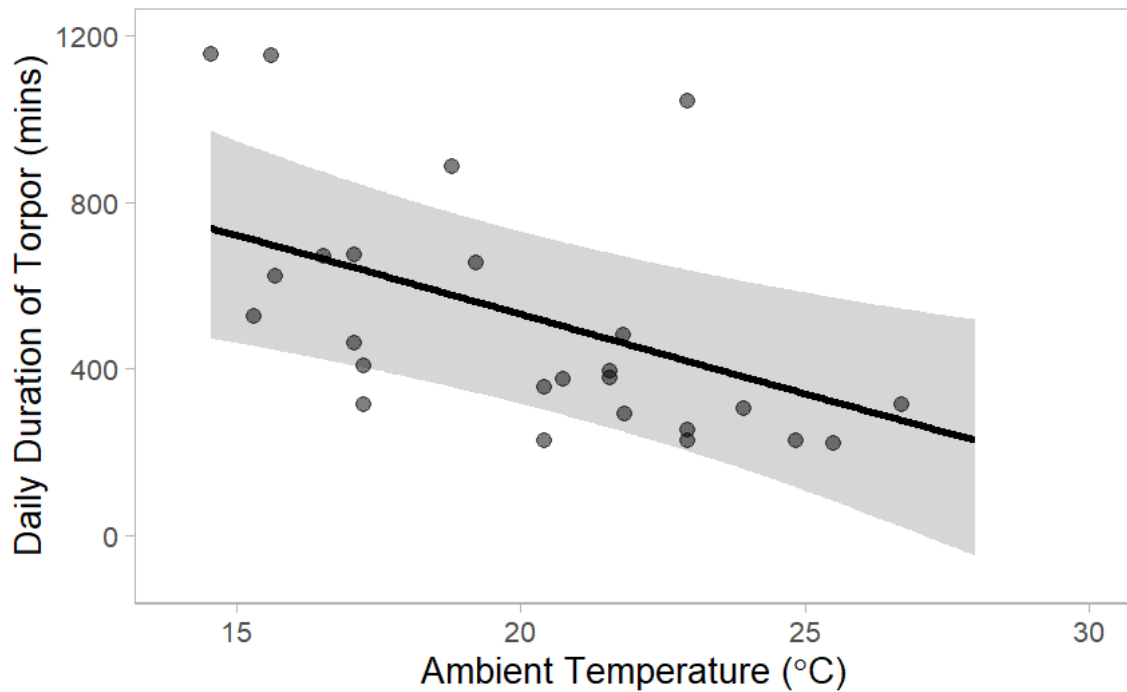

762

763

764   **Fig. 4**. Results of our simulation of daily energy expenditure by fringed myotis over

765   the range of temperatures observed in used roosts. Each point represents one day. The

766   red points represent estimated daily energy expenditure if bats never used torpor. The

767   blue points represent our estimate of energy expenditure over the course of a day if

768   part of the day is spent in torpor (with the daily duration of torpor a function of daily

769   ambient temperature as observed during our study). The lines represent loess

770   regressions of the relationship between roost temperature and daily energy

771   expenditure. Estimates of daily energy expenditure incorporating observed bat

772   behaviour are steady across all roost temperatures observed during our study. The

773   blue points in this figure correspond with Row A in Fig. 2, and are most closely

774   matched by Fig 2.3A.

775
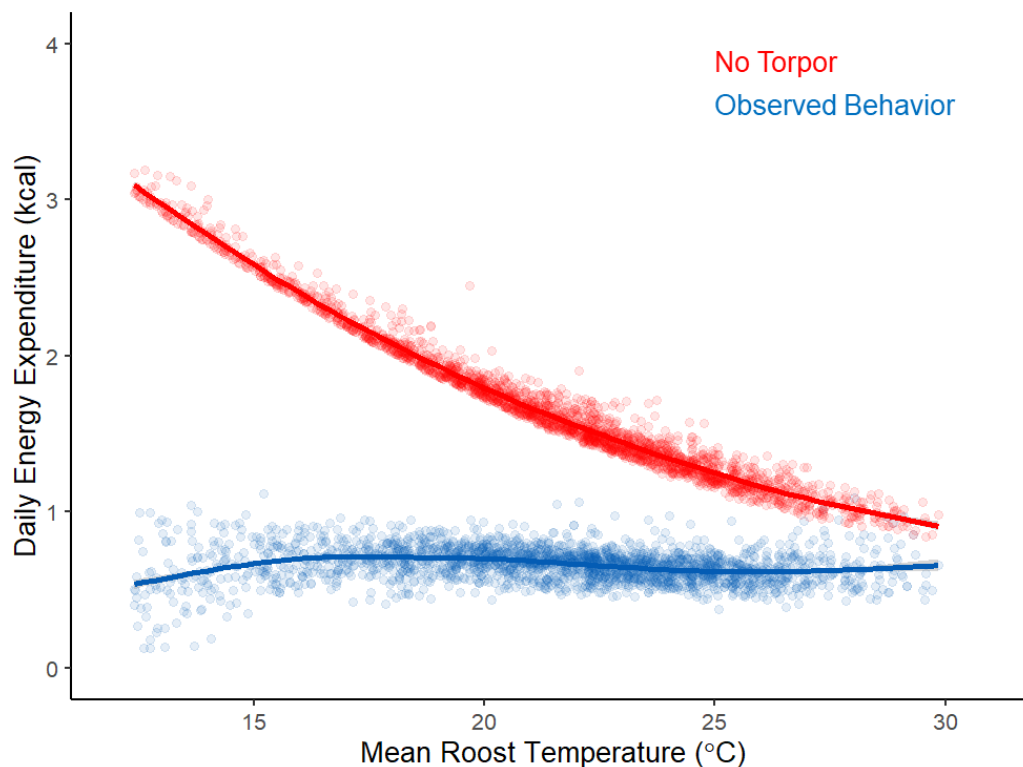
776

777   **Fig. 5**. Kernel density plots comparing thermal characteristics within used and available roost structures: mean temperature (A), time of day at

778   peak temperature (B), and the standard deviation of temperature (C). Blue distributions represent used roosts, while orange distributions

779   represent available roosts. These plots illustrate the results of our binomial model of roost selection. Used roosts were slightly warmer on

780   average than available roosts, but their distributions largely overlapped (A). Temperatures peaked slightly earlier in used roosts than available

781   roosts, but this was a function of temperatures in warmer roosts tending to peak earlier in the day ($r = -0.19$ for the relationship between mean

782   temperature within roost structures and time of day at peak temperature) and their distributions largely overlap (B). The standard deviation in

783   temperatures within used roosts is very similar to the standard deviation in temperatures within available roosts, although bats did not use the

784   few roost structures with very high standard deviations (C). Panel A in this figure corresponds with Row B in Fig. 2, and is most closely matched

785   by Fig. 2.3B.
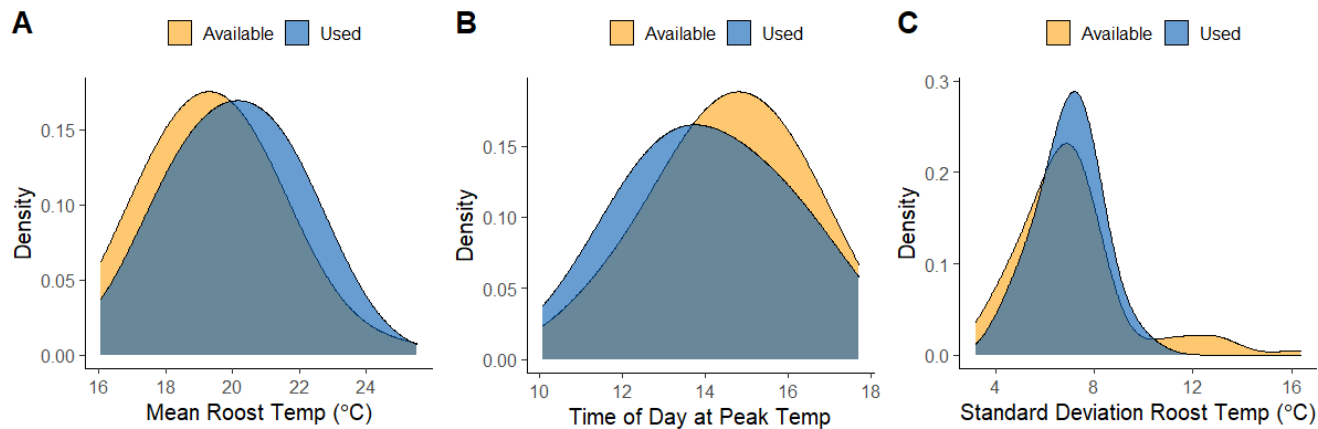
786

787   **Fig. 6**. Scatter plot of the relationship between ambient temperature on a given day

788   and the mean temperature within used roosts. Each point is based on observed data,

789   and represents a roost used for one day; some roosts (n = 14) were used on multiple

790   days and thus are represented by multiple data points on this plot. The line represents

791   the regression line for this relationship and the grey band represents 95% confidence

792   intervals around this line. Ambient temperature on a given day did not influence

793   whether bats used warm or cool roosts ($p = 0.06$; $R^2 = 0.04$). This figure corresponds

794   with Row C in Fig. 2, and is most closely matched by Fig. 2.3C.

795
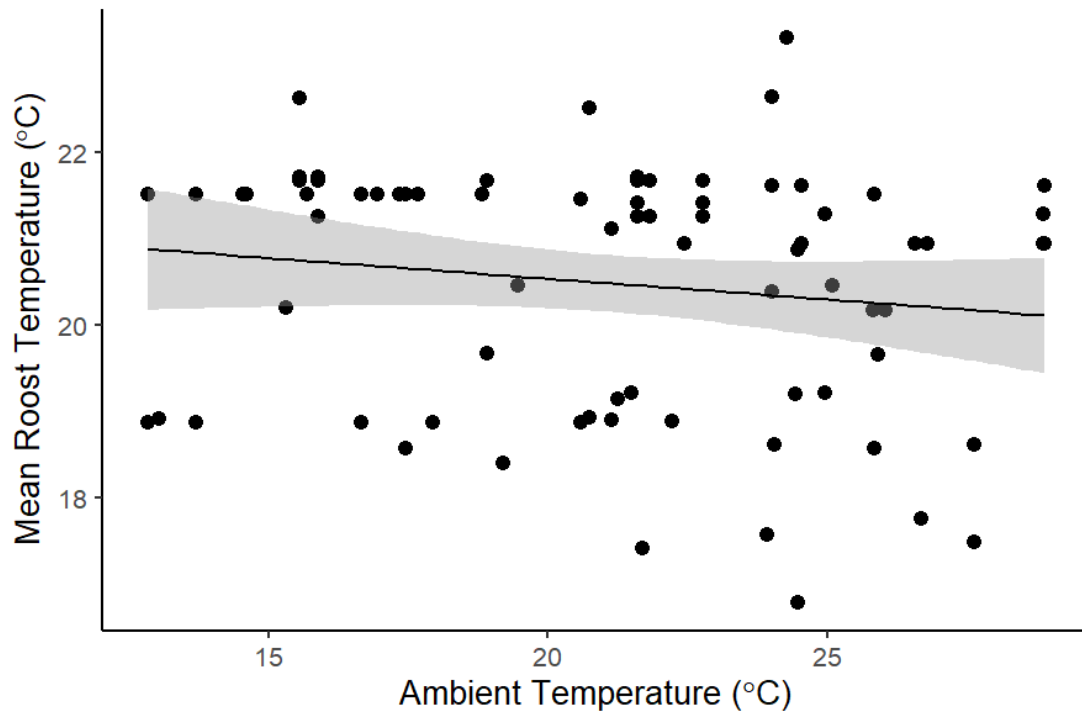
Appendix A: Supplementary Data

Descriptive Statistics for Rock vs. Tree Roost Structures

Temperatures within used rock crevices averaged 20.5˚C (range: 16.8˚ – 23.3˚C) while temperatures within available rock crevices averaged 19.9˚C (range: 16.5˚ – 24.2˚C). Temperatures within used tree roosts averaged 18.6˚C (range: 17.4˚ – 20.4˚C) while temperatures within available tree cavities averaged 19.2˚C (range: 16.1˚ – 25.5˚C) and temperatures within available spaces under sloughing bark averaged 18.4˚C (range: 16.1˚ – 21.0˚C).

Temperatures within used rock crevices peaked on average at 1414 hrs (range: 1105 – 1719 hrs), while temperatures within available rock crevices peaked on average at 1458 hrs (range: 1005 – 1742 hrs). Temperatures within used tree roosts peaked on average at 1447 hrs (range: 1125 – 1659 hrs), while temperatures within available tree cavities peaked on average at 1410 hrs (range: 1120 – 1608 hrs) and temperatures within available spaces under sloughing bark peaked on average at 1349 hrs (range: 1056 – 1608 hrs).

The standard deviation of temperatures within used rock crevices was 6.7˚C (range: 4.3˚ – 10.0˚C), while the standard deviation of temperatures within available rock crevices was 6.2˚C (range: 3.2˚ - 11.0˚C). The standard deviation of temperatures within used tree roosts was 7.7˚C (range: 6.7˚ - 9.1˚C), while the standard deviation of temperatures within available tree cavities was 8.7˚C (range: 5.9˚ - 16.4˚C) and within available spaces under sloughing bark was 7.7˚C (range: 6.5˚ - 11.0˚C).

There was no difference in ambient temperature between days where rock crevices were used and days where tree roost structures were used (Mann-Whitney U = 299; p = 0.968).
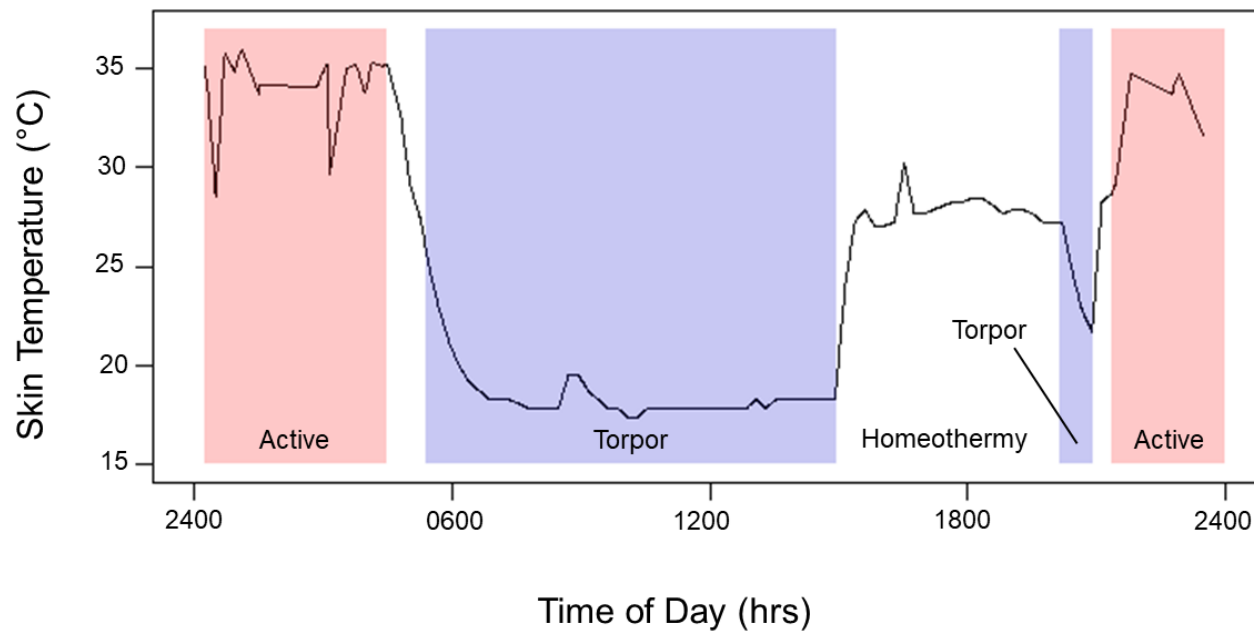
820 **Table A1**. Information on torpor use by bats tracked during our study, including an ID number for each individual, the dates for which we have

821 data, the mass of bats at time of capture, the timing of torpor entry and exit for morning and afternoon bouts of torpor, the duration of periods of

822 periods of torpor in both mornings and afternoons, and the total duration of torpor across the day.

Bat ID	Date	Mass (grams)	AM Torpor Start Time (hrs)	AM Torpor End Time (hrs)	Duration of AM Torpor (mins)	PM Torpor Start Time (hrs)	PM Torpor End Time (hrs)	Duration of PM Torpor (mins)	Total Torpor Duration (mins)
172_063	8/5/2017	6.02	517	1456	579	2013	2055	42	621
172_063	8/6/2017	6.02	451	1210	439	1910	2037	87	526
172_063	8/7/2017	6.02	2245	1557	1032	1840	2044	124	1156
172_904	6/28/2018	6.75	425	733	188	1825	2057	125	313
172_904	6/29/2018	6.75	419	1037	378	1603	2114	277	655
172_904	7/3/2018	6.75	525	944	259	1834	2029	115	374
172_904	7/4/2018	6.75	412	1446	634	1709	2122	253	887
172_904	7/5/2018	6.75	424	1458	597	1930	2043	73	670
172_904	7/6/2018	6.75	511	1016	305	-	-	0	305
172_904	7/7/2018	6.75	438	818	220	-	-	0	220
172_692	7/13/2018	6.92	445	830	225	1936	2043	67	292
172_692	7/14/2018	6.92	435	815	220	-	-	0	220
172_632	7/20/2018	8.04	426	1102	396	1916	2041	85	481
172_753	7/27/2018	8.16	133	2045	1152	-	-	0	1152
172_753	7/28/2018	8.16	2300	2031	1291	-	-	0	1291
172_453	8/4/2018	7.1	449	959	310	1915	2039	84	394
172_784	8/4/2018	7.53	442	1028	346	1951	2023	32	378
172_453	8/5/2018	7.1	459	1156	417	1613	2028	255	672

172_784	8/5/2018	7.53	445	1100	375	1852	2019	87	462
172_453	8/6/2018	7.1	441	916	275	1823	2034	131	406
172_784	8/6/2018	7.53	449	1003	314	-	-	0	314
172_453	8/7/2018	7.1	444	1041	357	-	-	0	357
172_784	8/7/2018	7.53	502	850	228	-	-	0	228
172_063	8/8/2018	6.02	2335	1427	892	1737	2009	152	1044
172_453	8/8/2018	7.1	451	839	228	-	-	0	228
172_784	8/8/2018	7.53	439	852	253	-	-	0	253
172_453	8/10/2018	7.1	456	843	227	-	-	0	227

823

824   **Fig. A1.** An example of raw skin temperature data that we used to delineate bouts of torpor. Periods of time in red blocks represent periods of

825   activity (flying, foraging, etc.), periods of time in blue blocks represent periods of torpor, and periods in white represent periods of homeothermy

826   or transition between torpor and homeothermy/activity. To delineate bouts of torpor, we used the definition suggested in Barclay, Lausen, &

827   Hollis (2001).

828