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1 **Individual flexibility in energy saving: body size and condition**
2 **constrain torpor use**

3

4

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11

12 **Running headline:** Body constitution constrains heterothermy

13

14 **Summary**

- 15 **1.** Phenotypic flexibility is a major mechanism in compensating climate-driven changes
16 in resource availability. Heterotherms can use daily torpor to overcome resource
17 shortages and adverse environmental conditions. The expression of this adaptive
18 energy saving strategy varies among individuals, but the factors constraining
19 individual flexibility remain largely unknown.
- 20 **2.** Since energy availability depends on individual stores and/or on the ability to acquire
21 food, the propensity and flexibility in torpor use are expected to be constrained by
22 body condition and/or size, respectively. The aim of this study was to test whether the
23 dependency of torpor depth on air temperature was constrained by body condition
24 and/or body size in a small heterothermic primate, the grey mouse lemur (*Microcebus*
25 *murinus*). During the onset of the dry season, we monitored air temperature as well as
26 skin temperatures of 14 free-ranging individuals (12 females, 2 males) of known body
27 mass and size.
- 28 **3.** Unexpectedly, torpor depth depended as much on air temperature as on body condition
29 and size. Fatter, or larger, mouse lemurs underwent deeper torpor than smaller, or lean
30 ones. Individual reaction norms of torpor depth to air temperature also revealed that
31 the propensity to undergo deep torpor and the flexibility in torpor depth were
32 enhanced by large body size and high body condition, whereas small, lean, individuals
33 remained normothermic.
- 34 **4.** Our study illustrates that alternative physiological strategies to overcome temperature
35 constraints co-occur in a population, with body size and condition being key
36 determinants of the energy conservation strategy that an individual can launch.

37

38 **Key-words:** air temperature, body constitution, energy availability, heterothermy,
39 individual reaction norm, *Microcebus murinus*, phenotypic flexibility

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44 **Introduction**

45 Energy-saving strategies are adaptive responses to recurrent energetic challenges. Daily
46 torpor and hibernation (heterothermy) enable endothermic species to reduce their energy
47 expenditure during episodes of energetic constraint (Heldmaier, Ortmann & Elvert 2004;
48 McKechnie & Mzilikazi 2011). These mechanisms rely on a controlled reduction of the body
49 temperature and metabolic rate during periods of rest (Geiser 2004; Heldmaier *et al.* 2004).
50 Their use improves the chances of survival during prolonged periods of resource shortage or
51 of harsh climatic conditions (Turbill, Bieber & Ruf 2011). Although prevalent in temperate
52 regions to overcome winter (Ortmann & Heldmaier 2000; McKechnie & Mzilikazi 2011),
53 heterothermy is also frequent in the tropics where it enables small endotherms to cope with
54 the dry season (Dausmann *et al.* 2004; McKechnie & Mzilikazi 2011; Canale, Levesque &
55 Lovegrove 2012).

56 Individuals with high levels of flexibility in physiological and behavioural traits are more
57 likely to successfully overcome environmental constraints, like climate change, by fine-tuning
58 their energy expenditure, and its timing, according to fluctuations in energy availability
59 (Nussey *et al.* 2005; Charmantier *et al.* 2008; Canale & Henry 2010). Facultative, daily torpor
60 is actually highly flexible, and this flexibility markedly differs between individuals (Schmid
61 & Kappeler 1998; Kobbe, Ganzhorn & Dausmann 2011; Canale *et al.* 2011; Canale & Henry
62 2011). However, the factors constraining individual flexibility in the use of this energy saving
63 mechanism remain unknown.

64 With decreasing air temperature, heterothermic mammals are able to substantially
65 decrease their body temperature, hence increasing torpor bout duration and depth (e.g. Geiser
66 & Kenagy 1988; Schmid 2000; Aujard & Vasseur 2001; Heldmaier *et al.* 2004). As the
67 energy benefits associated to torpor expression are positively related to torpor depth and

68 duration, low air temperature can enhance energy savings in thermo-conforming torpid
69 animals (Heldmaier *et al.* 2004). Heterothermy expression is also expected to depend on
70 energy availability, i.e. on stored energy reserves or the capacity to acquire food. Energy
71 reserves, like internal lipid stores, constitute the main fuel to sustain metabolic activity during
72 torpor bouts, and to offset the thermogenic cost associated with the regular returns to
73 normothermia (arousals; Geiser 2004; Heldmaier *et al.* 2004). Indeed, hibernating individuals
74 consume a large fraction of their energy reserves during these brief peaks of thermogenesis
75 associated with arousals (e.g. 19% in ground squirrels: Wang 1979; 72% in marmots:
76 Heldmaier *et al.* 2004). Therefore, animals must have stored energy (internally or externally)
77 when resources are abundant to be able to survive by using torpor when resources are scarce
78 (Schmid & Kappeler 1998; Kobbe *et al.* 2011). The acquisition of resources likely depends on
79 body size as a larger size is usually associated with better access to resources, for instance
80 through social dominance (Price 1984). Hence, both a good body condition and a large body
81 size are predicted to increase the ability to use torpor. Up to date, at the individual level, only
82 two studies reported a positive correlation between body mass and torpor use in chipmunks
83 (Levesque & Tattersall 2010) and hedgehogs (Hallam & Mzilikazi 2011), and three between
84 body condition and torpor use in bats (Kelm & von Helversen 2007; Stawski & Geiser 2010),
85 and mouse lemurs (Kobbe *et al.* 2011). However, none of these studies disentangled the
86 respective roles of body condition and body size on the individual ability to flexibly adjust
87 torpor use to fluctuations in air temperatures.

88 In this study, we investigated the expression of heterothermy by free-ranging grey mouse
89 lemurs (*Microcebus murinus*), small (60-120 g) primates inhabiting the dry forests of
90 Madagascar. Because Madagascar is characterized by a high climatic unpredictability (Dewar
91 & Richard 2007), the grey mouse lemur represents a good model to investigate the flexibility
92 of energy saving strategies in response to environmental constraints. During the dry season,

93 mouse lemurs experience shortfalls of food and water (Dammhahn & Kappeler 2008a), and
94 face high circadian air temperature fluctuations (daily amplitudes of up to 28 °C; Schmid
95 2001). They complement energy storage with energy conservation and enter daily torpor
96 when environmental conditions become unfavourable (Ortmann *et al.* 1997; Aujard, Perret &
97 Vannier 1998; Schmid 2001; Génin & Perret 2003). In this study, we aimed to quantify the
98 relative dependence of skin temperature (T_{sk}) to air temperature (T_a), body condition and body
99 size, using an individual reaction norm approach – a suitable statistical framework to quantify
100 and compare phenotypic plasticity between individuals (Nussey *et al.* 2007; Martin *et al.*
101 2011). The principle is to obtain biologically meaningful statistical parameters that describe
102 the range of phenotypes (here, T_{sk}) that an individual expresses in response to an
103 environmental gradient (here, T_a).

104

105 **Material and methods**

106 STUDY SITE AND ANIMALS

107 The study was conducted in the dry deciduous forest of Kirindy in western Madagascar, at the
108 onset of the dry season (April - May 2011). We captured 14 free-ranging adult grey mouse
109 lemurs (12 females and 2 males; Fig. 1) using baited Sherman live traps (see Dammhahn &
110 Kappeler 2008b for details). Individuals were briefly anesthetized (10 µl ketamine per 100 g),
111 weighed and measured (body length, head width, head length; Dammhahn & Kappeler
112 2008b). All individuals were equipped with collar-mounted temperature-sensitive radio-
113 transmitters (PIP3 button celled tag, Biotrack Ltd., UK, with a mass of approximately 3 g),
114 which allow to monitor manually T_{sk} , a reliable indicator of core body temperature
115 (Dausmann 2005). Transmitters were previously calibrated in a water bath ranging from 10 to
116 40 °C against a reference iButton (DS1921G, Alpha Mach Inc., Sainte-Julie, Canada). As

117 mouse lemurs generally rest in tree holes (Schmid 1998; Luthermann, Verburgt & Rendigs
118 2010), we recorded T_a in 8 tree holes using iButtons, every 15 min, throughout the study
119 period. iButtons were placed in small plastic bottles (diameter of 2.5 cm, length of 7 cm) to
120 prevent direct contact between the iButton and the trunk, and bottles were hollowed at the top
121 and the bottom to allow air flow.

122

123 PARAMETERS MEASURED

124 Parameter measures are presented as means \pm standard deviation of the means. T_{sk} was
125 measured twice per individual and per morning, once at $6:53 \pm 18$ min and then at $8:08 \pm 17$
126 min, using the method described in Schmid & Speakman (2000). Based on evidences from
127 previous studies (Ortmann *et al.* 1997; Schmid 2000; 2001), we chose the 6:00-9:00 a.m. time
128 window so that minimal T_{sk} measurements could be assumed to be indicative of individual,
129 daily maximal torpor depth. Since T_a was the lowest during our time window of measurement
130 (at $6:13 \pm 2:57$ on average), and since nocturnal heterotherms passively rewarm with the
131 morning rise in T_a (Schmid 2000; 2001; Turbill *et al.* 2008), it is unlikely that torpid
132 individuals reached a lower T_{sk} later than this time window. For the analyses of torpor depth,
133 we used the lowest T_{sk} measurement per morning per individual, which occurred at $7:49 \pm 37$.
134 In total, we obtained 17 ± 10 T_{sk} measures per individual. T_a values at the time of T_{sk}
135 measurement were averaged across the 4 spatially closest iButtons.

136 Body mass (BM) cannot be used as a direct index of inter-individual variation in internal
137 energy stores because it also covaries with body size. A high BM does not distinguish a small,
138 fat individual from a large, lean one. Thus, we computed an individual body condition index
139 (BCI) using the scaled mass index method (Peig & Green 2009). This index was calculated as
140 the mass of an individual standardized to the mean body size of all individuals in the

141 population retaining the population-specific allometric relationship. The population-level
142 statistical relationship between body mass and body size was calibrated on an independent
143 data set, composed of 226 adult individuals (97 females and 120 males) caught during
144 previous field surveys in the study population (M. Dammhahn, unpublished data). The
145 morphometric measure taken to account for body size was head width (HW; ± 0.1 mm), i.e.
146 the distance between the two bizygomatics, as it was the morphometric parameter the most
147 tightly correlated to BM (Peig & Green 2009). First, we extracted the slope of the regression
148 of BM to HW (β):

$$149 \log(BM_i) = \alpha + \beta \times \log(HW_i) + \varepsilon_i \quad (1)$$

150 Then, we extracted the Pearson coefficient of correlation of log-transformed BM and HW (φ):

$$151 \varphi = \text{corr}(\log(BM), \log(HW)) \quad (2)$$

152 Finally, individual BCI values were obtained using the following formula:

$$153 BCI_i = BM_i \times (\overline{HW} / HW_i)^\beta \quad (3)$$

154 BCI values are independent of HW (Pearson's R = -0.10, $p = 0.73$).

155

156 STATISTICAL ANALYSES

157 Because we used temporally repeated measures on the same individuals, T_{sk} data were
158 analysed using linear mixed effects models (built with the 'nlme' function), to account for the
159 different sources of non-independence among data points. Explanatory variables were the
160 fixed effects of T_a , HW, BCI, and their interactions. All variables were standardized to
161 achieve comparable ranges of variation (for a given variable, values were divided by its
162 standard deviation after subtraction of its mean). Individual identity was entered as random
163 individual intercept, and a random individual slope parameter was entered to account for
164 inter-individual variation in T_{sk} response to T_a (Schielzeth & Forstmeier 2009). To account for

165 the remaining non-independence between data points (i.e. non-random residual error), we also
 166 parameterized two structures for residual variance. An auto-regressive structure of order 1
 167 ('corAR1' function, parameter ρ) was included to account for temporal autocorrelation
 168 between residuals (Pinheiro & Bates 2000: p. 229), and we allowed variability in T_{sk} to
 169 exponentially increase with BCI and HW and decrease with T_a , by adding a variance function
 170 for each covariate ('varExp' function, respectively parameters δ , γ and ω ; Zuur *et al.* 2009: p.
 171 80, as in Peig & Green 2009). Hence, the starting model had the following form (notation
 172 follows Zuur *et al.* 2009), where i is the index for the individual, j is the index for air
 173 temperature (T_a) on day k , and l is the index for the measure:

$$Tsk_{ijkl} = \alpha + \beta_1 \times Ta_{ij} + \beta_2 \times BCI_i + \beta_3 \times HW_i + \beta_4 \times Ta_{ij} \times BCI_i + \beta_5 \times Ta_{ij} \times HW_i \\ + \beta_6 \times BCI_i \times HW_i + b_{i1} + b_{i2} \times Ta_{ij} + \varepsilon_{ijkl}$$

with

174 random intercept $b_{i1} \sim N(0, d_{11}^2)$,
 random slope $b_{i2} \sim N(0, d_{22}^2)$, $\text{corr}(b_{i1}, b_{i2}) \sim N(0, d_{12})$,
 $\text{corr}(\varepsilon_{ijk'l}, \varepsilon_{ijkl}) = \rho^{|k'-k|}$ if $k' \neq k$,
 $\varepsilon_{ijkl} \sim N(0, \sigma^2 \times e^{2\delta \times BCI_i} \times e^{2\gamma \times HW_i} \times e^{2\omega \times Ta_j})$.

175 The final model, containing only significant effects, was obtained by deletion of the non-
 176 significant interactions and additive effects from the fixed part of this starting model. The
 177 maximum likelihood-ratio tests of the significance of effects were computed with the final
 178 model.

179 Individual linear reaction norms of T_{sk} to T_a were estimated using a random slope - random
 180 intercept model. For this analysis, we transformed T_a values so that intercept values of T_{sk}
 181 were estimated for the highest air temperature experienced during the study period, i.e. 24.5
 182 °C. The used transformation for the T_a values was: $T_a' = 24.5 - T_a$. Doing so, individual
 183 intercept values can be interpreted as the individual propensity to use deep torpor at non-
 184 challenging air temperature, 25 °C being the temperature of thermoneutrality for the grey
 185 mouse lemur (i.e. the temperature at which the resting metabolic rate is the lowest; Aujard,

186 Perret & Vannier 1998). Then, the higher T_a' , the stronger is the thermal constraint (cold). The
187 model had the following form, where i is the index for the individual and j is the index for air
188 temperature (T_a'):

$$Tsk_{ijk} = \alpha + \beta_1 \times Ta'_{ij} + b_{i1} + b_{i2} \times Ta'_{ij} + \varepsilon_{ijk}$$

with

189 random intercept $b_{i1} \sim N(0, d_{11}^2)$,
random slope $b_{i2} \sim N(0, d_{22}^2)$, $\text{corr}(b_{i1}, b_{i2}) \sim N(0, d_{12})$,
 $\varepsilon_{ijk} \sim N(0, \sigma^2)$.

190 Individual intercept b_{i1} measures torpor depth at 24.5 °C, and individual slope b_{i2} measures
191 the linear response of T_{sk} to T_a' . d_{11}^2 is the between individual variance of the intercept
192 parameter, d_{22}^2 is the between individual variance of the slope for the effect of T_a' , d_{12} is the
193 covariance between individual intercepts and slopes, and σ^2 the residual variance for the error
194 term. Significant inter-individual variation in the linear response of T_{sk} to T_a' (i.e., $H_0: d_{22} = 0$)
195 was tested by a likelihood-ratio test between the restricted maximum likelihood fit of this
196 model with the fit of the same model but excluding parameters d_{22} and d_{12} . Individual
197 intercepts b_{i1} (also called elevation; Nussey *et al.* 2005) and individual slopes b_{i2} were
198 estimated with the model (Fig. 3, Best Linear Unbiased Predictions obtained with the 'ranef'
199 function). These parameters allowed to estimate individual propensity to undergo deep torpor
200 and individual flexibility in torpor depth, respectively. The effects of HW and BCI on these
201 individual slopes and intercepts were then tested using linear models, where significances of
202 effects were tested by ANOVAs.

203 Normality of model's residuals was checked with normal quantile-quantile plots. The
204 significance level was set to $P < 0.05$. All analyses were implemented with R version 2.13.1
205 (R Development Core Team 2008; *R: A language and environment for statistical computing*,
206 Vienna, Austria). Model parameter estimates are presented as means \pm standard error of the
207 means.

208

209 **Results**

210 Throughout the study period, mouse lemurs experienced a mean T_a of 18.5 ± 2.8 °C (averaged
211 across all iButtons and all mornings) and exhibited an average T_{sk} of 28.9 ± 6.7 °C, at $7:49 \pm$
212 37 min. Mean T_a was 12.2 °C for the coldest and 24.5 °C for the warmest morning,
213 respectively. Mouse lemurs expressed torpor in 45.0% of the sampled mornings (considering
214 that animals were torpid when $T_{sk} < 30$ °C; justified in Schmid 2001). Their body condition
215 and body size, i.e. head width, were 79.6 ± 12.2 g and 21.8 ± 0.7 mm, respectively, and they
216 had an initial body mass of 79.7 ± 19.2 g.

217 At the population level, T_{sk} increased with T_a ($\chi^2_1 = 12.93$, $p < 0.001$, $\beta = 1.61 \pm 0.32$), but
218 decreased with BCI ($\chi^2_1 = 6.55$, $p = 0.01$, $\beta = -1.79 \pm 0.70$) and tended to decrease with HW
219 ($\chi^2_1 = 2.86$, $p = 0.09$, $\beta = -2.50 \pm 0.89$). The slopes indicate that the effects of HW and BCI
220 were as strong as the effect of T_a . The positive relationship between T_{sk} and both HW and BCI
221 indicates that larger mouse lemurs with better body condition underwent deeper torpor than
222 those with lower body size and condition, at all T_a (Fig. 2). The responsiveness of T_{sk} to T_a
223 was greater in large individuals (T_a x HW interaction, $\chi^2_1 = 5.55$, $p = 0.02$, $\beta = 0.68 \pm 0.33$),
224 but did not depend on BCI (T_a x BCI interaction, $\chi^2_1 = 1.40$, $p = 0.24$, $\beta = 0.45 \pm 0.37$). The
225 residual variance of T_{sk} increased with increasing BCI ($\delta = 0.06$) and HW ($\gamma = 0.08$) and
226 decreased with increasing T_a ($\omega = -0.25$).

227 The linear reaction norm of T_{sk} to T_a significantly varied between individuals (random slope
228 for the linear effect of T_a , $\chi^2_2 = 13.66$, $p = 0.001$; Fig. 3, but see also Fig. S1 in Supporting
229 Information). The individual propensity to undergo deep torpor (random individual intercepts)
230 and to adjust torpor depth to T_a (random individual slopes for the effect of T_a) were strongly
231 positively correlated (correlation: 0.99), indicating that individuals using deep torpor were

232 also the most flexible. Both torpor propensity and flexibility increased with HW ($\beta = -2.48 \pm$
233 0.49 , $F_{1,12} = 25.29$, $p < 0.001$, and $\beta = -0.38 \pm 0.07$, $F_{1,12} = 25.32$, $p < 0.001$, respectively) and
234 with BCI ($\beta = -1.86 \pm 0.49$, $F_{1,12} = 14.22$, $p = 0.003$, and $\beta = -0.28 \pm 0.07$, $F_{1,12} = 14.11$, $p =$
235 0.003 , respectively; Fig. 4).

236

237 **Discussion**

238 We show for the first time that torpor use is largely determined by two independent
239 dimensions of body constitution, i.e. body size and body condition, in a small free-ranging
240 heterotherm (Fig. 4). Since torpid animals actually have a reduced energy expenditure (Geiser
241 2004; Heldmaier *et al.* 2004), it suggests that torpor-based energy saving are dependent on
242 individual body constitution. For a given air temperature, larger individuals or individuals
243 with a higher body condition underwent deeper torpor than smaller ones, or those with lower
244 body condition. Low air temperature is known to increase torpor expression (e.g. Geiser &
245 Kenagy 1988; Aujard & Vasseur 2001; Heldmaier *et al.* 2004), but body size and condition
246 proved to be as good predictors of torpor depth as air temperature. Individual propensity to
247 undergo deep torpor, and the responsiveness of torpor depth to air temperature, i.e. torpor
248 flexibility, were also strongly dependent on body size and body condition. Thus, as expected,
249 these two independent dimensions of body constitution appear to constrain individual
250 flexibility in torpor use. This result discards the hypothesis which posits that torpor is used as
251 an emergency response to adverse conditions by individuals with a poor body condition
252 (Christian & Geiser 2007). Studies on five other heterothermic mammals already suggested
253 that individuals with a high body mass or body condition had a greater use of torpor. Indeed,
254 both depth and duration of torpor bouts were positively related to body mass or body
255 condition in two bat species (*Glossophaga soricina*: Kelm & Von Helversen 2007;

256 *Nyctophilus bifax*: Stawski & Geiser 2010) and in the southern African hedgehog (*Atelerix*
257 *frontalis*: Hallam & Mzilikazi 2011). Frequency of torpor also increased with increasing body
258 condition in the food-hoarding Eastern chipmunk (*Tamias striatus*: Levesque & Tattersall
259 2010) and in the reddish-grey mouse lemur (*Microcebus griseorufus*: Kobbe *et al.* 2011), for
260 which torpor duration also increased. However, the conclusions were potentially confounded
261 by the effect of body size.

262 The amount of energy available to an individual would constrain its ability to make
263 torpor-based energy saving (Schmid & Kappeler 1998). If an individual does not have access
264 to a minimal, necessary amount of energy, it should not use torpor, otherwise incurring the
265 risk of not having enough energy to return to normothermia at the end of a profound torpor
266 bout (Terrien *et al.* 2009). Since large body size is often associated with social dominance,
267 particularly during contests for food or shelters (e.g. Price 1984), a larger size would enable
268 an animal to more easily acquire the energy needed. Hence, to over-winter, large individuals
269 could rely on both easy access to limited food as well as high energy savings. Independent of
270 body size, energy stores release individuals from daily resource acquisition to cover the
271 residual energetic costs associated with torpor. Thus, the larger the energy stores the more an
272 individual can rely on torpor-based minimization of energy expenditure to make it through the
273 dry season. This explains the relationship between body condition and torpor use observed
274 here. Torpor episodes between foraging bouts could also be used to maximize the amount of
275 energy allocated to fat storage (e.g. Carpenter & Hixon 1988), leading to a higher body
276 condition the more the animals express torpor (Schmid 2001). In this alternative scenario, a
277 better body condition would be the result, and not the facilitator, of increased torpor use.
278 Although both mechanisms may operate, in our study, lean individuals, i.e. those with the
279 highest need of fattening, did not use torpor. Since these individuals did not adjust their skin
280 temperature to air temperature, the good body condition is unlikely to be the result of torpor-

281 based energy saving. Hence the opposite is more likely: torpor-based energy saving may help
282 fat individuals to maintain a high body condition, whereas lean individuals would not improve
283 body condition by using torpor. Thus, our data support the view that sufficient body fattening
284 at the onset of the dry season determines an individual's ability to rely on torpor use to
285 survive the dry season (Schmid & Kappeler 1998; Kobbe *et al.* 2011).

286 Individuals that are too small or too lean to use torpor may not be systematically exposed
287 to higher mortality during the dry season, however. Alternative physiological strategies to
288 survive the unfavourable dry season may co-occur in the same population. Whereas large, fat
289 individuals would rely on energy conservation and saving, small sized, lean individuals would
290 remain active, with a reduced torpor use throughout the dry season, regularly feeding to
291 maintain a positive energetic balance. Their strategy would be based on optimized foraging
292 activity rather than on energy conservation, as has been hypothesised also for smaller
293 congeneric mouse lemurs (*Microcebus berthae*: Dammhahn & Kappeler 2012). Actually, a
294 large fraction of mouse lemurs remain active throughout the dry season, mainly males
295 (Schmid & Kappeler 1998; Kraus, Eberle & Kappeler 2008; Dammhanh & Kappeler 2008a;
296 b). Males fatten less than females prior to the dry season (Schmid & Kappeler 1998), and 81%
297 of them remain active, whereas most of the females (73%) are inactive for several weeks or
298 months (Schmid 1999). However, despite a significant reduced use of torpor and a higher
299 activity compared to females, males do not seem to suffer from excess mortality during the
300 dry season (Kraus *et al.* 2008). Their access to food may even be relatively high since the
301 densities of active individuals are the lowest during the lean period. Thus, the difference
302 between sexes in torpor use may be explained in some part by the differences in body
303 condition, as our results indicate. This hypothesis is supported by the fact that female grey
304 mouse lemurs have been shown to be dominant over males for the access to food resources
305 (Génin 2003), which enables them to achieve higher body mass.

306 Our study illustrates that alternative phenotypic strategies to overcome challenging
307 environmental conditions co-occur in a natural population, at the same time of the year.
308 Which strategy an individual will tend to use is mainly determined by body size and body
309 condition. There is probably a physiological continuum, ranging from individuals that largely
310 rely on torpor-based energy saving to others that remain normothermic and rely on feeding
311 opportunities. The study of individual reaction norms of physiological and behavioural
312 parameters to environmental constraints is needed to predict to what extent organisms will be
313 able to overcome such constraints, especially in the context of global changes (Pörtner &
314 Farrell 2008; Canale & Henry 2010; Chevin, Lande & Mace 2010; Chown *et al.* 2010).

315

316

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324

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326

327

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465 **SUPPORTING INFORMATION**

466 Additional supporting information may be found in the online version of this article.

467

468 **Figure S1.** Individual plots of the relationships between skin temperature and air temperature,
469 and the corresponding individual and population reaction norms.

470

471

472 **Figure legends**

473

474 Figure 1. Female grey mouse lemur (*Microcebus murinus*) in Kirindy forest, western Madagascar
475 (photograph by Pauline Vuarin).

476

477 Figure 2. Individual daily variations in torpor depth according to (a) body condition index and (b)
478 body size (indexed on head width) for 14 free-ranging adult grey mouse lemurs. Box plots show the
479 median (*bold line*), the 25% and 75% percentiles (*box*), and the non-outlier range (*whiskers*).

480

481 Figure 3. Individual linear reaction norms of minimal skin temperature (i.e. torpor depth) to air
482 temperature estimated for 14 free-ranging grey mouse lemurs.

483

484 Figure 4. Dependence of individual (a) intercept and (b) slope of reaction norms of skin temperature
485 to air temperature on body size (black dots) or body condition (open grey dots), for 14 free-ranging
486 adult grey mouse lemurs.

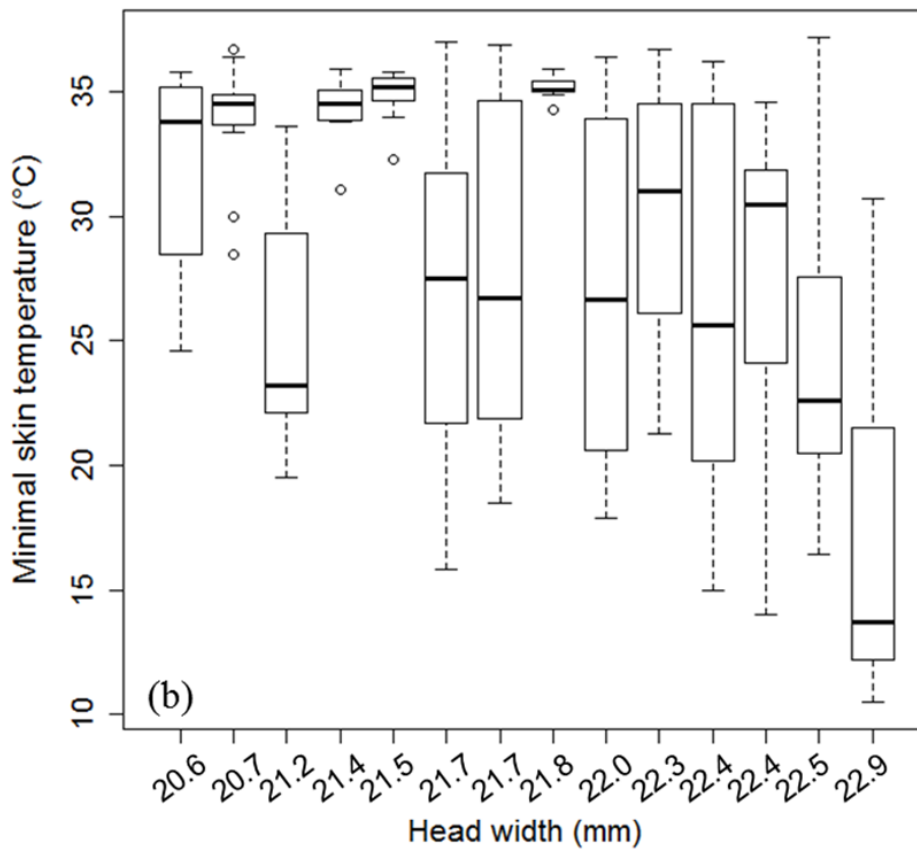
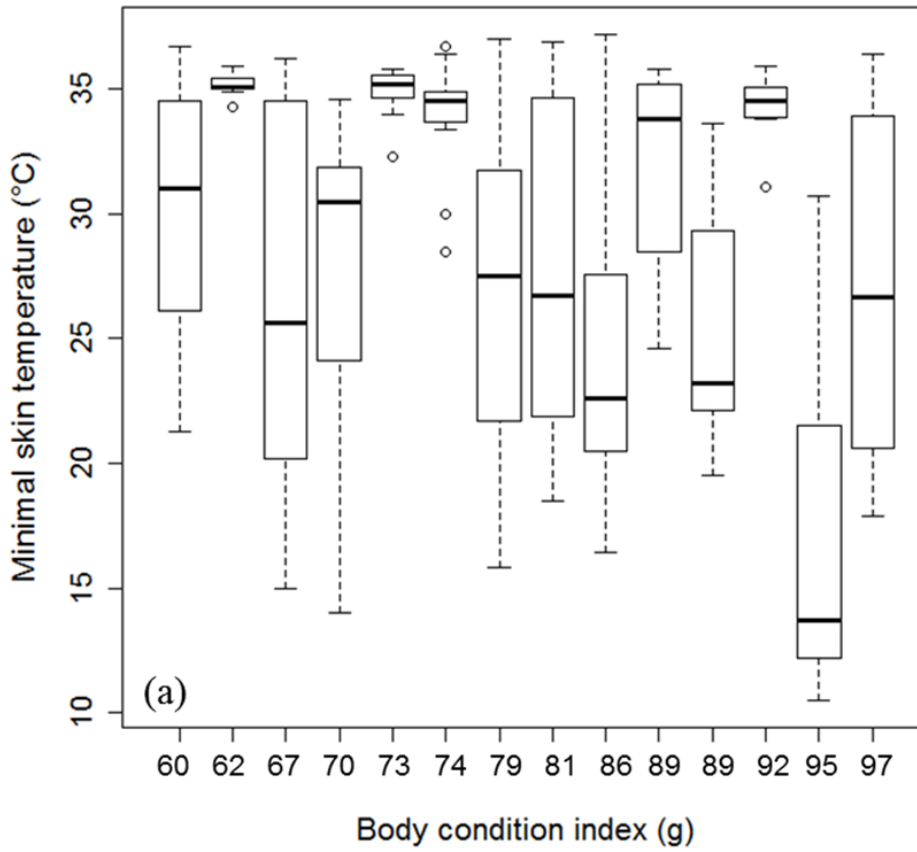
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488 Figure 1

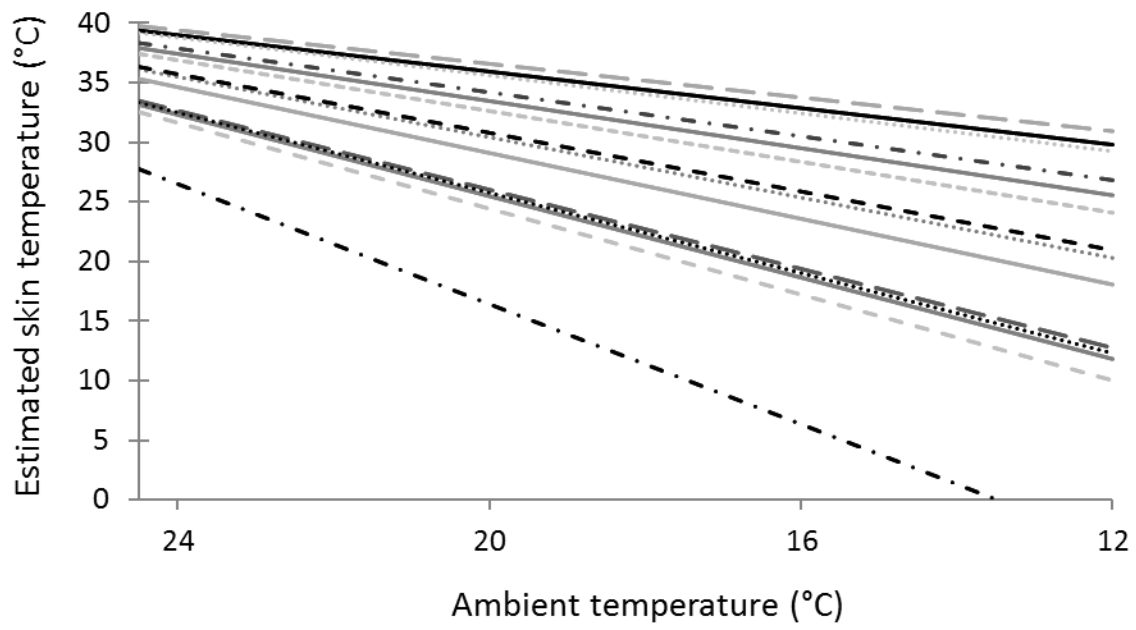


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493 Figure 3



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