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1 **Field evidence for a proximate role of food shortage in the**
2 **regulation of hibernation and daily torpor: a review**

3

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5

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15

16 **Abstract** Hibernation and daily torpor (heterothermy) have long been assumed to be adaptive
17 responses to seasonal energy shortage. Laboratory studies have demonstrated that food
18 shortage alone can trigger the use of heterothermy. However, their potential to predict
19 heterothermic responses in the wild is limited, and few field studies demonstrate the
20 dependence of heterothermy on food availability under natural conditions. Thus, the view of
21 heterothermy as an energy saving strategy to compensate for food shortage largely remains an
22 untested hypothesis. In this paper, we review published evidence on the proximate role of
23 food availability in heterothermy regulation by endotherms, and emphasize alternative
24 hypotheses that remain to be tested. Most studies have relied on correlative evidence.
25 Manipulations of food availability, that demonstrate the proximate role of food availability,
26 have been conducted in only five free-ranging heterotherms. Several other metabolic
27 constraints covary with food availability and can confound its effect. Shortage in water
28 availability, the nutritional composition of food, or subsequent conversion of food in fat
29 storage all could be actual proximate drivers of heterothermy regulation, rather than food
30 shortage. Social interactions, competition for food and predation also likely modulate the
31 relative strength of food shortage between individuals. The ecological relevance of the
32 dependence of heterothermy on food availability remains to be assessed in field experiments
33 that account for the confounding effects of covarying environmental and internal factors.

34

35 **Keywords** Heterothermy • Torpor • hibernation • Food availability • Food shortage • Field
36 experiments

37

38 **Abbreviations**

39 PUFA polyunsaturated fatty acids

40 **Introduction**

41

42 During energetically constraining periods, like cold exposure or food shortage, maintaining a
43 positive energy balance is crucial for survival and future reproduction. In contrast to
44 homoeothermic endotherms, which are constrained to continuously produce endogenous heat
45 to compensate for high heat loss, heterothermic endotherms have the ability to temporarily
46 reduce their energy expenditure by entering extended periods of controlled hypometabolism
47 and hypothermia (i.e. torpor; Geiser 2004; Heldmaier et al. 2004; Boyles et al. 2013; Geiser
48 2013). Heterothermic responses have been traditionally divided into hibernation and daily
49 torpor, hibernation being associated with torpor bouts lasting more than 24 hours, with deep
50 depression of the metabolic rate and massive fattening, whereas daily torpor is defined as
51 torpor bouts shorter than 24 hours, less effective at reducing energy expenditure, and
52 associated with lower fattening (Geiser and Ruf 1995; Geiser 2004, 2013; Boyles et al. 2011;
53 Lovegrove 2012). These bouts of hypometabolism allow a substantial reduction of energy
54 expenditure, down to 5% of the basal metabolic rate during hibernation and 30% during
55 torpor (reviewed in Körtner and Geiser 2000a; Geiser 2013). Hibernation and daily torpor are
56 not restricted to temperate and boreal regions to overcome cold, severe winter conditions, but
57 are also expressed under tropical and sub-tropical latitudes during the mild, dry season
58 (McKechnie and Mzilikazi 2011; Geiser 2013). Because heterothermy occurrence is often
59 seasonal and coincides with periods of natural energy bottlenecks, it has been regarded as an
60 adaptive strategy to cope with low ambient temperatures and/or seasonal food shortage
61 (Lovegrove 2000; Humphries et al. 2003b; Geiser 2004, 2013; Kronfeld-Schor and Dayan
62 2013; but see Geiser and Brigham 2012 for a review of alternative hypotheses). However, the
63 adaptive function of torpor to compensate energy shortage remains an untested hypothesis.
64 The fitness benefits in situation of reduced food availability still need to be demonstrated
65 (Humphries et al. 2003b; Angilletta et al. 2010; Kronfeld-Schor and Dayan 2013).

66 Heterothermy expression is predicted to be optimized according to external and internal
67 conditions, rather than maximized. Indeed, torpor use is supposed to come with physiological
68 costs, including increased oxidative stress (Giroud et al. 2009) and subsequent cellular
69 damage, transitory cognitive impairments (Roth et al. 2010) or reduced immunocompetence
70 (Canale and Henry 2011). Hence heterothermy should be used only when the benefits
71 (essentially energy saving) offset the costs (Humphries et al. 2003a,b). When unfavorable
72 conditions are predictable, the use of heterothermy can be anticipated without the risk that the
73 costs will outweigh the benefits. Heterotherms seem to largely rely on photoperiod to
74 anticipate and time seasonal acclimation (Helm et al. 2013; Williams et al. 2014), as day
75 length triggers seasonal behavioral and physiological adjustments including thermoregulation
76 and seasonal fattening (Körtner and Geiser 2000a). When seasonal fluctuations in weather
77 conditions and food availability are timed differently from year to year, the risk that the costs
78 offset the benefits is much higher. Sensitivity to proximal cues of energy shortage would then
79 be more adaptive as it would allow flexibility in the timing of heterothermy (Körtner and
80 Geiser 2000a; Canale and Henry 2010; Geiser 2013; Kronfeld-Schor and Dayan 2013). The
81 dependence on food availability is expected to be particularly strong in daily heterotherms,
82 which regulate torpor use on a daily basis, and in hibernators during the transitory periods of
83 irregular torpor use before and after the period of continuous hibernation (Geiser 2004;
84 Munro et al. 2005). The fact that some gut hormones involved in fuel homeostasis and energy
85 intake (ghrelin, glucagon-like peptide 1 and peptide YY) may be related to pre-wintering
86 mechanisms and torpor modulation (Giroud et al. 2009; Florant and Healy 2012) provides a
87 functional basis to the hypothesis of a proximate role of food shortage. The down regulation
88 of body temperature when food is limiting is also expected from a theoretical point of view,
89 when extending the output of theoretical models of thermal adaptation in ectotherms to
90 endotherms (Angilletta et al. 2010).

91 Food shortage is the energetic situation when food availability is insufficient to cover the
92 current or forthcoming energy expenditure of an organism (Kronfeld-Schor and Dayan 2013).
93 To formally isolate the effect of food shortage, both energy intake and expenditure should be
94 measured at the individual level. But up to now, nobody has achieved this challenge on free-
95 ranging heterothermic endotherms. Hence, we review the evidence for a proximate role of
96 food availability in the regulation of heterothermy-based energy saving under natural
97 conditions, assuming that it informs us on the role of food shortage. Given that field evidence
98 is scarce, we first briefly review the contributions of laboratory studies and point out their
99 strengths and limitations. Then, we review field evidence, looking at both correlative field
100 observations and experimental tests of the relationship between food availability and the use
101 of heterothermy. Finally, we outline future research directions to clarify and quantify the
102 respective roles of environmental and internal constraints that influence the use of
103 heterothermy and covary with food availability under natural conditions.

104

105 **Methods**

106

107 To identify published studies that addressed the role of food availability in heterothermy
108 regulation, we conducted a literature search with the database Web of Science[®] using the key
109 words ‘torpor’ or ‘hypotherm*’ or ‘hibernat*’ or ‘heterotherm*’ combined with ‘food
110 availability’ or ‘food shortage’ or ‘food restriction’ or ‘caloric restriction’ or ‘calorie
111 restriction’ or ‘energy availability’. Of the 319 returned references, only 68 fitted with the
112 scope of the present review (Table 1). For a study to be considered, (i) the model species had
113 to be a heterothermic endotherm (occasional use of shallow, rest-phase hypothermia by
114 homeotherms was excluded) and (ii) the study had to evaluate or suggest the dependence of
115 heterothermy on food availability based on experimental tests, or on correlations between

116 heterothermy patterns and food availability or environmental parameters supposedly
117 indicative of food availability.

118

119 **Laboratory-based evidence of heterothermy regulation by food availability**

120

121 Fifty-one laboratory experiments demonstrated that torpor or hibernation use depends on food
122 availability. They represent 70 % of the studies considered here (Table 1). We summarize the
123 most demonstrative results from these experiments. Experimental manipulation of food
124 availability under standardized controlled conditions are better at isolating causality than
125 correlative studies and allow the detailed characterization of the functional basis of the
126 heterothermic response.

127 As the unfavorable season approaches, food availability reduces, photoperiod shortens and
128 ambient temperature lowers. The combination of these seasonal changes gradually indicates
129 the start of a period of the year marked by strong energetic constraints, what can be expected
130 to trigger the use of heterothermy. These gradual seasonal changes likely allow acclimation to
131 the forthcoming unfavorable season, i.e. the reinforcement of physiological flexibility by
132 former exposure to energetic constraints (Canale et al. 2011). Nonetheless, the harshness of
133 the unfavorable season can be unpredictable, and the predictability of environmental
134 conditions may also modulate the use of heterothermy (Canale and Henry 2010; Kronfeld-
135 Schor and Dayan 2013).

136 Food limitation induced torpor or increased its use in several species of small mammals
137 such as the golden spiny mouse (*Acomys russatus*; Ehrhardt et al. 2005; Grimpo et al. 2013),
138 elegant fat-tailed mouse opossum (*Thylamys elegans*; Bozinovic et al. 2007), Japanese
139 dormouse (*Glirulus japonicus*; Otsu and Kimura 1993), Pallas's long-tongued tropical bat
140 (*Glossophaga soricina*; Kelm and von Helversen 2007), elephant shrews (*Elephantulus spp.*;
141 Lovegrove et al. 2001) and grey mouse lemur (*Microcebus murinus*; Giroud et al. 2008;

142 Canale et al. 2011). Food supplementation led to an earlier termination of hibernation in
143 eastern chipmunks (*Tamias striatus*; French 2000). In some species, the effect of food
144 deprivation on heterothermy can be more pronounced when combined with low ambient
145 temperatures. In the greater mouse-eared bat (*Myotis myotis*), food-deprived individuals spent
146 more time torpid in a cold environment than those exposed to higher ambient temperatures
147 (Wojciechowski et al. 2007). Food-restricted and cold exposed mouse lemurs increased both
148 depth and duration of their torpor bouts (Séguy and Perret 2005).

149 Photoperiod can modulate the influence of food shortage on heterothermy expression.
150 When exposed to a moderate caloric restriction (-40 % compared to *ad libitum*), grey mouse
151 lemurs under long photoperiod (mimicking summer) did not express torpor while those under
152 short photoperiod (mimicking winter) increased the depth and duration of torpor bouts.
153 Individuals exposed to a severe caloric restriction (-80 %) exhibited torpor whatever the
154 photoperiod, even though depth and duration of bouts were higher under short days (Giroud et
155 al. 2008). The sensitivity of torpor use to food shortage is also enhanced by prior exposure to
156 deficient energy availability: chronically calorie restricted individuals respond more rapidly to
157 an unpredicted food shortage than individuals fed *ad libitum* (Canale et al. 2011). Finally, the
158 predictability of resources may be more important than availability itself. Fat-tailed dunnarts
159 (*Sminthopsis crassicaudata*) increased the frequency and the duration of torpor bouts in
160 response to unpredictable levels of food, but not in response to a regular food restriction
161 (Munn et al. 2010). Temporal predictability of energetic resources may be of particular
162 importance in habitats exposed to high climatic unpredictability (Canale and Henry 2010), but
163 the effect of food predictability on torpor use has been formally tested in only one study
164 (Munn et al. 2010). More experiments are needed to evaluate the relative contribution of
165 intensity *versus* predictability of food shortage to heterothermy regulation.

166 Laboratory experiments have a limited potential to predict torpor patterns of free-ranging
167 heterotherms because artificial conditions largely differ from the actual conditions that free-

168 ranging animals experience. Laboratory studies likely underestimate torpor use and its impact
169 on energy expenditure under natural conditions (Geiser et al. 2000). In birds, torpor is
170 observed only under natural conditions (Smit and McKechnie 2010). Laboratory experiments
171 are obligate, over-simplifications of the mechanisms under study. Classical designs avoid the
172 role of noticeably influential ecological processes by (i) discarding the role of
173 thermoregulation (experiments at constant ambient temperature, even at thermo-neutrality;
174 Fig. 1), (ii) provisioning food on a predictable schedule, in quantity and quality largely
175 superior to natural food availability (Fig. 1), (iii) exposing animals to artificial light and
176 transitions between seasons (Fig. 1), (iv) protecting animals from exposure to parasites and
177 predators, (v) limiting movement (cages are smaller than natural home ranges), (vi) omitting
178 the social context (animals isolated from social interactions including competition), and (vii)
179 working on peculiar genetic backgrounds (drifted and inbred populations; Pelletier et al.
180 2009). Field studies are necessary to evaluate the transferability of laboratory results to
181 realistic ecological conditions.

182

183 **Review of field evidence**

184

185 Field evidence for heterothermy dependence on food availability were obtained using two
186 main methods of inference: correlative *versus* experimental evidence. Correlative evidence
187 refers to studies reporting correlations between heterothermy patterns and natural variation in
188 food availability or environmental variables supposedly indicative of food availability (64 %
189 of the field studies; Table 1). Experimental evidence refers to experimental manipulation of
190 food availability under (semi-)natural conditions (36 % of the field studies; Table 1).

191

192 Correlative evidence

193

194 Correlative evidence falls into one of two categories: studies suggesting that ambient
195 temperatures modulate heterothermy expressions through its impact on food availability were
196 considered as indirect field evidence (12 studies; Table 1), whereas studies showing that
197 heterothermy patterns correlate with natural fluctuations in food availability were considered
198 as direct field evidence (two studies; Table 1). The use of heterothermy generally correlates
199 with seasonal cycles of unfavorable conditions, such as low ambient temperatures, wet
200 conditions, deep snow cover or severe drought, which are associated with reduced food
201 availability (Körtner and Geiser 2000a; Lovegrove 2000; Humphries et al. 2003b; Geiser
202 2013). However, this seasonal contingency does not demonstrate a causal relationship
203 between the amount of food available and the patterns of heterothermy that are observed.

204

205 Indirect field evidence for the dependence of heterothermy expression on food availability
206 mediated by temperature-driven fluctuations of preys

207

208 As climate variability affects primary and secondary productions (Stenseth et al. 2002; Canale
209 and Henry 2010), and the activity of ectothermic invertebrate preys, it likely indirectly
210 modulates torpor use by birds and mammals through its influence on food availability (Fig.
211 1). Many insects, particularly aerial species, do not develop or cannot remain active at low
212 ambient temperature, or during rainfall episodes, resulting in important circadian, daily and
213 seasonal fluctuations in their abundance. These weather-driven drops in insect abundance
214 constitute major energetic constraints for aerial insectivores, like bats, nightjars and swifts
215 (Bize et al. 2007; Stawski et al. 2009; Stawski and Geiser 2010a; Doucette et al. 2012). The
216 dependency of invertebrate activity, and availability, on weather conditions is frequently put
217 forward to suggest that the use of heterothermy by insectivorous species during inclement
218 weather conditions is indeed driven by food shortage. In the subtropical, eastern long-eared
219 bat (*Nyctophilus bifax*), torpor depth and duration increased during cold winter nights

220 (Stawski et al. 2009; Stawski and Geiser 2010a). The same pattern was observed for summer
221 torpor use by desert free-tailed bats (*Mormopterus sp.*; Bondarenco et al. 2013). Hoary bats
222 (*Lasiurus cinereus*) entered torpor when ambient temperature was below 13 °C (Hickey and
223 Fenton 1996) or when storms occurred during the period of pregnancy (Willis et al. 2006).
224 And nestling alpine swifts (*Apus melba*) strongly reduce their body temperature during a
225 period of inclement weather, when parents stop feeding them (Bize et al. 2007). The strong
226 weather-dependency of torpor use mediated by limited food availability has also been
227 suggested for nectarivores. During rainy, cold nights, sugar gliders (*Petaurus breviceps*)
228 increased torpor use (Körtner and Geiser 2000b).

229 The main limitation of these studies is that the dependence of heterothermy expression on
230 food availability was only inferred from supposed correlations between food availability and
231 weather. The authors did not try to statistically distinguish their respective role in the
232 regulation of torpor use. Indeed, only three studies attempted to establish the link between
233 food availability and torpor use. In the studies on hoary bats and free-tailed bats, prey
234 abundance was positively correlated with ambient temperature, and torpor use increased with
235 low temperatures (Hickey and Fenton 1996; Bondarenco et al. 2013). And, in African scops
236 owls (*Otus senegalensis*), winter torpor use was not explained by fluctuations of ambient
237 temperature, and therefore was more likely attributable to the seasonal reduction in arthropod
238 abundance (Smit and McKechnie 2010). Species, for which resources are relatively
239 independent of daily weather conditions, such as granivorous, frugivorous or herbivorous
240 species, should be more suitable models to disentangle the proximate roles of food availability
241 and weather conditions in the regulation of torpor and hibernation. But until now, the link
242 between torpor use and food availability has been assessed in only one granivorous rodent
243 (the eastern chipmunk) and one frugivorous bird, the others dealing with insectivores (8
244 species) or omnivores (three species; Table 1).

245

246 Direct field evidence for the dependence of heterothermy expression on food availability
247
248 In the three following studies, the authors did measure the abundance of food and could relate
249 heterothermy patterns to the actual conditions of food availability that animals were
250 experiencing. The first study compared torpor use of Australian owlet-nightjars (*Aegotheles*
251 *cristatus*) over six winters and in three habitats that differed in ambient temperature, annual
252 rainfall and arthropod abundance (Doucette et al. 2012). Torpor use mainly depended on prey
253 abundance and to a lesser extent on rainfall, but not on minimum ambient temperature, while
254 depth and duration of torpor bouts depended on thermal constraints. Torpor frequency, depth
255 and bout length were also greater during the two periods of lowest arthropod biomass
256 (Doucette et al. 2012). This study is the most convincing demonstration of a proximate role of
257 prey availability in the regulation of torpor use in the wild, independent of ambient
258 temperature. To further improve the statistical support for a proximate role of food
259 availability independently of weather conditions, the dependent variable to be used should be
260 insect abundance adjusted for the dependence of insect activity/abundance on ambient
261 temperature and rainfall. A similar study on six freckled nightjars (*Caprimulgus tristigma*)
262 showed that moon phase was a better determinant of torpor use than air temperature, with
263 more torpor use during dark nights (Smit et al. 2011). This indirectly supports the role of food
264 availability on the regulation of torpor use as the foraging opportunities and foraging success
265 of these nocturnal birds that visually locate their insect preys are constrained by moon light
266 availability. Unfortunately, food abundance and foraging success could not be measured in
267 this study. The third study showed that hibernation patterns of eastern chipmunks, which rely
268 on hoards of seeds to sustain their energy needs during the hibernation period, were less
269 pronounced during years of high tree-seed production than during years of low production
270 (Landry-Cuerrier et al. 2008). The risk that the effect of food availability would be
271 confounded by ambient temperature is low as seed production is not strongly impacted by

272 daily fluctuations in weather conditions. More demonstrative is the fact that, within the year
273 of high production, inter-individual variations in torpor expression resulted from fine-scale
274 variations in resource availability: individuals inhabiting burrows close to trees with low seed
275 production exhibited longer and deeper torpor bouts than those closer to trees with high seed
276 production (Landry-Cuerrier et al. 2008). Previous studies had already suggested that the
277 decision to initiate hibernation may be partly dependent on hoard accumulation (Humphries et
278 al. 2002; Munro et al. 2008), but this study is the first to establish the correlation between
279 food availability and hibernation patterns.

280 Although these convincing studies document that variations in heterothermy patterns were
281 primarily explained by natural fluctuations in food availability, supporting that food
282 availability may be a proximate driver of torpor use in the wild, they still do not constitute
283 formal tests of heterothermy dependence on food availability. The natural fluctuations of food
284 availability could have been concomitant with other environmental constraints that
285 independently favor heterothermy expression (e.g., years of high seed-production could be
286 characterized with specific climatic conditions for instance).

287

288 Experimental evidence

289

290 Experimental manipulations of food availability under natural conditions are theoretically the
291 best way to test if energy availability determines heterothermy expression in the wild. To our
292 knowledge, such experiments have been conducted in only two hibernators and three daily
293 heterotherms, representing 11 % of all studies and 36% of field studies (Table1).

294 Food supplementation during periods of natural food shortage is the unique experimental
295 paradigm to investigate the dependence of heterothermy on energy availability, as food
296 restriction is unachievable with free-ranging animals. Humphries et al. (2003a,b), who
297 highlighted that hibernation as a response to natural food shortage remained an untested

298 hypothesis (Humphries et al. 2003b), were also the first ones to experimentally test if a
299 manipulation of food availability induced a change in hibernation patterns of free-ranging
300 heterotherms (Humphries et al. 2003a). Food-supplemented chipmunks spent more time
301 euthermic than controls during early winter, and when hypothermic, they also exhibited
302 shallower bouts of hypothermia. Chipmunks likely used available energy reserves to
303 minimize torpor use, supporting the torpor optimization hypothesis (Humphries et al. 2003b).
304 Another experimental manipulation of food availability was realized with golden spiny mice,
305 which are food limited in their natural habitat due to reduced insect abundance during winter,
306 the reduction being increased by exploitative competition with Cairo spiny mice (*A.*
307 *cahirinus*; Levy et al. 2012). Individuals kept in large field enclosures and exposed to natural
308 abiotic (photoperiod, ambient temperature) and biotic (predators) pressures, were offered
309 artificial foraging patches filled with seeds. Patches were refilled once per day. Mice that
310 arrived early at the food patches acquired more food and spent less time torpid, while later
311 foragers were energetically constrained and remained torpid longer (Levy et al. 2012). Two
312 other studies conducted under semi-natural conditions confirmed that food-supplemented
313 mice spent less time torpid than mice exposed to natural food availability (Levy et al.
314 2011a,b), supporting the idea that spiny mice reduce torpor use when they do not need to
315 minimize energy expenditure. We have also conducted a food supplementation experiment on
316 free-ranging grey mouse lemurs, small heterothermic primates that spontaneously enter torpor
317 during the dry season (Ortmann et al. 1997; Schmid 2001). Food-supplemented individuals
318 reduced their use of torpor, with shorter and shallower torpor bouts than individuals with
319 natural food availability (P. Vuarin, M. Dammhahn, P. Kappeler and P.-Y. Henry unpublished
320 data). However, this minimization of torpor use lasted for only one to two months
321 (respectively for males and females). Afterwards, food-supplemented mouse lemurs returned
322 to normal expression of torpor. Our study is the first to suggest that the dependence of
323 heterothermy regulation on food supply could be transitory, restricted to the period of

324 transition between summer and winter. This temporal organization of the responsiveness of
325 torpor to food availability could have resulted from an internal physiological schedule of
326 phenotypic transition that finally took over the control of torpor use. The supplementary food
327 could have also been used to build larger fat body stores before entering the core part of the
328 dry season, rather than to cover daily energetic needs.

329 The torpor optimization hypothesis also holds in birds. Woods and Brigham (2004) used
330 artificial lights to experimentally increase insect availability on the territory of three radio-
331 tagged common poorwills (*Phalaenoptilus nuttallii*), whereas control individuals had normal
332 access to prey, which varied with air temperature. Poorwills with supplemental illumination
333 used torpor at night less frequently (34.4 % of bird-nights) than control birds (72.3 % of bird-
334 nights), demonstrating that food availability had a strong influence on torpor use. Eventually,
335 food-supplemented speckled mousebirds (*Colius striatus*) kept in outdoor aviaries exhibited
336 higher body temperature than those exposed to restricted food availability (McKechnie et al.
337 2006).

338 Together, these experiments support the idea that reduced food availability is a proximate
339 driver of heterothermy, and that free-ranging heterotherms fine-tune the use of both
340 hibernation and torpor according to actual food availability. Hibernators can only rely on the
341 amount of energy stored before the beginning of hibernation, i.e. fat body reserves or food
342 hoards, while daily heterotherms have daily opportunities to forage throughout the
343 unfavorable season (Körtner and Geiser 2000a; Levy et al. 2012; Geiser 2013). However, the
344 model systems investigated are so few that they do not allow us to infer general patterns.

345

346 **Confounding effects of food availability**

347

348 Conceptually, most of the studies that have manipulated food availability aimed to manipulate
349 the amount of energy acquired by the animals. However, the ingestion of food is not always

350 only for energy intake; it is also the major way to control internal water, nutrient and anti-
351 nutrient balances, and energy stores (Fig. 1). Specifically designed experiments must be set up
352 to distinguish the role of food availability from the role of confounding effects. In this section,
353 we review all available literature independently of whether it reports results from laboratory
354 or natural conditions.

355

356 Water shortage rather than food shortage?

357

358 Depending on the ecological conditions, water may be limiting as much or even more than
359 energy availability. Both at high and low latitudes, freezing temperature of winter or dryness
360 of the dry season drastically reduce water bioavailability. Water and food shortages are
361 seasonally confounded, especially for species that acquire most their body water through
362 food. To our knowledge, experiments about the influence of water availability on
363 heterothermy have not yet been conducted in the wild.

364 Water availability modulates heterothermy expression under controlled conditions. In the
365 Syrian hamster (*Mesocricetus auratus*), water deprivation enhanced hibernation. An
366 unpredictable deprivation of water (randomly on 50 % of the days throughout the experiment)
367 had a stronger effect than a regular shortage (consistently every two days), as unpredictably
368 deprived individuals started hibernation earlier, spent more time hypothermic during winter
369 and remained torpid later in spring (Ibuka and Fukumura 1997). Such results demonstrate the
370 importance of both water availability and its uncertainty in torpor regulation.

371 Water availability can interact with food availability. Buffenstein (1985) exposed least
372 gerbils (*Gerbillus pusillus*) to different regimes of water and/or food restriction, generating
373 moderate to acute energetic and/or hydric stresses. The harshest conditions resulted in the
374 highest percentages of torpid animals, more gerbils being torpid when deprived of both food
375 and water (Buffenstein 1985). Further experiments remain to be conducted to determine if the

376 effects of food and water availability in heterothermy regulation are additive, as suggested by
377 the study on gerbils, or multiplicative (i.e. in interaction). A similar study, conducted on
378 stripe-faced dunnarts (*Sminthopsis macroura*), showed that heterothermy was not influenced
379 by water deprivation in this species, but was sensitive to food withdrawal (Song and Geiser
380 1997). Dunnarts seemed to be able to compensate for water shortage by consuming a larger
381 amount of moist food. Because they live in arid areas, they probably have physiological
382 adaptations peculiar to desert species (better kidney efficiency, low water turnover) that allow
383 them to cope with regular water limitations. Brooker and Withers (1994) reported that the
384 relative medullary thickness of the kidneys of stripe-faced dunnarts was one of the highest
385 among the 25 dasyurid marsupial species they examined. This might explain why a short-term
386 restriction in drinking water did not constitute an acute stress for this species (Song and
387 Geiser 1997). Species that acquire water essentially through food ingestion should be less
388 sensitive to water shortage than species relying on drinking water. The less a species drinks
389 water, the higher the risk that the effects of food and water shortages are confounded (Fig. 1).
390 Experimental supplementation of water during periods of natural water restriction should be
391 conducted in the field in order to confirm the role of water availability under relevant
392 ecological conditions.

393 Heterothermy could be primarily regulated according to water availability, as torpor is an
394 efficient strategy to cope with water shortage (Geiser and Brigham 2012; Ben-Hamo et al.
395 2013; Kronfeld-Schor and Dayan 2003). Schmid and Speakman (2000, 2009) suggested that
396 the primary function of torpor could be to save water, since torpid free-ranging grey mouse
397 lemurs had a lower daily water flux than normothermic ones but did not differ in daily energy
398 expenditure (Schmid and Speakman 2000). Daily water flux in torpid mouse lemurs from a
399 dry forest was also lower than that of lemurs from a rain forest, suggesting that the water
400 requirement was more constraining in the dry habitat (Schmid and Speakman 2009). The

401 large amount of time spent torpid by spiny mice during summer also suggests that torpor use
402 could be driven by water availability in this system (Levy et al. 2011a).

403

404 Food quality rather than food availability?

405

406 When foraging, animals do not only seek to acquire the maximum amount of food possible,
407 but also optimize food acquisition to compensate for deficiencies in some specific nutrients
408 (Fig. 1; Ruf and Arnold 2008). Nutrient deficiency may be particularly critical during
409 development, when the nutrient needs of fast growing offspring are maximal (Geiser and
410 Brigham 2012; Giroud et al. 2012). Nutrients are chemical components required for life, like
411 carbohydrates, lipids, or proteins. When a nutrient availability is reduced below a
412 physiological requirement, this deficiency may become a limiting factor and be responsible
413 for the induction of torpor, rather than food availability. Nutrient excess can also result in a
414 physiological incapacity to optimally control body temperature, like for yellow-bellied
415 marmot (*Marmota flaviventris*) that did not hibernate when fed with an excessive amount of
416 α -linoleic acid (Hill and Florant 2000). However, the role of the nutritional composition of
417 food in heterothermy regulation has been largely ignored.

418 Carbohydrates, lipids and proteins are expected to play a role in heterothermy regulation
419 given that they are major energy substrates (Fig. 1), but their roles in heterothermy regulation
420 have not been thoroughly studied. The nature of the metabolic fuel needed to induce torpor in
421 the eastern pygmy possum (*Cercartetus nanus*) was investigated by comparing the effects of
422 food deprivation, reduced fatty acid availability or glucose deprivation. All treatments
423 induced torpor, even though the metabolic rates and body temperatures in gluco-deprived
424 individuals remained higher than those of fat-limited or food-deprived ones (Westman and
425 Geiser 2004). Before the start of the hibernating season, semi-captive pichis (*Zaedyus pichiy*)
426 fed with a low-quality diet (1% protein, 0.1% lipid) expressed more frequent, deeper and

427 more prolonged torpor bouts than control individuals (Superina and Jahn 2013). Fatty acid
428 availability is likely to play a major role in heterothermy regulation. Stored body fat
429 constitutes the main fuel for hibernating big brown bats (*Eptesicus fuscus*). When selecting a
430 microclimate for hibernation, energy-limited individuals were expected to choose colder
431 temperatures to minimize energy expenditure, whereas non-limited ones were expected to
432 prefer warmer temperatures to minimize the costs of hibernation. Bats exposed to a reduced
433 fatty acid availability (through injection of mercaptoacetate) selected lower temperatures
434 (Boyles et al. 2007). For short-beaked echidnas (*Tachyglossus aculeatus*) and fat-tailed dwarf
435 lemurs (*Cheirogaleus medius*), monounsaturated fatty acids constitute the main fuel for
436 hibernation, as they were prevalent in the pre-hibernating fat depot of both species
437 (Falkenstein et al. 2001; Fietz et al. 2003). The respective roles of carbohydrates, lipids and
438 proteins in explaining the impact of food availability on heterothermy regulation remain to be
439 properly investigated.

440 Essential nutrients cannot be synthesized and must be obtained from food. They include
441 vitamins, dietary minerals, essential fatty acids and essential amino-acids. Among them,
442 polyunsaturated fatty acids (PUFA) are the only ones known to exert a strong influence on
443 heterothermy expression (Munro and Thomas 2004; Ruf and Arnold 2008). PUFA are essential
444 in maintaining optimal cell membrane functioning at varying temperatures, and a high PUFA
445 diet enhances torpor use, depth and duration, and reduces metabolic rate and mass loss (Munro
446 and Thomas 2004; Ruf and Arnold 2008). High PUFA content of the white adipose tissue in
447 the fall was associated with lower minimal body temperature and lower mass loss during winter
448 in free-ranging Alpine marmots (*Marmota marmota*; Ruf and Arnold 2008). Hibernators may
449 actively select diets rich in n-6 PUFAs before the onset of hibernation, given their properties of
450 heart protection at low body temperatures (Giroud et al. 2013). Free-ranging yellow-bellied
451 marmots were found to preferentially retain n-6 PUFA during winter (Hill and Florant 1999),
452 whereas an excessive amount of dietary n-3 PUFAs prevented them from hibernating (Hill and

453 Florant 2000). In contrast, free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*)
454 mainly stored n-3 PUFAs in their white adipose tissue during winter (Lehmer and van Horne
455 2001). The different PUFA dynamics between species were attributed to their different winter
456 strategies: marmots hibernate while prairie dogs express intermittent torpor (Lehmer and van
457 Horne 2001). To investigate how the amount of food interacts with its fatty acid composition,
458 Munro et al. (2005) compared torpor patterns of three groups of free-ranging eastern
459 chipmunks: a control group with natural food availability, a natural-PUFA food supplemented
460 group representing a manipulation of hoard size only, and a high-PUFA food supplemented
461 group representing a manipulation of both hoard size and dietary PUFA content. A natural-
462 PUFA supplement led to a reduction in torpor use as supplemented chipmunks spent more time
463 euthermic and exhibited higher skin temperatures than controls, but a high-PUFA supplement
464 led to a further reduction in torpor use and an advanced hibernation ending (Munro et al. 2005).
465 Food availability and fatty acid composition can vary over the year, but there is no evidence
466 that they necessarily covary positively. They could vary at different time or space scales, and
467 the direction and the strength of the interaction may change over the year.

468 Anti-nutrients are natural components that interfere with nutrient absorption and
469 utilization, like tannins in plants for example, but their potential role in heterothermy
470 regulation has been ignored so far (Fig. 1). Anti-nutrients can be expected to increase the
471 detoxification costs and associated metabolic costs of digesting food. In grey mouse lemurs
472 for example, individuals entering the dry season may not only face variations in food quantity
473 but also in quality, with potential changing concentrations of anti-nutrients. Even under *ad*
474 *libitum* food availability, mouse lemurs increase their avoidance of anti-nutrients under winter
475 photoperiod (Hellekant et al. 1993; Simmen et al. 1999). A way to test the effect of anti-
476 nutrients in heterothermy regulation would be to design a food supplementation experiment in
477 which animals at the onset of the unfavourable season would be exposed either to normal

478 seasonal food shortage (control), *ad libitum* food availability with normal nutritional content,
479 or to *ad libitum* food availability with enrichment in anti-nutrients.

480

481 Energy storage rather than energy shortage?

482

483 Animals remaining normothermic when food is available do not necessarily avoid the costs
484 associated with the use of heterothermy (Humphries et al. 2003a,b). Food-supplemented
485 animals may take the advantage of supplementary food to maximize food acquisition, and in
486 turn their energy reserves (internally as body fat, or externally as food hoards; Fig. 1). Larger
487 reserves should increase the chances to survive the unfavorable season by relying only on
488 heterothermy-based energy savings. This mechanism has been suggested in the food
489 supplementation experiment with grey mouse lemurs: individuals with increased access to
490 food postponed the use of torpor by one-two months, potentially to reach higher fat stores
491 than control individuals (P. Vuarin, M. Dammhahn, P. Kappeler and P.-Y. Henry unpublished
492 data). The energetic benefits associated with torpor expression are positively related to torpor
493 depth and duration (Heldmaier et al. 2004; Geiser 2013), and a higher body condition has
494 been associated with an increased use of heterothermy in mouse lemurs (Kobbe et al. 2011;
495 Vuarin et al. 2013) and bats (Stawski and Geiser 2010b). The amount of stored fat is actually
496 supposed to be the main determinant of the timing of hibernation initiation in several
497 heterotherms (Vuarin et al. 2013; Bieber et al. 2014).

498

499 Social interactions, competition and predation

500

501 Social interactions directly linked to thermoregulation, competition for food resources and
502 predation may modulate heterothermic responses to food availability (Kronfeld-Schor and
503 Dayan 2013). Animals roosting in groups may benefit from passive warming from their

504 congeners to reduce their own energy expenditure and save energy (Gilbert et al. 2010). In
505 contrast, competitive interactions for food could reinforce the strength of the food shortage
506 experienced (Levy et al. 2011b).

507 To our knowledge, only one field experiment has been conducted to test the conjoint
508 effects of food restriction and social interactions affecting thermoregulation (known as social
509 thermoregulation, huddling or communal roosting). In speckled mousebirds kept under semi-
510 natural conditions, food restriction induced the expression of heterothermic responses, but the
511 responses were less pronounced in birds resting in groups than in solitary birds (McKechnie et
512 al. 2006). The thermal conditions experienced by birds roosting in group were probably less
513 constraining than that of birds resting alone. Communal roosting may partly compensate for
514 food shortage. The fact that individuals rest alone or in groups should be taken into account
515 when working with social or gregarious species.

516 Competition for food resources, especially when they are already reduced due to natural
517 periods of food shortage, may also modulate heterothermy patterns. Under semi-natural
518 conditions, golden spiny mice spent less time torpid when supplementary food was provided
519 in the presence of a competitive species, but reduced torpor use when the competitor was
520 removed independently of food supplementation (Levy et al. 2011b). Inter- and intra- specific
521 competitive interactions should be taken into account when looking at the effect of food
522 availability on heterothermy expression.

523 Predation also likely modulates the use of heterothermy. The hypothermic state is
524 considered to increase survival probability (Turbill et al. 2011; Geiser 2013), and a possible
525 explanation could be that an increased use of heterothermy reduces predation risk because
526 animals can reduce the time they spent foraging, and minimize their exposure to predators
527 (Stawski and Geiser 2010b; Lebl et al. 2011). Free-ranging edible dormice (*Glis glis*) exhibit
528 unusual high longevity as well as prolonged hibernation duration up to >10 months (Bieber
529 and Ruf 2009), which led the authors to suggest that heterothermy evolved as a predator-

530 avoidance strategy in this species. The higher survival rate during the hibernation season
531 compared to the active season was also related to a reduced predation risk as animals were
532 protected from predators in their hibernacula (Lebl et al. 2011). However, hypothermic
533 individuals have reduced locomotor capacities, and have a lower efficiency at escaping
534 predators than normothermic ones (Carr and Lima 2013; but see Rojas et al. 2012). Hence the
535 selective pressure for using safe hibernacula should be high (Lebl et al. 2011). The predation
536 hypothesis to explain temporal fluctuations in heterothermy should also be considered in
537 future field studies testing the role of food availability.

538

539 **Conclusions and perspectives**

540 The reviewed field evidence revealed that food availability is unequivocally involved in the
541 regulation of hibernation and daily torpor, as heterotherms generally increase their use of
542 heterothermy when food availability is limited, and reduce it when supplementary food is
543 provided. However, the robustness and ecological generality of these conclusions must be
544 evaluated, as they are derived from very few convincing studies. Field studies account for a
545 third of all studies related to food availability and heterothermy expression. They are
546 dominated by correlative evidence, with studies based on correlations between heterothermy
547 patterns and environmental variables supposedly indicative of food availability (temperature,
548 rainfall), or between heterothermy patterns and food availability directly in very few cases.
549 Formal demonstrations of the dependence of heterothermy on food availability (through
550 experimental manipulations) account for only one-tenth of all studies.

551 More field studies are needed to gain a robust understanding of the proximate role of food
552 availability in the regulation of hibernation and daily torpor under natural conditions. Priority
553 should be given to experimental manipulations of food availability which is the best way to
554 identify a causal relationship between food availability and heterothermy patterns. Such an
555 approach has been used in only four species so far. Close attention should be paid to the

556 factors that covary with food availability and therefore confound its effects (Fig. 1). Their
557 respective roles in regulating heterothermy remain to be tested and quantified. Among field
558 evidence, only three temperate species have been studied (a rodent, a bat and a swift),
559 whereas ten different species have been studied for the tropics and subtropics (Table 1).
560 Because organisms from different latitudes are expected to face different energetic constraints
561 (climate and food availability being less predictable in dry tropical regions than in temperate
562 zones, for example; Boyles et al. 2013), a greater diversity of models species is needed.

563 To directly quantify the effect of food shortage, i.e. the internal energetic deficit at the
564 individual level, on torpor use, energy intake and expenditure should be measured on both
565 control and experimental individuals (Grimpo et al. 2013; Kronfeld-Schor and Dayan 2013).
566 Up to now, this is a significant technological challenge, which has never been overcome
567 under natural conditions. This review highlights how much basic research remains to be done
568 to gain an integrative understanding of the proximate drivers of heterothermy regulation under
569 realistic ecological conditions.

570

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577

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- 944

945 **Table 1** Published evidence of the role of food availability in torpor regulation for
946 heterothermic endotherms. Studies are ordered per method of inference, torpor patterns, class,
947 order and species names. For each species, their diet, latitudinal range and adult body mass (in
948 g) are reported as they influence the use of heterothermy (Geiser 2004; Boyles et al. 2013).
949 Methods of inference were ranked so that their order reflects the robustness of the inference
950 about the proximate role of food availability under natural conditions, starting from the most
951 convincing method: (i) field experiments, where food availability was manipulated *in situ*, (ii)
952 direct field evidence, i.e. when heterothermy use correlates with natural fluctuations in food
953 availability, after accounting for confounding environmental covariates (Fig. 1), (iii) indirect
954 field evidence, i.e. when heterothermy use correlates with ambient temperature supposedly
955 because of the temperature-dependence of food availability, and (iv) laboratory experiments
956 of food restriction. The categorical classification of torpor patterns per species followed
957 Geiser and Ruf (1995), and was complemented by subsequent reviews (Geiser 2004, 2013;
958 Boyles et al. 2011; McKechnie and Mzilikazi 2011; Lovegrove 2012; Dausmann 2014), or
959 information in the original reference. Species' traits were obtained from Boyles et al. (2013),
960 the cited references or online natural history information. For latitudinal range, tropical refers
961 to latitudes between the Tropic of Cancer and the Tropic of Capricorn, subtropical refers to
962 latitudes between the tropic circles and the 35th parallels, and temperate refers to latitudes
963 between the 35th parallels and the poles. The house mouse (*Mus musculus*) is classified as
964 widespread since it spreads across the whole latitudinal gradient.

Table 1

Torpor pattern	Class	Order	Species	Diet ^a	Latit. range ^b	Body mass	Reference(s)
(i) Field experiments							
Daily heterotherms	Mammals	Primates	Grey mouse lemur (<i>Microcebus murinus</i>)	Omn.	Trop.	77.5	(Vuarin et al. unpublished data)
		Rodents	Golden spiny mouse (<i>Acomys russatus</i>)	Omn.	Subt.	50.6	(Levy et al. 2011a,b, 2012) ^c
	Birds	Mousebirds	Speckled mousebird (<i>Colius striatus</i>)	Frug.	Trop.	52	(McKechnie et al. 2006) ^c
Hibernators	Mammals	Rodents	Eastern chipmunk (<i>Tamias striatus</i>)	Gran.	Temp.	97	(Humphries et al. 2003a; Munro et al. 2005)
	Birds	Nightjars	Common poorwill (<i>Phalaenoptilus nuttallii</i>)	Ins.	Subt.	50	(Woods and Brigham 2004)
(ii) Direct field evidence							
Daily heterotherms	Birds	Nightjars	Australian owlet-nightjar (<i>Aegotheles cristatus</i>)	Ins.	Subt.	47	(Doucette et al. 2012)
Hibernators	Mammals	Rodents	Eastern chipmunk (<i>Tamias striatus</i>)	Gran.	Temp.	97	(Landry-Cuerrier et al. 2008)
(iii) Indirect field evidence							
Daily heterotherms	Mammals	Marsupials	Sugar glider (<i>Petaurus breviceps</i>)	Omn.	Subt.	132	(Körtner and Geiser 2000b)
	Birds	Nightjars	Freckled nightjar (<i>Caprimulgus tristigma</i>)	Ins.	Subt.	73	(Smit et al. 2011)
		Owls	African scops owl (<i>Otus senegalensis</i>)	Ins.	Trop.	70	(Smit and McKechnie 2010)
		Swifts	Alpine swift (<i>Apus melba</i>)	Ins.	Temp.	69	(Bize et al. 2007)
Hibernators	Mammals	Bats	Free-tailed bat (<i>Mormopterus sp.</i>)	Ins.	Subt.	8.5	(Bondarenco et al. 2013)
			Hoary bat (<i>Lasiurus cinereus</i>)	Ins.	Temp.	19.9	(Hickey and Fenton 1996; Willis et al. 2006)
			Northern long-eared bat (<i>Nyctophilus bifax</i>)	Ins.	Subt.	10.1	(Stawski et al. 2009; Stawski and Geiser 2010a,b)
		Rodents	Eastern chipmunk (<i>Tamias striatus</i>)	Gran.	Temp.	97	(Humphries et al. 2002; Munro et al. 2008)
(iv) Laboratory experiments							

Daily heterotherms	Mammals	Bats	Common blossom bat (<i>Syconycteris australis</i>)	Nect.	Subt.	17.8	(Coburn and Geiser 1998)	
			Pallas's long-tongued bat (<i>Glossophaga soricina</i>)	Nect.	Trop.	10.1	(Kelm and von Helversen 2007)	
			Little yellow-shouldered bat (<i>Sturnira lilium</i>)	Frug.	Trop.	21.9	(Audet and Thomas 1997)	
	Marsupials		Seba's short-tailed bat (<i>Carollia perspicillata</i>)	Frug.	Trop.	18	(Audet and Thomas 1997)	
			Elegant fat-tailed mouse opossum (<i>Thylamys elegans</i>)	Ins.	Subt.	40.2	(Silva-Duran and Bozinovic 1999; Bozinovic et al. 2007)	
			Fat-tailed dunnart (<i>Sminthopsis crassicaudata</i>)	Ins.	Subt.	19	(Munn et al. 2010)	
			Stripe-faced dunnart (<i>Sminthopsis macroura</i>)	Ins.	Subt.	24	(Withers et al. 2000; Song and Geiser 1997)	
			Grey mouse lemur (<i>Microcebus murinus</i>)	Omn.	Trop.	77.5	(Génin and Perret 2003; Séguy and Perret 2005; Giroud et al. 2008; Canale et al. 2011, 2012)	
	Rodents		Arizona pocket mouse (<i>Perognathus amplus</i>)	Gran.	Temp.	11	(Reichman and Brown 1979)	
			Darwin's leaf-eared mouse (<i>Phyllotis darwini rupestris</i>)	Omn.	Subt.	35.9	(Bozinovic and Marquet 1991)	
			Djungarian hamster (<i>Phodopus sungorus</i>)	Gran.	Temp.	25	(Ruf et al. 1993 ; Bae et al. 2003)	
			Golden spiny mouse (<i>Acomys russatus</i>)	Omn.	Subt.	50.6	(Ehrhardt et al. 2005; Gutman et al. 2006, 2007; Grimpo et al. 2013)	
			House mouse (<i>Mus musculus</i>)	Omn.	Wid.	19.3	(Himmshagen 1985; Kanizsai et al. 2009; Schubert et al. 2010)	
			Least gerbil (<i>Gerbillus pusillus</i>)	Gran.	Trop.	12.6	(Buffenstein 1985)	
			White-footed mouse (<i>Peromyscus leucopus</i>)	Omn.	Temp.	18.1	(Tannenbaum and Pivorun 1987)	
	Birds	Hummingbirds	North American deer mouse (<i>P. maniculatus</i>)	Omn.	Temp.	22.5	(Tannenbaum and Pivorun 1987)	
			Rufous hummingbird (<i>Selasphorus rufus</i>)	Nect.	Trop.	4	(Hiebert 1991)	
	Hibernators	Mammals	Armadillos	Pichi (<i>Zaedyus pichiy</i>)	Omn.	Temp.	1000	(Superina and Jahn 2013) ^c
			Bats	Gould's long-eared bat (<i>Nyctophilus gouldi</i>)	Ins.	Subt.	10	(Geiser and Brigham 2000)
Greater mouse-eared bat (<i>Myotis myotis</i>)				Ins.	Temp.	25	(Wojciechowski et al. 2007)	

	Lesser long-eared bat (<i>Nyctophilus geoffroyi</i>)	Ins.	Trop.	7.1	(Ellis et al. 1991; Geiser and Brigham 2000)
Elephant shrews	Eastern rock elephant shrew (<i>Elephantulus myurus</i>)	Ins.	Subt.	57.2	(Lovegrove et al. 2001)
	North African elephant shrew (<i>E. rozeti</i>)	Ins.	Subt.	45.1	(Lovegrove et al. 2001)
Hedgehogs	Southern African hedgehog (<i>Atelerix frontalis</i>)	Ins.	Subt.	520	(Gillies et al. 1991)
Marsupials	Eastern pygmy possum (<i>Cercartetus nanus</i>)	Omn.	Subt.	36	(Westman and Geiser 2004)
	Monito del Monte (<i>Dromiciops gliroides</i>)	Omn.	Subt.	38	(Bozinovic et al. 2007; Nespolo et al. 2010)
Rodents	Alpine marmot (<i>Marmota marmota</i>)	Herb.	Temp.	3000	(Ortmann and Heldmaier 2000)
	Belding's ground squirrel (<i>Urocitellus beldingi</i>)	Gran.	Temp.	350	(French 1982)
	Eastern chipmunk (<i>Tamias striatus</i>)	Gran.	Temp.	97	(Wrazen and Wrazen 1982; French 2000)
	Golden-mantled ground squirrel (<i>Callospermophilus lateralis</i>)	Gran.	Temp.	200	(Mrosofsky 1980; Forger et al. 1986; Pulawa and Florant 2000)
	Groundhog (<i>Marmota monax</i>)	Herb.	Temp.	3200	(Potkewitz et al. 1982)
	Japanese dormouse (<i>Glirulus japonicus</i>)	Omn.	Temp.	28	(Otsu and Kimura 1993)
	Silky pocket mouse (<i>Perognathus flavus</i>)	Gran.	Subt.	9	(Wolff and Bateman 1978)
	Woodland dormouse (<i>Graphiurus murinus</i>)	Omn.	Subt.	45	(Webb and Skinner 1996)

66 ^a Frug.: frugivorous; Gran.: granivorous; Herb.: herbivorous; Ins.: insectivorous; Nect.: nectarivorous; Omn.: omnivorous

67 ^b Subt.: subtropical; Temp.: temperate; Trop.: tropical; Wid.: widespread

68 ^c semi-natural conditions with outdoor enclosure

969 **Figure legends**

970 **Fig. 1** Proximate role of food availability in heterothermy regulation, and potentially
971 confounding effects of environmental and internal covariates. Factors that act directly on
972 heterothermy regulation are represented with full arrows, and their relative contributions are
973 represented with percentages (w, x, y and z %). Factors that indirectly influence heterothermy
974 regulation through their effects on food availability are represented with broken arrows. The
975 effects of food availability can be subdivided in four categories as food ingestion is the major
976 way to regulate the acquisition of energy (through nutrients constituting energy substrates),
977 water, essential nutrients and anti-nutrient balances, and fat storage (respectively, z_1 , z_2 , z_3
978 and z_4 %). Energy substrates should be distinguished between carbohydrates, lipids and
979 proteins (respectively, $z_{1,1}$, $z_{1,2}$, $z_{1,3}$ %).

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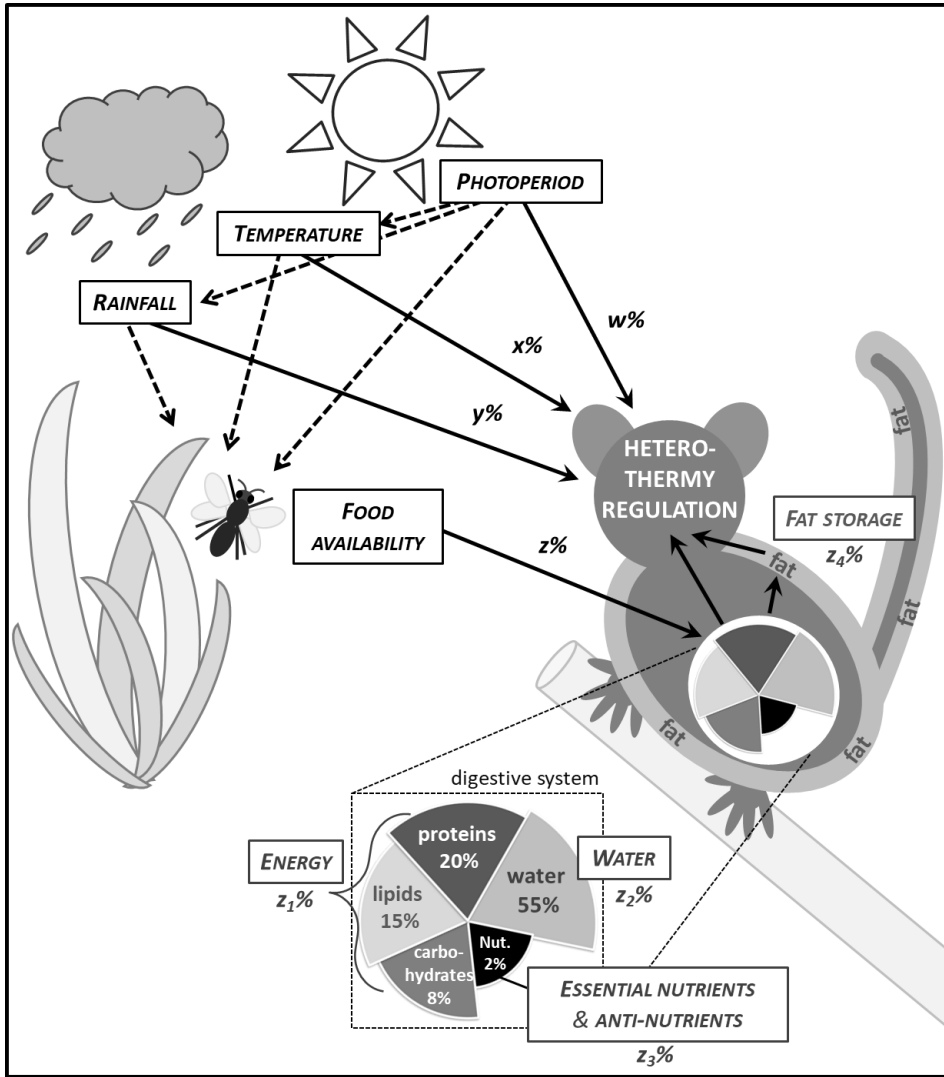
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