



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

Pauline Vuarin, Pierre-yves Henry

► To cite this version:

Pauline Vuarin, Pierre-yves Henry. Field evidence for a proximate role of food shortage in the regulation of hibernation and daily torpor: a review. *Journal of Comparative Physiology B*, 2014, 184 (6), pp.683-697. 10.1007/s00360-014-0833-0 . hal-03264247

HAL Id: hal-03264247

<https://hal.science/hal-03264247>

Submitted on 18 Jun 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Pauline Vuarin • Pierre-Yves Henry

UMR 7179 CNRS-MNHN, Muséum National d'Histoire Naturelle

1 avenue du petit Château, 91800 Brunoy, France

e-mail: pauline.vuarin@edu.mnhn.fr

Corresponding author:

e-mail: henry@mnhn.fr

Tel: +33 (0)1 60 47 92 28

Fax: +33 (0)1 60 47 92 18

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

Keywords Heterothermy • Torpor • hibernation • Food availability • Food shortage • Field experiments

Abbreviations

PUFA polyunsaturated fatty acids

Introduction

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

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

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

Methods

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

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

Laboratory-based evidence of heterothermy regulation by food availability

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

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

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

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

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

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

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

Review of field evidence

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

Correlative evidence

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

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

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

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

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

Direct field evidence for the dependence of heterothermy expression on food availability

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

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

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

Experimental evidence

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

Food supplementation during periods of natural food shortage is the unique experimental paradigm to investigate the dependence of heterothermy on energy availability, as food restriction is unachievable with free-ranging animals. Humphries et al. (2003a,b), who 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

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

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

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

Confounding effects of food availability

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

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

Water shortage rather than food shortage?

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

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

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

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

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

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

Food quality rather than food availability?

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

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

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

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

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

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

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

Energy storage rather than energy shortage?

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

Social interactions, competition and predation

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

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

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

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

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

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

Conclusions and perspectives

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

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

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

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

Acknowledgment We are very grateful to Ian D. Hume for inviting us to write this review. We also thank Martine Perret, Sylvain Giroud and four anonymous reviewers for their useful comments on earlier versions of this manuscript, and to Melanie Dammhahn, Fabien Pifferi and Bruno Simmen for inspiring discussions on the topic. This work was funded by Centre National de la Recherche Scientifique and Muséum National d'Histoire Naturelle (UMR 7179).

References

- Angilletta Jr MJ, Cooper BS, Schuler MS, Boyles JG (2010) The evolution of thermal physiology in endotherms. *Frontiers in Bioscience* E:861–881
- Audet D, Thomas DW (1997) Facultative hypothermia as a thermoregulatory strategy in the phyllostomid bats, *Carollia perspicillata* and *Sturnira lilium*. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 167:146–152

584 Bae HH, Larkin JE, Zucker I (2003) Juvenile Siberian hamsters display torpor and modified
585 locomotor activity and body temperature rhythms in response to reduced food
586 availability. *Physiological and Biochemical Zoology* 76:858–867 doi: 10.1086/381462

587 Ben-Hamo M, Munoz-Garcia A, Williams JB, Korine C, Pinshow B (2013) Waking to drink:
588 rates of evaporative water loss determine arousal frequency in hibernating bats. *Journal*
589 *of Experimental Biology* 216:573–577 doi:10.1242/jeb.078790

590 Bieber C, Ruf T (2009) Summer dormancy in edible dormice (*Glis glis*) without energetic
591 constraints. *Naturwissenschaften* 96:165–171. doi:10.1007/s00114-008-0471-z

592 Bieber C, Lebl K, Stalder G, Geiser F, Ruf T (2014) Body mass dependent use of hibernation:
593 Why not prolong the active season, if they can? *Functional Ecology* 28:167–177
594 doi:10.1111/1365-2435.12173

595 Bize P, Klopfenstein A, Jeanneret C, Roulin A (2007) Intra-individual variation in body
596 temperature and pectoral muscle size in nestling Alpine swifts *Apus melba* in response
597 to an episode of inclement weather. *Journal of Ornithology* 148:387–393 doi:
598 10.1007/s10336-007-0141-5

599 Bondarenko A, Koertner G, Geiser F (2013). Some like it cold: summer torpor by freetail bats
600 in the Australian arid zone. *Journal of Comparative Physiology B-Biochemical*
601 *Systemic and Environmental Physiology* 183:1113–1122 doi:10.1007/s00360-013-
602 0779-7

603 Boyles JG, Dunbar MB, Storm JJ, Brack V (2007) Energy availability influences
604 microclimate selection of hibernating bats. *The Journal of Experimental Biology*
605 210:4345–4350 doi: 10.1242/jeb.007294

606 Boyles JG, Smit B, McKechnie AE (2011) A new comparative metric for estimating
607 heterothermy in endotherms. *Physiological and Biochemical Zoology* 84:115–123
608 doi:10.1086/656724

609 Boyles JG, Thompson AB, McKechnie AE, Malan E, Humphries MM, Careau V (2013) A
610 global heterothermic continuum in mammals. *Global Ecology and Biogeography*
611 22:1029–1039 doi:10.1111/geb.12077

612 Bozinovic F, Marquet PA (1991) Energetics and torpor in the Atacama desert-dwelling rodent
613 *Phyllotis darwini rupestris*. *Journal of Mammalogy* 72:734–738

614 Bozinovic F, Muñoz JLP, Naya DE, Cruz-Neto AP (2007) Adjusting energy expenditures to
615 energy supply: food availability regulates torpor use and organ size in the Chilean
616 mouse-opossum *Thylamys elegans*. *Journal of Comparative Physiology B: Biochemical,*
617 *Systemic, and Environmental Physiology* 177:393–400 doi: 10.1007/s00360-006-0137-
618 0

619 Bozinovic F, Ruiz G, Rosenmann M (2004) Energetics and torpor of a South American
620 “living fossil”, the microbiotheriid *Dromiciops gliroides*. *Journal of Comparative*
621 *Physiology B: Biochemical, Systemic, and Environmental Physiology* 174:293–297 doi:
622 10.1007/s00360-004-0414-8

623 Brooker B, Withers P (1994) Kidney structure and renal indexes of dasyurid marsupials.
624 *Australian Journal of Zoology* 42:163–176 doi: 10.1071/ZO9940163

- 625 Buffenstein R (1985) The effect of starvation, food restriction, and water deprivation on
626 thermoregulation and average daily metabolic rates in *Gerbillus pusillus*. *Physiological*
627 *Zoology* 58:320–328
- 628 Canale CI, Henry P-Y (2010) Adaptive phenotypic plasticity and resilience of vertebrates to
629 increasing climatic unpredictability. *Climate Research* 43:135–147 doi:
630 10.3354/cr00897
- 631 Canale CI, Henry P-Y (2011) Energetic costs of the immune response and torpor use in a
632 primate. *Functional Ecology* 25:557–565
- 633 Canale CI, Perret M, Théry M, Henry P-Y (2011) Physiological flexibility and acclimation to
634 food shortage in a heterothermic primate. *The Journal of Experimental Biology*
635 214:551–560 doi: 10.1242/jeb.046987
- 636 Canale CI, Perret M, Henry P-Y (2012) Torpor use during gestation and lactation in a
637 primate. *Naturwissenschaften* 99: 159–163
- 638 Carr JM, Lima SL (2013) Nocturnal hypothermia impairs flight ability in birds: a cost of
639 being cool. *Proceedings of the Royal Society B: Biological Sciences* 280:20131846
640 doi:10.1098/rspb.2013.1846
- 641 Coburn DK, Geiser F (1998) Seasonal changes in energetics and torpor patterns in the
642 subtropical blossom-bat *Syconycteris australis* (Megachiroptera). *Oecologia* 113:467–
643 473 doi: 10.1007/s004420050399
- 644 Dausmann KH (2014) Flexible patterns in energy savings: heterothermy in primates. *Journal*
645 *of Zoology* 292:101–111 doi:10.1111/jzo.12104
- 646 Doucette LI, Brigham RM, Pavey CR, Geiser F (2012) Prey availability affects daily torpor
647 by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). *Oecologia* 169:361–
648 372 doi: 10.1007/s00442-011-2214-7
- 649 Ehrhardt N, Heldmaier G, Exner C (2005) Adaptive mechanisms during food restriction in
650 *Acomys russatus*: the use of torpor for desert survival. *Journal of Comparative*
651 *Physiology B: Biochemical, Systemic, and Environmental Physiology* 175:193–200 doi:
652 10.1007/s00360-005-0475-3
- 653 Ellis WAH, Marples TG, Phillips WR (1991) The effects of a temperature-determined food
654 supply on the annual activity cycle of the lesser long-eared bat, *Nyctophilus geoffroyi*
655 Leach 1821 (Microchiroptera: Vespertilionidae). *Australian Journal of Zoology*
656 39:263–271
- 657 Falkenstein F, Körtner G, Watson K, Geiser F (2001) Dietary fats and body lipid composition
658 in relation to hibernation in free-ranging echidnas. *Journal of Comparative Physiology*
659 *B: Biochemical, Systemic, and Environmental Physiology* 171:189–194 doi:
660 10.1007/s003600000157
- 661 Fietz J, Tataruch F, Dausmann KH, Ganzhorn JU (2003) White adipose tissue composition in
662 the free-ranging fat-tailed dwarf lemur (*Cheirogaleus medius*; Primates), a tropical
663 hibernator. *Journal of Comparative Physiology B: Biochemical, Systemic, and*
664 *Environmental Physiology* 173:1–10 doi: 10.1007/s00360-002-0300-1
- 665 Florant GL, Healy JE (2012) The regulation of food intake in mammalian hibernators: a
666 review. *Journal of Comparative Physiology B-Biochemical Systemic and*
667 *Environmental Physiology* 182:451–467 doi:10.1007/s00360-011-0630-y

- 668 Forger NG, Dark J, Barnes BM, Zucker I (1986) Fat ablation and food restriction influence
669 reproductive development and hibernation in ground-squirrels. *Biology of*
670 *Reproduction*, 34:831–840 doi:10.1095/biolreprod34.5.831
- 671 French AR (1982) Intraspecific differences in the pattern of hibernation in the ground squirrel
672 *Spermophilus beldingi*. *Journal of Comparative Physiology B: Biochemical, Systemic,*
673 *and Environmental Physiology* 148:83–91
- 674 French AR (2000) Interdependency of stored food and changes in body temperature during
675 hibernation of the eastern chipmunk, *Tamias sriatus*. *Journal of Mammalogy* 81:979–
676 985
- 677 Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily
678 torpor. *Annual Review of Physiology* 66:239–274 doi:
679 10.1146/annurev.physiol.66.032102.115105
- 680 Geiser F (2013) Hibernation. *Current Biology* 23:R188–R193 doi: 10.1016/j.cub.2013.01.062
- 681 Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-
682 eared bats (*Nyctophilus*). *Journal of Comparative Physiology B-Biochemical, Systemic*
683 *and Environmental Physiology* 170:153–162 doi:10.1007/s003600050270
- 684 Geiser F, Brigham RM (2012) The other functions of torpor. In: Ruf T, Bieber C, Arnold W,
685 Milesi E (eds) *Living in a seasonal world. Thermoregulatory and metabolic*
686 *adaptations*. Springer, Berlin, pp 109–121 doi: 10.1007/978-3-642-28678-0
- 687 Geiser F, Holloway J C, Körtner G, Maddocks T A, Turbill C, Brigham MR (2000) Do
688 patterns of torpor differ between free-ranging and captive mammals and birds? In:
689 Heldmaier G, Klingenspor M (eds) *Life in the cold, Eleventh International Hibernation*
690 *Symposium*, Springer, Berlin, pp 95–102
- 691 Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds : physiological
692 variables and classification of torpor patterns. *Physiological Zoology* 68:935–966
- 693 Génin F, Perret M (2003) Daily hypothermia in captive grey mouse lemurs (*Microcebus*
694 *murinus*): effects of photoperiod and food restriction. *Comparative Biochemistry and*
695 *Physiology Part B: Biochemistry and Molecular Biology* 136:71–81 doi:
696 10.1016/S1096-4959(03)00172-6
- 697 Gilbert C, McCafferty D, Le Maho Y, Giroud S, Blanc S, Ancel A (2010) One for all and all
698 for one: the energetic benefits of huddling in endotherms. *Biological Reviews* 85:545–
699 569 doi: 10.1111/j.1469-185X.2009.00115.x
- 700 Gillies AC, Ellison GTH, Skinner JD (1991) The effect of seasonal food restriction on
701 activity, metabolism and torpor in the South-African hedgehog (*Atelerix frontalis*).
702 *Journal of Zoology* 223:117–130
- 703 Giroud S, Blanc S, Aujard F, Bertrand F, Gilbert C, Perret M (2008) Chronic food shortage
704 and seasonal modulations of daily torpor and locomotor activity in the grey mouse
705 lemur (*Microcebus murinus*). *American journal of physiology Regulatory, Integrative*
706 *and Comparative Physiology* 294:R1958–R1967 doi: 10.1152/ajpregu.00794.2007
- 707 Giroud S, Perret M, Le Maho Y, Momken I, Gilbert C, Blanc S (2009) Gut hormones in
708 relation to body mass and torpor pattern changes during food restriction and re-feeding
709 in the gray mouse lemur. *Journal of Comparative Physiology B: Biochemical, Systemic,*
710 *and Environmental Physiology* 179:99–111 doi: 10.1007/s00360-008-0294-4

711 Giroud S, Turbill C, Ruf T (2012) Torpor use and body mass gain during pre-hibernation in
712 late-born juvenile garden dormice exposed to food shortage. In: Ruf T, Bieber C,
713 Arnold W, Millesi E (eds) Living in a seasonal world. Thermoregulatory and metabolic
714 adaptations. Springer, Berlin, pp 481–491

715 Giroud S, Frare C, Strijkstra A, Boerema A, Arnold W, Ruf T (2013) Membrane phospholipid
716 fatty acid composition regulates cardiac SERCA activity in a hibernator, the Syrian
717 hamster (*Mesocricetus auratus*). PLoS ONE 8:e63111 doi:
718 10.1371/journal.pone.0063111

719 Grimpo K, Legler K, Heldmaier G, Exner C (2013) That's hot: golden spiny mice display
720 torpor even at high ambient temperatures. Journal of Comparative Physiology B-
721 Biochemical Systemic and Environmental Physiology 183:567–581
722 doi:10.1007/s00360-012-0721-4

723 Gutman R, Choshniak I, Kronfeld-Schor N (2006) Defending body mass during food
724 restriction in *Acomys russatus*: a desert rodent that does not store food. American
725 Journal of Physiology – Regulatory, Integrative and Comparative Physiology
726 290:R881–R891 doi: 10.1152/ajpregu.00156.2005

727 Gutman R, Yosha D, Choshniak I, Kronfeld-Schor N (2007) Two strategies for coping with
728 food shortage in desert golden spiny mice. Physiology and Behavior 90:95–102 doi:
729 10.1016/j.physbeh.2006.08.033

730 Heldmaier G, Ortmann S, Elvert R (2004) Natural hypometabolism during hibernation and
731 daily torpor in mammals. Respiratory physiology and neurobiology 141:317–29 doi:
732 10.1016/j.resp.2004.03.014

733 Hellekant G, Hladik CM, Dennys V, Simmen B, Roberts TW, Glaser D (1993) On the
734 relationship between sweet taste and seasonal body-weight changes in a primate
735 (*Microcebus murinus*). Chemical Senses 18:27–33

736 Helm B, Ben-Shlomo R, Sheriff MJ, Hut RA, Foster R, Barnes BM, Dominoni D (2013).
737 Annual rhythms that underlie phenology: biological time-keeping meets environmental
738 change. Proceedings of the Royal Society of London Series B-Biological Sciences
739 280:20130016 doi:10.1098/rspb.2013.0016

740 Hickey MBC, Fenton MB (1996) Behavioural and thermoregulatory responses of female
741 hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey
742 availability. Ecoscience 3:414–422

743 Hiebert SM (1991) Seasonal differences in the response of Rufous hummingbirds to food
744 restriction: body mass and the use of torpor. The Condor 93:526–537

745 Hill VL, Florant GL (1999) Patterns of fatty acid composition in free-ranging yellow-bellied
746 marmots (*Marmota flaviventris*) and their diet. Canadian Journal of Zoology 77:1494–
747 1503 doi: 10.1139/cjz-77-9-1494

748 Hill VL, Florant GL (2000) The effect of a linseed oil diet on hibernation in yellow-bellied
749 marmots (*Marmota flaviventris*). Physiology and Behavior 68:431–437
750 doi:10.1016/S0031-9384(99)00177-8

751 Himmshagen J (1985) Food restriction increases torpor and improves brown adipose tissue
752 thermogenesis in OB/OB mice. American Journal of Physiology 248:E531–E539

- 753 Humphries MM, Thomas DW, Hall CL, Speakman JR, Kramer DL (2002) The energetics of
754 autumn mast hoarding in eastern chipmunks. *Oecologia* 133:30–37 doi:
755 10.1007/s00442-002-1014-5
- 756 Humphries MM, Kramer DL, Thomas DW (2003a) The role of energy availability in
757 mammalian hibernation: an experimental test in free-ranging eastern chipmunks.
758 *Physiological and Biochemical Zoology* 76:180–186 doi: 10.1086/367949
- 759 Humphries MM, Thomas DW, Kramer DL (2003b) The role of energy availability in
760 mammalian hibernation: a cost-benefit approach. *Physiological and Biochemical*
761 *Zoology* 76:165–179 doi: 10.1086/367950
- 762 Ibuka N, Fukumura K (1997) Unpredictable deprivation of water increases the probability of
763 torpor in the Syrian hamster. *Physiology and Behavior* 62:551–556
- 764 Kanizsai P, Garami A, Solymar M, Szolcsanyi J, Szelenyi Z (2009) Energetics of fasting
765 heterothermia in TRPV1-KO and wild type mice. *Physiology and Behavior* 96:149–154
766 doi:10.1016/j.physbeh.2008.09.023
- 767 Kelm DH, von Helversen O (2007) How to budget metabolic energy: torpor in a small
768 Neotropical mammal. *Journal of Comparative Physiology B: Biochemical, Systemic,*
769 *and Environmental Physiology* 177:667–677 doi: 10.1007/s00360-007-0164-5
- 770 Kobbe S, Ganzhorn JU, Dausmann KH (2011) Extreme individual flexibility of heterothermy
771 in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *Journal of*
772 *Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*
773 181:165–173 doi: 10.1007/s00360-010-0507-5
- 774 Körtner G, Geiser F (2000a) The temporal organization of daily torpor and hibernation:
775 circadian and circannual rhythms. *Chronobiology International* 17:103–128
- 776 Körtner G, Geiser F (2000b) Torpor and activity patterns in free-ranging sugar gliders
777 *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357 doi:
778 10.1007/s004420051021
- 779 Kronfeld-Schor N, Dayan T (2013) Thermal ecology, environments, communities, and global
780 change: energy intake and expenditure in endotherms. *Annual Review of Ecology,*
781 *Evolution, and Systematics* 44:461–480 doi:10.1146/annurev-ecolsys-110512-135917
- 782 Landry-Cuerrier M, Munro D, Thomas DW, Humphries MM (2008) Climate and resource
783 determinants of fundamental and realized metabolic niches of hibernating chipmunks.
784 *Ecology* 89:3306–3316
- 785 Lebl K, Bieber C, Adamik P, Fietz J, Morris P, Pilastro A, Ruf T (2011) Survival rates in a
786 small hibernator, the edible dormouse: a comparison across Europe. *Ecography* 34:683–
787 692 doi:10.1111/j.1600-0587.2010.06691.x
- 788 Lehmer EM, van Horne B (2001) Seasonal changes in lipids, diet, and body composition of
789 free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). *Canadian Journal of*
790 *Zoology* 79:955–965 doi: 10.1139/z01-060
- 791 Levy O, Dayan T, Kronfeld-Schor N (2011a) Adaptive thermoregulation in golden spiny
792 mice: the influence of season and food availability on body temperature. *Physiological*
793 *and Biochemical Zoology* 84:175–184 doi: 10.1086/658171

- 794 Levy O, Dayan T, Kronfeld-Schor N (2011b) Interspecific competition and torpor in golden
795 spiny mice: two sides of the energy-acquisition coin. *Integrative and Comparative*
796 *Biology* 51:441–448 doi: 10.1093/icb/icr071
- 797 Levy O, Dayan T, Rotics S, Kronfeld-Schor N (2012) Foraging sequence, energy intake and
798 torpor: an individual-based field study of energy balancing in desert golden spiny mice.
799 *Ecology Letters* 15:1240–1248 doi: 10.1111/j.1461-0248.2012.01845.x
- 800 Lovegrove BG (2000) Daily heterothermy in mammals: coping with unpredictable
801 environments. In: Heldmaier G, Klingenspor M (eds) *Life in the cold*, Eleventh
802 *International Hibernation Symposium*. Springer, Berlin, pp 29–40
- 803 Lovegrove BG (2012) The evolution of endothermy in Cenozoic mammals: a plesiomorphic-
804 apomorphic continuum. *Biological Reviews* 87:128–162 doi:10.1111/j.1469-
805 185X.2011.00188.x
- 806 Lovegrove BG, Raman J, Perrin MR (2001) Daily torpor in elephant shrews (*Macroscelidea*:
807 *Elephantulus* spp.) in response to food deprivation. *Journal of Comparative Physiology*
808 *B: Biochemical, Systemic, and Environmental Physiology* 171:11–21
- 809 McKechnie AE, Mzilikazi N (2011) Heterothermy in Afrotropical mammals and birds: a
810 review. *Integrative and Comparative Biology* 51:349–363 doi: 10.1093/icb/icr035
- 811 McKechnie AE, Körtner G, Lovegrove BG (2006) Thermoregulation under semi-natural
812 conditions in speckled mousebirds: the role of communal roosting. *African Zoology*
813 41:155–163
- 814 Mrosovsky N (1980) Circannual cycles in golden-mantled ground squirrels: experiments with
815 food deprivation and effects of temperature on periodicity. *Journal of Comparative*
816 *Physiology A: Sensory, Neural, and Behavioral Physiology* 136:355–360 doi:
817 10.1007/BF00657357
- 818 Munn AJ, Kern P, McAllan BM (2010) Coping with chaos: unpredictable food supplies
819 intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (*Sminthopsis*
820 *crassicaudata*). *Naturwissenschaften* 97:601–605 doi: 10.1007/s00114-010-0670-2
- 821 Munro D, Thomas DW (2004) The role of polyunsaturated fatty acids in the expression of
822 torpor by mammals: a review. *Zoology* 107:29–48 doi: 10.1016/j.zool.2003.12.001
- 823 Munro D, Thomas DW, Humphries MM (2005) Torpor patterns of hibernating eastern
824 chipmunk *Tamias striatus* vary in response to the size and fatty acid composition of
825 food hoards. *Journal of Animal Ecology* 74:692–700
- 826 Munro D, Thomas DW, Humphries MM (2008) Extreme suppression of aboveground activity
827 by a food-storing hibernator, the eastern chipmunk (*Tamias striatus*). *Canadian Journal*
828 *of Zoology* 86:364–370 doi: 10.1139/Z08-008
- 829 Nespolo RF, Verdugo C, Cortés P a, Bacigalupe LD (2010) Bioenergetics of torpor in the
830 microbiotherid marsupial, monito del monte (*Dromiciops gliroides*): the role of
831 temperature and food availability. *Journal of Comparative Physiology B: Biochemical,*
832 *Systemic, and Environmental Physiology* 180:767–773 doi: 10.1007/s00360-010-0449-
833 y
- 834 Ortmann S, Heldmaier G (2000) Regulation of body temperature and energy requirements of
835 hibernating Alpine marmots (*Marmota marmota*). *American Journal of Physiology –*
836 *Regulatory, Integrative and Comparative Physiology* 278:R698–R704

- 837 Ortmann S, Heldmaier G, Schmid J, Ganzhorn JU (1997) Spontaneous daily torpor in
838 Malagasy mouse lemurs. *Naturwissenschaften* 84:28–32
- 839 Otsu R, Kimura T (1993) Effect of food availability and ambient temperature on hibernation
840 in the Japanese dormouse, *Glirulus japonicus*. *Journal of Ethology* 11:37–42
- 841 Pelletier F, Reale D, Watters J, Boakes EH, Garant D (2009) Value of captive populations for
842 quantitative genetics research. *Trends in Ecology and Evolution* 24:263–270
843 doi:10.1016/j.tree.2008.11.013
- 844 Potkewitz LG, Baldwin BH, Tennant BC (1982). Food availability and hibernation in
845 laboratory woodchucks. *Laboratory Animal Science* 32:432–433
- 846 Pulawa LK, Florant GL (2000) The effects of caloric restriction on the body composition and
847 hibernation of the golden-mantled ground squirrel (*Spermophilus lateralis*).
848 *Physiological and Biochemical Zoology* 73:538–546 doi: 10.1086/317752
- 849 Reichman OJ, Brown JH (1979) The use of torpor by *Perognathus amplus* in relation to
850 resource distribution. *Journal of Mammalogy* 60:550–555
- 851 Rojas AD, Körtner G, Geiser F (2012) Cool running: locomotor performance at low body
852 temperature in mammals. *Biology Letters* 8:868–870 doi:10.1098/rsbl.2012.0269
- 853 Roth TCII, Rattenborg NC, Pravosudov VV (2010) The ecological relevance of sleep: the
854 trade-off between sleep, memory and energy conservation. *Philosophical Transactions*
855 *of the Royal Society B-Biological Sciences* 365:945–959 doi:10.1098/rstb.2009.0209
- 856 Ruf T, Arnold W (2008) Effects of polyunsaturated fatty acids on hibernation and torpor: a
857 review and hypothesis. *American Journal of Physiology - Regulatory, Integrative and*
858 *Comparative Physiology* 294:R1044–R1052 doi: 10.1152/ajpregu.00688.2007
- 859 Ruf T, Stieglitz A, Steinlechner S, Blank JL, Heldmaier G (1993) Cold exposure and food
860 restriction facilitate physiological responses to short photoperiod in Djungarian
861 hamsters (*Phodopus sungorus*). *Journal of Experimental Zoology* 267:104–112
862 doi:10.1002/jez.1402670203
- 863 Schmid J (2001) Daily torpor in free-ranging Gray Mouse Lemurs (*Microcebus murinus*) in
864 Madagascar. *International Journal of Primatology* 22:1021–1031
- 865 Schmid J, Speakman JR (2000) Daily energy expenditure of the grey mouse lemur
866 (*Microcebus murinus*): a small primate that uses torpor. *Journal of Comparative*
867 *Physiology B: Biochemical, Systemic, and Environmental Physiology* 170:633–641
- 868 Schmid J, Speakman JR (2009) Torpor and energetic consequences in free-ranging grey
869 mouse lemurs (*Microcebus murinus*): a comparison of dry and wet forests.
870 *Naturwissenschaften* 96:609–620 doi: 10.1007/s00114-009-0515-z
- 871 Schubert KA, Boerema AS, Vaanholt LM, de Boer SF, Strijkstra AM, Daan S (2010) Daily
872 torpor in mice: high foraging costs trigger energy-saving hypothermia. *Biology Letters*,
873 6:132–135 doi:10.1098/rsbl.2009.0569
- 874 Séguéy M, Perret M (2005) Factors affecting the daily rhythm of body temperature of captive
875 mouse lemurs (*Microcebus murinus*). *Journal of Comparative Physiology B:*
876 *Biochemical, Systemic, and Environmental Physiology* 175:107–115 doi:
877 10.1007/s00360-004-0467-8

- 878 Silva-Duran IP, Bozinovic F (1999) Food availability regulates energy expenditure and torpor
879 in the Chilean mouse-opossum *Thylamys elegans*. *Revista Chilena de Historia Naturale*
880 72:371–375
- 881 Simmen B, Josseume B, Atramentowicz M (1999) Frugivory and taste responses to fructose
882 and tannic acid in a prosimian primate and a didelphid marsupial. *Journal of Chemical*
883 *Ecology* 25:331–346
- 884 Smit B, McKechnie AE (2010) Do owls use torpor? Winter thermoregulation in free-ranging
885 pearl-spotted owlets and African scops-owls. *Physiological and Biochemical Zoology*
886 83:149–156 doi: 10.1086/605457
- 887 Smit B, Boyles JG, Brigham RM, McKechnie AE (2011) Torpor in dark times: patterns of
888 heterothermy are associated with the lunar cycle in a nocturnal bird. *Journal of*
889 *Biological Rhythms* 26:241–248 doi:10.1177/0748730411402632
- 890 Song X, Geiser F (1997) Daily torpor and energy expenditure in *Sminthopsis macroura*:
891 interactions between food and water availability and temperature. *Physiological*
892 *Zoology* 70:331–337
- 893 Stawski C, Geiser F (2010a) Seasonality of torpor patterns and physiological variables of a
894 free-ranging subtropical bat. *The Journal of experimental biology* 213:393–399 doi:
895 10.1242/jeb.038224
- 896 Stawski C, Geiser F (2010b) Fat and fed: frequent use of summer torpor in a subtropical bat.
897 *Naturwissenschaften* 97:29–35 doi: 10.1007/s00114-009-0606-x
- 898 Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat
899 (*Nyctophilus bifax*). *Journal of Comparative Physiology B: Biochemical, Systemic, and*
900 *Environmental Physiology* 179:433–441 doi: 10.1007/s00360-008-0328-y
- 901 Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological
902 effects of climate fluctuations. *Science* 297:1292–1296 doi: 10.1126/science.1071281
- 903 Superina M, Jahn GA (2013) Effect of low-quality diet on torpor frequency and depth in the
904 pichi *Zaedyus pichiy* (Xenarthra, Dasypodidae), a South American armadillo. *Journal of*
905 *Thermal Biology* 38:280–285 doi:10.1016/j.jtherbio.2013.03.004
- 906 Tannenbaum MG, Pivorun EB (1987) Differential effect of food restriction on the induction
907 of daily torpor in *Peromyscus maniculatus* and *Peromyscus leucopus*. *Journal of*
908 *Thermal Biology* 12:159–162 doi:10.1016/0306-4565(87)90057-X
- 909 Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the
910 evolution of slow life histories among mammals. *Proceedings of the Royal Society B-*
911 *Biological Sciences* 278:3355–3363 doi:10.1098/rspb.2011.0190
- 912 Vuarin P, Dammhahn M, Henry P-Y (2013) Individual flexibility in energy saving: body size
913 and condition constrain torpor use. *Functional Ecology* 27:793–799 doi: 10.1111/1365-
914 2435.12069
- 915 Webb PI, Skinner JD (1996) Summer torpor in African woodland dormice *Graphiurus*
916 *murinus* (Myoxidae: Graphiurinae). *Journal of Comparative Physiology B:*
917 *Biochemical, Systemic, and Environmental Physiology* 166:325–30
- 918 Westman W, Geiser F (2004) The effect of metabolic fuel availability on thermoregulation
919 and torpor in a marsupial hibernator. *Journal of Comparative Physiology B:*

- 920 Biochemical, Systemic, and Environmental Physiology 174:49–57 doi:
921 10.1007/s00360-003-0388-y
- 922 Williams CT, Barnes BM, Kenagy GJ, Buck CL (2014) Phenology of hibernation and
923 reproduction in ground squirrels: integration of environmental cues with endogenous
924 programming. *Journal of Zoology* 292:112–124 doi:10.1111/jzo.12103
- 925 Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging
926 bats. *Naturwissenschaften* 93:80–83 doi:10.1007/s00114-005-0063-0
- 927 Withers KW, White DH, Billingsley J (2000). Torpor in the carnivorous marsupial
928 *Sminthopsis macroura*: effects of food quality and quantity. In: Heldmaier G,
929 Klingenspor M (eds) *Life in the cold*, Eleventh International Hibernation Symposium,
930 Springer, Berlin, pp 127–137
- 931 Wojciechowski MS, Jefimow M, Tegowska E (2007) Environmental conditions, rather than
932 season, determine torpor use and temperature selection in large mouse-eared bats
933 (*Myotis myotis*). *Comparative Biochemistry and Physiology Part A, Molecular and*
934 *Integrative Physiology* 147:828–840 doi: 10.1016/j.cbpa.2006.06.039
- 935 Wolff JO, Bateman GC (1978) Effects of food availability and ambient temperature on torpor
936 cycles of *Perognathus flavus* (Heteromyidae). *Journal of Mammalogy* 59:707–716
- 937 Woods CP, Brigham RM (2004) The avian enigma: “hibernation” by Common Poorwills
938 (*Phalaenoptilus nuttalli*). In: Barnes BM, Carey HV (eds) *Life in the cold: evolution,*
939 *mechanisms, adaptation, and application*. Twelfth International Hibernation
940 Symposium. Biological Papers of the University of Alaska, number 27. Institute of
941 Arctic Biology, University of Alaska, Fairbanks, Alaska, pp 129–138
- 942 Wrazen JA, Wrazen LA (1982) Hoarding, body mass dynamics, and torpor as components of
943 the survival strategy of the eastern chipmunk. *Journal of Mammalogy* 63:63–72
- 944

Table 1 Published evidence of the role of food availability in torpor regulation for heterothermic endotherms. Studies are ordered per method of inference, torpor patterns, class, order and species names. For each species, their diet, latitudinal range and adult body mass (in g) are reported as they influence the use of heterothermy (Geiser 2004; Boyles et al. 2013). Methods of inference were ranked so that their order reflects the robustness of the inference about the proximate role of food availability under natural conditions, starting from the most convincing method: (i) field experiments, where food availability was manipulated *in situ*, (ii) direct field evidence, i.e. when heterothermy use correlates with natural fluctuations in food availability, after accounting for confounding environmental covariates (Fig. 1), (iii) indirect field evidence, i.e. when heterothermy use correlates with ambient temperature supposedly because of the temperature-dependence of food availability, and (iv) laboratory experiments of food restriction. The categorical classification of torpor patterns per species followed Geiser and Ruf (1995), and was complemented by subsequent reviews (Geiser 2004, 2013; Boyles et al. 2011; McKechnie and Mzilikazi 2011; Lovegrove 2012; Dausmann 2014), or information in the original reference. Species' traits were obtained from Boyles et al. (2013), the cited references or online natural history information. For latitudinal range, tropical refers to latitudes between the Tropic of Cancer and the Tropic of Capricorn, subtropical refers to latitudes between the tropic circles and the 35th parallels, and temperate refers to latitudes between the 35th parallels and the poles. The house mouse (*Mus musculus*) is classified as 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	(Bondarenko 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)
		Primates	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; Grimpot 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)
			North American deer mouse (<i>P. maniculatus</i>)	Omn.	Temp.	22.5	(Tannenbaum and Pivorun 1987)
	Birds	Hummingbirds	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	(Mrosovsky 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)

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

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

^c semi-natural conditions with outdoor enclosure

Figure legends

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

