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► To cite this version:

Pauline Vuarin, Pierre-Yves Henry. Food shortage can drive body temperature regulation in wild heterothermic vertebrates. *Temperature*, 2015, 2 (1), pp.29-30. 10.4161/23328940.2014.952210 . hal-03257176

HAL Id: hal-03257176

<https://hal.science/hal-03257176>

Submitted on 10 Jun 2021

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Food shortage can drive body temperature regulation in wild heterothermic vertebrates

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Abstract: Food availability is expected to trigger hibernation and torpor (i.e. heterothermy) use. Yet, laboratory experiments under controlled conditions dominate, and this hypothesis remains largely untested under natural conditions. Further experimental manipulations of food availability must therefore be conducted in the wild, accounting for other covarying environmental stressors.

Keywords: heterothermy, hibernation, torpor, food availability, food shortage, field experiments

Heterothermy, in reference to hibernation and daily torpor, has been commonly assumed to be an adaptive response to energetically constraining conditions, like low ambient temperature and/or seasonal food shortage. In a recent paper¹, we reviewed published evidence for a proximate role of food shortage in heterothermy regulation of vertebrates. Heterothermy is a widespread energy saving mechanism that enables heterothermic organisms to reduce their energy expenditure through a controlled reduction of metabolism and body temperature². Because heterothermy expression is also associated with physiological costs (like increased oxidative stress or cognitive impairments), its use should be optimized rather than maximized, so that the benefits offset the costs³. When unfavorable conditions are predictable, heterothermy may be anticipated based on fixed seasonal cues such as photoperiod, which is responsible for seasonal acclimation in many animals. But when such conditions are poorly predictable, an alternative hypothesis is that heterotherms may rather rely on proximal cues such as food availability to time their use of heterothermy. Such mechanism would allow them to flexibly time and fine-tune their use of heterothermy according to actual energetic constraints. However, the adaptive function of heterothermy at compensating food shortage remains largely untested under natural conditions.

Our literature review highlighted 73 relevant papers, including both laboratory and field studies. Laboratory experiments largely dominate (70%, Fig. 1). Although they demonstrate that heterothermy use depends on food availability under controlled conditions, they do not permit to conclude on the actual role of food availability in the wild¹. Among the 22 field studies, only 36% reported experimental evidence by manipulating food availability under (semi)-natural conditions (Fig. 1), which is yet the unique way to test the dependence of heterothermy on food availability¹. 64% reported correlations between heterothermy patterns and natural variation in food availability or environmental variables supposedly indicative of food availability (Fig. 1). Correlative studies either related increased heterothermy use with unfavorable climatic conditions (low ambient temperature or rainfall episodes) that are negatively correlated with prey abundance for insectivores (indirect evidence), or related heterothermy patterns to natural fluctuations of food availability (direct evidence). Over all field studies, food shortage appears to be associated with increased hibernation or torpor use under natural conditions, as was observed in controlled laboratory experiments. Food supplementation during periods of natural food shortage has been conducted in only two hibernators and three daily heterotherms so far. Food supplemented individuals reduced their use of heterothermy, spending less time torpid and exhibiting shallower torpor bouts¹. These

results support that food availability is a proximate driver of heterothermy, free-ranging heterotherms fine-tuning its use according to actual food availability. Nonetheless, due to the paucity of data, further experiments need to be conducted in the wild to properly quantify the role of food availability, after adjusting for other covarying factors.

The effect of food shortage could be confounded by several covarying environmental (extrinsic) or internal (intrinsic) stressors¹. First, water availability can be limited and water shortage is generally associated to seasonal food shortage. Therefore, its role may be of as much, or even higher, importance as that of food, but has never been studied in the wild. Second, the nutritional composition of food is expected to play a role in heterothermy regulation because carbohydrates, lipids and proteins are major energy substrates, but food quality has largely been ignored. The role of essential nutrients (including vitamins, dietary minerals, essential fatty acids and essential amino-acids) and anti-nutrients also remains to be tested. Up to now, polyunsaturated fatty acids are the only ones known to be involved in heterothermy expression, mostly through studies on mammalian hibernators. Third, energy storage, rather than food shortage, may be determinant. Torpor use and flexibility being enhanced by higher body condition, body fat reserves are supposed to determine the timing of heterothermy initiation. For correlative field studies, that document many collinear environmental and internal parameters that can influence the regulation of body temperature (like food or water availability, temperature, rainfall, daylength), path analyses should be a relevant statistical tool to diagnose which are the environmental conditions that primarily drive the flexible use of heterothermy.

Finally, social interactions related to thermoregulation, competition for food resources and predation may also modulate heterothermic responses to food availability¹. In case of social thermoregulation, huddling or communal roosting, animals may benefit from passive rewarming from the group to reduce the amount of energy invested into their own thermoregulation, saving energy. Inter- and intra-specific competitive interactions for similar food resources could reinforce the strength of the experienced food shortage. An increased use of heterothermy and the associated inactivity may reduce the exposure to predators, and thus enhance survival probability. Ideally, these parameters should also be considered in future field studies on the role of food availability in heterothermy regulation.

Most of the work still needs to be done to obtain a robust, integrative understanding of the major, proximate drivers of heterothermy regulation and flexibility in the wild. Such studies

are likely to have profound implications in physiological ecology, particularly when considering global change. Phenotypic flexibility is indeed the main adaptive response of vertebrates to compensate environmental change⁴. Most research has focused on flexible adjustments of the phenology of major biological events (e.g., reproduction or migration)⁵, but flexibility for energy saving mechanisms has rarely been considered. Because such flexibility would allow heterotherms to rapidly adjust and fine-tune their energetic balance to environmental fluctuations, it may contribute to their resilience to global changes. At a broader scale, physiological responses of animals mainly depend on temperature⁶. Therefore, any study on the regulation of body temperature will potentially bring new insights in comparative and evolutionary physiology.

Disclosure of potential conflicts of interest

No potential conflicts of interest are disclosed.

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Figure 1. Relative proportion of studies that documented the role of food availability in heterothermy regulation based on experimental field evidence, direct or indirect correlative field evidence, and laboratory experiments.

