The ecology and evolution of mammalian heterothermy in a changing world

Andrew E. McKechnie

Mammal Research Institute
Department of Zoology and Entomology
University of Pretoria
Private Bag X20
Hatfield 0028
South Africa

Email: aemckechnie@zoology.up.ac.za

One of the most intriguing ways in which mammals offset the energetic cost of continuous endothermic homeothermy is by reducing their metabolic rate and body temperature (T_b) far below normothermic levels, over time scales ranging from hours to months. Although humans have been aware of the existence of hibernation and torpor among small mammals for many centuries, recent decades have radically changed our perceptions of the ecological and evolutionary significance of these heterothermic responses. Indeed, some small mammals spend well over half their lives in a state of hibernation; in Arctic ground squirrels (*Urocitellus parryii*), for instance, the average annual hibernation duration is ~ 230 days (Buck & Barnes, 1999). Prolonged hibernation is not, however, restricted to high-latitude environments characterised by long, severe winters. Recent work in the forests of Madagascar, a tropical habitat characterised by year-round mild temperatures but pronounced patterns of rainfall seasonality, has revealed that several species including the greater hedgehog tenrec (*Setifer setosus*), fat-tailed dwarf lemur (*Cheirogaleus medius*) and reddish-gray mouse lemur (*Microcebus griseorufus*) hibernate for periods in excess of one month under natural conditions (Dausmann *et al.*, 2005; Kobbe, Ganzhorn & Dausmann, 2011; Lovegrove *et al.*, in press). There is evidence that some mammals from tropical and sub-tropical latitudes can hibernate for much longer when necessary; an Australian eastern pygmy-possum (*Cercartetus nanus*), for example, hibernated for more than a year in captivity (Geiser, 2007).

It is against the backdrop of heterothermy having far-reaching consequences for the ecology, evolution and conservation of mammals in a changing world that this mini-series of reviews was commissioned. The goal of the mini-series is to synthesise recent developments in the field of mammalian heterothermy and provide novel perspectives in which physiology, ecology and evolution are integrated. Authors were invited to write reviews focusing on specific taxa, because it was felt that this would be the most effective way to achieve integrative overviews of how heterothermy relates to other aspects of species' ecology and influences fitness. The mini-series consists of four papers. Riek & Geiser (in press) analyse the data currently available on heterothermy in marsupials, and provide new insights into the scaling and phylogenetic inertia of heterothermy-related variables in this infraclass. Bats - one of the most heterothermic of eutherian orders - are the focus of a review by Stawski, Willis & Geiser (in press), in which these authors draw attention to the functions of heterothermy other than energy conservation. Dausmann (in press) provides an overview of heterothermy in primates, and the diverse and flexible patterns of thermoregulation that occur in species from Madagascar and other subtropical regions with strong seasonality of rainfall. Finally, the processes underlying the phenology of hibernation and reproduction in sciurids, one of the classic groups of north-temperate heterotherms, are reviewed by Williams *et al*. (in press).

Heterothermy has far-reaching implications for understanding the evolution of endothermy. It is becoming steadily more apparent that heterothermy is an ancestral, plesiomorphic trait in mammals, rather than a recent adaptation to specific environmental conditions (Geiser, 1998; Grigg, Beard & Augee, 2004; Lovegrove, 2012; Malan, 1996). This view is strongly supported by the widespread occurrence of heterothermy in small mammals from phylogenetically ancient taxa such as marsupials and afrotherians (Lovegrove, 2012). Moreover, because groups such as Madagascar's tenrecs and lemurs inhabit regions whose climates have been comparatively stable since the late Cretaceous, and where selection pressures associated with insularity may be expected to have led to the retention of ancestral physiological traits, studies of extant members of these taxa shed considerable light on the patterns of thermoregulation that likely existed in early mammals (Lovegrove, 2012). Lovegrove has argued that the "classic" pattern of mammalian endothermic homeothermy (*sensu* Scholander *et al.*, 1950) is in fact an apomorphic, derived phenomenon that evolved from a plesiomorphic condition involving periods of normothermy interspersed with hibernation or torpor. Thus, whereas a few decades ago the study of mammalian hibernation was almost completely restricted to Palaearctic species inhabiting north-temperate latitudes, it has more recently become clear that the future of the field lies as much in the tropical forests of South America, Africa and southeast Asia as it does in the colder parts of North America and Eurasia.

Besides heterothermy being of fundamental importance for elucidating the evolutionary history of thermoregulation in mammals, understanding the physiology and ecology of torpor and hibernation has direct relevance in the face of several pressing environmental issues. One of these is anthropogenic climate change: the increases in global temperatures and frequencies of extreme weather events driven by greenhouse gas emissions (IPCC, 2007) will have diverse and far-reaching impacts on mammals (Boyles *et al.*, 2011; Canale & Henry, 2010; Fuller *et al.*, 2010; Humphries, Thomas & Speakman, 2002; Humphries, Umbanhowar & McCann, 2004; Lovegrove *et al.*, in press; Welbergen *et al.*, 2008). One clear link between rising temperatures and heterothermy concerns the temperature-dependence of metabolism during hibernation and hence the fat reserves needed to survive the hibernation season. Humphries *et al*. (2002) modelled the impacts of increases in hibernaculum temperatures on winter energy requirements in little brown bats (*Myotis lucifugus*), and predicted that the northern geographical limit for winter hibernation in this species will shift markedly pole-ward by the 2080s. The link between the temperature-dependence of metabolism and the impacts of climate change effects has also recently been highlighted by Lovegrove *et al*. (in press), who found that in four small, nocturnal tropical mammals, namely tarsiers (*Tarsius syrichta*), tenrecs (*S. setosus*) and mouse lemurs (*Microcebus ravelobensis* and *M. griseorufus*), rest-phase (i.e., daytime) T_b during torpor was higher than night-time active phase T_b. Increases in rest-phase metabolic rate driven by Arrhenius effects associated with higher future air temperatures may be expected to negatively affect fitness due to increases in maintenance metabolism and concomitant decreases in the energy allocated to growth and reproduction (Lovegrove *et al.*, in press). Others have emphasised the importance of phenotypic plasticity in the expression of hibernation and/or torpor in coping with the greater environmental variability predicted under future climate scenarios, noting that the rapid pace of climate change will result in phenotypic plasticity being more important than genotypic adaptation for buffering mammals from its effects (Canale & Henry, 2010). Collectively, these studies highlight the importance of incorporating heterothermy in mechanistic models predicting the impacts of climate change on many mammals, particularly in the tropics.

A second issue of major current concern to which the study of heterothermy is directly relevant is white-nose syndrome (WNS), the emerging infectious disease among North American bats caused by the fungus *Pseudogymnoascus destructans*. Apparently the result of the accidental introduction of *P. destructans* from Europe, since 2006 WNS has caused catastrophic levels of mortality among bats in the eastern half of North America (Frick *et al.*, 2010; Warnecke *et al.*, 2012). Mortality associated with WNS appears to result from the disruption of normal patterns of hibernation, with infected bats rewarming far more frequently than they would otherwise, leading to depletion of fat reserves before the end of winter (Boyles & Willis, 2009; Warnecke *et al.*, 2012). The latter observation has led to the proposal that WNS-linked mortality rates could potentially be reduced by artificially warming localized areas within hibernacula, thereby reducing the energy needed for rewarming and increasing the probability of fat reserves lasting for the entire winter (Boyles & Willis, 2009). Although many questions regarding WNS remain, is it clear that an understanding of hibernation patterns in bats holds the key to predicting many of its consequences for populations of bats.

The goal of this mini-series was also to identify emerging questions and new areas of research. Over the last few decades, the availability of ever-smaller temperature loggers and transmitters has led to a proliferation of studies of thermoregulation involving small, heterothermic mammals in their natural habitats. Collectively, these studies have shown that heterothermy is far more phylogenetically widespread and used in a much greater variety of ecological contexts than we had previously thought. They have also highlighted the importance of solar radiation in rewarming from heterothermy, both in extant taxa and during the evolution of mammalian endothermy (Geiser & Drury, 2003; Mzilikazi, Lovegrove & Ribble, 2002). But many questions remain, particularly with regards to the energetic consequences of heterothermy in free-ranging mammals. Very few studies have involved direct measurements of energy expenditure during heterothermy via doubly-labelled water or heart rate telemetry (e.g., Dechmann *et al.*, 2011; Schmid & Speakman, 2000). Such measurements are becoming increasingly feasible; indeed, the last decade has seen the development of miniaturized heart rate transmitters suitable for estimating energy expenditure in even the smallest endotherms (see e.g., Dechmann *et al.*, 2011; Steiger *et al.*, 2009), as well as the advent of liquid water isotope analysers that are much cheaper, more portable and easier to use than traditional isotope ratio mass spectrometers. The inclusion of measurements of energy expenditure in future studies of heterothermy in free-ranging individuals will make possible a much deeper understanding of the ecological and evolutionary significance of mammalian heterothermy.

References

Boyles, J. G., Seebacher, F., Smit, B. & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*: **51**: 676-90.

Boyles, J. G. & Willis, C. K. R. (2009). Could localized warm areas inside cold caves reduce mortality of hibernating bats affected by white-nose syndrome? *Frontiers in Ecology and the Environment*: **8**: 92-98.

Buck, C. L. & Barnes, B. M. (1999). Annual cycle of body composition and hibernation in free-living Arctic ground squirrels. *Journal of Mammalogy*: **80**: 430-42.

Canale, C. I. & Henry, P.-Y. (2010). Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. *Climate Research*: **43**: 135-47.

Dausmann, K. H. (in press). Flexible patterns in energy savings: heterothermy in primates. *Journal of Zoology, London*.

Dausmann, K. H., Glos, J., Ganzhorn, J. U. & Heldmaier, G. (2005). Hibernation in the tropics: lessons from a primate. *Journal of Comparative Physiology B*: **175**: 147-55.

Dechmann, D. K. N., Ehret, S., Gaub, A., Kranstauber, B. & Wikelski, M. (2011). Low metabolism in a tropical bat from lowland Panama measured using heart rate telemetry: an unexpected life in the slow lane. *Journal of Experimental Biology*: **214**: 3605-12.

Frick, W. E., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., Butchkoski, C. M. & Kunz, T. H. (2010). An emerging disease causes regional population collapse of a common North American bat species. *Science*: **329**: 679-82.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R. S., Mitchell, D. & Maloney, S. K. (2010). Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology*: **83**: 713-20.

Geiser, F. (1998). Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clinical and Experimental Pharmacology and Physiology*: **25**: 736-40.

Geiser, F. (2007). Yearlong hibernation in a marsupial mammal. *Naturwissenschaften*: **94**: 941-44.

Geiser, F. & Drury, R. L. (2003). Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *Journal of Comparative Physiology B*: **173**: 55-60.

Grigg, G. C., Beard, L. A. & Augee, M. L. (2004). The evolution of endothermy and its diversity in mammals and birds. *Physiological and Biochemical Zoology*: **77**: 982-97.

Humphries, M. M., Thomas, D. W. & Speakman, J. R. (2002). Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature*: **418**: 313-16.

Humphries, M. M., Umbanhowar, J. & McCann, K. S. (2004). Bioenergetic predictions of climate change impacts on northern mammals. *Integrative and Comparative Biology*: **44**: 152-62.

IPCC (2007). *Climate change 2007: Fourth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge: Cambridge University Press.

Kobbe, S., Ganzhorn, J. U. & Dausmann, K. H. (2011). Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *Journal of Comparative Physiology B*: **181**: 165-73.

Lovegrove, B. G. (2012). The evolution of endothermy in Cenozoic mammals:a Pleisiomorphic-Apomorphic continuum. *Biological Reviews*: **87**: 128-62.

Lovegrove, B. G., Canale, C. I., Levesque, D., Fluch, G., Řeháková-Petrů, M. & Ruf, T. (in press). Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? . *Physiological and Biochemical Zoology*.

Malan, A. (1996). The origins of hibernation: a reappraisal. In *Adaptations to the cold: Tenth International Hibernation Symposium.*: 1-6. Geiser, F., Hulbert, A. J. & Nicol, S. C. (Ed.). Armidale: University of New England Press.

Mzilikazi, N., Lovegrove, B. G. & Ribble, D. O. (2002). Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. *Oecologia*: **133**: 307-14.

Riek, A. & Geiser, F. (in press). Heterothermy in pouched mammals – a review. *Journal of Zoology, London*.

Schmid, J. & Speakman, J. R. (2000). Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *Journal of Comparative Physiology B*: **170**: 633-41.

Scholander, P. F., Hock, R., Walters, V., Johnson, F. & Irving, L. (1950). Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin*: **99**: 237-58.

Stawski, C., Willis, C. K. R. & Geiser, F. (in press). The importance of heterothermy in bats. *Journal of Zoology, London*.

Steiger, S. S., Kelley, J. P., Cochran, W. W. & Wikelski, M. (2009). Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. *Physiological and Biochemical Zoology*: **82**: 580-89.

Warnecke, L., Turner, J. M., Bollinger, T. K., Lorch, J. M., Misra, V., Cryan, P. M., Wibbelt, G., Blehert, D. S. & Willis, C. K. R. (2012). Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences*: **109**: 6999-7003.

Welbergen, J. A., Klose, S. M., Markus, N. & Eby, P. (2008). Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B*: **275**: 419-25.

Williams, C.T., Barnes, B.M., Kenagy, G.J. & Buck, C.L. (in press). Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. *Journal of Zoology, London*.