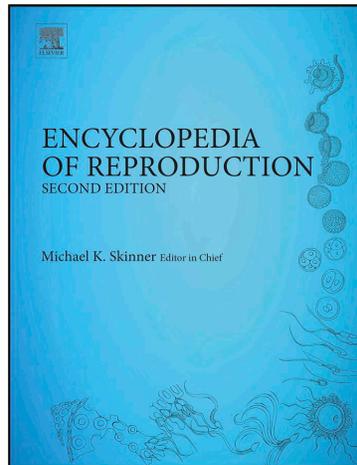


Provided for non-commercial research and educational use.  
Not for reproduction, distribution or commercial use.

This article was originally published in Encyclopedia of Reproduction, Second Edition, published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<https://www.elsevier.com/about/our-business/policies/copyright/permissions>

From McAllan, B. M., & Geiser, F. (2018). Torpor During Reproduction in Mammals and Birds: Balancing Energy Expenditure for Survival. In M. K. Skinner (Ed.), Encyclopedia of Reproduction. vol. 6, pp. 757–763. Academic Press: Elsevier.

<http://dx.doi.org/10.1016/B978-0-12-809633-8.20625-0>

ISBN: 9780128118993

Copyright © 2018 Elsevier Inc. All rights reserved.

Academic Press

## Torpor During Reproduction in Mammals and Birds: Balancing Energy Expenditure for Survival

**BM McAllan**, The University of Sydney, Sydney, NSW, Australia; and University of New England, Armidale, NSW, Australia  
**Fritz Geiser**, University of New England, Armidale, NSW, Australia

© 2018 Elsevier Inc. All rights reserved.

### Glossary

**Heterothermy** Condition where birds and mammals can change their body temperatures in a regulated manner.

**Homeothermy** Condition where birds and mammals maintain a single body temperature in a regulated manner.

### Nomenclature

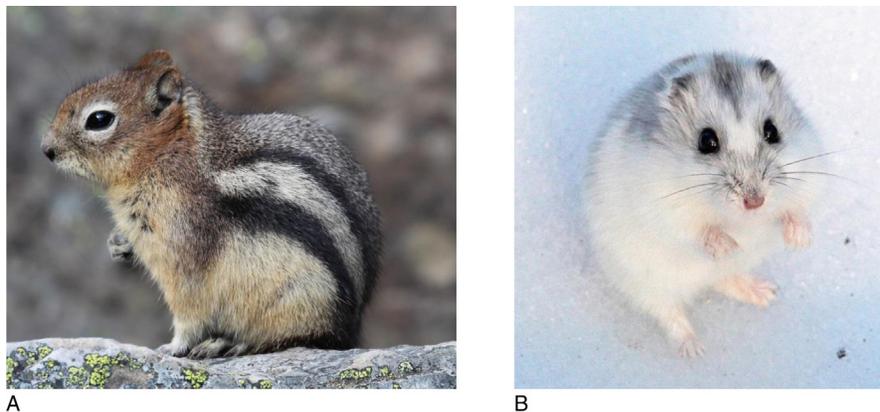
$T_b$  Body temperature

### Introduction

Mammalian reproduction and expression of torpor are often viewed as mutually incompatible processes. Reproduction typically requires acquisition of nutrients and high energy expenditure for mating behaviour and the production of young (Tyndale-Biscoe and Renfree, 1987), whereas torpor is characterised by a substantial reduction of energy expenditure by up to 90%–99% and also a fall body temperature ( $T_b$ ) to between 0 and 25°C, depending on the species. Animals usually remain torpid between a few hours up to about 6 weeks (Ruf and Geiser, 2015). Birds and mammals that use torpor or hibernation and change  $T_b$  over time are called ‘heterotherms’ in contrast to ‘homeothermic’ species that maintain a constant high  $T_b$ .

To avoid the energetic incompatibility many species use a sequence of torpor followed by reproduction during the yearly cycle. In typical heterothermic rodents from the Northern Hemisphere torpor is expressed from autumn to early spring, after which reproduction commences in spring and summer (Geiser *et al.*, 2008). This pattern is especially observed in cricetid (hamsters) and sciurid (ground squirrel family) rodents (Fig. 1), which live in strongly seasonal environments with highly productive summers. These species refuse to express torpor during the reproduction season, reduce their gonads during the torpor season and even may remain homeothermic when reproductive hormones are administered.

Interestingly, not all species conform to this dogma. Torpor during the reproductive season has been observed during both pregnancy and lactation in many mammals, and also during incubation and brooding in birds (Brigham *et al.*, 2012; McKechnie and Mzilikazi, 2011; McAllan and Geiser, 2014; Geiser *et al.*, 2017). This is especially true for small mammals from the Australian arid zone, who seem to not only use torpor during reproduction, but to enable reproduction on limited resources (McAllan and Geiser, 2014). We aim to summarise available information about those mammals and birds that enter torpor during reproduction and examine the taxonomic diversity of the phenomenon.



**Fig. 1** Examples of mammals that use torpor or hibernation, however the golden-mantled ground squirrel and the Djungarian hamster do not express torpor during the reproductive season. (A) Golden-mantled ground-squirrel *Callospermophilus lateralis* (Sciuridae); (B) The Djungarian hamster *Phodopus sungorus* (Cricetidae). Photos are by Fritz Geiser and cannot be reproduced without permission of Fritz Geiser.

### Torpor and Reproduction in Heterothermic Birds

Birds from at least nine orders are known to be heterothermic (McKechnie and Mzilikazi, 2011; Brigham *et al.*, 2012). These include barbet relatives, kingfishers, mousebirds, swifts, hummingbirds (Fig. 2(A)), nightjar relatives, owls, pigeons and songbirds. Although heterothermy is less common in non-reproductive birds than for similarly-sized mammals (Ruf and Geiser, 2015), some use torpor while incubating eggs. For example Andean broad-tailed hummingbirds, *Selasphorus platycercus*, incubate eggs with a  $T_b$  as low as 6.5°C and in this species torpor may be as pronounced as in non-reproductive birds.

There is only one known avian hibernator, the poorwill, *Phalaenoptilus nuttallii* (Brigham *et al.*, 2012). Like many mammalian hibernators it can enter torpor for several days and drop their  $T_b$  to 5°C (Brigham *et al.*, 2012). When reproductive, few individuals reluctantly become torpid and with a cost to reproductive output (Brigham *et al.*, 2012).

### Torpor and Reproduction in the Monotremes (Egg-Laying Mammals)

Echidnas (*Tachyglossus aculeatus*, Fig. 2(B)) will hibernate when non-reproductive in many areas of Australia (Morrow and Nicol, 2009). The echidnas, although having a distinct seasonal biology, also have overlapping hibernation and reproductive seasons (Morrow and Nicol, 2009). In Tasmania reproductively active males hibernate from mid-February to mid-June, while reproductively active females hibernate from early March until mid-July. Reproductive males have been found with torpid females, or with females that re-entered hibernation after mating (Morrow and Nicol, 2009). Pregnant, torpid, recently mated females also have been observed in the wild (Morrow and Nicol, 2009). Unlike other hibernators, male echidnas have enlarged testes during hibernation but not all males mate each year, and those that are not involved in reproduction continue to hibernate (Morrow and Nicol, 2009).



**Fig. 2** Examples of birds and mammals that use torpor or hibernation. The blossom bat, hummingbird, feathertailed glider and echidna are all capable of using torpor or hibernation during reproduction. (A) Volcano hummingbird (*Selasphorus flammula*, Apodiformes Trochilidae). (B) Echidna *Tachyglossus aculeatus* (Monotremata). (C) Feathertailed glider *Acrobates pygmaeus* (Acrobatidae). (D) The Australian blossom bat *Syconycteris australis* (Pteropodidae). Photos are by Fritz Geiser and cannot be reproduced without permission of Fritz Geiser.

## Torpor and Reproduction in Marsupials

Daily torpor and hibernation are known to occur in a number of marsupial families. Many dasyurids (carnivorous marsupials) have been observed to use torpor for most of the year, including the reproductive season. Fat-tailed dunnarts (*Sminthopsis crassicaudata*) enter daily torpor throughout the year and do so during lactation for females, and in males when testes are large and they are reproductive. Unlike many rodents, torpor patterns are similar in fat-tailed dunnarts no matter their reproductive condition (McAllan and Geiser, 2014). Pregnant stripe-faced dunnarts (*S. macroura*), can use torpor, but only in the first half of the short pregnancy. Males used torpor when reproductive hormones were present or absent, however torpor traits such as torpor bout duration, were affected by presence of testosterone in males. In females the effects of reproductive hormones on patterns of torpor use are mixed, with only the pregnancy hormone progesterone really disrupting torpor use. This contrasts to data from heterothermic rodents, where presence of testosterone abolishes the use of torpor in males, and oestrogen inhibits torpor use in females (McAllan and Geiser, 2014).

Another carnivorous marsupial the Mulgara [*Dasyercus cristicauda (blythi)*] uses daily torpor with minimum  $T_b$  around 14°C and reproduce in winter (Körtner *et al.*, 2008). Reproductively active males and pregnant females use torpor under both winter field and even mild laboratory conditions (Körtner *et al.*, 2008). Females can increase their body mass by 35% during pregnancy by frequently using torpor to conserve energy, but because neonates weigh less than 1% of the mother's body mass, it seems that females try to enhance fat storage for the more energetically demanding period of lactation, which is the main time of energy and nutrient transfer to growing young in marsupials (McAllan and Geiser, 2014). In contrast to most other mammals for which there are data, the use of torpor in mulgaras appeared to increase during pregnancy in comparison to non-reproductive individuals. However, free-ranging males displayed only shallow and brief torpor during the mating season in early winter, but after mating daily torpor was pronounced (Körtner *et al.*, 2008).

Torpor during the reproductive season also occurs in kowaris (*Dasyuroides byrnei*). Similar to the mulgaras, reproduction also influenced thermoregulation in females in the field. Pregnant female kowaries can enter torpor, but maintain high normothermic  $T_b$ 's throughout lactation in McAllan and Geiser (2014). Moreover, pregnant antechinus (*Antechinus flavipes*) enter daily torpor in captivity (Stawski and Rojas, 2016).

Torpor during reproduction also occurs in possums (diprotodont marsupials). In contrast to the dasyurids, which predominantly express torpor during pregnancy, possums appear to use torpor mainly during lactation, perhaps because their neonates are substantially larger than those of dasyurids. Feathertail gliders (*Acrobates pygmaeus*, Fig. 2(C)) undergo both short and prolonged torpor when non-reproductive with  $T_b$  falling as low as 2°C and torpor bouts lasting for up to a week in Geiser *et al.* (2008). Torpor has been observed in lactating females with pouch young in the reproductive season (Austral Spring). Similarly, free-ranging female sugar gliders (*Petaurus breviceps*), displayed daily torpor during lactation, when the pouch young were 19–34 days of age (Geiser *et al.*, 2008). During pregnancy wild female sugar gliders maintained a high and rather constant  $T_b$ , males only use torpor occasionally.

## Torpor and Reproduction in the Afrotheria

The Afrotherians are often considered as basal clade in eutherian phylogeny and include elephants, sea cows, hyraxes tenrecs, golden moles, sengis, and aardvarks (McKechnie and Mzilikazi, 2011). Torpor use has been described in many tenrecs. Generally these species typically have a hibernation season over the winter and can show prolonged torpor bouts from 2–4 days although more frequently the bouts are shorter are less than 24 h duration (McKechnie and Mzilikazi, 2011), whereas others may remain in shallow torpor for weeks (Lovegrove *et al.*, 2014). There is a large variability in gestation periods within each tenrec species, which is perplexing until it is noted that this phenomenon may be linked to the opportunistic use of torpor during the reproductive season, similar to marsupials. The  $T_b$ s of torpid shrew-tenrecs (*Microgale dobsoni* and *Microgale talazaci*) and large-eared tenrecs (*Geogale aurita*) are higher when females are pregnant or lactating than when they are non-pregnant and torpid (see McKechnie and Mzilikazi, 2011). Torpor was not observed during pregnancy in other tenrec species (*Hemicentetes semispinosus*, *H. nigriceps*, *Echinops telfairi*, *Setifer setosus*; see McKechnie and Mzilikazi, 2011; McAllan and Geiser, 2014). Torpor use in pregnant females appears to lengthen the gestation period (see McKechnie and Mzilikazi, 2011; McAllan and Geiser, 2014). Sengis (elephant shrews, Macroscelidea), express daily torpor or short-term hibernation when non-reproductive and exhibit seasonal torpor patterns (McKechnie and Mzilikazi, 2011). Their torpor use is adaptive to the weather conditions, as they can respond to changing conditions in spring, by returning to occasional torpor use if the weather is poor. For the sengis, the interaction between torpor use and reproduction is not clear (Lovegrove *et al.*, 2014).

## Torpor and Reproduction in the Xenarthra (Anteaters, Armadillos, and Sloths)

Torpor is used by the pichi (*Zaedyus pichiy*) and these temperate zone armadillos appear to have distinct non-overlapping hibernation and reproductive seasons in Ruf and Geiser (2015). However, there is one record of "hypothermia" in a pregnant three-toed sloth, (*Bradypus griseus griseus*, Morrison 1945 in McAllan and Geiser (2014)).

### Torpor and Reproduction in the Eulipotyphla (Shrews, Moles and Hedgehogs)

In contrast to reports from the past, torpor has been recorded in many shrews *Crocidura russula*, *C. leucodon*, *C. suaveolens* and in *Suncus etruscus* (McAllan and Geiser, 2014). Data are scant because the very small shrews are difficult to keep in captivity and there are technological limitations for measuring their thermal physiology in the field. Data on thermoregulation of shrews during reproduction are even sparser. Hedgehogs readily use torpor both in captivity and in the wild with long torpor bouts lasting up to 27 days in some species, although 2–4 days are more usual (Dmi'el and Schwartz, 1984). In all hedgehogs studied torpor could be induced at any time of year by cool weather (Dmi'el and Schwartz, 1984). However, only one study has specifically examined the use of torpor by reproductive animals (Fowler, 1988). Pregnant European hedgehogs (*Erinaceus europaeus*) demonstrated the same daily fluctuations in  $T_b$  as non-pregnant animals, and defended their normothermic  $T_b$  only during late pregnancy (Fowler, 1988).

### Torpor and Reproduction in Primates (Lemurs and Bushbabies)

Several species of primates belonging to the Cheirogaleidae (Malagasy lemurs) from five genera and in the South African lesser bushbaby (*Galago moholi*, Dausmann, 2014) all express torpor. Some of the dwarf lemurs hibernate with a distinct hibernation season, separated temporally from the reproductive season (Dausmann, 2014) and if food is scarce or the habitat is poor animals will choose not to reproduce, instead using torpor during the reproductive season (Dausmann, 2014).

In contrast the mouse-lemurs (*Microcebus* spp.) are very flexible in their use of heterothermy with some species using only daily torpor occasionally (e.g. *Microcebus berthae*, in Dausmann, 2014), whereas others showing an extended regular pattern of torpor, depending fat reserves accumulated during the active season (*M. griseorufus*, *M. murinus* in Dausmann, 2014). For the most part torpor use has not been seen in pregnant or lactating females, with most observations of torpor occurring in the “winter” (dry) period (Dausmann, 2014). The exception to this was found in *M. murinus*, in which severe food restriction in the laboratory induced torpor use in both pregnant and lactating females (Dausmann, 2014). While the experiment may seem divorced from the animals' experiences in nature, the unpredictable environment and pronounced changes in water availability in their natural environment may require torpor use during pregnancy and lactation in wild mouse-lemurs (Dausmann, 2014). In contrast to the Madagascan lemurs, the African lesser bushbaby, *Galago moholi*, uses torpor only rarely as an emergency mechanism for energy savings, suggesting that torpor and reproduction in bushbabies are likely to be mutually exclusive (Dausmann, 2014).

### Torpor and Reproduction in Bats

Many insectivorous bats (Microchiroptera) typically exhibit prolonged torpor in winter, but also short bouts of torpor during the summer reproductive season. There are many examples of bats using torpor during pregnancy and lactation (McAllan and Geiser, 2014; Stawski et al., 2014). Torpor use in reproductive bats can cause a delay in gestation in pregnant females, and a possible reduction in milk production. The main physiological disadvantage for female bats and their offspring could be that delays in parturition and embryonic and postnatal growth could result in insufficient pre-winter fattening to fuel the energy requirements during the long hibernation season in winter (Ruf and Geiser, 2015). The physiological advantage is that any transient energy shortfalls are managed such that both mother and offspring remain viable, although reproductive activities are delayed (Willis et al., 2006).

Many vespertilionid bats mate in late summer and early autumn (Stawski et al., 2014; Ruf and Geiser, 2015). After mating, sperm is stored in the oviduct and following the hibernation season, pregnancy starts immediately after fertilization. The demanding energetic costs of pregnancy and lactation continue to increase until weaning thus food consumption increases for lactating females, however female *M. lucifugus* will use torpor during pregnancy and lactation, although the bouts are shallower and shorter than in non-reproductive individuals (Stawski et al., 2014).

Torpor extends the length of pregnancy of many bats (mouse-eared bat *M. myotis*, mouse-eared bat *M. blythii*, pipistrelle *Pipistrellus pipistrellus*). Food availability coupled with cooler temperatures seems to be the main trigger for torpor use during pregnancy and lactation in these bats. In the wild this results in variable gestation lengths in animals between roost sites and over several years in the lump-nosed bat, *Corynorhinus* (= *Plecotus*) *rafinesquei* (Pearson et al., 1952). Similar to other mammals, torpor bout duration and depth was reduced in reproductive females (Stawski et al., 2014). Miniopertid bats also mate in autumn or winter, but females enter hibernation in a pregnant condition, embryonic development is delayed, and births do not occur until the following summer (Stawski et al., 2014). In the desert-dwelling Hemprich's long-eared bats (*Otonycteris hemprichii*) torpor use occurred in pregnant female bats up to the third trimester of pregnancy, when  $T_b$  could be still lower than during normothermia, but torpor was shallower than in non-reproductive bats (Stawski et al., 2014). Shallow torpor was also expressed in lactating females, although the incidence of torpor use was reduced. In the big brown bat (*Eptesicus fuscus*), torpor has been observed during both pregnancy and lactation (Audet and Fenton, 1988; Stawski et al., 2014). Deep torpor (ie. a skin temperature drop by more than 10°C) was regularly observed during pregnancy and also during lactation.

Male *Miniopterus* also show seasonal changes in reproduction, with spermatogenesis and fertility unimpaired by hibernation use (Pearson et al., 1952). Similar to *M. schreibersii*, the vespertilionid male Daubentons's bats (*Myotis daubentonii*) and male Bechstein's bats (*M. bechsteini*) also use torpor during the reproductive periods in summer, although to a lesser extent than other times of year

(Stawski *et al.*, 2014). Male big brown bats regularly used torpor throughout the year, but show a seasonal cycle in torpor use (Audet and Fenton, 1988).

The differences in torpor use between many small insectivorous bats may be because of their different roost selections. Roosting alone and in exposed roosts incurs much higher costs for maintenance of homeothermy when compared to roosting in maternity colonies in well-insulated roosts (Willis *et al.*, 2006). The importance of roost selection or thermal condition for torpor use by reproductive bats is supported by laboratory work where captive pregnant and lactating female and male long-eared bats (*Nyctophilus geoffroyi* and *N. gouldi*) studied under identical thermal conditions, showed indistinguishable thermal physiology (McAllan and Geiser, 2014). The reluctance by reproductive females to enter torpor in the field may be because of ecological rather than physiological differences, and may explain why many females roost together whereas male bats roost alone (Willis *et al.*, 2006).

Subtropical insectivorous bats also use torpor. Long-eared non-reproductive male bats (*N. bifax*) continue to use torpor no matter what the season suggesting that torpor use is beneficial throughout the year even in the subtropics (McAllan and Geiser, 2014; Ruf and Geiser, 2015). However, non-reproductive males used torpor more frequently than pregnant females during spring, similarly to male big brown bats and male Daubenton's bats (McAllan and Geiser, 2014; Stawski *et al.*, 2014). It appears that occasionally pregnant females may have been energetically constrained and therefore needed to enter torpor for short periods in McAllan and Geiser (2014).

We know less about torpor use in the Megachiroptera. The nectarivorous blossom-bat (*Syconycteris australis* Fig. 2(D)) displays daily torpor in captivity (Stawski *et al.*, 2014; Ruf and Geiser, 2015). Torpor in non-reproductive *S. australis* is used by all individuals and lasts for up to 12 h, metabolic rate falls to about 15% of resting animals and  $T_b$  drops to a minimum of about 18°C. Torpor has been observed in one of three pregnant bats, but the torpor bout of this female was shorter and the reduction of the metabolic rate was less pronounced than in most non-reproductive individuals (Stawski *et al.*, 2014). Interestingly, pregnant *R. aegyptiacus* depress their metabolism by 19% of resting metabolic rates of non-pregnant females, perhaps enabling them to spend more time on foraging or to allocate more energy to fat storage or milk production (Stawski *et al.*, 2014).

### Torpor and Reproduction in Other Rodents (Dormice)

Torpor use has also been observed in several rodent families besides the sciurids and cricetids. Many species of dormice (Gliridae) use torpor (Ruf and Geiser, 2015) and use is linked to food availability, with complex relationships observed between torpor, seasonal food availability and reproduction. The hibernation cycle of the edible dormouse (*Glis glis*) is closely tied to the seasonal change, but successful reproduction is associated with seed production by beech trees (Mast years), and females may not reproduce every year (Lebl *et al.*, 2011). Because of the secretive nature of this dormouse it is unclear whether the females use torpor while in reproductive condition in the wild although being in good physical condition does not preclude their use of summer torpor (Lebl *et al.*, 2011).

Food scarcity also promotes torpor use in any season in garden dormice (*Eliomys quercinus*, in Ruf and Geiser, 2015). Torpor regularly occurs in summer in African woodland dormice (*Graphiurus murinus*, in Ruf and Geiser, 2015). Both spontaneous torpor (with food) and induced torpor (food removed) was observed in this species, although it was not stated whether the animals were reproductive, it was certainly during their reproductive season. Wild common dormice (*Muscardinus avellanarius*) hibernate for prolonged periods in winter but torpor was also observed in reproductive males and females, pregnant females, females with litters and in nestlings during the breeding season (Juškaitis, 2005). Similar to some bats, torpor bouts for pregnant females were not as deep as those found in females at other times of year (Juškaitis, 2005).

### Torpor and Reproduction in the Carnivora (Bears and Badgers)

Torpor use is restricted to bears (Ursidae) and some badgers (Mustelidae). Hibernating black bears (*Ursus americanus*) and brown bears (*Ursus arctos*) show long periods of dormancy in winter and actually give birth during their hibernation period. All animals remain aware and capable of moving throughout hibernation (Tøien *et al.*, 2011). Bears do not eat, drink, defecate, or urinate during the 3–6 month hibernation period, and unlike many small hibernators, which often allow their  $T_b$  to fall near 0°C (Ruf and Geiser, 2015), their core  $T_b$  decreases to only about 30°C. Even so, because metabolic rate is very low, considerable energy savings are made over winter. Pregnancy and birth are only weakly associated with activity patterns in the brown bear (Tøien *et al.*, 2011), and circulating sex steroids have been found to be independent of torpor activity in black bears and in polar bears in McAllan and Geiser (2014).

Badgers have a hibernation season that appears independent of the reproductive season for males, and delayed embryonic implantation occurs in females, with post-implantation gestation occurring during the height of winter conditions. The European badger (*Meles meles*) will remain heterothermic when delayed implantation occurs, although in one female  $T_b$  was raised somewhat from 28.4°C before implantation to between 32.1 and 34.7°C during the remainder of the gestation period (Fowler and Racey, 1988). In males increased circulating testosterone concentrations are seasonal and begin to rise in winter, when hibernation is still common (Fowler and Racey, 1988). Similar patterns of heterothermy are seen in the American badger (*Taxidea taxus*), although  $T_b$ s have not been measured for pregnant females (McAllan and Geiser, 2014).

## Discussion

Torpor use during reproduction in birds and mammals is widespread, occurring in many taxa (e.g., Monotremata, Marsupialia, Afrotheria, Eulipotyphla, Chiroptera). However, we lack information on torpor and reproduction in other mammalian groups. We clearly need more information about thermoregulatory capacities of species from several orders.

Most monotremes and marsupials have short pregnancies and the mass of an echidna egg and that of single neonates or neonate litters of marsupials is less than 0.3% of the mothers' masses (Tyndale-Biscoe and Renfree, 1987; McAllan and Geiser, 2014). Energy expenditure/day for gestation in both groups and lactation in marsupials is relatively low even over the long lactational time that they have compared to eutherians (Nicoll and Thompson, 1987). Small rodents, such as the scurids and circetids who do not have an overlap of reproduction and torpor use, have a relatively short gestation periods, heavy neonate litters (10%–65% of maternal weight) and fast development after birth and both gestation and lactation are thus energetically expensive (Nicoll and Thompson, 1987). Bats have one large neonate (13%–40% of maternal weight), but growth of fetal and young bats, as in marsupials and monotremes, is slow and energy expenditure/day during gestation is much lower than in small rodents (Nicoll and Thompson, 1987). In contrast carnivores have small altricial young with fast neonatal growth rates, but because of their size heterothermic carnivores have vastly different energetic demands than most other heterotherms.

Similarly for the birds the nightjar relatives (Caprimulgiformes) and hummingbirds (Trochiliformes) have relatively small clutch sizes and relatively long rearing periods and the additional energy expenditure required during reproduction should be small. We can conclude that mammals and birds that produce few offspring or spread the reproductive effort and the associated metabolic costs over a long time, may display torpor during the period of reproduction. The rate of development of young may be slower, but the chance of survival in offspring is unaffected because a small delay in growth within the long period of development has minimal impact.

Many of the species that use torpor during reproduction are animals from unpredictable environments, where seasonal availability of food can be cut short by abrupt weather changes. For some species the adverse weather conditions or the food shortages must be severe for induction of heterothermy (Dausmann, 2014), for others, such as bats heterothermy during pregnancy is part of the yearly cycle. For bears and badgers heterothermy during pregnancy seems part of the yearly cycle in a predictable environment, but their body size also plays an important role for carnivores. For these mammals the small extension of pregnancy or lactation may be an important strategy to optimise reproductive outcomes later in spring and summer.

Besides reproductive strategies another explanation for the differences between thermoregulatory patterns during reproduction in different mammalian groups and birds, could be diet. Abundance of most insects (and other arthropods) and nectar strongly fluctuate with season and use of torpor during reproduction may be linked to their availability. If food supply is predictable food supplies and a species can reproduce during a period of high primary productivity then strict homeothermy during reproduction will be an advantage, whereas species with relatively unpredictable food supplies may be better off using torpor when the cost is only a small extension of the reproductive period. The use of heterothermy during the reproductive season appears to be quite widespread and is a strategy for small birds and mammals to weather temporary unpredictable energetic adversities, while continuing to invest in reproduction.

## Acknowledgments

This work was supported by grants from the Australian Research Council (DP130101589 to BMM, and DP130101506 to FG).

## References

- Audet, D., & Fenton, M. B. (1988). Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: vespertilionidae): A field study. *Physiol. Zool.*, *61*, 197–204.
- Brigham, R.M., McKechnie, A.E., Doucette, L.I., Geiser, F., 2012. Heterothermy in caprimulgid birds: A review of inter- and intraspecific variation in free-ranging populations. In: Ruf, T., Bieber, C., Arnold, W. and Millesi, E. (Eds.), *Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations*, pp. 175–187.
- Dausmann, K. H. (2014). Flexible patterns in energy savings: Heterothermy in primates. *J. Zool.*, *292*, 101–111.
- Dmi'el, R., & Schwartz, M. (1984). Hibernation patterns and energy expenditure in hedgehogs from semi-arid and temperate habitats. *J. Comp. Physiol. B*, *155*(117), 123.
- Fowler, P. A. (1988). Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season. *J. Reprod. Fertility*, *82*, 285–292.
- Fowler, P. A., & Racey, P. A. (1988). Overwintering strategies of the badger, *Meles meles*, at 57° N. *J. Zool., Lond.*, *214*, 635–651.
- Geiser, F., Christian N., Cooper C.E., et al., 2008. Torpor in marsupials: Recent advances. In: Lovegrove, B.G., McKechnie, A.E. (Eds), *Hypometabolism in Animals: Torpor, Hibernation and Cryobiology*. Proceedings of the 13th International Hibernation Symposium. University of KwaZulu-Natal, Pietermaritzburg. pp 297–306.
- Geiser, F., Stawski, C., Wacker, C. B., & Nowack, J. (2017). Phoenix from the ashes: Fire, torpor and the evolution of endothermy. *Front. Physiol.*, *8*, 842. <https://doi.org/10.3389/fphys.2017.00842>.
- Juškaitis, R. (2005). Daily torpor in free-ranging common dormice (*Muscardinus avellanarius*) in Lithuania. *Mamm. Biol.*, *70*, 242–249.
- Körtner, G., Pavey, C. R., & Geiser, F. (2008). Thermal biology, torpor and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. *Physiol. Biochem. Zool.*, *81*, 442–451.
- Lebl, K., Rotter, B., Kürbisch, K., Bieber, C., & Ruf, T. (2011). Local environmental factors affect reproductive investment in female edible dormice. *Journal of Mammalogy*, *92*, 926–933.
- Lovegrove, B. G., Lobban, K. D., & Levesque, D. L. (2014). Mammal survival at the Cretaceous-Paleogene boundary: Metabolic homeostasis in prolonged tropical hibernation in tenrecs. *Proc R Soc B*, *281*, 20141303.
- McAllan, B. M., & Geiser, F. (2014). Torpor during Reproduction in Mammals and Birds: Dealing with an Energetic Conundrum. *Integr. Comparative Biol.*, *54*(3), 516–532.

- McKechnie, A. E., & Mzilikazi, N. (2011). Heterothermy in afrotropical mammals and birds: A review. *Integrative and Comparative Biology*, *51*, 349–363.
- Morrow, G., & Nicol, S. C. (2009). Cool sex? Hibernation and reproduction overlap in the echidna. *PLOS ONE*, *4*(6), e6070. <https://doi.org/10.1371/journal.pone.0006070>.
- Nicoll, M. E., & Thompson, S. D. (1987). Basal metabolic rates and energetics of reproduction in therian mammals: Marsupials and placentals compared. *Symp. zool. Soc. Lond.*, *57*, 7–27.
- Pearson, O. P., Koford, M. R., & Pearson, A. K. (1952). Reproduction of the lump-nosed bat *Corynorhinus rafinesquei* in California. *J. Mammal.*, *33*, 273–320.
- Ruf, T., & Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biol. Rev.*, *90*, 891–926.
- Stawski, C., & Rojas, A. D. (2016). Thermal physiology of a reproductive female marsupial, *Antechinus flavipes*. *Mammal Res.*, *61*, 417–421.
- Stawski, C., Willis, C. K. R., & Geiser, F. (2014). The importance of temporal heterothermy in bats. *J. Zool.*, *292*, 86–100.
- Tøien, Ø., Blake, J., Edgar, D. M., et al. (2011). Hibernation in black bears: Independence of metabolic suppression from body temperature. *Science*, *331*(6019), 906–909.
- Tyndale-Biscoe, H., & Renfree, M. B. (1987). *Reproductive Physiology of Marsupials*. Cambridge: Cambridge University Press.
- Willis, C. K. R., Brigham, R. M., & Geiser, F. (2006). Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften*, *93*, 80–83.