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INVITED REVIEW

Torpor during Reproduction in Mammals and Birds: Dealing with an Energetic Conundrum

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Synopsis Torpor and reproduction in mammals and birds are widely viewed as mutually exclusive processes because of opposing energetic and hormonal demands. However, the reported number of heterothermic species that express torpor during reproduction is ever increasing, to some extent because of recent work on free-ranging animals. We summarize current knowledge about those heterothermic mammals that do not express torpor during reproduction and, in contrast, examine those heterothermic birds and mammals that do use torpor during reproduction. Incompatibility between torpor and reproduction occurs mainly in high-latitude sciurid and cricetid rodents, which live in strongly seasonal, but predictably productive habitats in summer. In contrast, torpor during incubation, brooding, pregnancy, or lactation occurs in nightjars, hummingbirds, echidnas, several marsupials, tenrecs, hedgehogs, bats, carnivores, mouse lemurs, and dormice. Animals that enter torpor during reproduction often are found in unpredictable habitats, in which seasonal availability of food can be cut short by changes in weather, or are species that reproduce fully or partially during winter. Moreover, animals that use torpor during the reproductive period have relatively low reproductive costs, are largely insectivorous, carnivorous, or nectarivorous, and thus rely on food that can be unpredictable or strongly seasonal. These species with relatively unpredictable food supplies must gain an advantage by using torpor during reproduction because the main cost is an extension of the reproductive period; the benefit is increased survival of parent and offspring, and thus fitness.

Introduction

Reproduction in endothermic mammals and birds is an expensive process because it involves increased expenditure of energy during courtship and mating, production of gametes, and acquisition and provision of nutrients and energy to the growing young (Wimsatt 1969; Renfree and Tyndale-Biscoe 1987). Reproduction can also be associated with an increase in activity or foraging (Körtner and Geiser 1995; McAllan et al. 2008). Torpor on the other hand is characterized by a pronounced and regulated, temporal fall in metabolic rate (MR) and body temperature (T_b), which results in an overall reduction in expenditure of energy (Boyer and Barnes 1999; Carey et al. 2003; Geiser 2004; Kronfeld-Schor and Dayan 2013) and typically occurs when the animal is at rest. Because of these opposing demands, reproduction and torpor in endotherms are widely viewed as energetically exclusive physiological processes. Importantly, reproduction requires not only an increase of MR for processing nutrients and transferring them to the growing offspring (Kenagy et al. 1989) but also high levels of reproductive hormones (Hinds et al. 1996). In contrast, torpor is widely associated with extremely low levels of reproductive hormones and it is therefore often assumed from an endocrinological perspective that the physiological states of reproduction and torpor are incompatible.

To avoid this energetic conundrum, many species simply use a temporal sequence of torpor and reproduction within a yearly cycle. For example, in several heterothermic rodents, the reproductive period in spring and summer is followed by a period of heterothermy in autumn and winter when animals exhibit torpor, but there is no temporal overlap in the two states (Kenagy 1989; Ruf et al. 2006).

Although reproduction and torpor may be mutually exclusive in many rodents and presumably many other heterothermic endotherms, torpor during the reproductive season has been observed during both incubation and brooding in birds, and during pregnancy and lactation in several mammals, (Calder and Booser 1973; Racey 1973; Morton 1978; Audet and Fenton 1988; Kissner and Brigham 1993; Stephenson and Racey 1993a, 1993b; Geiser and Masters 1994; Geiser 1996). However, although the knowledge about this topic has expanded substantially over the past two decades, a recent review has not been conducted. We therefore aim in this review to update new information about the mammals and birds that enter torpor during reproduction and examine the taxonomic diversity of the phenomenon. Firstly, we summarize current knowledge concerning the use of torpor and reproduction in endotherms, first in birds, and then in mammals, using the phylogeny proposed by Song et al. (2012). Then, we examine information for heterothermic rodents that is responsible for the view that torpor and reproduction are incompatible (sciurids and cricetids), because in these mammals reproduction and torpor apparently are required to occur in a temporal sequence. Finally, we discuss the physiological and ecological constraints and advantages of heterothermy with regard to the production of offspring and survival of the parent.

Torpor and reproduction in heterothermic birds

Species from nine avian orders are known to be heterothermic (McKechnie and Lovegrove 2002; Geiser 2004; McKechnie and Mzilikazi 2011; Brigham et al. 2012), and although heterothermy seems to be less common in birds than for similarly-sized mammals, it is by no means rare (McKechnie and Lovegrove 2002; McKechnie and Mzilikazi 2011). With regard to the interaction between torpor and reproduction, one of the first observations of heterothermy in reproductive birds was for broad-tailed hummingbirds, *Selasphorus platycercus* (Apodiformes; Calder and Booser 1973). These birds enter nocturnal torpor while incubating their eggs (Calder and Booser 1973). The data were obtained in the Andes in the wild by using a synthetic temperature-sensitive incubated egg. The temperature of the egg fell after midnight to a minimum of 6.5°C, whereas ambient temperature (T_a) fell to about 0°C, suggesting regulation of T_b by the torpid bird at about 6.5°C. The egg was rewarmed after several hours at low temperature. Because a T_b of 6.5°C is extremely low for hummingbirds (Dawson and Hudson 1970; Reinertsen 1983; McKechnie and Lovegrove 2002), the data suggest that torpor during incubation of this species may be as pronounced as in non-reproductive birds.

Heterothermy in birds is especially widespread among the Caprimulgiformes; however, there is only one known avian hibernator, the poorwill, *Phalaenoptilus nuttallii* (Brigham 1992; Smit and McKechnie 2010; Brigham et al. 2012). When non-reproductive, poorwills enter torpor regularly; their bouts of torpor may last for several days and their T_b falls to a minimum of about 5°C as in many mammalian hibernators (Brigham 1992; French 1993; Brigham et al. 2012). In contrast, when reproductive, few individuals became torpid. Torpor was observed in only 3 of 203 bird-nights in brooding or incubating birds (Kissner and Brigham 1993). Skin temperature in these poorwills fell only to 11.5°C, but it appears that they also remained torpid for several days. Moreover, torpor was observed in a brooding male and a chick and both were able to arouse from torpor (Kissner and Brigham 1993). Although torpor was observed in these birds, Csada and Brigham (1994) concluded that the use of torpor during the reproductive period did constrain their reproductive output. Moreover, not all poorwill species readily use torpor. For example, whip-poorwills use torpor only reluctantly and only non-brooding males demonstrate bouts of torpor during the breeding season (Lane et al. 2004).

Torpor and reproduction in egg-laying mammals

Echidnas (*Tachyglossus aculeatus*, Monotremata) are known to hibernate when non-reproductive in many areas of Australia (Grigg et al. 1992; Nicol and Andersen 1996). Animals in cold climates show a prolonged hibernation season; bouts of torpor last of up to 30 days and T_b may fall as low as 4°C (Grigg et al. 1992). The first observation on torpor in reproductive echidnas was restricted to a single captive female during the breeding season. This individual had a T_b of 21°C 2 days before she laid her egg, and was again lethargic briefly after oviposition (Geiser and Seymour 1989). Initial observations on free-living individuals, however, suggested that this may have been a laboratory artefact because in the wild the hibernation season is terminated in mid-winter when echidnas mate and appear to remain normothermic (Beard et al. 1992). In contrast, recent studies have demonstrated that echidnas, although having a distinct seasonal biology, also have overlapping hibernation and reproductive seasons (Morrow and Nicol 2009; Morrow et al. 2009). Throughout their range echidnas show some degree of seasonal inactivity, but in Tasmania (subspecies *T. a. setosus*) reproductively active males hibernate from mid-February to mid-June, while reproductively active females hibernate from early March until mid-July. During this time, 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). If pregnant females do re-enter torpor after mating, this extends the pregnancy by the number of days that torpor is used (Nicol and Morrow 2012). However, during the 10–11 days of incubation and during the first 30 days of lactation, Tasmanian echidnas are in a closed nursery burrow and protected from the weather (Morrow et al. 2009). Thus, it seems unlikely that pregnant female echidnas enter deep torpor to postpone the energetic costs of lactation. In contrast to many other hibernators, male echidnas have enlarged testes during hibernation, which is perhaps related to mating in mid-winter (Morrow and Nicol 2009; Morrow et al. 2009). However, not all males mate each year, and those that are not involved in reproduction continue to hibernate (Morrow and Nicol 2009).

Torpor and reproduction in Marsupials

Daily torpor and hibernation in marsupials have been extensively described for a number of genera (Geiser and Körtner 2010). Several species of insectivorous/carnivorous dasyurids have been observed to use torpor for most of the year, including the reproductive season. One of the first observations of this phenomenon was of fat-tailed dunnarts (*Sminthopsis crassicaudata*) which enter daily torpor throughout the year. A lactating female with pouch young (i.e., young living in the mother's pouch) was found torpid in the field (Morton 1978). These young were subsequently raised successfully (Morton 1978). Torpor in non-reproductive individuals lasts for about 6–12 h and T_b falls to about 14°C (Geiser and Baudinette 1987; Warnecke et al. 2008). Captive male dunnarts responded to long photoperiod by increasing their testes size, and to short photoperiod by reducing testes size, a pattern similar to that seen for many heterothermic rodents (Holloway and Geiser 1996). However, in contrast to many rodents, patterns of torpor were similar in fat-tailed dunnarts no matter what the state of their testes and independent of current photoperiodic exposure (Holloway and Geiser 1996).

More detailed observations of the interactions between reproduction and torpor have been made for the closely related stripe-faced dunnart (*Sminthopsis macroura*). Torpor use was quantified in a pregnant *S. macroura*, but was observed only in the first half of the short pregnancy (Geiser et al. 2005) (Fig. 1). When male and female *S. macroura* were experimentally manipulated to explore the effects of reproductive hormones on thermal energetics, it was found that males used torpor irrespective of hormonal influences; however, various traits of torpor, especially duration of bouts, were affected by presence of testosterone in males (McAllan et al. 2012). In females, disruption of reproductive cycles occurred with hormone antagonists; however, resting MR was not affected, and only presence of progesterone affected patterns of torpor in females. Consequently, the results differ substantially from those found for heterothermic rodents, in which presence of testosterone abolishes the use of torpor in males, and oestrogen inhibits use of torpor in females (Hall and Goldman 1980; Goldman et al. 1986; Lee et al. 1990; Ouarour et al. 1991; McAllan et al. 2012).

Mulgaras (*Dasycercus cristicauda* [*blythi*] Dasyuridae) use daily torpor with minimum T_b of about 14°C and they reproduce in winter (Körtner et al. 2008). Reproductively active males and especially pregnant females (76% of observations) frequently entered spontaneous torpor (when food and water are available) in the laboratory even under mild thermal conditions (Geiser and Masters 1994); frequent torpor in pregnant females was also observed in the field in winter (Körtner et al. 2008). The gestation period in the captive females was up to 18 days longer than that reported in other studies. Despite (or because of) the high incidence of torpor, females increased their body mass by 35% during pregnancy, which was not due to the mass of the young, because neonatal litters weigh less than 1% of the mother's body mass (Geiser and Masters 1994). It thus appears that females try to enhance storage of fat for the more energetically demanding period of lactation (which is the main time that energy is transferred to the growing young in marsupials), by becoming torpid and saving energy during their daily period of inactivity. Females ceased to express torpor 4–5 days before young were born and were not observed to use torpor during lactation (Geiser and Masters 1994) and a

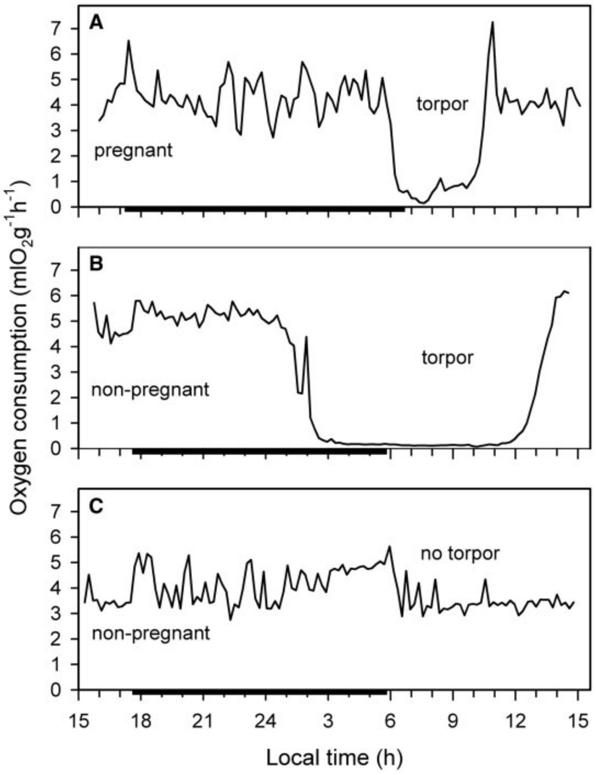

Fig. 1 Oxygen consumption of female dunnarts (*Sminthopsis macroura*) measured over 1 day at T_a 16.8°C. The female in the top panel (**A**) was pregnant and entered an approximately 4-h bout of torpor lasting from about 06:00 to about 10:00 h, the female in the middle panel (**B**) was non-pregnant and entered an approximately 10-h bout of torpor lasting from about 02:00 to about 12:30 h, and the female in the bottom panel (**C**) was non-pregnant and the only individual that remained normothermic. The black bar indicates the period of darkness. Figure modified from Geiser et al. (2005).

similar observation was made in the field (Körtner et al. 2008). Interestingly for this species, and in contrast to most others for which data are available, the use of torpor appeared to increase during pregnancy in comparison to non-reproductive individuals. Males in the field, on the other hand, displayed only shallow, brief torpor during the mating season in early winter, but after mating daily torpor was deep and long (Körtner et al. 2008).

Mulgaras are in the critical weight range of 35–3500 g in which mammal extinctions are most prevalent, and have a relatively predictable pattern of life history (Masters and Dickman 2012). In contrast to the population crashes suffered by other mammals in this weight range, mulgaras persist in the arid zone of Australia, and a strong predictor for their resilience against extinction, as for other many Australian mammals, is their extensive use of torpor at all times of the year. Torpor minimizes their requirements for energy and foraging and permits reproduction even on limited resources (Geiser and Turbill 2009; Geiser and Körtner 2010; Masters and Dickman 2012; Hanna and Cardillo forthcoming 2014).

Torpor during the reproductive season has also been observed in kowaris (*Dasyuroides byrnei*), which are another small (110 g) dasyurid found in Australia's arid zone (Körtner and Geiser 2011). Similar to the mulgaras, reproduction also influenced thermoregulation in females in the field. Although pregnant female kowaries entered torpor, they maintained high normothermic T_bs throughout lactation (Körtner and Geiser 2011).

Torpor during reproduction in marsupials is, however, not only restricted to the carnivorous/insectivorous dasyuromorphs, but also occurs in the diprotodont possums. However, unlike 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*) undergo both short and multi-day torpor when non-reproductive with T_b falling as low as 2°C and bouts of torpor lasting for up to a week (Geiser and Ferguson 2001). Unlike other marsupials, which appear to mainly express torpor during pregnancy, torpor in these gliders was observed on six occasions in lactating females with pouch young in the reproductive season between September and November (austral spring) (Frey and Fleming 1984). Similarly, free-ranging female sugar gliders (*Petaurus breviceps*) displayed daily torpor (T_b 20–27°C) 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. In contrast, dominant males only used torpor occasionally before the time females were pregnant.

Torpor and reproduction in the Afrotheria

The Afrotherian superorder includes the Paenungulata (elephants, sea cows, and hyraxes) and the Afroinsectiphilia (including tenrecs, golden moles, sengis, and aardvarks) and, with the Xenarthra, are often considered as basal clades in eutherian phylogeny (Song et al. 2012). Torpor has been described for many of the tenrecs (Gould and Eisenberg 1966; Eisenberg and Gould 1967; Scholl 1974; Lovegrove and Génin 2008). Quantitative data are available on several species, including the lesser hedgehog tenrec (*Echinops telfairi*; Scholl 1974; Lovegrove and Génin 2008), the large-eared tenrec (*Geogale aurita*;

Stephenson and Racey 1993a), and the shrew-tenrecs (*Microgale dobsoni* and *Microgale talazaci*; Stephenson and Racey 1993b). These species typically have a torpor season over winter when T_b falls to 10–15°C (*E. telfairi*; Scholl 1974). They can show prolonged bouts of torpor lasting 2–4 days (*E. telfairi*) although more frequently bouts of torpor are shorter, and usually are of less than 24 h duration (*E. telfairi*; Lovegrove and Génin 2008).

One of the more perplexing aspects of tenrec biology is the large variability in gestation periods within each species (Stephenson 1993; Künzle et al. 2007; Lovegrove and Génin 2008). This phenomenon has been observed in many of the heterothermic species and may be linked to the opportunistic use of torpor during the reproductive season, as is the case for marsupials (see above). Non-reproductive large-eared tenrecs (*G. aurita*) have a minimum T_b of about 17°C and shrew-tenrecs (*M. dobsoni* and *M. talazaci*) one of about 25°C (Stephenson and Racey 1993a, 1993b). The T_b of pregnant and lactating shrew-tenrecs fell to only about 29°C and in the large-eared tenrec to about 22°C (Stephenson and Racey 1993a, 1993b). However, in two captive pregnant female *Hemicentetes semispinosus* and *Hemicentetes nigriceps* torpor was not observed (Stephenson and Racey 1994); nor was it observed in pregnant and lactating *E. telfairi* (Poppitt et al. 1994). Torpor was also not observed in wild pregnant *Setifer setosus*; although a long bout of inactivity was observed in a lactating female (Levesque et al. 2013). However, in several of these insectivores, use of torpor by pregnant females appears to lengthen the gestation period (Stephenson 1993; Stephenson and Racey 1993a, 1993b).

Extensive quantitative data are also available for the sengis (elephant shrews, Macroscelidea), which express daily torpor or short-term hibernation when non-reproductive (Mzilikazi and Lovegrove 2004; McKechnie and Mzilikazi 2011). These species exhibit seasonal torpor, but can adapt to changing conditions in spring, by returning to occasional torpor if weather conditions are poor. In free-ranging rock elephant shrews (*Elephantulus myurus*), daily torpor was routinely observed during winter, and although occurrence of torpor was low in spring, they could readily extend torpor to periods of up to 39 h if late cold fronts passed through the interior of southern Africa (Mzilikazi and Lovegrove 2004). Western rock elephant shrews (*Elephantulus rupestris*) also display torpor in summer, and females use torpor more frequently than do males (Oelkrug et al. 2012), although the interaction between torpor and reproduction is not clear.

Torpor and reproduction in the Xenarthra

The Xenarthrans include the anteaters, armadillos, and sloths. Torpor is used by the pichi (*Zaedyus pichiy*) (Superina and Boily 2007) although these temperate-zone armadillos appear to have distinct non-overlapping hibernation and reproductive seasons (Superina et al. 2009). However, there is one record of "hypothermia" in a pregnant three-toed sloth (*Bradypus griseus griseus*) (Morrison 1945).

Torpor and reproduction in the Eulipotyphla

The Eulipotyphla (shrews, moles, and hedgehogs) were until recently taxonomically associated with the Afroinsectiphilia in the order Insectivora; however, they have been removed to their own phylogenetic grouping (Song et al. 2012). Some of the highest basal and resting MRs have been recorded in the shrews, and in the past it was often assumed that they did not enter torpor at all. However, quantitative data on torpor are now available for several species (Nagel 1977; Genoud 1988; Symonds 1999). Torpor has been recorded in, for example, *Crocidura russula*, *Crocidura leucodon*, and *Crocidura suaveolens* and in *Suncus etruscus* (Nagel 1977; Fons et al. 1997), and it has been suggested that the reason for the limited quantitative data in the literature on shrews is the difficulty in maintaining the animals in captivity (Genoud 1988); also, of course, the size of transmitters limits field work on very small species.

Data on thermoregulation of Eulipotyphla during reproduction are even more scant. Torpor has been observed in the Malaysian moon-rat (*Echinosorex gymnurus*; Whittow et al. 1977) but does not appear to overlap with reproduction in this species. Hedgehogs readily use torpor both in captivity and in the wild with long bouts lasting up to 27 days in some species, although 2–4 days are more usual (Dmi'el and Schwartz 1984; Fowler and Racey 1990; Gillies et al. 1991; Król 1994; Hallam and Mzilikazi 2011). The South African hedgehog (*Atelerix frontalis*) has a hibernation season over the winter when T_b falls to as low as 1°C and while they can have bouts as long as 2–4 days, more frequently the bouts are shorter, and are less than 24 h duration (Hallam and Mzilikazi 2011). Not surprisingly, use of torpor is highest during the winter hibernation season in the European hedgehog (*Erinaceus europaeus*; Fowler and Racey 1990), but can be induced at any time of year by cool weather (Dmi'el and Schwartz 1984; Fowler and Racey 1990). During the spring/summer breeding season, shallow torpor can be induced in adult Eastern hedgehogs (*Erinaceus concolor*; Król 1994), and although these animals were sexually mature, they were not pregnant or lactating. Torpor can also be induced by low T_a during summer in long-eared hedgehogs (*Hemiechinus auritus*) (Dmi'el and Schwartz 1984). However, only one study has specifically examined the use of torpor by reproductive animals (Fowler 1988). Pregnant European hedgehogs demonstrated the same daily fluctuations in T_b as non-pregnant animals, and only during late pregnancy was there a defense of normothermic T_b by females (Fowler 1988).

Torpor and reproduction in bats

Information available on torpor in relation to reproduction in bats is more detailed than for all other groups. Indeed, it is well known that many small insectivorous bats typically exhibit multi-day torpor in winter, as well as also short bouts of torpor during the summer reproductive season. The considerable discussion over the advantages and disadvantages of torpor in reproductive bats focusses mainly on the delay of gestation in pregnant females, and the possible reduction in milk production caused by torpor. Reduced milk production may considerably slow postnatal growth (Eisentraut 1937; Racey and Swift 1981; Wilde et al. 1999) and therefore should be avoided. 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 (Ransome 1990; Thomas et al. 1990). The physiological advantage is that any transient shortfalls in energy are managed such that both mother and offspring remain viable, although reproductive activities are delayed (Willis et al. 2006). Despite the perceived disadvantages associated with the effect of torpor on embryonic development and the growth of pups, there are many examples of bats using torpor during pregnancy and lactation (Audet and Fenton 1988; Hamilton and Barclay 1994; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Willis et al. 2006; Dzal and Brigham 2013; Klug and Barclay 2013; Johnson and Lacki 2014), clearly demonstrating that this is a successful approach.

Many vespertilionid bats mate in late summer and early autumn when sperm production reaches a peak in males and when females are in oestrus (Racey and Tam 1974; Encarnação et al. 2004). After mating, sperm is stored in the oviduct throughout winter and hibernation (Racey 1973). Following the hibernation season, pregnancy starts immediately after fertilization. For females the demanding energetic costs of pregnancy and lactation continue to increase until weaning (Racey and Speakman 1987; Kurta et al. 1989; McLean and Speakman 2000). Consequently, food consumption increases for lactating females and in the transition from pregnancy to lactation this increase can be by as much as 45% in *Myotis lucifugus* (Anthony and Kunz 1977) and *Myotis velifer* (Kunz 1974). However, despite an apparent physiological advantage in maintaining normothermia during pregnancy and lactation, female *M. lucifugus* will use torpor during pregnancy and lactation, although the bouts are shallower and shorter than in non-reproductive individuals (Dzal and Brigham 2013).

It has long been known that torpor extends the gestation period of the mouse-eared bat (*M. myotis*; Eisentraut 1937). Pregnant females lowered T_b when held in a cold room and embryonic development was slowed in proportion to the degree of reduction in temperature. Conversely, embryonic development was accelerated when bats were kept in warm places (Eisentraut 1937). Detailed information on the phenomenon of slowed embryonic growth is also available for the pipistrelle (*Pipistrellus pipistrellus*; Racey 1973). When deprived of food and exposed to low T_a pipistrelles became torpid and their gestation period was extended by a period similar to that of the induced torpor (Racey 1973). In the insectivorous mouse-eared bat *M. blythii* availability of food can dictate the timing of parturition (Arlettaz et al. 2001), with deprivation delaying parturition. Food deprivation is known to promote opportunistic use of torpor in many bat species during the summer months (Racey 1973; Kurta 1990; Hosken 1997). Fetal development in bats in general appears to be inversely related to temperature and lower T_a generally delays embryonic development (Eisentraut 1937; Pearson et al. 1952; Racey 1969, 1973; Racey and Swift 1981; Banerjee et al. 2007). Embryonic delay in *P. pipistrellus* can even take place after fetuses have reached a palpable size, although a successful reproductive outcome was maintained (Racey 1973). Pearson et al. (1952) estimated that the duration of gestation in the lump-nosed bat, *Corynorhinus* (=*Plecotus*) *rafinesquei*, varied considerably between roost sites and over several years, with estimated durations of between 56 and 100 days. The variability was attributed to selection of T_a and roosts, and it was noted that there did not seem to be much delay in subsequent development once the embryo was fully implanted (Pearson et al. 1952). Torpor in pregnant and lactating *C. rafinesquei* was observed and quantified by Johnson and Lacki (2014) who found that the duration of bouts and the depth of torpor were reduced in reproductive females, although it still occurred.

Similar to the verspertilionids, the miniopterid bats 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 spring (Dwyer 1963; Wimsatt 1969). Delayed implantation of the embryo is associated with low concentrations of progesterone in the plasma but unchanged concentrations of estradiol in female *Miniopterus schreibersii* (Crichton et al. 1989; Bernard et al. 1991a). During this time of year females may be active, and also readily use torpor (Crichton et al. 1989; Bernard et al. 1991a).

Male *Miniopterus*, too, show seasonal changes in reproduction, with spermatogenesis and fertility that are not impaired by hibernation; this pattern also is seen in other hibernating bats (Pearson et al. 1952; Bernard et al. 1991b). Similar to *M. schreibersii*, males of vespertilionid Daubentons's bats (*Myotis daubentonii*) also use torpor during reproductive periods in summer, although to a lesser extent than at other times of year (Becker et al. 2013). The cycle of reproductive activity, including spermatogenesis, does not affect torpor in male *M. daubentonii* nor in male Bechstein's bats (*Myotis bechsteinii*) (Dietz and Hörig 2011).

Hemprich's long-eared bats (*Otonycteris hemprichii*) are desert-dwelling bats. Females bear two offspring per litter in small maternal colonies of up to 10 individuals, and in contrast to many other vespertilionids, they take care of their pups alone (Daniel et al. 2010). In these bats, torpor 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 (Daniel et al. 2010). 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; Grinevitch et al. 1995; Rintoul and Brigham forthcoming 2014). Deep torpor in the big brown bat (i.e., a drop in skin temperature by more than 10°C) was regularly observed during pregnancy with more than 50% of females demonstrating torpor, but it was rare during lactation (about 5% of females; Grinevitch et al. 1995). This study contrasted with the observations by Hamilton and Barclay (1994) who found no difference in the incidence of torpor between pregnant and lactating females. Similar to observations for Daubenton's bat, male big brown bats also regularly use torpor throughout the year, but show a seasonal cycle in its use (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. 1995).

Some of the differences in use of torpor among many small insectivorous bats have been attributed to interspecific differences in roost selections. Obviously, roosting alone and in exposed roosts incurs much higher costs for maintenance of homeothermy compared with roosting in maternity colonies in well-insulated roosts (Willis and Brigham 2007). This could explain why pregnant and lactating temperate bats roosting in rock crevices or in foliage, and those that roost alone will reduce T_b more frequently than, for example, reproducing female Bechstein's bats and Daubenton's bats that communally roost in tree cavities (Lausen and Barclay 2003; Dietz and Kalko 2006; Solick and Barclay 2007; Willis et al. 2006). It has been observed that *E. fuscus*, which usually roost in rocky areas, usually become torpid on at least 40% of "bat days" (defined as starting at morning twilight [civil], or when the bat returned to the roost for the last time, and ending when the bat emerged to forage that night), independently from their reproductive condition (Lausen and Barclay 2003).

The importance of roost selection or thermal condition for use of torpor by reproductive bats is supported by laboratory work conducted under the same thermal conditions. Captive male and pregnant and lactating female long-eared bats (*Nyctophilus geoffroyi* and *Nyctophilus gouldi*) studied under identical thermal conditions during the reproductive season, almost all entered torpor and showed indistinguishable thermal physiology. This suggests that the observed reluctance by reproductive females to enter torpor in the field is indeed predominantly because of ecological rather than physiological differences, which also reflects the fact that females roost gregariously whereas male bats typically roost solitarily (Turbill and Geiser 2006).

The use of torpor by subtropical insectivorous bats is well-known (Geiser and Stawski 2011). In long-eared bats (*Nyctophilus bifax*) even during the reproductive season in spring, non-reproductive males continue to use torpor regularly (94% of days), suggesting that overall the use of torpor is beneficial throughout the year even in the subtropics (Stawski 2010). However, non-reproductive males used torpor more frequently than did pregnant females during spring, similarly to male big brown bats (*E. fuscus*) and male Daubenton's bats (*M. daubentonii*) (Grinevitch et al. 1995; Dietz and Kalko 2006;

Stawski 2010). For the subtropical *N. bifax*, the costs incurred by pregnant bats employing torpor usually appear to outweigh the energetic benefits gained by torpor under the warm subtropical conditions. It may be, however, that occasionally pregnant females were energetically constrained and therefore needed to enter torpor for short periods (Stawski 2010).

Although knowledge about the use of torpor by small insectivorous bats is substantial, much less is known about it in the ''fruit bats'' (Pteropodidae) (Geiser and Stawski 2011). The nectarivorous blossom-bat (*Syconycteris australis*), one of the better-known pteropodid species with regard to heterothermy, displays daily torpor in captivity (Coburn and Geiser 1998). Torpor in non-reproductive *S. australis* is used by all individuals and lasts for up to 12 h, MR falls to about 15% that of resting animals and T_b drops to a minimum of about 18°C. Although for this species torpor has been observed in one of three pregnant bats, the bout of torpor of this female was shorter and the reduction of the MR was less pronounced than in most non-reproductive individuals (Geiser et al. 2001). In contrast, torpor has not been observed in other reproductive female nectarivorous phyllostomid bats (Voigt 2003) nor in another frugivorous megachiropteran bat (Egyptian fruit bat; *Rousettus aegyptiacus*) (Korine et al. 2004). However, for pregnant *R. aegyptiacus* a metabolic depression of 19% of resting MRs of non-pregnant females was observed (Korine et al. 2004). The authors of this study concluded that the decrease in MR of pregnant females during the resting phase may enable them to spend more time on other activities such as foraging, or potentially to allocate more energy to fat storage or milk production (Korine et al. 2004).

Torpor and reproduction in the Carnivora

Torpor is rarely observed in the carnivores, and appears to be largely restricted to bears (Ursidae) and some badgers (Mustelidae). Many carnivores, such as dogs (Canidae, including the raccoon dog, *Nyctereutes procyonoides*) and cats (Felidae) appear to be largely homeothermic during the winter, although reproduction is seasonal and shallow torpor has been observed in aardwolfs (*Proteles cristata*; Hyaenidae) (Anderson 2004; Szafrańska et al. 2013). Hibernating black bears (*Ursus americanus*) and brown bears (*Ursus arctos*) show prolonged periods of dormancy in winter and, interestingly, do give birth during their hibernation season. Although the MR of hibernating bears is as low as that in many other hibernators (Tøien et al. 2011), all animals remain aware and capable of moving throughout hibernation (Fedorov et al. 2009; Friebe et al. 2013), albeit at much higher T_b than in some other heterothermic mammals that are capable of movement during torpor at T_b*s* as low as 14.8°C (Rojas et al. 2012). Bears do not eat, drink, defecate, or urinate during the 3- to 6-month hibernation period, and unlike many small hibernators, which often allow their T_b to fall near 0°C (Geiser 2004), the core T_b of bears decreases to only 30–36°C (Fedorov et al. 2009; Tøien et al. 2011). However, because MR in hibernating black bears is reduced by approximately 75% (Tøien et al. 2011), considerable savings of energy are made over winter. Some, but not all, black bears maintained a higher T_b during pregnancy in comparison to non-pregnant bears (Tøien et al. 2011; Shimozuru et al. 2013). Pregnancy and birth are only weakly associated with activity patterns in the brown bear (Friebe et al. 2013), and circulating sex steroids have been found to be independent of torpor in black bears and polar bears (Palmer et al. 1988; Tsubota et al. 1999).

Badgers have a torpor season that appears independent of the reproductive season for males, although delayed embryonic implantation occurs in females, with post-implantation gestation occurring during the height of winter conditions in *Taxidea taxus* (Harlow 1981) and *Meles meles* (Fowler and Racey 1988). The European badger (*M. 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°C and 34.7°C during the remainder of the gestation period (Fowler and Racey 1988). In males, increased concentrations of circulating testosterone are seasonal, and are correlated with behavioral activity (Buesching et al. 2009). Different phenotypes of testosterone patterns have been observed, and high summer concentrations correlate with parasite load and with over-wintering demise (Buesching et al. 2009). Testosterone concentrations begin to rise in winter when hibernation is still common (Fowler and Racey 1988; Buesching et al. 2009). Similar patterns of heterothermy have been found in the American badger (*T. taxus*) (Harlow 1981); although T_b*s* have not been measured for pregnant females, a study of food restriction aimed at emulating the period of food restriction during pregnancy that is part of the annual cycle found that pregnancy and the subsequent development of the cub were not impaired by restriction of the mother's food (Harlow et al. 1985).

Torpor and reproduction in primates

Several species of primates belonging to the Cheirogaleidae (Malagasy lemurs) from four of the five genera (Dausmann 2014) and in the South African lesser bushbaby (*Galago moholi*) (Nowack et al. 2010) express torpor. Some of the dwarf lemurs hibernate with a distinct hibernation season, separated temporally from the reproductive season (Dausmann 2014). This phenomenon is best described for the fat-tailed dwarf lemur (*Cheirogaleus medius*), which hibernates over the Madagascan winter for up to 7 months in tree hollows (Dausmann et al. 2004). The dichotomous pattern is repeated for several members of the family and if food is scarce, or the habitat is poor, animals will choose not to reproduce, and have not been observed to use torpor during the reproductive season (Lahann and Dausmann 2011).

In contrast, the mouse-lemurs (*Microcebus* spp.) are very flexible in their use of heterothermy (Ortmann et al. 1997; Schmid et al. 2000; Kobbe and Dausmann 2009; Kobbe et al. 2011; Canale et al. 2012). Some species appear to use only daily torpor occasionally (e.g., *Microcebus berthae*; Schmid et al. 2000), whereas others can show an extended regular pattern of torpor, although this is dependent on accumulating enough fat during the active season (*M. griseorufus*) (Kobbe and Dausmann 2009; *M. murinus*; Ortmann et al. 1997). For the most part torpor 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 restriction of food in the laboratory induced torpor both in pregnant and lactating females (Canale et al. 2012). Although restriction of food provoked torpor in late gestation and also during lactation, females remained normothermic until body mass was significantly reduced. Restriction of food for lactating females also caused a reduced growth rate in the pups, although it was not clear if this was from the reduced nutrient uptake or from the use of torpor because of temperature effects (Canale et al. 2012). Although the experiment may seem divorced from the animals' experiences in nature, the unpredictable environment and pronounced changes in availability of water in their natural environment may require torpor during pregnancy and lactation in wild mouse-lemurs (Canale et al. 2012; Dausmann 2014).

In contrast to the Madagascan lemurs, the African lesser bushbaby, *G. moholi*, uses torpor only rarely, and never as a routine seasonal response. Indeed, one of the first studies to comprehensively examine thermoregulation in this species found no evidence of torpor (Mzilikazi et al. 2006), although a later study found that only a small proportion of the population ever enters torpor and usually only on single occasions (Nowack et al. 2010). This species only uses torpor as an emergency mechanism for saving energy, with another study showing that regular use of torpor was confined to animals in poorer condition and sometimes resulted in animals failing to arouse from torpor (Nowack et al. 2013). This suggests that torpor and reproduction in bushbabies is likely to be mutually exclusive.

Torpor and reproduction in ground squirrels (Sciuridae) and hamsters (Cricetidae), the "dichotomous" rodents in which torpor and reproduction do not temporally overlap

Typically hibernation and torpor have been studied during the winter when T_a is low and when many animals are non-reproductive and have low levels of reproductive hormones (Barnes 1996; Mzilikazi and Lovegrove 2002). These studies were to a large extent conducted on two groups of rodents, the ground squirrels and hamsters, many of which are naturally found in cold, strongly seasonal climates. A striking characteristic of these species is that in both sexes the gonads regress before the beginning of the hibernation season (Hoffman 1964; Wimsatt 1969; Barnes et al. 1986). Indeed for some species the complete regression of the gonads is necessary for hibernation to begin (Figala et al. 1973; Darrow et al. 1988).

It is also well documented that reproductive hormones, in particular testosterone in males, inhibit torpor in several species of hamster (Goldman et al. 1986) and that male ground squirrels with scrotal testes refuse to hibernate (Landau and Dawe 1960). High circulating concentrations of testosterone are correlated with enhanced breeding capabilities on one hand, but are also inversely correlated with hibernation in yellow pine chipmunks, *Tamias amoenus* (Place et al. 2002), Uinta ground squirrels, *Spermophilus* (now *Urocitellus*) *armatus* (Ellis et al. 1983), golden-mantled ground squirrels, *Spermophilus* (*Urocitellus*) *lateralis* (Barnes 1986), European ground squirrels *Spermophilus citellus* (Strauss et al. 2008), and the Mongolian hamster, *Allocricetulus curtatus* (Feoktistova et al. 2013). Interactions between circulating testosterone and hibernation are more complex in the woodchuck (*Marmota monax*), although this may be related to their reluctance to hibernate in captivity and disturbances to the animals during experimental regimes

(Concannon et al. 1989). Paradoxically, in arctic ground squirrels (*S. parryii*), androgens do not decrease in response to onset of winter, and this is believed to promote anabolism of muscle in preparation for catabolism during the long hibernation season (Boonstra et al. 2011). Reproductive capability, however, is not maintained over winter (Buck and Barnes 1999; Boonstra et al. 2011).

Administration of testosterone inhibits torpor in male hamsters and ground-squirrels (Hall and Goldman 1980; Goldman et al. 1986; Lee et al. 1990; Ouarour et al. 1991), whereas castration after the final arousal from the winter hibernation season in spring reinstates hibernation in golden-mantled ground-squirrels, *S. lateralis* (Dark et al. 1996). Castrated males later not only remain normothermic (i.e., do not enter torpor), but their circadian thermoregulatory response can be phase-shifted by administration of physiological doses of testosterone (Darrow et al. 1988). In many of these species, the inhibition of torpor by testosterone is impervious to the effects of low T_a and animals remain normothermic in all but the most extreme cold (Hall and Goldman 1980; Lee et al. 1990; Ouarour et al. 1991). The "resistance" of reproductively intact animals to thermal challenges examined to date is regulated by photoperiod, in which short (winter) photoperiods induce gonadal involution and promote heterothermy in all sciurid and cricetid species that have been studied, largely independent of T_a (Steinlechner et al. 1986; Darrow et al. 1987; Geiser et al. 2013). Testosterone-administered castrates also refuse to hibernate, which underscores the strict separation between reproduction and hibernation in the members this group of rodents that have so far been investigated (Hall and Goldman 1980, Goldman et al. 1986; Lee et al. 1990, Darrow et al. 1988, Ouarour et al. 1991; Ruby et al. 1993).

Similar patterns for the discontinuity between reproductive activity and hibernation are observed for females in sciurid and cricetid rodents. Data, however, are scant. Female Turkish (*Mesocricetus brandti*) hamsters do not show oogenic activity if they hibernate and T_a does not affect this response (Jagiello et al. 1992). Moreover, uterine receptors for progesterone and oestrogen are absent in hibernating Turkish hamsters (Okulicz et al. 1988). Follicular development is also absent in hibernating European ground squirrels (*S. citellus*), and concentrations of circulating oestradiol and progesterone parallel these follicular changes, with barely detectable values circulating during hibernation (Millesi et al. 2008). Administration of prolactin inhibits torpor in non-breeding female hamsters (Ruby et al. 1993). In contrast, oestradiol inhibits torpor, although only partially so, and progesterone has no effect on other variables of torpor in hamsters (Hall and Goldman 1980; Darrow et al. 1988). Thus, in these female rodents the effects of steroid sex hormones on thermal physiology are mixed, with administration of oestradiol or progesterone affecting thermoregulatory activities in some species, but not in others (Darrow et al. 1988; Lee et al. 1990). Nevertheless, there are no data on an overlap between torpor and reproduction in females, unlike in the other rodents addressed below.

Torpor and reproduction in other "non-dichotomous" rodents

Torpor is, of course, not restricted to sciurids and cricetids and has also been observed in several other families of rodents. However, the relationship between hibernation and reproductive seasons is less straightforward than for ground squirrels and hamsters. Many species of dormice (Gliridae) use torpor (Wyss 1932; Montoya et al. 1979; Webb and Skinner 1996; Juškaitis 2005; Kart Gür et al. 2014). The use of torpor often is closely linked to the availability of food in these species, with complex relationships observed between torpor, seasonal availability of food, storage of body fat, and reproduction (Bieber et al. 2014). The edible dormouse (*Glis glis*) is locally called the "Siebenschläfer" or "seven-sleeper" in German-speaking parts of Europe because of its disappearance for about 7 months of the year. However, although its hibernation cycle is closely tied to the seasonal change, successful reproduction is associated with seed production by beech trees (mast years), and females may not reproduce every year (Lebl et al. 2011). Torpor in captive non-reproductive females occurs in summer (Bieber and Ruf 2009) and body mass is not directly associated with successful reproduction. The secretive nature of the Siebenschläfer makes it unclear whether the females use torpor while in reproductive condition in the wild, although good physical condition does not preclude their use of summer torpor (Bieber and Ruf 2009; Lebl et al. 2011).

Scarcity of food not cold also promotes torpor in any season in garden dormice, *Eliomys quercinus* (Giroud et al. 2012) and it appears to be driven to some extent by low-protein diets (Ambid and Agid 1972; Montanya et al. 1979). Torpor regularly occurs in summer in African woodland dormice (*Graphiurus murinus*; Webb and Skinner 1996). 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. However, in wild common dormice, *Muscardinus avellanarius*, which hibernate for prolonged periods in winter (Pretzlaff and Dausmann 2012), torpor was also observed in reproductive pairs of males and females, pregnant females, females with litters, and in nestlings during the breeding season (Juškaitis 2005). Similar to some bats, bouts of torpor for pregnant females were not as deep as those of females at other times of year (Juškaitis 2005).

Pouched mice, *Saccostomus campestris* (Muridae) use torpor opportunistically and do not appear to have any seasonal preference for the use of torpor, which is believed to be a response to the unpredictable environments in their habitats and therefore may be used during reproduction (Mzilikazi and Lovegrove 2002). However, sexually mature males are generally resistant to using torpor and this is related to elevated concentrations of circulating testosterone (Mzilikazi and Lovegrove 2002).

Discussion

The occurrence of torpor during reproduction in birds and mammals suggests that it is convergent in the two endothermic classes. However, within the mammals, information on torpor during reproduction is more confined to the more ancestral taxa (Monotremata, Marsupialia, Afrotheria, Eulipotyphla, and Chiroptera). This could be interpreted as evidence for a plesiomorphic evolution of torpor in reproductive individuals and in non-reproductive individuals, or as lack of information on torpor and reproduction in other mammalian groups. Lovegrove (2012) argued for a monophyletic evolution of heterothermic responses in mammals, and placed the high-latitude Sciuridae and Cricetidae in the most derived group of adaptive heterothermy, rather than expressing plesiomorphic characteristics of many of the other rodents. This interpretation is not fully supported, however, by developmental data in mammals and also birds, suggesting that an independent evolution of torpor in the two classes or even between monotreme, marsupial, or eutherian mammals currently cannot be excluded (Geiser and Martin 2013). Indeed, information about thermoregulatory capacities of species from several orders is lacking, and general conclusions cannot be drawn without this information.

Although many of the rodents investigated to date appear to be strictly homeothermic during the reproductive season, many of these data are drawn from the two heterothermically predictable groups of rodents, the sciurids and cricetids. New information from the temperate zones of the world and from more long-lived rodents in other latitudes suggest that the dichotomous response seen in ground squirrels and hamsters may not reflect the general response of all rodents, and definitely not for all endotherms. There are two possible energetic reasons for the differences seen in the separation of reproduction from heterothermic metabolic responses: maternal investment and unpredictable environments.

Most monotremes and marsupials have short gestation periods and the mass of an echidna egg and that of single neonates or neonate litters of marsupials is less than 1% of the mothers' masses (Renfree and Tyndale-Biscoe 1987; Geiser and Seymour 1989). Energy expenditure/day for gestation in both groups therefore should be relatively low, and this has been verified for some marsupials (Thompson and Nicoll 1986; Nicoll and Thompson 1987). Similarly, energetic costs/day during lactation in marsupials also tend to be relatively low (Thompson and Nicoll 1986; Nicoll and Thompson 1987), because of their slow growth, but of course it extends over a long period. In contrast, small rodents typically have a relatively short gestation period, relatively heavy neonate litters (10–65% of maternal weight) (Eisenberg 1981) and relatively rapid development after birth; both gestation and lactation are therefore energetically expensive (Nicoll and Thompson 1987). Bats appear to be similar to rodents in having relatively large, but usually single, neonates (13–40% of maternal weight) (Ransome 1990). However, growth of fetal and young bats, as in marsupials and monotremes, is slow and energy expenditure/day at least during gestation is much lower than in small rodents (Racey and Speakman 1987; Nicoll and Thompson 1987). In contrast, carnivores have small altricial young with fast neonatal growth rates (Harlow et al. 1985), but heterothermic carnivores have vastly different energetic demands from most other heterotherms, simply because of their larger size.

Similar arguments as for mammals may be applied to birds. Both 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 relatively small. It therefore appears 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. This may slow the rate of development of the young, but may not adversely affect the chance of survival in offspring because a small delay in growth within the long period of development may not have a strong negative impact.

Many of the species that are heterothermic during reproduction also are animals that are found in unpredictable environments, where availability of food can be cut short by abrupt changes in weather. Although for some species adverse weather conditions or food shortages apparently need to be severe for induction of heterothermy (Canale et al. 2012; Nowack et al. 2013), for others heterothermy during pregnancy appears to be part of the yearly cycle (Crichton et al. 1989; Bernard et al. 1991a). For bears and badgers, heterothermy during pregnancy is part of the yearly cycle in a predictable environment (Harlow et al. 1985; Fowler and Racey 1988; Fedorov et al. 2009; Friebe et al. 2013), but, as pointed out above, size *per se* plays an important role in this group. Reproduction in winter is also found for some marsupials and bats, in which reproductive effort coincides with winter seasons, and torpor is employed. For these mammals, the small extension of pregnancy or lactation seems to be an important strategy that optimizes reproductive outcomes later in spring and summer.

Although reproductive strategies may provide a possible explanation for the differences between thermoregulatory patterns during reproduction in different mammalian groups and birds, other influences also have to be considered. It is evident that many species in which torpor has been observed during the reproductive period are fully or partially insectivorous, nectarivorous, or carnivorous. Abundance of most insects (and other arthropods) and nectar strongly fluctuate with season and vertebrate prey is often difficult to obtain. Occurrence of torpor during reproduction therefore may be linked to the food consumed by the organism. Species that have access to relatively predictable food supplies and that reproduce during a period of high primary productivity may be able to adopt strict homeothermy during reproduction, 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.

Our review has consolidated the knowledge and understanding of the use of heterothermy during reproduction in many mammals and some birds. The restriction of the use of heterothermy to a non-reproductive part of an animal's life history may be a derived characteristic, and may be confined to just a few groups. Certainly, 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.

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