

Torpor in reproductive endotherms

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Reproduction in endotherms is an energetically demanding process. Torpor on the other hand is a state of reduced energy expenditure and it is often assumed that the two physiological states are incompatible. This view is supported by observations on heterothermic rodents. In many rodents the reproductive period during which metabolic rate may increase substantially is followed by a period of heterothermy, but there is no temporal overlap (Kenagy 1989). The gonads of these rodents regress before the beginning of the hibernation season (Hoffman 1964; Wimsatt 1969; Barnes *et al.* 1986). It is also well documented that reproductive hormones, in particular testosterone, inhibit torpor in several hamster species (Goldman *et al.* 1986) and that ground squirrels with scrotal testes do not hibernate (Landau & Dawe 1960).

While 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 pregnancy and lactation in several mammals and during incubation and brooding in birds (Calder & Booser 1973; Racey 1973; Morton 1978; Audet & Fenton 1988; Stephenson & Racey 1993a, b; Kissner & Brigham 1993; Geiser & Masters 1994). In the present overview, I will summarise the data from various species that use torpor during the reproductive season and attempt to explain how and why these species differ from those which appear to be strictly homeothermic when reproducing.

The assumption is often made that if reproductive individuals enter torpor, it must be restricted to short bouts and high body temperatures (T_b) because a small and brief reduction of T_b may not adversely affect the development of the embryo or growing young. However, torpor during the reproductive season has been observed in both daily heterotherms (species which show daily torpor) and hibernators (species which show prolonged torpor). While torpor during the reproductive season is usually less pronounced than during the non-reproductive season this is not always the case. Observations on the various species are briefly described below and summarised in Table 1.

Broad-tailed hummingbirds (*Apodiformes*) enter nocturnal torpor while incubating their eggs (Calder & Booser 1973). The temperature of a synthetic incubated egg fell after midnight to a minimum of 6.5°C, while the air temperature fell to about 0°C, suggesting regulation of T_b at around 6.5°C. The eggs were rewarmed after several hours at low temperature. A T_b of 6.5°C is extremely low for hummingbirds (Dawson & Hudson 1970; Reinertsen 1983) which suggests that torpor during incubation of this species is similar to that in non-reproductive birds.

Poorwills (*Caprimulgiformes*) are the only known avian hibernator. When non-reproductive they show torpor bouts of several days and their T_b falls to about 5°C (Brigham 1992; French 1993). When reproductive, few individuals became torpid. Torpor was

observed in only 3 of 203 bird-nights in brooding or incubating birds (Kissner & Brigham 1993). Skin temperature in these poorwills fell as low as 11.5°C and it appears that they remained torpid for several days. Moreover, torpor was observed in a brooding male and a chick and both were able to arouse (Kissner & Brigham 1993).

Echidnas (*Monotremata*) are known to hibernate when non-reproductive. Animals in cold climates show a prolonged hibernation season with torpor bouts of up to 30 days and T_b may fall as low as 4°C (Grigg *et al.* 1992). Observations on torpor in reproductive echidnas are restricted to a single captive individual during the breeding season. This individual had a T_b of 21°C two days before she laid her egg, and was again lethargic briefly after oviposition (Geiser & Seymour 1989). Observations on free-living individuals, however, suggest that the hibernation season is terminated when animals begin reproduction (Beard *et al.* 1992).

Fat-tailed dunnarts (*Marsupialia*) enter daily torpor throughout the year when food is withheld. Torpor in non-reproductive individuals lasts for about 6 hours and T_b falls to about 14°C (Geiser & Baudinette 1987). A lactating female with pouch young was found torpid in the field. These young were raised successfully (Morton 1978). Males responded to long photoperiod by increasing their testes size, however, torpor patterns were similar to those in short photoperiod when testes were small (Holloway 1992).

Mulgaras (*Marsupialia*) use daily torpor with minimum body temperatures around 14°C. Reproductively active males and pregnant females (76% of observations) frequently entered spontaneous (food and water available) torpor in the laboratory. The gestation period in these 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 (Geiser & Masters 1994). It is possible that females try to build up fat stores for the more energetically demanding period of lactation (Thompson & Nicoll 1986) by becoming torpid and saving energy during their daily period of inactivity. Females ceased entering torpor 4-5 days before young were born and were not observed to use torpor during pregnancy (Geiser & Masters 1994). In this species, the use of torpor appeared to increase during pregnancy in comparison to non-reproductive individuals.

Feathertail giders (*Marsupialia*) undergo both daily and prolonged torpor when non-reproductive with T_b falling to as low as 2°C and torpor bouts lasting for up to a week (Jones & Geiser 1992). During the reproductive season daily torpor was observed on six occasions in females with pouch young between September and November (spring)(Frey & Fleming 1984).

Hedgehog-tenrecs (*Insectivora*) also show prolonged torpor, but with T_b around 10-15°C (Scholl 1974). Non-reproductive large-eared tenrecs have T_b of about 17°C and shrew-tenrecs around 25°C (Stephenson & Racey 1993a, b). 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 & Racey 1993a, b). In several of these insectivores, torpor in pregnant females appears to slow development of young (Stephenson 1993).

It is well known that insectivorous bats (*Microchiroptera*) exhibit prolonged torpor in winter and daily torpor during summer. Information available on torpor in relation to reproduction in bats is more detailed than for other groups. It has been known for many years that bats of the genus *Miniopterus* mate in autumn or winter. Females enter hibernation in a pregnant condition, embryonic development is retarded, and births do not occur until the following summer (Dwyer 1963; Wimsatt 1969). In the big brown bat,

torpor has been observed during both pregnancy and lactation (Audet & Fenton 1988; Grunevitch *et al.* 1995). Deep torpor in the big brown bat (i.e. a skin temperature drop by more than 10°C) was regularly observed during pregnancy (about 50% of bats), but rare during lactation (about 5% of bats). It is also known that torpor extends the gestation period of the mouse-eared bat (Eisenraut 1937) and detailed information on this phenomenon is available on the pipistrelle (Racey 1973). When deprived of food and exposed to cold temperatures pipistrelles became torpid and their gestation period was extended by a period similar to that of induced torpor (Racey 1973). Exposure to low temperatures alone did not induce torpor in pregnant pipistrelles (Racey 1973).

The common blossom-bat (Megachiroptera) displays daily torpor in captivity (Geiser *et al.* 1996). Torpor lasts for up to 12 hours, metabolic rate (MR) falls to about 15% of that of resting animals and T_b drops to a minimum of about 18°C. Although torpor has been observed in one of three pregnant bats, the torpor bout was shorter and the reduction of the MR was less pronounced than in most non-reproductive bats.

Table 1. Summary of observations on torpor in reproductive endotherms

GROUP/Species	Mass (g)	Diet	Observation	Source
BIRDS				
<i>Setophorus platycercus</i>	3.5	Nectar / Insects	Deep torpor in incubating birds	Caldler & Boater 1973
Broad-tailed hummingbird				
<i>Phalaenoptilus nuttallii</i>	48	Insects	Inrequent torpor during brooding and incubation	Kissner & Brigham 1993 Caada & Brigham 1994
Poorwill				
MAMMALS				
MONOTREMES				
<i>Tachylotus aculeatus</i>	4500	Insects	$T_b = 21^\circ\text{C}$ in pregnant female	Geiser & Seymour 1989
Echidna				
MARSUPIALS				
<i>Smimulopsis crassicaudata</i>	17	Insects	Torpor in free-living lactating females; torpor while testes large	Morton 1978
Fat-tailed dunnart				
<i>Dasyurus cristicauda</i>	100	Insects	Frequent torpor in pregnant females and reproductive males	Holloway 1992 Geiser & Mauters 1994
Mulgara				
<i>Acrobates pygmaeus</i>	12	Insects / Nectar	Torpor in free-living lactating gliders	Frey & Fleming 1984
Feastertail glider				
PLACENTALS				
<i>Microgale dobsoni</i>	45	Insects	Shallow torpor in reproductive females	Stephenson & Racey 1993b
Shrew-tenrec				
<i>Microgale talazaci</i>	45	Insects	Shallow torpor in reproductive females	Stephenson & Racey 1993b
Shrew-tenrec				
<i>Geogale aurila</i>	6.7	Insects	$T_b = 22^\circ\text{C}$ in pregnant & lactating females	Stephenson & Racey 1993a
Large-eared tenrec				
<i>Scotter setosus</i>	225	Insects	Gestation length variance likely due to torpor	Stephenson 1993
Greater hedgehog tenrec				
<i>Echinops telfairi</i>	176	Insects	Gestation length variance likely due to torpor	Stephenson 1993
Lesser hedgehog tenrec				
<i>Myotis myotis</i>	25	Insects	Pregnant bats torpid for several days	Eisenraut 1937
Mouse-eared bat				
<i>Pipistrellus pipistrellus</i>	6	Insects	Torpor during pregnancy slows fetal development	Racey 1973
Pipistrelle				
<i>Eptesicus fuscus</i>	19	Insects	Torpor during pregnancy & lactation in both sexes; deep torpor rare during lactation	Audet & Fenton 1988 Grunevitch <i>et al.</i> 1995
Big brown bat				
<i>Miniopterus schreibersii</i>	15	Insects	Retarded embryo growth during hibernation	Dwyer 1963
Common bent-wing bat				
<i>Miniopterus australis</i>	7	Insects	Retarded embryo growth during hibernation	Dwyer 1963 Wimsatt 1969
Little bent-wing bat				
<i>Syconcretus australis</i>	18	Nectar / Pollen	80% reduction of MR in pregnant, torpid bat	Geiser, Köster & Law unpublished observations
Common blossom-bat				

Thus, torpor in reproductive individuals has been observed in two bird species and in members of all three mammalian subclasses. Whether torpor is daily or prolonged it seems to occur during reproduction only in species that show opportunistic torpor rather than in species that show a strong seasonal cycle in thermal physiology. However, it is obvious that observations on torpor during reproduction are far less common than observations on torpor in non-reproductive animals. This is most likely due to a reduced proclivity towards torpor; however, it is also possible that reproductive individuals are often spared from cold exposure and food withdrawal in the laboratory to ensure survival of the young.

The occurrence of torpor during reproduction in birds and mammals suggests that it is a convergent development. However, within the mammals, information on torpor during reproduction is clearly restricted to the more ancestral taxa (monotremes, marsupials, insectivores, bats). This could be interpreted as evidence for a monophyletic development of torpor in reproductive individuals, or as lack of information on torpor and reproduction in other mammalian groups. It is possible that as the phenomenon receives more attention, members of other mammals (eg. rodents) may also show torpor during reproduction.

Since the rodents investigated so far are strictly homeothermic during the reproductive season, the question arises how they differ from species that do show torpor when they reproduce. 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 0.3% of the mothers' masses (Tyndale-Biscoe 1973; Geiser & Seymour 1989). Energy expenditure for gestation in both groups therefore should be relatively low as has been verified for some marsupials (Thompson & Nicoll 1986; Nicoll & Thompson 1987). Similarly, energetic costs during lactation in marsupials also tend to be relatively low (Thompson & Nicoll 1986; Nicoll & Thompson 1987), because of their slow growth. In contrast, small rodents have a relatively short gestation period, relatively heavy neonate litters (10-65% of maternal weight; Eisenberg 1981) and a relatively fast development after birth and thus both gestation and lactation are energetically expensive (Nicoll & Thompson 1987). Bats, in contrast to rodents, usually have single neonates, but appear similar to rodents in having relatively large neonates (13-40% of maternal weight; Ransome 1990). However, growth of foetal and young bats is slow as in marsupials and monotremes and energy expenditure, at least during gestation, is much lower than in small rodents (Racey & Speakman 1987; Nicoll & Thompson 1987). Similar arguments as for mammals may be applied for the birds. Both Caprimulgiformes and hummingbirds have relatively small clutch sizes and relatively long rearing periods and the additional energy expenditure 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 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.

While reproductive strategies may provide a possible explanation for the differences between thermoregulatory patterns during reproduction in different mammalian groups and birds, other influences have to be considered. It is evident that all species in which torpor has been observed during the reproductive period are insectivorous or nectarivorous. Abundance of most insects (and other arthropods) and nectar strongly fluctuate with season.

Occurrence of torpor during reproduction therefore may be linked to the food consumed by the animals. Species that have access to relatively predictable food supplies during the period of reproduction should be able to adopt strict homeothermy during reproduction, whereas species with relatively unpredictable food supplies may be better off using torpor at a cost of only a small extension of the reproductive period.

The present overview shows that while there is some information available on torpor in reproductive endotherms it is in many cases based on observations from only a few individuals and often without quantitative data. It is clear that future studies require a more systematic approach, which includes endocrinological analyses, in an effort to understand this most interesting phenomenon.

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