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 regressed 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 & Dave 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 1993; a; Kiessner & 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, they must be restricted to short bouts and high body temperatures (Tb) because a small and brief reduction of Tb 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 various species are briefly described below and summarised in Table 1.

Broad-tailed hummingbirds (Aplodinotes) 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 Tb at around 6.5°C. The eggs were rewarmed after several hours at low temperature. A Tb 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 Tb falls to about 5°C (Brigham 1992; French 1993). When reproductive, few individuals become torpid. Torpor was observed in only 3 of 203 birds in brooding or incubating birds (Kiessner & 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 (Kiessner & Brigham 1993).

Echidnas (Tachyglossidae) 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 Tb may fall as low as 4°C (Grigg et al. 1992). Observations on echidnas in reproductive conditions are restricted to a single captive individual during the breeding season. This individual had a Tb of 21°C two days before she laid her egg, and was again lethargic briefly after oviposition (Geiser & Seymor 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 Tb falls to about 14°C (Geiser & Baednait 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 33% 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 & Nicol 1986) by becoming torpid and saving energy during their daily periods of inactivity. Females ceased entering torpor 4.5 days before young were born and were not observed to use torpor during lactation (Geiser & Masters 1994). In this species, the use of torpor appeared to increase during pregnancy in comparison to non-reproductive individuals.

Featherless gliders (Marsupialia) undergo both daily and prolonged torpor when non-reproductive with Tb 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 Tb around 10-15°C (Scholl 1974). Non-reproductive large-eared tenrecs have Tb of about 17°C and shrew tenrecs around 25°C (Stephenson & Racey 1993a, b). The Tb 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 insects, 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 Mioupeus 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 (Aued & Fenton 1988; Grinevich 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 (Eisenbraut 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 Tₚ drops to a minimum of about 18°C. Although torpor has been observed in at least 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

<table>
<thead>
<tr>
<th>GROUP</th>
<th>SPECIES</th>
<th>Mass (g)</th>
<th>Diet</th>
<th>Observation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIRDS</td>
<td>Sphenophora platyrhynchos</td>
<td>3.1</td>
<td>Insect</td>
<td>Deep torpor in incubating birds</td>
<td>Geiser &amp; Boomer 1973</td>
</tr>
<tr>
<td></td>
<td>Eptesicus fuscus</td>
<td>46</td>
<td>Insect</td>
<td>Torpor in breeding and incubation</td>
<td>Kinnaird &amp; Brigham 1993</td>
</tr>
<tr>
<td></td>
<td>Myotis myotis</td>
<td>450</td>
<td>Insect</td>
<td>Torpor in pregnant female</td>
<td>Geiser &amp; Seymour 1989</td>
</tr>
<tr>
<td></td>
<td>Antrozous pallidus</td>
<td>17</td>
<td>Insect</td>
<td>Torpor in non-breeding females</td>
<td>Noyes 1978</td>
</tr>
<tr>
<td></td>
<td>Myotis evotis</td>
<td>100</td>
<td>Insect</td>
<td>Torpor in pregnant females and reproductive males</td>
<td>Geiser &amp; Murri 1994</td>
</tr>
<tr>
<td></td>
<td>Rhinolophus megalophyllus</td>
<td>12</td>
<td>Insect</td>
<td>Torpor in non-breeding females</td>
<td>Frey &amp; Fleming 1984</td>
</tr>
<tr>
<td></td>
<td>Myotis lucifugus</td>
<td>45</td>
<td>Insect</td>
<td>Deep torpor in reproductive season</td>
<td>Stephens &amp; Racey 1990a</td>
</tr>
<tr>
<td></td>
<td>Tadarida brasiliensis</td>
<td>45</td>
<td>Insect</td>
<td>Deep torpor in reproductive season</td>
<td>Stephens &amp; Racey 1990b</td>
</tr>
<tr>
<td></td>
<td>Argyrodes griseus</td>
<td>67</td>
<td>Insect</td>
<td>Torpor in pregnant females</td>
<td>Stephens &amp; Racey 1992a</td>
</tr>
<tr>
<td></td>
<td>Vespertilio murinus</td>
<td>215</td>
<td>Insect</td>
<td>Torpor in pregnant females</td>
<td>Stephens &amp; Racey 1992b</td>
</tr>
<tr>
<td></td>
<td>Hipposideros rouxii</td>
<td>116</td>
<td>Insect</td>
<td>Torpor in pregnant females</td>
<td>Stephens &amp; Racey 1992c</td>
</tr>
<tr>
<td></td>
<td>Mammals</td>
<td>25</td>
<td>Insect</td>
<td>Torpor in pregnant females</td>
<td>Eisenbraut 1937</td>
</tr>
<tr>
<td></td>
<td>Dasyptila fuscomaculata</td>
<td>6</td>
<td>Insect</td>
<td>Torpor during pregnancy slow postnatal development</td>
<td>Racey 1973</td>
</tr>
<tr>
<td></td>
<td>Pipistrellus pipistrellus</td>
<td>19</td>
<td>Insect</td>
<td>Torpor during pregnancy and lactation in both sexes</td>
<td>Aued &amp; Fenton 1988</td>
</tr>
<tr>
<td></td>
<td>Nyctinomus albiventris</td>
<td>15</td>
<td>Insect</td>
<td>Reduced embryo growth during lactation</td>
<td>Dayan 1983</td>
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<tr>
<td></td>
<td>Myotis grisegena</td>
<td>7</td>
<td>Insect</td>
<td>Reduced embryo growth during lactation</td>
<td>Wyman 1980</td>
</tr>
<tr>
<td></td>
<td>Myotis mystacinus</td>
<td>18</td>
<td>Nectar</td>
<td>10% reduction of MR in pregnant, torpid bat</td>
<td>Geiser, Krüger &amp; Law 1993</td>
</tr>
</tbody>
</table>

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 the 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 the phenomenon receives more attention, members of other mammals (e.g., 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 mother's mass (Yuendle-Bischof 1973; Geiser & Seymour 1989). Energy expenditure for gestation in both groups therefore should be low as has been verified for some marsupials (Thompson & Nicol 1988; Nicol & Thompson 1987). Similarly, energy costs during lactation in marsupials also tend to be relatively low (Thompson & Nicol 1986; Nicol & 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 (Nicol & 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; Rasmussen 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 & Speelman 1987; Nicol & Thompson 1987). Similar arguments as for mammals may be applied for 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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References