

S22-4 Torpor in Australian birds

Fritz GEISER^{1*}, Gerhard KÖRTNER¹, Tracy A. MADDOCKS¹, R. Mark BRIGHAM²

1. Dept. of Zoology, BBMS, University of New England, Armidale, NSW 2351, Australia; *fgeiser@metz.une.edu.au

2. Dept. of Biology, University of Regina, Regina, SK S4S 0A2, Canada; mark.brigham@uregina.ca

Abstract Energy-conserving torpor is characterized by pronounced reductions in body temperature and metabolic rate and, in Australian birds, is known to occur in the Caprimulgiformes (spotted nightjar, Australian owlet-nightjar, tawny frogmouth), Apodiformes (white-throated needletail) and the Passeriformes (dusky woodswallow). Anecdotal evidence suggests that it also may occur in the white-fronted honeyeater, crimson chat, banded whiteface, red-capped robin, white-backed swallow, mistletoebird, and perhaps welcome swallow. Daily torpor (bouts lasting for several hours) appears to be the most common pattern, although anecdotal evidence indicates that white-backed swallows can undergo prolonged torpor. Diurnal birds enter torpor only during the night but nocturnal birds may use it by the day and/or night, and often in more than one bout/day. Body temperatures fall from ~38–41°C during activity to ~29°C during torpor in spotted nightjars, tawny frogmouths, dusky woodswallows and white-throated needletails, and to ~22°C in Australian owlet-nightjars. In the spotted nightjar, a reduction in T_b by ~10°C resulted in a 75% reduction in metabolic rate, emphasizing energy conservation potential. Since torpor is likely to be more crucial for the survival of small birds, a detailed understanding of its use is important, not only for physiologists but also ecologists and wildlife managers. It is thus disappointing that so much information on torpidity in Australian birds is anecdotal, and that so little effort has been made to characterize its patterns and quantify the resulting energy savings and survival benefits for birds in the wild.

Key words Australia, Energy expenditure, Thermoregulation, Torpor

1 Introduction

Endothermic birds and mammals differ from ectotherms primarily in their ability to regulate body temperature (T_b) using internal heat produced from combustion of food fuels. Because the surface area/volume ratio of animals increases with decreasing size, many small endotherms must produce an enormous amount of heat to compensate for heat loss during exposure to cold. Obviously, prolonged periods of high metabolic heat production can only be sustained by high food intake; and, during adverse environmental conditions and/or shortage of food, the cost of thermoregulation may be prohibitively high. Therefore, not all mammals and birds maintain permanent homeothermy, but during certain times of the day or year enter a state of torpor (Lyman et al., 1982; Geiser and Ruf, 1995).

Torpor in these “heterothermic endotherms” is characterized by a controlled reduction of T_b , metabolic rate (MR), and other physiological processes with the main apparent function of reducing energy expenditure substantially. Torpor conserves energy because (i) over a wide range of ambient temperatures (T_a), no thermoregulatory heat production is required, and (ii) the substantial fall of T_b , and in some species inhibition of MR, can substantially lower energy expenditure to well below the basal metabolic rate (BMR). Torpor is commonly used to cope with acute environmental challenges or food shortages, but can also be employed to balance daily energy expenditure without ob-

vious stress or even to enhance fuel storage to cope with future energy bottlenecks (Carpenter and Hixon, 1988; Geiser and Masters, 1994).

Although both birds and mammals can use torpor (MacMillen and Trost, 1967; Dawson and Hudson, 1970; Reinertsen, 1983; Prinzinger and Siedle, 1988; Geiser and Ruf, 1995; Schleucher, 2001; Downs and Brown, 2002; McKechnie and Lovegrove, 2002), it is widely believed that torpor in small birds is far less common than in small mammals because birds can migrate to avoid adverse conditions. This argument is based on the assumption that birds in general use long distance migration, which is, of course, not the case. Many Australian birds are sedentary or nomadic instead and, because the Australian continent is characterized by low rainfall, high evaporation rates, prolonged droughts and low primary productivity, food will be limiting periodically, in addition to the usual seasonal challenges experienced elsewhere. Sedentary insectivores and frugivores, in particular, should suffer energetic bottlenecks under such conditions; and since they do not migrate far, they are likely to use physiological adaptations that help them to survive.

Australian birds are an interesting group from an evolutionary point of view. Many species are endemic, and the majority of passerines appear to be the result of a massive Australian radiation (Sibley and Ahlquist, 1985; Schodde and Mason, 1999), and therefore are especially likely to be

physiologically adapted to the idiosyncrasies of the continent.

In this paper we review published information on torpor in Australian birds, and also present some unpublished data. Worldwide, heterothermic species, judged by capacity to reduce $T_b > 6^\circ\text{C}$ (McKechnie and Lovegrove, 2002), are known from seven bird orders, but so far from only three include them in Australia (Table 1).

2 Caprimulgiformes (nightjars and allies)

Anecdotal reports of torpor in Australian birds have been around since the 1920s, but the first quantitative data were provided by Dawson and Fisher (1969) for captive spotted nightjars (*Eurostopodus argus*). The T_b of one individual fell from $\sim 39^\circ\text{C}$ during normothermia (regulating a high T_b) to 29.6°C during torpor, and MR was reduced to only $\sim 25\%$ of resting MR in normothermic individuals. More data on torpor in Australian caprimulgiforms have become available recently. Free-ranging Australian owl-nightjars (*Aegotheles cristatus*) frequently entered torpor in the early morning in winter, with T_b falling to a minimum of 22°C (Brigham et al., 2000). Torpor lasted for ~ 4 hours through the morning and birds re-warmed near midday, perhaps using radiant heat from the sun which substantially reduces the energetic costs of re-warming (Geiser and Drury, 2003). Only one third of monitored birds re-entered a second bout in the afternoon, before arousing for nocturnal activity. Captive owl-nightjars entered torpor as well, but it was shallower and shorter than in the field (Geiser et al., 2000).

Although laboratory investigations suggested that tawny frogmouths (*Podargus strigoides*) are homeothermic (McNab and Bonaccorso, 1995; Bech and Nicol, 1999), and the species is ~ 10 -fold larger than any caprimulgid recorded with torpor, they do enter torpor in the wild (Körtner et al., 2000, 2001). Its pattern, however, differs substantially from that in owl-nightjars: frogmouths entered torpor at night, typically after a brief period of activity. Moreover, the minimum T_b of frogmouths (29°C) was well above that in owl-nightjars. After a bout of night torpor lasting ~ 7 hours, frogmouths always re-warmed actively before sunrise before flying to a day roost, and there often re-entered a second, dawn torpor that terminated in the late morning.

Torpor in tawny frogmouths occurred exclusively during winter, and was correlated with average night T_a . During cold dry winters, when night T_a frequently dropped $< 5^\circ\text{C}$, night torpor frequency reached up to 60% of observations; but during warmer, wetter winters, it fell to $\sim 30\%$. In all winters, morning torpor was less common than night torpor (Körtner and Geiser, 2000).

Although both owl-nightjars and tawny frogmouths enter torpor in the same habitats in the wild, pattern and timing differ substantially. These differences appear to be related to differences in size, mode of foraging and roosting.

Frogmouths at 500 g mass carry fat reserves and seem to be able to survive over several nights without foraging; they are sit-and-wait predators of active arthropods and are unlikely to be very successful when cold T_a limits insect activity. Owllet-nightjars at 50 g mass, in contrast, have a much lower capacity to store fat; they also forage actively on the ground, and may be able to find food on most nights.

A possible reason for differences in the timing of their torpor may also be related to roosting. Owllet-nightjars roost in tree cavities potentially protected from diurnal predators, whereas Frogmouths, although well camouflaged, roost on branches in the open (Brigham et al., 2000). Differences in the minimum T_b between the two species (frogmouths 29°C , owllet-nightjars 22°C) are probably related to body mass. Small birds have lower minimum T_b than large birds (Geiser and Ruf, 1995), which maximizes the reduction of MR, and thus energy-savings during torpor.

Thus it appears that Australian caprimulgids use torpor extensively, as on other continents (Jaeger, 1948; Bartholomew et al., 1957; Peiponen, 1965; Withers, 1977; Brigham, 1992; French, 1993). Ecological factors influencing torpor use by caprimulgids are discussed elsewhere in this symposium (Brigham et al., 2006).

3 Apodiformes (swifts and hummingbirds)

The only observations of torpor in Australian swifts are those by Pettigrew and Wilson (1985) for a white-throated needletail (*Hirundapus caudacutus*). A captive bird went into torpor every night over several nights, and body mass declined during that time. On one night when cloacal T_b was continually monitored, T_b fell from 38.5°C to 28°C and the bird remained torpid for 10 hours. The bird aroused actively the following morning after human disturbance. In view of the large size of *Hirundapus* swifts (85 g), we think it likely that other Australian swifts, all of which are smaller, are also heterothermic.

4 Passeriformes

The oldest report on a torpor-like state in passerines claims that welcome swallows (*Hirundo neoxena*) show "semi hibernation", huddling in rock crevices in winter and foraging only on warm days (Dove, 1923). This report implies that the birds remained in the crevices for several days, but it was not quantified systematically and it is not clear whether birds simply huddled or were torpid.

Heumann (1926) reported a torpor-like state in mistletoebirds (*Dicaeum hirundinaceum*). He recorded that six birds froze close to death while in transit to America and were resuscitated four times. He also observed that captive mistletoebirds became cold regularly in winter in an aviary, but no quantitative measurements were taken.

Reports on torpor in white-backed swallows (*Cheramoeca leucosternum*) are based on observations made near Perth, Western Australia (Serventy, 1970). A group

Table 1 Torpor in Australian birds

	Body mass (g)	Minimum T_b (°C)	Torpor duration (h)	Notes	Source
Caprimulgiformes					
Spotted nightjar <i>Eurostopodus argus</i>	75	29.6		Torpor in captive bird in summer	Dawson and Fisher, 1969
Australian owl-nightjar <i>Aegotheles cristatus</i>	50	22.4	4–6	Dawn torpor in winter, arousal near midday, and 2nd bout in afternoon; nocturnal torpor only on cold winter nights	Brigham et al., 2000
Tawny frogmouth <i>Podargus strigoides</i>	500	29	7	Nocturnal torpor on cold winter nights, arousal near sunrise, 2nd dawn bout common	Körtner et al., 2000, 2001
Apodiformes					
White-throated needletail <i>Hirundapus caudacutus</i>	85	28	~10	Nocturnal torpor in captive bird in summer	Pettigrew and Wilson, 1985
Passeriformes					
White-fronted honeyeater <i>Phylidonyris albifrons</i>	~20			Nocturnal torpor	Ives, 1973
Noisy miner <i>Manorina melanocephala</i>	70	33	~10	Nocturnal shallow torpor	Geiser, unpublished
Crimson chat <i>Epthianura tricolor</i>	~10			Nocturnal torpor in juveniles lasting till late morning	Ives, 1973
Banded whiteface <i>Aphelocephala nigricincta</i>	~10			Regular nocturnal torpor in winter	Ives, 1973
Red-capped robin <i>Petroica goodenovii</i>	~9			Nocturnal torpor	Ives, 1973
Dusky woodswallow <i>Artamus cyanopterus</i>	35	29	~12	Regular spontaneous nocturnal torpor in outdoors aviary in autumn/winter	Maddocks and Geiser 1999
White-backed swallow <i>Cheramoeca leucosternum</i>	13			Diurnal torpor in group of birds in burrow on cold winter day	Serventy, 1970; Congreve, 1972
Welcome swallow <i>Hirundo neoxena</i>	12			Torpor in groups of birds huddling in tree cavities or rock crevices in winter?	Dove, 1923
Mistletoe bird <i>Dicaeum hirundinaceum</i>	9			Birds in intercontinental transit appeared dead, resuscitated after rewarming	Heumann, 1926

of ~20 torpid swallows were found in a burrow; they did not move and were cold to touch when removed for examination. The birds had disappeared a week later. As this observation was made during the daytime on a cold winter's day, it is not an example of the nocturnal torpor common in diurnal birds but may instead represent prolonged torpor. This interpretation is supported by further observations on four individuals (Congreve, 1972) that were found at the end of a tunnel during the collection of sand. When first discovered at 13:15 h the birds were cold to touch, by 13:35 h they were shivering and at 14:00 h they could fly. Congreve suggests that the swallows may spend some of the winter in a state of torpor, again implying that this species may enter prolonged bouts of torpor.

Ives (1973) reported behavioral observations of tor-

por in several Australian arid-zone birds. Young crimson chats (*Epthianura tricolor*) disperse from the nest early in development, and spend the night on the ground. During the night they appear to enter a torpid state and when handled on the following morning remain inert, reviving only after passive re-warming. Captive banded whitefaces (*Aphelocephala nigricincta*) enter torpor each night and re-warm when T_a rises in the morning. Nocturnal torpor was also reported in red-capped robins (*Petroica goodenovii*) and white-fronted honeyeaters (*Phylidonyris albifrons*), but no details were provided.

Honeyeaters are a successful endemic Australian bird family. They are relevant to the context of this paper as they mainly eat insects and nectar, the availability of which fluctuates with weather or season. Free-ranging noisy miners

(*Manorina melanocephala*), a medium sized honeyeater (70g), showed substantial and predictable reductions of T_b on every night in winter (T_b measured $\pm 0.5^\circ\text{C}$ with implanted iButtons). The most extreme fluctuation of T_b occurred during mid-winter (July), with daily shifts of up to 9°C . Although minimum T_b of 33°C was relatively high, it would still be classified as torpor under many definitions. Daily T_b fluctuations followed the dark- and light- phases very closely, with a steep decline of T_b at the beginning of the night, a further reduction of T_b until $\sim 2\text{--}3$ am, which was followed by slow rise of T_b before sunrise and finally a steep rise back to normothermic T_b of $\sim 41^\circ\text{C}$ after sunrise. When food was withheld, captive noisy miners showed a similar nightly reduction of T_b and reduced MR to $\sim 50\%$ of that during the day (Maddocks, 2001).

Dusky woodswallows (*Artamus cyanopterus*) at 35 g also enter nocturnal torpor in captivity. They feed mainly on the wing on flying insects, and roost in tightly packed communal swarms in the wild. They also exhibit predictable daily changes in T_b , which are even more pronounced than in noisy miners. T_b fell at dusk, even when food was available throughout the day, and birds remained torpid throughout the night, re-warming at dawn. Especially in May/June, T_b fell regularly from $\sim 41^\circ\text{C}$ to $\sim 30^\circ\text{C}$ and on some occasions to 29°C (Maddocks and Geiser, 1999).

Torpor thus appears to be commonly used by Australian birds for energy conservation. However, more quantitative work is required to establish its impact on avian survival in general.

Acknowledgements This study was supported by a grant from the Australian Research Council.

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