Passive Rewarming from Torpor in Mammals and Birds: Energetic, Ecological and Evolutionary Implications

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Abstract. Endothermic rewarming from torpor requires an enormous increase in energy expenditure and is widely viewed as one of the major disadvantages of torpor. However, recent evidence suggests that passive rewarming, by the increase of ambient temperature (T_a), by basking in the sun, or by social thermoregulation, is common in heterothermic birds and mammals. Passive rewarming has been observed in a number of mammals, including echidnas, several dasyurid marsupials, pygmy possums, marmots, elephant shrews, lemurs, several insectivorous bats, and possibly numbats and sugar gliders. In birds, passive rewarming occurs in poor-wills, whip-poor-wills, Australian owlet-nightjars, tawny frogmouths, and roadrunners. Passive rewarming is employed by both hibernators (species capable of prolonged torpor) and daily heterotherms (species displaying exclusively daily torpor), presumably to reduce energy expenditure during arousal. In captivity, passive rewarming due to increased T_a reduced energy expenditure of a small marsupial during rewarming by ~65% and, with a radiant heat source, by ~85% of that required for active, endothermic rewarming. We estimate that the use of daily torpor, combined with passive rewarming from torpor, and basking in the sun during the rest phase can reduce daily energy expenditure by ~50%. The low energy expenditure required during passive rewarming may explain how ancestral endotherms with presumably a low capacity

for heat production were able to rewarm from low body temperatures (T_b) before they commenced activity. In addition, it may explain why torpor is more common in sunny regions or in regions with daily T_a fluctuations including T_a maxima > T_b minima during torpor. As a consequence, many other species that have access to sun or high daily fluctuations of T_a may use torpor because they can save energy during torpor and arouse at minimal rewarming costs via passive rewarming and do not require a high thermogenic capacity.

Introduction

It is widely accepted that torpor in mammals and birds, which is characterised by periodic reductions of body temperature (T_b) and metabolic rate (MR), is primarily used for energy conservation (Lyman et al., 1982; Boyer and Barnes, 1999). Nevertheless, a major drawback to this physiological strategy is the high expenditure of energy that is required for endothermic arousals at the end of a torpor bout. This is especially true for short bouts of torpor such as during daily torpor, which usually lasts < 12 hours within a 24-hour cycle. Although MR may be reduced by ~90% during a bout of daily torpor compared with that for normothermic, resting individuals, daily energy savings through the use of torpor are usually only ~20–30% because of the high costs of activity and rewarming (Kenagy, 1989; Holloway and Geiser, 1995; Lovegrove et al., 1999). Even during hibernation, when MR during torpor (TMR) may be <1% of that in normothermic individuals (Geiser, 2004), endothermic arousals that occur after torpor periods of several days or weeks require most of the energy used during the hibernation season (Wang, 1978; Thomas et al., 1990).

Estimates of energy expenditure during torpor have largely been based on laboratory data obtained under constant ambient temperature (T_a). However, recent evidence from field studies in both mammals and birds demonstrates that rewarming in many species is to a large extent a passive process (Schmid, 1996; Körtner et al., 2000; Brigham et al., 2000; Dausmann et al., 2000; Geiser et al., 2002; Mzilikazi et al., 2002; Geiser, 2003; Lane et al., 2004; McKechnie and Wolf, 2004). For captive animals, rewarming costs can be reduced significantly by passive rewarming associated with a rise in T_a (Lovegrove et al., 1999), by exposure to radiant heat (Geiser and Drury, 2003), or by social thermoregulation (Arnold 1993). Consequently, the energetic costs of rewarming in many species may have been substantially over-estimated in the past and the potential energetic benefits of torpor in free-ranging animals under-estimated.

In this paper we summarise current knowledge about passive rewarming by heterothermic mammals and birds and how passive rewarming may reduce energy expenditure.

Passive Rewarming in Mammals and Birds

Passive rewarming from torpor appears to be widespread in both mammals and birds (Table 1). It occurs in all three mammalian subclasses, but in birds is currently known only from the Caprimulgiformes and roadrunners, although it is likely that other birds (e.g., mouse birds or hummingbirds) use exogenous heat in the rewarming process. Passive rewarming occurs in both hibernators and daily heterotherms. Passive rewarming has been observed from T_b <10° C in some hibernators, but usually begins at T_b ~20° C. In most species passive rewarming does not appear to involve movement, although it may involve active selection of an appropriate torpor site in which to rewarm passively on the following day. However, active movement at low T_b from a torpor site to a favourable basking site has been observed in fat-tailed antechinus and tawny frogmouths. In species with social thermoregulation, such as marmots or sugar gliders, passive rewarming may simply involve delayed arousal and absorbing heat from adjacent individuals. Most observations on passive rewarming have been made recently, reflecting the greater use of small temperature transmitters and data loggers in the field. Thus it is likely that passive rewarming will be reported in many other heterothermic species when these are investigated in nature.

For those species for which MR measurements are available, MR remained low (below or near basal MR, BMR) during the initial part of the rewarming process. However, in species in which high or rising T_a caused the increase of T_b, endothermic arousal associated with a sharp rise of MR commenced when T_b reached ~25° C. It has been estimated that passive rewarming via an increase in T_a from 15 to 25° C reduces the rewarming costs in dunnarts (*Sminthopsis macroura*) to ~35% relative to active rewarming (Lovegrove et al., 1999). During radiant heat assisted passive rewarming in *S. macroura* basking under a heat lamp, which provided much less radiant heat than the sun, endothermic heat production remained low (below BMR) throughout most of the rewarming process, without the sharp rise near T_b 25° C. As a consequence, radiant heat assisted passive rewarming reduced rewarming costs by *S. macroura* to ~15% of that required for active endothermic rewarming at the same T_a (Geiser and Drury, 2003).

Table 1. Observations on passive rewarming from torpor in mammals and birds.

	Body mass (g)	Observations	Source
MAMMALS			
Monotremata			
Tachyglossus aculeatus Echidna	~4000	Partially passive rewarming in free-ranging individual in a burrow in spring.	Brice et al. 2002
Marsupialia			
Planigale tenuirostis Narrow-nosed planigale	7	Basks in winter, but not clear whether during or after rewarming from torpor.	Read 1995a
Planigale gilesi Giles' planigale	8	Displays daily torpor in captivity and basks in winter in the wild, but not clear whether during or after rewarming.	Read 1995b; Geiser 2003
Sminthopsis murina Common dunnart	16	Partially passive rewarming with T_a in the field from T_b ~20° C.	Paull 2004
Sminthopsis macroura Stripe-faced dunnart	25	Has been observed basking in captivity; individuals reduce energetic cost of rewarming from torpor to ~35% of endothermic rewarming when exposed to rise of T_a, and to ~15% endothermic rewarming when exposed to radiant heat.	Lovegrove et al. 1999; Geiser & Drury 2003
Pseudantechinus macdonnellensis Fat-tailed antechinus	31	Torpid individuals emerge from deep rock crevices to commence morning basking at T_b 19.3 to 31.3° C; remain in sun throughout rewarming process and for much of the afternoon.	Geiser et al. 2002
Dasycercus cristicauda Mulgara	110	Displays daily torpor in captivity and basks in the wild, but not clear whether during or after rewarming from torpor.	Woolley 1995; Geiser 2003
Myrmecobius fasciatus Numbat	500	Observed basking in the morning, but not clear whether during or after rewarming from torpor.	Serventy & Raymond 1973
Cercartetus concinnus Western pygmy-possum	18	Partially passive rewarming of free-ranging individual in the morning from T_b ~9 to 17° C.	Geiser & Körtner 2004

Petaurus breviceps Sugar glider	100	Synchronised arousals among individuals sharing a nest; a slight delay in onset of arousal will result in partially passive rewarming in that individual.	Körtner & Geiser 2000

Placentalia

Marmota marmota Alpine marmot	~3000	Synchronised endogenous arousals reduce energy expenditure during periodic arousals; adults provide heat for juveniles.	Arnold 1993
Elephantulus myurus Rock elephant shrew	56	Short bouts of torpor with T_b <10° C common in captivity and field, but occasional bouts of >1d. Most bouts in the field terminated within 2 hour after sunrise, T_a and T_b rise are tightly coupled, and basking may be used during rewarming.	Lovegrove et al. 2001; Mzilikazi et al. 2002
Eremitalpa granti Namib golden mole	20	Displays daily variations of T_b from ~20° C in the morning to ~30° C in the afternoon tracking sand temperature.	Fielden et al. 1990
Microcebus myoxinus Pygmy mouse lemur	33	Passive rewarming with T_a in outdoor enclosure. T_b rises from ~19 to 27° C with small rise of MR.	Schmid 1996
Microcebus murinus Grey mouse lemur	80	Passive rewarming with T_a in outdoor enclosure. T_b rises from ~18 to 26° C and MR increases by less then 2-fold. Endothermic arousal at T_b>26° C.	Schmid 1996
Cheirogaleus medius Fat-tailed lemur	250	Hibernates for several months in dry, warm winter of Madagascar, but daily partial arousals from T_b ~20 to ~30° C. T_b rise to ~27° C is largely passive, at higher T_b active heat production commences with MR > BMR.	Dausmann et al. 2000
Vespadelus pumilus Eastern forest bat	4	Partial passive arousal in the morning in a subtropical area in summer with an increase of T_b from ~16 to 23° C in parallel with rising T_a.	Turbill et al. 2003a

Species		Description	Reference
Myotis lucifugus Little brown bat	6	Partially passive rewarming from T_b ~18–23° C via increasing T_a under simulated roost conditions; MR remains low until T_b ~25–28° C is reached and increases steeply thereafter.	Kurta 1990
Myotis evotis Western long-eared bat	7	Partially passive rewarming of a pregnant bat from T_b ~19 to 30° C.	Chruszcz & Barclay 2002
Nyctophilus geoffroyi Australian long-eared bat	7	Prolonged torpor bouts of up to 2 weeks in winter, daily passive rewarming from T_b ~ 2–8 to 10–20° C, active arousals after 1–2 weeks in torpor with T_b > 30° C. In summer partially passive arousal near midday on most days.	Turbill et al. 2003b, c
Eptesicus fuscus Big brown bat	20	Passive rise of T_b with T_a from T_b ~10° C in outdoor enclosure; partially passive rewarming in free-ranging bat.	Lausen & Barclay 2003; Willis & Brigham 2003

BIRDS

Caprimulgiformes

Species		Description	Reference
Phalaenoptilus nuttallii Poor-will	45	Prolonged and deep torpor (T_b < 10° C) in winter, daily partially passive arousals due to solar radiation; endogenous arousal after ~5 days in shaded birds.	Brigham et al. 2004
Caprimulgus vociferus Whip-poor-will	55	Rise of T_b with T_a from T_b ~20 to 30° C in late spring.	Lane et al. 2004
Aegotheles cristatus Owlet-nightjar	50	Dawn torpor in winter common, arousal near midday when birds were observed basking.	Brigham et al. 2000
Podargus strigoides Tawny frogmouth	500	Nocturnal torpor on cold winter nights, arousal near sunrise; second dawn torpor bout commonly terminated by partially passive rewarming in the sun.	Körtner et al. 2000, 2001

Cuculiformes

Species		Description	Reference
Geococcyx californicus Roadrunner	300	Passive rewarming in mildly hypo-thermic birds from T_b ~34 to 38° C under artificial sunlight in captivity.	Ohmart & Lasiewski 1971

The potential effect of radiant energy on daily energy expenditure by *S. macroura* is substantial (Fig. 1). To estimate daily energy expenditure we assume both passive rewarming from torpor as well as basking during normothermia, which is common in both mammals and birds, and allows a reduction of energy expenditure to ~BMR over a wide range of T_a. We calculate that energy expenditure of individuals remaining normothermic throughout the day with an activity phase at night and rest phase during the daytime is 48 kJ/d (average from 6
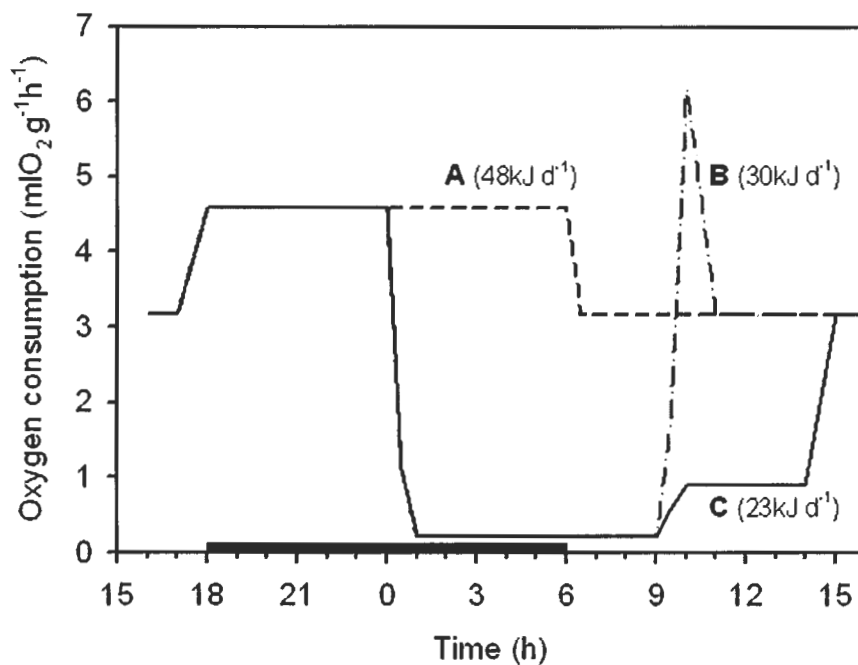

Fig. 1. Time course of metabolic rate measured as oxygen consumption of Sminthopsis macroura *(25 g) exposed to T_a 16° C with or without access to radiant heat. Heat was provided by a 60W reflector globe with 99% color rendering index and 2850K, which produced ~5% of the lux of natural solar radiation. (A) Animals without access to radiant heat remaining normothermic throughout (active night, rest day), (B) animals entering torpor at midnight without access to radiant heat and endothermic arousal from 09:00h, and (C) animals entering torpor at midnight and having access to radiant heat during rewarming and for most of the afternoon, assuming that during basking in the sun MR falls to near BMR as during basking under a 60W reflector globe. The black bar on the x-axis indicates the dark phase (MR data based on six individuals from Geiser and Drury 2003).*

individuals held at T_a 16° C without access to radiant heat). If animals entered torpor at midnight as commonly observed and used endothermic arousal, daily energy expenditure is reduced by 37%. However, if they used passive rewarming in the morning and basked for most of the afternoon, daily energy expenditure is reduced by 52%. These calculations indicate that access to solar energy during passive rewarming from torpor and during the normothermic rest phase, combined with low TMR, enable animals to benefit more substantially from torpor than previously thought.

Passive rewarming also has implications for torpor use. Access to solar radiation and/or exposure to daily T_a fluctuations, including T_a maxima > T_b minima during torpor may be important factors that determine whether or not a species uses torpor, in addition to unpredictable changes in climate and food availability that often are associated with daily torpor (Lovegrove, 2000). Most species in Table 1 live in areas that receive substantial amounts of solar radiation or experience pronounced daily T_a fluctuations such as deserts and high altitudes, which may be limiting with respect to food availability but provide alternative energy in the form of sunshine. Because moderate, changing T_a and basking can substantially reduce arousal costs and because species diversity increases towards the equator in most taxa, it is likely that the number of heterothermic endotherms living at low latitudes may have been underestimated in the past. Thus, our summary challenges the traditional view that torpor is especially common in cold climates.

We speculate that passive rewarming was probably also involved in the evolution of endothermic thermoregulation. The >10-fold increase in thermogenic capacity from ectotherms to endotherms (Hulbert and Else, 1989) must have involved numerous generations of individuals with intermediate thermogenesis. Ancestral endotherms were small, likely unable to maintain a constant high T_b during rest, and lacked the thermogenic capacity required for endothermic rewarming, but probably relied on high T_bs for efficient function. If passive rewarming reduced energy expenditure during the rewarming phase by 65 to 85% of that required for active rewarming, a small thermogenic capacity would have sufficed to raise T_b to levels that allowed efficient function.

Our observations suggest that ancestral endotherms were heterothermic and became torpid when thermally challenged or when food supply was low (Johansen, 1961; Cade, 1964; Grigg and Beard, 2000). However, it is improbable that the pattern of torpor was identical to that in modern heterotherms with thermoregulatory control of T_b during torpor and the capacity for full endother-

mic arousal. It therefore seems likely that ancestral endotherms required external heat, not primarily to save energy as in extant species, but either to speed up the rewarming process or be able to rewarm at all.

Acknowledgements

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