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Ontogeny and phylogeny of endothermy and torpor in mammals and birds☆

Fritz Geiser *

Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale NSW 2351, Australia

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ABSTRACT

Endothermic thermoregulation in small, altricial mammals and birds develops at about one third to half of adult size. The small size and consequently high heat loss in these young should result in more pronounced energetic challenges than in adults. Thus, employing torpor (a controlled reduction of metabolic rate and body temperature) during development would allow them to save energy. Although torpor during development in endotherms is likely to occur in many species, it has been documented in only a few. In small, altricial birds (4 orders) and marsupials (1 order), which are poikilothermic at hatching/birth, the development of competent endothermic thermoregulation during cold exposure appears to be concurrent with the capability to display torpor (i.e. poikilothermy is followed by heterothermy), supporting the view that torpor is phylogenetically old and likely plesiomorphic. In contrast, in small, altricial placental mammals (2 orders), poikilothermy at birth is followed first by a homeothermic phase after endothermic thermoregulation is established; the ability to employ torpor develops later (i.e. poikilothermy–homeothermy–heterothermy). This suggests that in placentals torpor is a derived trait that evolved secondarily after a homeothermic phase in certain taxa perhaps as a response to energetic challenges. As mammals and birds arose from different reptilian lineages, endothermy likely evolved separately in the two classes, and given that the developmental sequence of torpor differs between marsupials and placentals, torpor seems to have evolved at least thrice.

1. Introduction

Body mass strongly affects the function of adult and juvenile animals (Brody, 1945; Schmidt-Nielsen, 1984; Calder, 1996; McNab, 2002). Influences of size on physiology during development are most profound in small, altricial species, which are born at an undeveloped stage, are poikilothermic at birth, and develop independent endothermic thermoregulation when they are about one third to half adult size (Morrison and Petajan, 1962; Dawson and Hudson, 1970; Schleucher, 1999; Brown and Downs, 2002). Small endotherms, which comprise the vast majority of all species, have large surface to volume ratios resulting in high loss of heat during cold exposure, high mass-specific basal MR (BMR) in thermoneutrality, high mass-specific energy expenditures during locomotion, and a proportionally low capacity for fat storage for insulation and/or energy storage (Withers, 1992; Calder, 1996). Consequently, in small endotherms the energetic costs for maintenance of homeothermy (constant high body temperature, T_b) may become prohibitively high, especially during cold exposure and/or periods of food shortage.

Unlike homeotherms, heterothermic endotherms are capable of employing torpor, and thereby can substantially reduce energy expenditure during certain parts of the day or the year, which minimizes the impacts of energetic challenges. Torpor, characterised by controlled reductions of metabolic rate (MR) and T_b, is therefore an important survival strategy in many mammals and birds, and is especially common in small species (Morrison, 1960; Hiebert, 1993; Barnes and Carey, 2004; Geiser, 2004; Willis et al., 2005). Although it is generally accepted that body size is one important factor that determines whether or not adults of a species are heterothermic, little is known about impacts of size and growth on the development of both endothermy and heterothermic responses by endotherms when high energy costs are likely to provide a strong selection pressure for heterothermy. This information is not only important from an energetic point of view, but also in relation to evolution of endothermy and torpor, because it remains unresolved and is often debated whether torpor in endotherms is ancestral and plesiomorphic, or a derived trait (Bartholomew and Hudson, 1962; Twente and Twente, 1964; Mrosovsky, 1971; Augee and Gooden, 1992; Malan, 1996; Geiser, 1998; Lovegrove et al., 1999; Carey et al., 2003; Grigg et al., 2004).

The purpose of the present article is to synthesize current knowledge about the development of endothermic thermoregulation and that of torpor in mammals and birds. The data are used to discuss implications of the ontogenetic sequence of development of endothermic

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* Fax: +61 2 6773 3814.
E-mail address: fgeiser@une.edu.au.

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Table 1
Development of torpor in mammals and birds

	Adult body mass (g)	Observations and source
Mammals		
Marsupials		
Sminthopsis macroura	25	Juvenile dunnarts enter torpor immediately after endothermic thermoregulation is established at ~40% adult mass. Torpor in small young is longer and deeper than in large young and adults. Development of endothermic thermoregulation and torpor concurrent (Geiser et al., 2006).
Antechinus flavipes	25	Antechinus are endothermic at weaning ~12–14 g, torpor from ~18 g. Development of endothermic thermoregulation and torpor likely concurrent (Geiser, 1988; Westman et al., 2002).
Antechinus stuartii	40	
Dasyuroides byrnei	110	Kowaris are endothermic at ~35 g and capable of entering torpor at ~50 g. Development of endothermic thermoregulation and torpor concurrent, but there is a brief homeothermic phase late during development at ~80 g before adult heterothermy (Geiser et al., 1986).
Placentals		
Crocidura russula	13	Juvenile shrews enter torpor on day 7 at ~5 g after an apparent homeothermic phase at day 4 at ~3 g, following poikilothermy at <3 g. Development of endothermy and torpor not concurrent (Nagel, 1977).
Phodopus sungorus	25	Juvenile hamsters enter food restriction-induced torpor 13 days after endothermic thermoregulation is established. Development of endothermic thermoregulation and torpor not concurrent (Bae et al., 2003).
Spermophilus saturatus	250	After poikilothermy, endothermic juvenile ground squirrels refuse to enter torpor during development in summer. In autumn, 2 weeks prior to hibernation, food withdrawal induces torpor. Development of endothermic thermoregulation and torpor not concurrent (Geiser and Kenagy, 1990).
Birds		
Ephthianura tricolor	10	Nocturnal torpor in juvenile Crimson chats lasting till late morning (Ives, 1973).
Delichon urbica	19	Juvenile martins from day 11 enter torpor after starvation. Minimum T_b in nest increases from ~26 °C at 12 g to 32 °C at 18 g. Development of endothermic thermoregulation and torpor concurrent (Prinzinger and Siedle, 1988).
Apus apus	42	Juvenile swifts enter daily torpor over several nights after fasting with T_b as low as 21 °C; adults also enter torpor. Development of endothermic thermoregulation and torpor apparently concurrent (Koskimies, 1948).
Urocolius macrourus	60	Near fledging (10 days) mousebirds enter torpor at ~55% adult mass before they can fly. Development of endothermic thermoregulation and torpor concurrent (Finke et al., 1995).
Oceanodroma furcata	60	Juvenile storm-petrels become endothermic at ~5 d, but enter torpor from that time until 28 d (~10 to 50 g) if parents do not provide enough food. Development of endothermic thermoregulation and torpor concurrent (Boersma, 1986).

thermoregulation and the ability of displaying torpor with regard to the evolution of endothermy and heterothermy.

2. Methods

2.1. Data collection

Data for this summary were taken from the literature or from unpublished measurements on *Sminthopsis macroura* by the author. Published information on torpor during development could be found on four marsupial mammals, three placental mammals, and five birds (Table 1). For several of these species detailed developmental studies on thermoregulatory capabilities of individuals preceded investigations on quantification of the expression of torpor in the same individuals; in other species published data were used to estimate the time of independent endothermic thermoregulation for the developing young. Most studies were conducted in captivity, whereas storm-petrels and chats were observed in the wild. With the exception of the study on chats, which provides only qualitative observations, all studies contain some quantitative measurements of T_b and/or MR.

2.2. Measurements on *S. macroura*

For MR measurements (quantified as the rate of oxygen consumption) of *S. macroura*, animals were exposed to a constant air temperature (T_a) of 16.0±0.5 °C for ~23.5 h commencing in the late afternoon; food and water were not available during measurements, but were available *ad libitum* at all other times. Juvenile *S. macroura* (n=11) were measured once/month over 5 months during their development beginning at a body mass of about 11 g. Experiments were discontinued once they approached adult body mass of 20 to 24 g. A single-channel oxygen analyser (FOX, Sable Systems, Las Vegas, NV, USA) was used for these measurements. MR for two or three individuals and outside air as a reference were measured in sequence for 3 min each using solenoid valves to switch between channels (i.e. each individual and outside air were measured every 9 to 12 min). The flow-rate of dry air passing through the respirometry chamber was controlled with rotameters (7908, Aarlborg, New York, NY, USA) and measured with mass flowmeters (FMA-5606, Omega, Stamford, CT, USA). Torpor was defined as a reduction of MR below 75% of resting MR (RMR) at T_a 16 °C and torpor bout duration was calculated as the time when MR remained below 75% RMR (further details in Geiser et al., 2006). Entry times and arousal times were derived from the times when MR fell below or rose above 75% of RMR. T_a was measured to the nearest 0.1 °C every 3 min in the respirometry chambers with calibrated thermocouple probes that were inserted 1 cm into the chamber and recorded with a digital thermometer (Omega DP116). Outputs from the flowmeter, oxygen analyser and digital thermometer were interfaced to a personal computer.

Numerical values are presented as mean±1 standard deviation (SD); n is the number of individuals. Linear regressions were fitted using the method of least squares; pseudo-replication was minimized because each individual was represented by a similar number of data points.

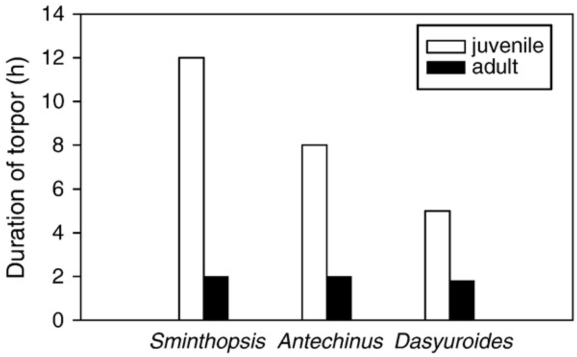

Fig. 1. Change of the duration of torpor during the development in three marsupial genera. Data for the same individuals at 50 to 58% of adult body mass are compared with data when they reached adult body mass. Body masses were: *Sminthopsis macroura* 11 g vs 22 g; *Antechinus* spp. 18 g vs 34 g (*Antechinus stuartii* and *A. flavipes* are combined as in the original investigation); *Dasyuroides byrnei* 70 g vs 120 g.