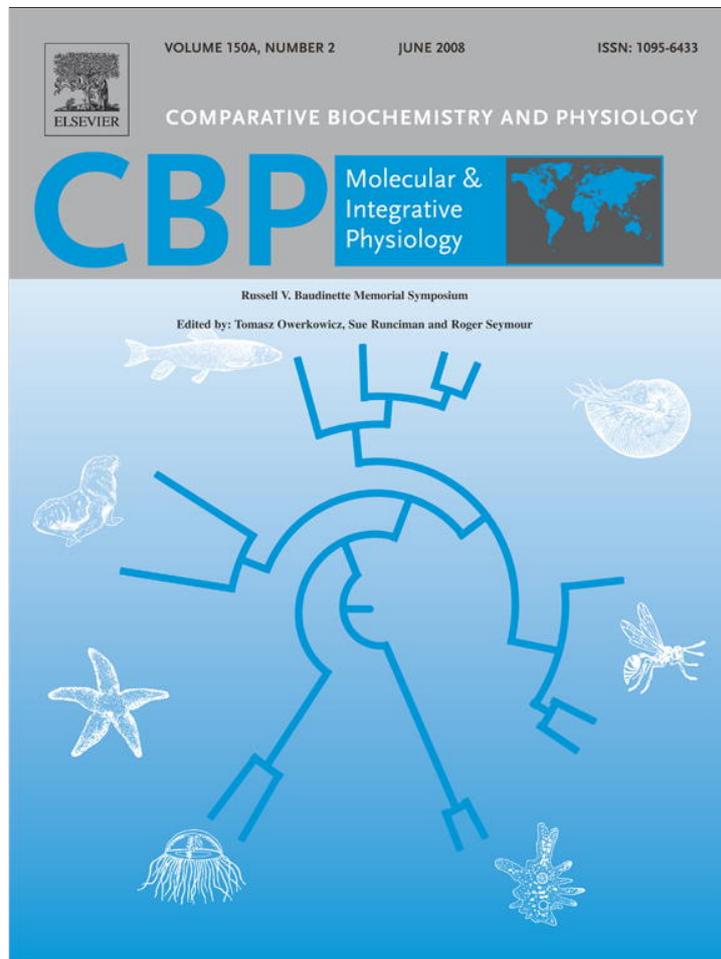


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Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpaOntogeny and phylogeny of endothermy and torpor in mammals and birds[☆]Fritz Geiser^{*}

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ARTICLE INFO

Article history:

Received 20 January 2006

Received in revised form 10 November 2006

Accepted 8 February 2007

Available online 1 May 2008

Keywords:

Development

Endothermy

Energetics

Evolution

Growth

Heterothermy

Homeothermy

Poikilothermy

Thermoregulation

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.

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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

[☆] Presented as part of the Russell V. Baudinette Memorial Symposium held in Adelaide, Australia, 1–2 October 2005.

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Table 1
Development of torpor in mammals and birds

	Adult body mass (g)	Observations and source
Mammals		
Marsupials		
<i>Sminthopsis macroura</i>	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).
<i>Antechinus flavipes</i>	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).
<i>Antechinus stuartii</i>	40	
<i>Dasyuroides byrnei</i>	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		
<i>Crocodyra russula</i>	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).
<i>Phodopus sungorus</i>	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).
<i>Spermophilus saturatus</i>	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		
<i>Ephthianura tricolor</i>	10	Nocturnal torpor in juvenile Crimson chats lasting till late morning (Ives, 1973).
<i>Delichon urbica</i>	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).
<i>Apus apus</i>	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).
<i>Urocolius macrourus</i>	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).
<i>Oceanodroma furcata</i>	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 \pm 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.

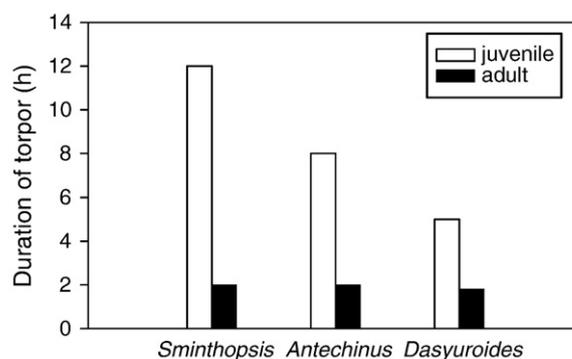


Fig. 1. Change of the duration of torpor during the development in three marsupial genera. Data for the same individuals at 50 to 58% of adult body mass are compared with data when they reached adult body mass. Body masses were: *Sminthopsis macroura* 11 g vs 22 g; *Antechinus* spp. 18 g vs 34 g (*Antechinus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

3. Results and discussion

3.1. Development of endothermy and torpor

3.1.1. Marsupials

All marsupial mammals in which development of torpor has been investigated belong to the order Dasyuromorphia, family Dasyuridae (insectivorous/carnivorous marsupials), most of which appear to enter daily torpor (Geiser, 2003). Adult body mass of the species ranges from 25 to 110 g and all four species are known to enter daily torpor as adults. In all four species (*Sminthopsis* and *Dasyuroides* from the arid zone, *Antechinus* from coastal, mesic or subtropical areas) torpor was more pronounced (i.e. deeper and longer) at some stage of juvenile development; average maximum torpor duration was three- to six-fold of that in the same individuals once they had reached adult size (Fig. 1).

In *S. macroura* the duration of torpor decreased linearly with body mass during growth. Interestingly, both the times of torpor entry as well as the times of arousal from torpor were related to body mass (Fig. 2). Thus, the prolongation in torpor duration early during development of *S. macroura* was achieved by both earlier torpor entries as well as later arousals. In contrast, it has been suggested for adult placental mammals that a change in the duration of daily torpor bouts in response to different food rationing or T_a is primarily achieved by a change of time of torpor entry, whereas the time of arousal appears largely fixed by a circadian rhythm and occurs at about the same time of day for a certain species (Tucker, 1966; Brown and Bartholomew, 1969). The developmental data presented here suggest that daily heterotherms are more flexible with regard to torpor duration than has been proposed previously and that both earlier torpor entries as well as later arousals may contribute to a prolongation of daily torpor.

In small dasyurid marsupials (<50 g), torpor expression appears to develop concurrently with the ability for endothermic thermoregulation. In juvenile *S. macroura*, the ability of entering torpor was present immediately after endothermic thermoregulation had developed. In *Antechinus* spp. torpor was observed soon after the time endothermic thermoregulation was established. The data on the temporal relationship between competent endothermy and expression of torpor were investigated in the same individuals for *S. macroura*, and therefore are continuous (Geiser et al., 2006), whereas for *Antechinus* spp. development of endothermy and torpor expression were investigated in different individuals (Geiser, 1988; Westman et al., 2002). Nevertheless, it is unlikely that *Antechinus* spp. exhibit a homeothermic phase after endothermic thermoregulation is established in summer because soon after that period, torpor in juveniles was most pronounced.

Interestingly, the closely related, but larger (~110 g), kowari (*Dasyuroides byrnei*) exhibited a somewhat different temporal pattern

of thermoregulation (Geiser et al., 1986). As in the other three dasyurid species, deep and long torpor bouts were expressed soon after endothermic thermoregulation was established suggesting that development of endothermy and torpor are concurrent. However, torpor expression declined with growth until a homeothermic phase was observed in sub-adults during summer, suggesting an additional seasonal influence on thermal biology during development. Torpor was expressed again once individuals approached adult body mass.

3.1.2. Placentals

Torpor in developing placental mammals has been described in two orders: the Insectivora and the Rodentia. However, juveniles from other orders, as for example bats, are known to enter torpor (Hollis, 2004), but to my knowledge no detailed developmental sequences, identifying the transition between poikilothermy and heterothermy or homeothermy, have been published. The temporal sequence from poikilothermy to heterothermy differs between the placentals and the investigated marsupials because in the placentals a clear homeothermic phase intervenes between the initial period of poikilothermy and the period of heterothermy later in life.

In the insectivorous shrew (*Crocodyrus russula*) from a cool-temperate area in Europe, the observed homeothermic phase was brief (about 3 days) and began around day 4 post-partum at a body mass of ~3 g (Nagel, 1977). Individuals entered daily torpor from day 7 post-partum at a body mass of ~5 g (~40% of adult mass).

The herbivorous hamster *Phodopus sungorus* originating from Siberia/Mongolia, which also is a daily heterotherm rather than a hibernator, did not display torpor after food restriction for 13 days after endothermic thermoregulation had developed (Bae et al., 2003), suggesting an about 2-week homeothermic phase. Daily torpor after food restriction was expressed only after this 2-week homeothermic phase. However, a torpor-like state could be induced in *P. sungorus* soon after endothermy was established by administration of the metabolic inhibitor 2-deoxy-D-glucose (2-DG). Because this 2-DG-induced state of lowered T_b differs functionally from natural torpor (Westman and Geiser, 2004) and clearly differs from the methodologies employed in the other studies, the 2-DG data are not further considered in this article. Thus, when the same experimental approach is compared among placental mammals, all species investigated appear to display a homeothermic phase after endothermic thermoregulation is established that is followed, after different time intervals, by a heterothermic phase.

The homeothermic phase after establishment of endothermic thermoregulation in a seasonal hibernator, the herbivorous ground squirrel *Spermophilus saturatus* living in montane areas of western North America, appears unequivocal. Endothermic thermoregulation was established in late June. From June to late August (i.e. for more

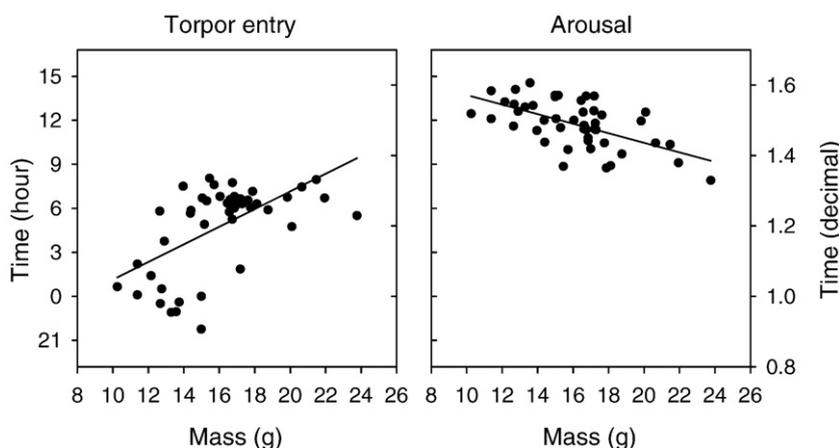


Fig. 2. The time of torpor entry and the time of arousal from torpor in *Sminthopsis macroura* during the growth phase as a function of body mass. Decimal time (i.e. times within one day are expressed as fractions ranging from 0 to 1, shown on right y-axis) was correlated with torpor entry: entry time (decimal) = $0.797 + 0.025$ body mass (g); $r^2 = 0.33$; $p < 0.0001$; arousal time (decimal) = $1.71 - 0.014$ body mass (g); $r^2 = 0.33$; $p < 0.0001$.

than 2 months) it was impossible to induce torpor in juveniles even after withdrawal of food and water for 2 days and cold exposure, which resulted in a substantial (~15 to 20%) reduction in body mass (Geiser and Kenagy, 1990). Only in autumn, two weeks before all juveniles began to hibernate (i.e. displayed prolonged, multi-day torpor bouts) with surplus of food and water, could torpor be induced in some juveniles by withdrawal of food and water.

3.1.3. Birds

Avian species known to be heterothermic during development have been found in the orders Charadriiformes (shorebirds), Coliiformes (mousebirds), Apodiformes (swifts) and Passeriformes (songbirds). Detailed measurements are available only for four species listed in Table 1. For chats, the fifth species, information is limited to field observations by a naturalist. In contrast to all mammals investigated to date in relation to the development of torpor, one of the species (the storm-petrel) is not known to be heterothermic as an adult. Information about patterns of thermoregulation in adult chats is to my knowledge not available.

Juveniles of the plankton and crustacean eating storm-petrel in their natural burrows in the arctic Barren Islands, Alaska, became endothermic at ~5 days post-hatching and, when adults did not provide sufficient food, entered torpor soon thereafter over a period of ~2 weeks during the growth phase (Boersma, 1986). Body mass during this time increased from ~10 to 60 g (the latter is the adult mass).

In herbivorous/frugivorous mousebirds from the Afrotropics, torpor was first observed 10 days after hatching, essentially at the same time when they were capable of endothermic thermoregulation (Finke et al., 1995). Body mass at that time was ~55% of adult mass. Torpor was quantified by respirometry and, because active arousal was induced by T_b measurements to insure that individuals were torpid and not simply hypothermic without the ability of endothermic arousal, torpor bout length was not determined.

Juveniles of insectivorous swifts from Finland (Koskimies, 1948) displayed torpor after 6 days of fasting and T_b fell to lower values on consecutive fast days (~29 °C on day 6, ~26 °C on day 12 during exposure to T_a 24 °C; during exposure to 19 °C, T_b fell to 20.1 °C on the 7th fast day). T_b began to decline at about 1900 h, nocturnal T_b minima were observed between 0100 and 0300 h, and T_b then increased to normothermic levels (~37 °C) by 0500 h, with the exception of day 12 when it remained lower. Young swifts were able to survive fasting for up to 12 days likely because of their large storage of fat and use of nocturnal torpor. Adult swifts also entered torpor with a T_b of 29 °C apparently after a shorter period of starvation than in juveniles.

Young of the insectivorous/granivorous Crimson chat from arid-zone Australia disperse early during development from the nest and spend the night on the ground (Ives, 1973). On the following morning juveniles were found in an inert, torpid state, but revived after passive rewarming. When undisturbed these juveniles must have been able to elevate T_b to normothermic levels either by endogenous heat production or via passive rewarming.

Juvenile insectivorous martins from cool-temperate Europe were capable to enter and arouse from torpor 11 days post-hatching, one day after endothermic thermoregulation was established (Prinzinger and Siedle, 1988). Torpor could be induced by starvation at a body mass of about 12 g (~60% of adult mass), but the time required for torpor induction increased with increasing body mass.

3.2. Evolution of endothermy and torpor

In all species investigated here, the majority of which are members of phylogenetically old groups, endothermy developed after a period of poikilothermy, suggesting that endothermic thermoregulation evolved during, not prior to, the evolution of mammals and birds. With regard to torpor, available data suggest that at least two general patterns of development of endothermy and torpor occur in birds and

mammals and there is no evidence that these are related to climate, habitat or diet. The most frequent temporal pattern appears to be the concurrent development of endothermic thermoregulation and the capability of entering torpor (i.e. poikilothermy followed by heterothermic endothermy). This pattern appears to occur in dasyurid marsupials and birds. The similarity of the developmental sequence of endothermy and torpor in both passerine and non-passerine birds suggests that evolution of torpor is similar in the avian orders that have been investigated (cf. McKechnie and Lovegrove, 2003) (Fig. 3). Only one of the species investigated, the storm-petrel, appears to be an obligate homeotherm as an adult after a heterothermic phase. The second temporal pattern, observed in the placental mammals, is characterised by initial poikilothermy, followed by a homeothermic phase after endothermic thermoregulation is established, and finally a heterothermic phase that may be interrupted by seasonal homeothermy in the adult stage. Thus, the two general developmental patterns of heterothermic species appear to be: (i) poikilothermy–heterothermy and (ii) poikilothermy–homeothermy–heterothermy.

While Haeckel's view that ontogenesis is a brief and rapid recapitulation of phylogenesis is often criticised when applied literally, developmental data are widely used to explore possible functional changes during phylogeny (Dawson and Hudson, 1970; Seymour et al., 2004). If we apply this approach to the developmental data on torpor in relation to endothermic thermoregulation, the observed differences in temporal sequences suggest that the evolution of torpor differs among vertebrate classes and orders.

In four avian orders and one marsupial order, the concurrent development of endothermic thermoregulation and torpor suggest that in these groups torpor is a plesiomorphic trait. It seems, that in these taxa, reptilian eurythermy was maintained although endothermy, made possible by an increased capacity for heat production, had evolved (Hulbert and Else, 1989; Grigg et al., 2004). These groups support the view that torpor occurred early in the evolutionary history of endotherms, perhaps via initial facultative endothermy, and that heterothermy was maintained in these groups throughout their evolutionary history (Augee and Gooden, 1992; Malan, 1996; Grigg et al., 2004). Some now apparently homeothermic lineages, as for example storm-petrels and likely the majority of homeothermic birds and marsupials, must have abandoned the heterothermic phase later in their evolutionary history. Obviously, as birds and mammals are derived from separate reptilian lineages, and endothermy in the two groups most likely evolved independently (Dawson and Hudson, 1970; Hohtola, 2004), torpor in marsupials and birds must also have evolved independently.

In contrast, developmental data on the placental mammals suggest a different evolutionary scenario. As the heterothermic phase in two

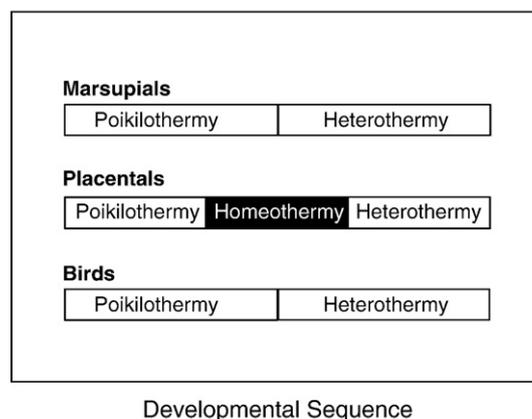


Fig. 3. Developmental sequence of thermal biology of small, altricial marsupial mammals (1 order), placental mammals (2 orders), and birds (4 orders) that are heterothermic at some stage.

placental orders is preceded by a homeothermic phase, the data indicate that in this subclass torpor is a derived trait. This interpretation supports the view that torpor is a secondary adaptation to the environment expressed by certain endothermic taxa and that torpor evolved independently in placental mammals when environmental conditions required a reduction of the high homeothermic metabolism for survival (Bartholomew and Hudson, 1962; Twente and Twente, 1964; Mrosovsky, 1971). Because a derived polyphyletic evolutionary pattern, as proposed by this hypothesis, is currently only supported by data on placentals, it may be restricted to this subclass. Thus, assuming the developmental data reported here are representative and reflect evolutionary sequences, rather than activation of certain ubiquitous genes that may be present in mammals and birds (Carey et al., 2003), they suggest that torpor evolved independently at least thrice. Plesiomorphic torpor appears to have evolved in the birds, and independently in marsupials, whereas torpor in the placentals seems to be a derived trait.

While the arguments presented here may sound plausible with regard to the developmental data, they do require some caveats. These include: (i) The data do not explain the extraordinary similarities in torpor patterns among various endothermic taxa; however, these might reflect limited functional options for a reduction in endothermic metabolism. (ii) Heterothermic birds appear to be predominantly members of modern bird groups, which does not support the argument supported by developmental data; however, lack of knowledge about torpor in old bird taxa may simply be due to lack of detailed investigations on torpor in most avian orders. (iii) Seasonal influences may be more pronounced in northern hemisphere placentals (especially ground squirrels), which could explain the observed differences between marsupials and placentals; however, the data on torpor during the reproductive season in shrews and hamsters do not support the interpretation of a strong seasonal influence on thermoregulatory patterns during the development. (iv) The species/groups that have been investigated may not be representative and temporal developmental patterns may not reflect evolutionary events.

Thus, while the comparative ontogenetic analysis presented here provides a new addition to the hypotheses about the evolution of endothermy and torpor and also provides an experimental avenue for testing evolutionary hypotheses, it does not resolve all the remaining questions. More work investigating the developmental sequence of endothermy and torpor on more taxa, including precocial species such as elephant shrews, is needed to further elucidate the understanding of this evolutionary riddle.

Acknowledgements

Special thanks go to Russ Baudinette for his encouragement and help with the original marsupial study on kowaris. I also wish to thank Rebecca Drury, Sara Hiebert, Esa Hohtola, Gerhard Körtner, Bronwyn McAllan and Lisa Warnecke for help and constructive comments on the manuscript, and the organisers of the R.V. Baudinette symposium and special publication. The work was supported by a grant from the Australian Research Council.

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