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The Evolution of Endothermy and Its Diversity in Mammals and Birds

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ABSTRACT

Many elements of mammalian and avian thermoregulatory mechanisms are present in reptiles, and the changes involved in the transition to endothermy are more quantitative than qualitative. Drawing on our experience with reptiles and echidnas, we comment on that transition and on current theories about how it occurred. The theories divide into two categories, depending on whether selection pressures operated directly or indirectly on mechanisms producing heat. Both categories of theories focus on explaining the evolution of homeothermic endothermy but ignore heterothermy. However, noting that hibernation and torpor are almost certainly plesiomorphic (= ancestral, primitive), and that heterothermy is very common among endotherms, we propose that homeothermic endothermy evolved via heterothermy, with the earliest protoendotherms being facultatively endothermic and retaining their ectothermic capacity for “constitutional eurythermy.” Thus, unlike current models for the evolution of endothermy that assume that hibernation and torpor are specialisations arising from homeothermic ancestry, and therefore irrelevant, we consider that they are central. We note the sophistication of thermoregulatory behavior and control in reptiles, including precise control over conductance, and argue that brooding endothermy seen in some otherwise ectothermic Boidae suggests an incipient capacity for facultative endothermy in reptiles. We suggest that the earliest insulation in protoendotherms may have been internal, arising from redistribution of the fat bodies that are typical of reptiles. We note that short-beaked echidnas provide a useful living model of what an (advanced) protoendotherm may have been like. Echidnas have the advantages of endo-

thermy, including the capacity for homeothermic endothermy during incubation, but are very relaxed in their thermoregulatory precision and minimise energetic costs by using ectothermy facultatively when entering short- or long-term torpor. They also have a substantial layer of internal dorsal insulation. We favor theories about the evolution of endothermy that invoke direct selection for the benefits conferred by warmth, such as expanding daily activity into the night, higher capacities for sustained activity, higher digestion rates, climatic range expansion, and, not unrelated, control over incubation temperature and the benefits for parental care. We present an indicative, stepwise schema in which observed patterns of body temperature are a consequence of selection pressures, the underlying mechanisms, and energy optimization, and in which homeothermy results when it is energetically desirable rather than as the logical endpoint.

Introduction

Endothermy has arisen in insects, fishes, reptiles, birds, and mammals, as well as in some plants. However the evolution of endothermy in mammals has attracted the most debate and attention, and it is regarded as one of the most significant transitions in vertebrate evolution. We bring two perspectives to the debate that are different from published views of other authors; a focus on the relevance of thermoregulatory mechanisms in reptiles, many of which foreshadow those used by mammals and birds, and a consideration of the implications of the view that mammalian and avian torpors are probably plesiomorphic (see review by Grigg [2004]). Although we will concentrate on mammalian endothermy, many of our considerations are relevant to birds also.

What endotherms have is the capacity for substantial heat production as a by-product of cellular work, either with or without muscular contractions, and its retention or loss governed by mechanisms that regulate thermal conductance. The heat-production, heat-loss equation is such that endotherms have the capacity to display body temperature patterns that are conspicuously different from those within the capacities of ectotherms.

Current ideas about the evolution of endothermy focus on the evolution of homeothermic endothermy. This is not surprising because it is usually assumed that endotherms are typically homeothermic, with a stable, high body temperature.

However, homeothermy may not be characteristic of even the majority of endotherms. Substantial daily and seasonal T_b variations occur in very many mammals and birds (reviews by McKechnie and Lovegrove [2002] and Geiser [2004]) and, as data accumulate from studies of free-ranging species, more and more are found to show heterothermic patterns. Even some primates are heterothermic (e.g., Madagascan lemurs; Dausmann et al. 2000). Not only is heterothermy common, but there is good evidence to suggest that hibernation is probably plesiomorphic (Augee and Gooden 1992) and that hibernation and short-term (daily) torpor are likely to be homologous (Grigg 2004), implying that torpor in the broader sense is plesiomorphic. This has implications for thinking about the evolution of endothermy (Grigg and Beard 2000; Grigg 2004). In this article we will review the evidence available from among reptiles, show that short-beaked echidnas have many of the attributes that might be expected in a putative protoendotherm and draw the threads together to propose a logical stepwise scenario for the evolution of endothermy in a way that incorporates the implications of torpor being plesiomorphic. The scenario also includes a new idea about the vexed question of the evolution of insulation. We think our scenario is broadly compatible with much of what has been written by others about probable selection pressures but extends and expands it.

Current Ideas about the Evolution of Endothermy

Ruben (1995, 1996), Hayes and Garland (1995), and Farmer (2000) all provide excellent and comprehensive reviews of the literature on this topic. Numerous models have been proposed, and they fall broadly into two categories. One category includes models that assume direct selection for the benefits of high T_b and high resting metabolic rate, such as the thermal niche expansion model (Bakken and Gates 1975; Crompton et al. 1978), the homeothermy and increased metabolic efficiency model (Heinrich 1977; Avery 1979), the endothermy via inertial homeothermy model (McNab 1978), and the parental care model (Farmer 2000). Implicit in all these models is the notion that warmth allows a higher resting metabolic rate and, therefore, has a high selective value. These ideas are sometimes referred to collectively as the thermoregulatory hypotheses.

The second broad category includes models that consider the benefits of warmth per se to be insufficient to warrant the costs, and that the high metabolic rates typical of endotherms must have arisen as a consequence of selection for other advantages such as postural changes that increase exercise (Heath 1968; Bakker 1971), increased brain size (Hulbert 1980), or higher aerobic capacity (Bennett and Ruben 1979; Bennett 1991; Ruben 1995). The aerobic capacity model has gained prominence in recent years. According to this model, selection for increased aerobic capacity to support a higher level of sustained activity has led consequentially to higher resting metabolic rates and, apparently as a more or less accidental by-

product, higher resting heat production and the capacity for homeothermic endothermy.

The difficulty of establishing that a higher active metabolic rate implies a high resting rate as well has been a problem with this model (see discussion by Hayes and Garland [1995]), and this may be why Ruben (1995) included the possibility of “inertial homeothermy” (sensu McNab 1978), in which homeothermy comes as a correlate of higher thermal inertia at large body size.

Our aim is not necessarily to try to discriminate between these two groups of models but to use our own research on reptiles and echidnas to better define the appropriate questions, broaden the discussion, and further develop some ideas we presented previously (Grigg and Beard 2000).

Who were the earliest protoendotherms? It is thought that mammals arose late in the Triassic, from the cynodont therapsid reptiles about 200 mya (Rowe 1992). Ruben and Jones (2000) noted that because endothermy occurs in all three classes of extant mammals, by parsimony their last common Mesozoic ancestor, about 160 mya, must also have been endothermic, with a high resting metabolic rate and hair. However, endothermy almost certainly arose even earlier than the evolution of mammals. Hillenius (1994) suggested that the presence of respiratory turbinates in the nasal passages provides a useful marker for the possession of endothermy, implying that “mammalian” endothermy first arose in the Permian therapsid reptiles, about 250 mya in the late Permian. Thus, the first “mammalian” protoendotherms were likely to be the dog- or bear-sized therocephalians. These animals are thought to have been active carnivores, 20–100 kg, living in tropical and subtropical climates, essentially reptilian in most features and apparently lacking hair or any external insulation (Ruben and Jones 2000). These authors also considered that these animals may have been inertial homeotherms, but, as we will discuss later, that idea can be dismissed.

The Relevance of Torpor Being Plesiomorphic

Torpor, hibernation, and estivation in mammals are all qualitative descriptions of deviations from what has come to be regarded as “normal” mammalian homeothermy. Lyman and Blinks (1959) considered hibernation to be functionally advanced and specialized, and Wang (1989, p. 392) wrote that “the wide occurrence of torpor in species from at least six mammalian and eight avian orders suggests that it is polyphyletic in origin.” This remains the prevailing view. Ruben (1995) accepted Wang’s (1989) judgment and dismissed the relevance of torpor/hibernation to considerations about the evolution of endothermy.

However, this dismissal may not be justified. A more parsimonious interpretation of the taxonomic distribution and other aspects of both short- and long-term torpor, reviewed by Grigg and Beard (2000) and Grigg (2004), leads to the

alternate conclusion that daily torpor and hibernation are likely to be plesiomorphic and, furthermore, are supported by similar mechanisms expressed to different extents. Augee and Gooden (1992) proposed that the ability to hibernate, occurring as it does in such a wide diversity of mammalian groups and across all three orders of extant mammals, argues for a plesiomorphic origin, not a polyphyletic one. Quite independently, Malan (1996, p. 2) noted similarities in the T_b patterns expressed by hibernators to those seen seasonally in many reptiles and came to the same conclusion: that “we should now consider the phylogeny of hibernation, not as the repetitive and independent occurrence of a secondary adaptation in various phyla, but simply as a recurring expression of primitive traits.”

The idea is not new; Cade (1964) interpreted the occurrence of torpor/hibernation in five out of 14–15 distinct lineages within the Rodentia as evidence of intermediate stages in the “history of rodent evolution of homeothermic mechanisms and the associated loss of tolerance for deep hypothermia.” He also drew particular attention to the significance of torpidating/hibernating mammals’ tolerance for low T_b , which Eisentraut (1960) had called “constitutional eurythermy.” More recently, Lovegrove et al. (1999) interpreted the finding of torpor in elephant shrews (Macroscelidae) as support for a plesiomorphic origin of heterothermy.

Furthermore, while there is strong evidence that endothermy must have arisen independently in birds and mammals, the mechanisms underlying torpor/hibernation in both groups could well be monophyletic in origin. Malan (1996) certainly saw these attributes in both mammals and birds as stretching back to a common ancestry in the reptiles. With torpor/hibernation being found in 11 out of 26 orders of birds, and still counting, including the ancient mousebirds (Coliidae; McKechnie and Lovegrove 2002), parsimony again suggests plesiomorphy, as argued by these authors. As in mammals, avian evidence continues to accumulate; Lane et al. (2004) concluded that heterothermy within the Caprimulgiformes is plesiomorphic. It seems likely that the physiological mechanisms that support torpor in birds and mammals share the same ancient origins and, therefore, the evolution of their endothermy may be more similar than is usually acknowledged.

The plesiomorphic model makes it easy to see how attributes shown by a heterotherm in a milder climate could be selected for and enable range expansion into more severe climates, with attendant specializations to fine-tune behaviors, tie them to relevant day-length cues, and even to change membrane structure, which may be necessary if drops to very low T_b will be encountered (Aloia et al. 1986). That is, we interpret the patterns shown by the “classic” hibernators not as specializations from homeothermic endothermy but as specializations at one end of a whole spectrum of examples with attributes deriving from ancestral heterothermic capabilities differentially expressed (Grigg 2004). The complex physiology and behaviour in arctic ground squirrels, for example (Barnes 1989; Boyer and

Barnes 1999), keyed tightly to seasonal events and enabling survival through Arctic winters, are specializations from more facultative styles of heterothermy seen in their relatives still living in less severe conditions (Grigg 2004). Echidnas provide another example (see later), with both facultative and obligate hibernation being shown within the one species, depending on where they live (Grigg and Beard 2000; Kuchel 2003). In mild climates where food is available all year, echidnas hibernate facultatively, perhaps depending on overall energy status. In areas snow clad in winter, where both harsh conditions and food shortage prevail, they match the pattern seen in classical hibernators, and all individuals hibernate every year.

If the physiological and behavioral capacities for short-term torpor and hibernation are expressions of persistent/reemergent capacities reflecting reptilian ancestry, and because the thermoregulatory systems present in reptiles foreshadow so strongly those of mammals and birds, it seems reasonable to suggest that studies of torpor and hibernation should be a central theme in studies of the evolution of endothermy. Indeed, the entry into daily torpor or hibernation may involve a reversal of some of the same physiological mechanisms that accompanied the evolution of endothermy from ectothermy (Grigg and Beard 2000).

Evidence from Living Reptiles

If endothermy arose in a lineage of therapsid reptiles, clues to its origin may survive among extant reptiles. Few, if any, reptiles are simply passive thermoconformers. There are behavioural and physiological mechanisms that cause many reptiles to have a high (and often relatively stable) body temperature during daytime hours (see review chapters in Gans and Pough 1982), and these have been selected for, presumably, because of the benefits accruing from being warm. It could be argued that there are few associated costs when the heat source is external, but this overlooks the potential high cost of predation exposure in a cool, basking lizard. A really impressive example of the benefits accruing from warmth is provided by Australia’s freshwater crocodile, *Crocodylus johnstonii*, in which social hierarchy and the competition for basking sites dictates which individuals in the population are thermoregulators rather than thermoconformers, with undoubted advantages in growth and reproductive success (Seebacher and Grigg 1997).

Modern reptiles provide a rich source of information relevant to the evolution of endothermy, but, before exploring that, we will examine an idea that has been influential even to the extent of possible inclusion in variants of the aerobic capacity hypothesis (Ruben 1995; Ruben and Jones 2000), the hypothesis that endothermy arose via passive homeothermy. (Note that the term “homeothermy” is used in older literature and even some modern literature as if it were synonymous with what would now be termed “homeothermic endothermy.”)

Endothermy did not evolve via “inertial homeothermy.”

Table 1: Comparison of patterns, mechanisms, and regulation between reptilian ectotherms and their descendants, the endothermic mammals and birds

	Reptilian Ectotherm	Mammalian Endotherm	Avian Endotherm
Pattern of T_b	Daily and seasonal fluctuations, T_b may be high and stable during activity periods. Size related. Facultative endothermy in brooding pythons.	Commonly high and stable, commonly heterothermic, modal values differ between three classes. Many show torpor and/or hibernation.	Mostly high and stable, commonly heterothermic, modal values higher than in the three mammalian classes. Many show torpor, few show hibernation.
Mechanisms	Primarily behavioral, heat production from RMR low, little heat from leaky membranes, physiological mechanisms include panting, changes in peripheral blood flow. Muscle thermogenesis in brooding pythons foreshadows some attributes of endotherms, including the capacity to increase metabolic rate when ambient temperature falls.	Behavior still important, heat production from RMR high (leakier membranes), physiological mechanisms include changes in peripheral blood flow, panting, sweating, insulation. Locomotion. Shivering. Regulatory NST from unknown source in marsupials (skeletal muscle?) and possibly all mammals. BAT a specialized tissue forming a thermogenic organ in many eutherian mammals, particularly eutherian hibernators and young.	Behavior still important, heat production from RMR high (leakier membranes), physiological mechanisms include changes in peripheral blood flow, panting (gular flutter), insulation. Locomotion. Shivering. Regulatory NST, possibly from sarcoplasmic reticulum.
Regulation	Role of hypothalamus in regulating behavior and physiology relevant to thermoregulation.	Role of hypothalamus in regulating behavior and physiology relevant to thermoregulation.	Role of hypothalamus in regulating behavior and physiology relevant to thermoregulation.

MacNab (1978) proposed ingeniously that endothermy evolved via inertial (passive) homeothermy, gained through large body size and maintained by selection for the advantages accompanying homeothermy as body sizes decreased. It is therefore relevant to explore extant species to see how large a reptile would have to be to show passive homeothermy across both daily and seasonal timescales. Data from a study of daily and seasonal changes in T_b in estuarine crocodiles, *Crocodylus porosus*, in a tropical habitat and over a size range from 32 to 1,000 kg (Grigg et al. 1998; Seebacher et al. 1999) show clearly that dog- or bear-sized protoendotherms in a tropical or subtropical climate could not have been inertial homeotherms. Movements to and from the water and between sun and shade minimized daily changes in T_b . T_b cycled daily through about 7°C in the smallest animals (32–42 kg) decreasing to 2°–3°C in the largest animals (600–1,000 kg). So the largest individuals were essentially passive homeotherms at the timescale of a single day and, if thermostability within 2°C is accepted as homeothermy, this pattern was observed in animals larger than about 500 kg. That is, inertial homeothermy over the course of even a single day is found in only quite large individuals, even in a tropical environment. What was interesting, however, and very relevant to this discussion, is that at a seasonal scale the range

in modal daily T_b between winter and summer was similar in both larger and smaller individuals, 4°–5°C. Even a 1-ton crocodile, seeking sun or shade, water or land, and doing so in a way that minimizes change in T_b , is not thermostable across seasons. Inertial homeothermy at a seasonal scale could occur in only very large reptiles, much larger than 1 ton, at any latitude. Furthermore, the acquisition of inertial homeothermy does not necessarily imply the acquisition of warmth as well. Admittedly, T_b in reptiles large enough to be passively homeothermic does increase with an increase in body size (Seebacher et al. 1999), but the crocodilian data show that the combination of passive homeothermy and substantially above-ambient T_b could not occur in reptiles in the size range of the Permian theriocephalians (i.e., less than 100 kg). The evidence suggests that MacNab's idea that endothermy evolved via passive homeothermy can be disregarded.

A comparison between reptiles and the higher vertebrate endotherms. The extent to which reptilian thermoregulatory systems foreshadow those in mammals and birds is striking; most of the differences are more quantitative than qualitative (Table 1).

Reptiles have sophisticated control over thermal conductance. Reptiles can effect considerable control over thermal conduc-

tance through changes in peripheral blood flow. The hysteresis between rates of heating and cooling was described initially by Bartholomew and Tucker (1963) in a laboratory study of bearded dragons, *Pogona* (= *Amphibolorus*) *barbata*. Its occurrence and relevance to reptiles under natural conditions was confirmed in a field study by Grigg and Seebacher (1999) in the same species. Increased blood flow allows a cool reptile to gain heat rapidly while basking; after basking, decreased flow leads to decreased conductance and allows a warm reptile to maintain its heat load for longer in a cooling environment. Excitingly, the fieldwork showed that this species also has the capacity to reduce peripheral blood flow and avoid further warming under high operative temperatures, that is, a “reverse hysteresis.” These carefully regulated changes in conductance foreshadow mechanisms seen in both mammals and birds.

Shivering thermogenesis in brooding pythons, and its integration with basking. Shivering thermogenesis by brooding female Boidae is usually dismissed as a curious adaptation in a few very specialized reptiles. However, the shivering thermogenesis in brooding pythons (Hutchison et al. 1966; Harlow and Grigg 1984) shows that reptiles have more of the capacities of endotherms than is generally recognized and, therefore, is very relevant to discussions about the evolution of endothermy. These snakes are able to shiver and raise the temperature of their eggs above a threshold allowing development, as well as increasing the rate of development. They are, therefore, facultative endotherms. Very significantly, and just like mammals and birds, they respond to a lowered ambient temperature by increasing their metabolic rate by increased shivering, thus maintaining T_b .

Furthermore, their integration of shivering with typical ectothermic basking behaviour is particularly interesting. When the snake in Harlow and Grigg's (1984) study on *Morelia spilota* had an ambient heat source available a short distance away, she would leave the eggs each morning to bask and, when warmed to 32°–33°C, return and coil once more around the eggs, shivering from then on as required to maintain T_b . This is very reminiscent of the way ectothermy and endothermy are integrated in an energetically sensible way in some mammalian endotherms, for example, in the torpidating carnivorous marsupial, *Pseudantechinus macdonnellensis*, which uses the morning sun to rewarm following an overnight torpor (Geiser et al. 2002), and in two species of mouse lemur, *Microcebus*, in which the early morning T_b rises passively with ambient temperature until the start of the next activity session (Schmid 1996). In general, though often overlooked, behaviour is a very important element in thermoregulation of all mammals and birds, just as it is in reptiles.

Some additional observations from reptiles. Tosini and Menaker (1995) described physiologically generated circadian rhythms in T_b in iguanas, *Iguana iguana*, kept at constant temperature, in which activity cycles were not the cause of the increases in T_b . This seems to be an example among reptiles

of limited endogenous heat production not associated with muscular work, the sort of difference upon which, presumably, natural selection can operate. Leakiness in membranes, although less than in mammals (Else and Hulbert 1987), is a feature of reptilian tissues also, so it is possible to imagine selection pressures operating to increase this to the extent of providing substantial heat as a by-product. The temperature increases in *I. iguana* were only small, 1°–2°C, and oxygen consumption was not measured simultaneously, but the results are provocative.

Also provocative, Rismiller and McKelvey (2000) described patterns of T_b in a varanid lizard in winter that appear strikingly similar to the spontaneous arousals that characterize hibernating mammals. Will study of reptiles shed light on the enigmatic but characteristic periodic arousals that characterize hibernation in eutherian, marsupial, and monotreme hibernators?

Selection for warmth rather than increased aerobic capacity? The “thermoregulatory hypothesis” assumes that there was positive selection for increased resting metabolic rate in the evolution of the higher body temperatures, presumably within the therapsid-cynodont lineage in the case of mammals, because of the advantages accrued by warmth. As discussed, reptiles show a number of mechanisms that operate to collect, retain, and even, in a couple of instances, generate warmth quite apart from increased aerobic capacity. Much of the heat production associated with high resting metabolic rate in endotherms comes from otherwise futile work, and that by itself might be offered as an argument in favor of the thermoregulatory hypothesis.

The “protoendotherms” may have been facultative endotherms. Many elements of endothermy are present and functional in living reptiles: excellent peripheral vascular control, a sophisticated regulatory control of thermoregulation, examples of facultative endothermy by shivering thermogenesis, and an example of small circadian increases in T_b not associated with activity. Given this, we propose that the evolution of endothermy is likely to have occurred via stages in which selective pressures favored the enhancement of elements present within reptiles and that the early “protoendotherms” were facultative rather than obligate endotherms, like the only known extant reptilian endotherms.

Echidnas and the Protoendotherm

Having identified characteristics of reptiles that seem to be foreshadowing endothermy, can we find extant mammals or birds that seem to echo strongly the features likely to be found in a putative protoendotherm? Among the extant mammals, short-beaked echidnas seem to have many of them. Martin (1903) wrote about echidnas in the context of the development of “homeothermism.” After a comprehensive study of captive echidnas in outdoor pens in Melbourne, Australia, and based

on their heterothermy, low T_b , reliance on muscular work for heat, and apparent lack of NST, Augée (1978, p. 118) wrote, “unless fossil evidence is obtained to the contrary, the best interpretation of monotremes in regard to endothermy/homeothermy is that they represent an early stage in its evolution.”

Both of these studies predated the availability of data from radiotelemetry of echidnas free-ranging in their natural habitat and, therefore, the realization that echidnas are hibernators (Grigg et al. 1989) and also torpidators (Grigg et al. 1992a). These studies, combined with data from other workers, provide a much better understanding of echidna thermal relations, and, therefore, a reappraisal of their relevance to ideas about the evolution of endothermy is timely.

Short-beaked echidnas match in many respects the attributes that one might design in a putative protoendotherm. They occur all over Australia, from the tropics to cold temperate regions, above the snowline, and by the coast. This distribution implies very substantial adaptability to different thermal regimes, and their thermal relations have now been studied in detail across a wide variety of habitats and climates (Grigg et al. 1989, 1992a; Beard et al. 1992; Nicol and Andersen 1993, 2000; Rismiller and McKelvey 1996; Grigg and Beard 2000; Brice et al. 2002a, 2002b; Kuchel 2003).

A number of generalizations emerge that we will illustrate using published information supplemented with previously unpublished data from our study site near Stanthorpe in SE Queensland, a comparatively mild, subtemperate climate:

1. Although the modal T_b of echidnas is close to 32°C (the same as the other monotremes; Dawson et al. 1978; Grigg et al. 1989, 1992a, 1992b, 2003), they are relaxed about maintaining a stable T_b , with typical daily cycles of 2°–5°C (Fig. 1a), sometimes larger (Fig. 1b), that correlate with their daily activity cycle. Daily maxima and minima may not correlate with ambient temperatures (Grigg et al. 1992a; Kuchel 2003). A facultatively endothermic protoendotherm might have been similarly relaxed about regulating T_b and might have had a lower modal T_b than is typical of most mammals or of birds.

2. Behaviour is important in echidna thermal relations, and shifts in the time of day at which echidnas are active contribute significantly to the similarity of daily patterns seen in markedly different climates. Thus they are more diurnal in cooler climates and more nocturnal in warmer climates and often shift their active period seasonally. For example, in the hot, semiarid continental climate of central Queensland, they may be active at any time of the day during winter and spring (unless hibernating) but are strictly nocturnal in summer, seeking shelter in caves and burrows to avoid the heat (Brice et al. 2002a). Avoiding heat is important, for they lack sweat glands and presumably rely on the heat sink provided by ambient conditions to counter heat production associated with exercise. On unusually warm days in the Australian Alps, where they are normally active during the day, we recorded them losing heat quickly after seeking shade or a cool stream when T_b reached 34°C (Grigg

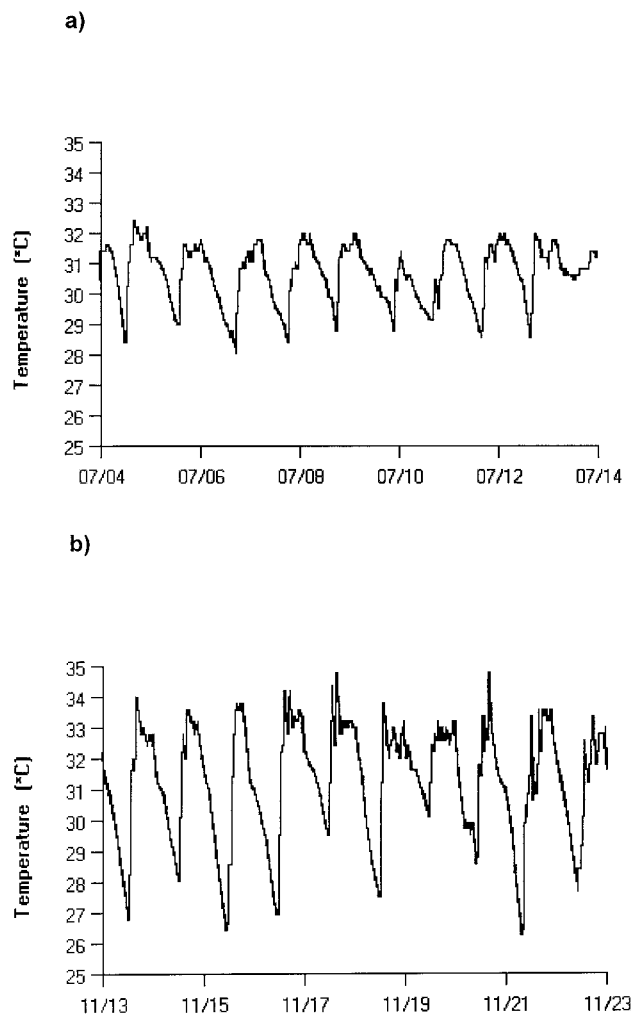


Figure 1. Two examples of daily cycles in body temperature in a male echidna (95) at our southeast Queensland study site, which has a warm temperate climate. *a*, July 4–14, 2001 (southern winter). *b*, November 13–23, 2001 (southern summer).

et al. 1992a). A protoendotherm would presumably also have had to rely on behaviour to assist in its thermoregulation.

3. An early endotherm might have been expected to make considerable use of basking. Basking has rarely been observed in short-beaked echidnas in the wild, perhaps because they seem to spend all their waking hours foraging actively. Echidnas in captivity and in the wild occasionally do lie in full sun, giving every impression of basking. T_b in a 3.3-kg individual rose from 28.0° to 30.8°C in about 90 min, during which she shifted position occasionally as if to remain in the sun. How much of this increase can be attributed to insolation is, however, unknown. Manning and Grigg (1997), working on freshwater turtles, have shown that observations on apparent basking behaviour can be very misleading, and more work is needed to establish how much echidnas make use of basking.

4. Echidnas have good capacity for changes in thermal conductance. By analogy with reptiles, and mammals and birds, the putative protoendotherm could be expected to have good control over thermal conductance. Dawson et al. (1978, p. 100) described a fourfold increase in conductance in *Zaglossus* (long-beaked echidna) between T_a 15°C and T_a 30°C, which they attributed to a “considerable increase in peripheral blood flow to facilitate heat dissipation.” Schmidt-Nielsen et al. (1966) described similar changes in thermal conductance in *Tachyglossus*. The changes in conductance can be ascribed to changes in peripheral blood flow. In both echidnas there is a substantial muscle layer (*panniculus carnosus*) external to the fat layer (*panniculus adiposus*) in which the spines are deeply embedded and that is well supplied with blood. This dorsal fat layer is ideally placed to act as effective insulation. However, it can be bypassed by blood flowing peripherally either during basking for heat gain or when heat loss is required. Echidnas in cooler climates are conspicuously more hairy than in warm climates, where they have almost no hair between the spines.

5. Echidnas lack sweat glands and do not pant (Augee 1976) and on the basis of this and early experimental work (Robinson 1954, cited in Griffiths 1968) echidnas have come to be regarded as intolerant of heat (Griffiths 1978). However, Brice et al. (2002a) have shown in fieldwork that they rest in surprisingly warm daytime shelters and maintain T_b below T_a . Further work on this is in progress in our laboratory. Do they reduce metabolic rate and show patterns reminiscent of the “reverse hysteresis” discovered in *Pogona*, as might be expected in a protoendotherm?

6. Short-beaked echidnas also show both short-term and long-term hypothermias that fit the patterns usually identified as short-term torpor and hibernation, respectively. Of particular interest in the context of the present topic, echidnas often and at any time of the year show large, short-term drops in T_b , sometimes in a daily cycle (Fig. 1b) and sometimes the result of a day in which the activity period was foregone (Fig. 2). Such large departures from “normal” T_b are usually identified as torpor events, even if no information is recorded about the capacity for locomotor coordination (see below).

Short-beaked echidna long-term torpors may last for weeks or months, interrupted by periodic arousals to normal body temperatures (Fig. 3), matching the pattern of so-called classical hibernation thought originally to occur only in Eutheria. Thus, short-beaked echidnas were the first mammals in which both torpor and hibernation were described (Grigg et al. 1992a), a phenomenon now known also in the edible dormouse, *Glis glis* (Wilz and Heldmaier 2000). The occurrence of both daily torpor and hibernation in the same species begs questions about the extent to which these patterns are supported by different mechanisms or simply expressions of the same mechanism expressed to different extents. Kuchel (2003) found that it was impossible to make distinctions in echidnas; 1-, 2-, and 3-d torpors merged indistinguishably into longer periods that, in

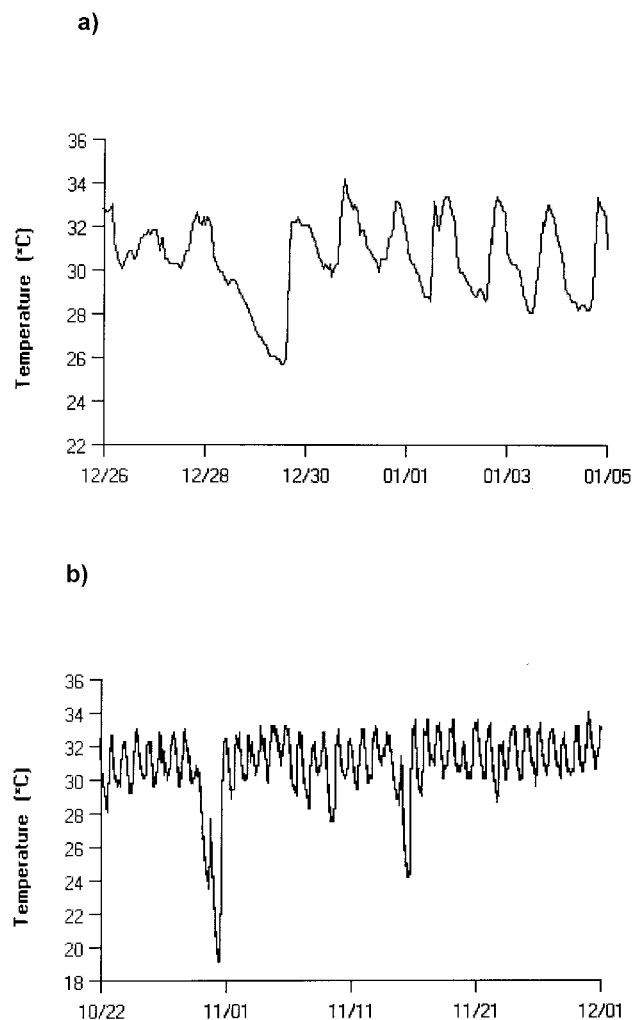


Figure 2. Two examples at our southeast Queensland study site of departures from the normal daily pattern of body temperature caused by the echidna foregoing its normal daily foraging activity. By analogy with common practice, such departures might be said to be indicative of daily torpor. a, Echidna 117, male, December 26, 2000–January 5, 2001. b, Echidna 93, female, October 22–December 1, 2000.

winter, were broken by periodic arousals and qualified as hibernation. She could not find a distinction on the basis of metabolic rate either. Grigg (2004) took up this question further and concluded that daily torpor and hibernation are likely to be supported by similar mechanisms. That is, they share a high degree of homology. Such flexibility in the adoption of ectothermy or endothermy could be expected in an early, facultative endotherm.

7. Likewise logical in a protoendotherm, and particularly significant for our present topic, echidnas show hibernation in surprisingly mild climates. The biggest differences in T_b patterns found so far between studies at different locations is that echidnas in warmer climates spend less time in hibernation than

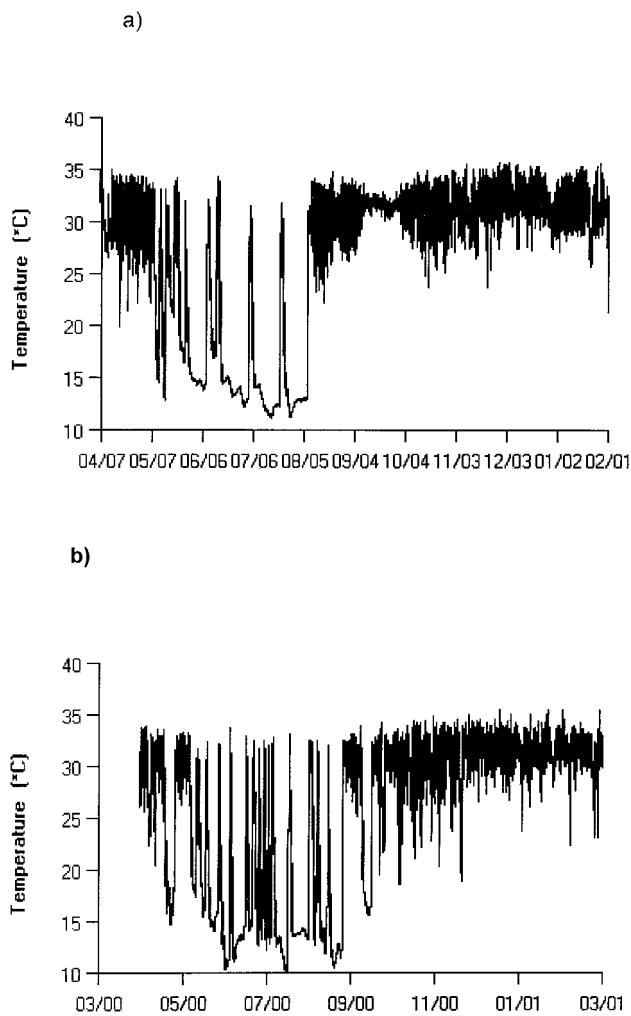


Figure 3. Two examples of patterns of hibernation shown at our warm temperate, southeast Queensland study site. *a*, Echidna 90, female, April 2000–February 2002. Note the conspicuous period of “homeothermy” in late September, from before laying the single egg, during incubation, and for a short period thereafter, showing a capacity to regulate T_b very tightly. *b*, Echidna 115, female, nonbreeding that year, March 2000–March 2001.

those in colder climates, and in the warmer areas hibernation seems to be facultative rather than obligate. All individuals in the Tasmanian and Australian Alps studies hibernated, every year, for periods up to about 7 mo. Males entered earlier and aroused earlier than females at both locations. In these colder climates, some (younger?) individuals remain in hibernation until well into the spring, missing the breeding season. In contrast, hibernation is facultative in the warm, temperate, continental climate of our study site near Stanthorpe, Queensland. Here, Kuchel (2003) found that hibernation occurred in nine out of 15 echidna-years of data, males being less likely to hibernate than females, and that the length of the hibernation

season varied considerably between individuals—approximately 1–4 mo. Data from other sites are less numerous, making generalizations more difficult. In the hot, semiarid continental climate of Idalia National Park in central Queensland, all three individuals from which data loggers were recovered showed hibernation for about 3 mo, and all showed torpor events (Brice et al. 2002a and personal communication).

That echidnas often hibernate in very mild climates where food shortages are unlikely, and display such a diversity of hibernation patterns, has prompted considerable interest (Nicol and Andersen 1996, 2000; Grigg and Beard 2000; Kuchel 2003). We (Grigg and Beard 2000) concluded that the purpose of hibernation in benign climates is to achieve an energetic advantage. Animals well prepared for the spring breeding season might be “putting themselves on ice” for the winter. This predicts that in a climate where hibernation is facultative, animals with good body condition in autumn would hibernate, while animals in lesser condition would choose to continue to forage through the winter. Kuchel (2003) explored this proposition and found somewhat equivocal results. She did, however, confirm that hibernation represents a saving on the year’s energy expenditure though, as would be expected, less than in hibernators in colder climates.

8. Despite being conspicuously heterothermic, echidnas do have the capacity for homeothermic endothermy, as clearly shown during incubation. Just before laying their single egg, during incubation, and for a few days thereafter, a total of 2–3 wk, they have the capacity to regulate T_b very tightly (Beard and Grigg 2000; see also Fig. 3a). The exact source or sources of heat during this time remain unresolved.

9. Another aspect of short-beaked echidna thermal relations is that they have the clear capacity for apparently normal activity at very low body temperatures in comparison to other mammals. Although this has received only passing mention in previous accounts, it is very important in the present context. Echidnas can be foraging at the lowest T_b of their daily cycle, presumably shortly after emerging from the resting site. The lowest T_b at which Kuchel (2003) sighted an animal active and foraging was 20.6°C. It is apparent that they have the capacity to be active over a T_b range of more than 15°C. This capacity for constitutional eurythermy is characteristic of reptiles as well and would be expected in an early, facultative endotherm, and its loss in homeothermic endotherms (that show constitutional stenothermy) was identified by Cade (1964) as an important correlate of the evolution of ectothermy to “homeothermy” (=homeothermic endothermy). It could be argued that the term “torpor” should not be used unless T_b falls below the point where coordinated activity ceases. In echidnas, this would be below 20°C (Kuchel 2003). At one level, this throws doubt on whether defining torpor according to the extent of the drop in T_b (see Barclay et al. 2001) is sufficient, as has been discussed by McKechnie and Lovegrove (2002) and Grigg (2004). At another level, however, it is worth remembering that the terms

“torpor” and “hibernation,” like “poikilothermy” and “homeothermy,” are descriptive of patterns, not mechanisms. They are useful because of the descriptive information they convey but cannot be defined tightly because of the diversity of patterns to which they are applied. When we have sufficient understanding of the mechanisms at work that explain the observed patterns, those terms, like poikilothermy and homeothermy (in the old sense), will be replaced.

In short, echidnas are facultative ectotherms that, although having resting metabolic rates much higher than reptiles, shivering thermogenesis, a conspicuous heat input from locomotor activity, and the capacity for homeothermic endothermy, also show a strikingly heterothermic pattern of T_b most of the time. They also show striking abandonments of their normal daily pattern, in the form of periods of daily torpor at any time of the year and periods of classical winter hibernation of widely varying duration that are longest in cooler climates. We do not consider that the short-beaked echidna displays a primitive or inadequate monotreme grade of thermoregulatory capacity. Rather, within its lineage, and like many marsupials and eutherians, it has retained and refined the capacity to tolerate low body temperatures and, for reasons dictated primarily by energy management, can enter a diversity of torpor/hibernation states that may not be very different physiologically from each other. We think, therefore, that in having many attributes that one might expect to find in an advanced protoendotherm, short-beaked echidnas provide a useful, living model.

Physiological Steps in the Evolution of Endothermy

Any model for the evolution of endothermy must accommodate realistic interpretations of each of the elements of difference between reptilian ectothermy and mammalian or avian endothermy, as well as elements carried over. The elements of difference relate particularly to the various sources of heat production and the acquisition and control of lowered thermal conductance.

Increased Biochemical Heat Production

We identify five endogenous sources of heat in mammals; muscular work associated with locomotion and other activity, otherwise futile muscular work (shivering), heat produced from whatever comprises basal metabolic rate (including futile work associated with maintaining gradients across leaky membranes), heat produced by the uncoupling of oxidative phosphorylation using the uncoupling protein UCP1 in brown adipose tissue (BAT; review by Cannon and Nedergaard 2004; usually referred to as regulatory nonshivering thermogenesis, NST) and, quite possibly, an additional source of regulatory, controllable NST located in skeletal muscle, similar to that described in birds (see review by Bicudo et al. [2002]).

The most obvious source of increased heat production (and

possibly the oldest?) is from muscular work, either as a consequence of locomotor activity or from shivering. There is little work on heat production as a by-product of activity in reptiles. What might be the significance of muscular heat production in the evolution of endothermy in birds and mammals?

1. *Locomotor activity.* The daily increases in T_b in both short-beaked (detailed analysis by Kuchel 2003; Fig. 1) and long-beaked (Grigg et al. 2003) echidnas coincide with their daily foraging activities. Indeed, Augee (1978) considered that the main source of heat in short-beaked echidnas was their muscular activity. The picture cannot be so simple, however, because otherwise the daily T_b minima, at the end of rest periods, would depend upon ambient temperatures, and this is not the case (Grigg et al. 1992a; Kuchel 2003). It is comparatively easy to imagine that the benefits of warmth gained from muscular work could be recognised in an evolutionary sense and lead to direct selection for less visible and probably less expensive mechanisms of heat production that do not involve muscular work. Perhaps the evolution of higher resting metabolic rates in mammals and birds, via leaky membranes, came as the evolution of a replacement for heat produced by muscular work. The strong expression of heat produced by muscular work on the daily T_b cycle of echidnas may provide an example of a situation that could have been present among protoendotherms.

2. *Shivering thermogenesis.* Shivering thermogenesis occurs in birds and mammals (and boid snakes). It occurs in all three classes of mammals, including our model protoendotherm, the short-beaked echidna. It is a significant contributor to the increased oxygen consumption seen at ambient temperatures below the thermoneutral zone. In birds and those mammals that lack BAT, many authors would assume that all of that increased oxygen consumption is attributable to shivering, but this may not be so (see point 5 below).

3. *High resting metabolic rates.* Resting metabolic rates are, by definition, measured within the thermoneutral zone, and the heat produced as a consequence of that metabolism, fed into a heat balance equation, will account for the maintenance of a high and stable T_b . Importantly, because it suggests that heat from this source is a continuing background production rather than a regulated source, this heat production is an intrinsic property of the tissues themselves for, when the metabolic rate of excised tissues (liver, heart, brain) is determined, that of mammalian tissue exceeds that of reptilian tissue by a factor of approximately 5 (Else and Hulbert 1987). Whole-organism metabolic rates reflect a similar difference between mammals and reptiles. Further, these and other authors have explored the source of the measured difference and found higher mitochondrial densities and increased leakiness in mammalian membranes, in both visceral tissues and in skeletal muscle. Heat is produced as a consequence of the additional ionic pumping necessary to maintain or reestablish concentration gradients (Else et al. 1996, 2004; Rolfe and Brand 1997; Rolfe et al. 1999).

This source of higher “background” or resting heat production is a major difference between the endotherms and the reptiles. Shivering (as in pythons) and muscular work (e.g., foraging echidnas) can provide substantial periods of regulated high T_b . However, understanding the evolution of endothermy depends on understanding the evolution of the capacity for high rates of metabolic heat production in animals at rest. This is particularly interesting in the context of the aerobic capacity hypothesis, in which it is envisaged that higher resting metabolic rates evolved only as a correlate of selection for higher, aerobically driven activity levels. Hayes and Garland (1995) have drawn attention to the difficulty of validating this experimentally. It seems unlikely but is difficult to prove that otherwise futile biological work would evolve as an automatic correlate of higher aerobic capacity. In other words, heat production by futile work across leaky membranes seems to be a specific mechanism for producing heat, which could be selected for directly, as was, presumably, thermogenic BAT in the eutherian mammals.

4. Brown adipose tissue (BAT) and nonshivering thermogenesis.

Note that BAT is not a prerequisite for endothermy nor, indeed, diagnostic of mammals, as was asserted by Cannon et al. (2000, p. 387), who wrote that “our mammalian prerogative of being able to produce extra metabolic heat without muscular activity (i.e., nonshivering thermogenesis), is anatomically localized to a unique mammalian tissue, brown adipose tissue, and, molecularly, to the unique mammalian protein UCP1 (thermogenin), uniquely found in the brown adipose tissue.” This is an important point because BAT seems not to be present in monotremes (Augee 1969, 1978), the metatheria (Hayward and Lisson 1992; Kabat et al. 2003a, 2003b) although controversially reported in a single dasyurid (Hope et al. 1997). BAT is also not commonly present in eutherian mammals (Rothwell and Stock 1985) and has not been found in birds (Brigham and Trayhurn 1994). Nevertheless, Rose et al. (1999) and Kabat et al. (2003a, 2003b) have clearly demonstrated that norepinephrine-stimulated NST occurs in cold-acclimated Tasmanian bettongs, *Bettongia gaimardi*, and Tasmanian devils, *Sarcophilus harrisi*, both of which are homeothermic endotherms that lack both BAT and UCP1.

This is not to detract from the importance of BAT as a source of heat in the many species of Eutheria in which it does occur, and particularly those eutherian hibernators that rely on its capacities during rewarming. However, arousals from hibernation in marsupial hibernators and in the short-beaked echidna are equally impressive events and not at all dependent on BAT. It seems more likely that BAT and the thermogenic organs it comprises are a specialization that occurred within the eutherian. It is clear that the step from ectotherm to endotherm did not depend on the evolution of BAT.

5. *Another heat source?* There may be another, as yet not understood source of regulatory NST in mammals, as has apparently been found in the skeletal muscle of birds (review by

Bicudo et al. [2002]). Ye et al. (1995, 1996), aware of the reported lack of BAT in marsupials, explored other possible sources of NST in the macropodid marsupial Tasmanian bettong, *B. gaimardi*. Working on an isolated, perfused hindleg preparation, they found that catecholamines modified skeletal muscle oxygen consumption and lactate and glycerol production and concluded that the skeletal muscle vascular bed made a significant contribution to whole-body thermogenesis of bettongs. Further work on bettongs has reinforced this hypothesis. Bettongs are homeothermic endotherms that lack both BAT and UCP1 (Rose et al. 1999; Kabat et al. 2003a) but that show norepinephrine-stimulated NST (Rose et al. 1998, 1999). Furthermore, *B. gaimardi* does have UCP2 and UCP3 (Kabat et al. 2003a) and, as pointed out by these authors, although these are identified as uncoupling proteins mainly by their structural similarity to UCP1, rat white adipose tissue is known to up-regulate UCP2 in response to cold stress (Loncar 1991). Both UCP2 and UCP3 are known from both skeletal muscle and white adipose tissue in eutherians as well, including those lacking BAT, at least as adults.

Comprising such a large proportion of total body tissue, skeletal muscle is a very logical potential source of regulatory NST, and a catecholamine control over the production of metabolites with the thermogenic potential of glycerol and lactate, metabolized to lipids and carbohydrate in the liver (Ye et al. 1995), provides an attractive hypothesis. Alternatively, the source could be in the sarcoplasmic reticulum, as in birds (Bicudo et al. 2002). Either way, there is a need for an explanation for what remains a mystery at present: the mechanism that provides controllable, regulatory NST in mammals that lack brown fat. It seems likely that a widespread, ancient, and controllable mechanism of regulatory NST will be found in the skeletal muscle of mammals. If it turns out to be the same mechanism in both birds and mammals, that could imply that endothermy in these two groups stems from a common origin (Grigg 2004).

Whether or not echidnas have the capacity for regulatory NST is unknown at present. That they do is suggested by observations that daily T_b minima can be independent of ambient temperature (Grigg 1992a; Kuchel 2003). On the other hand, Augee (1978) injected an echidna with the neuromuscular-junction-blocking drug Flaxedil and found that it was unable to maintain T_b . He concluded that echidnas are dependent on heat produced by locomotor activity and shivering. However, echidnas in captivity cannot be relied on to maintain T_b when T_a falls (Kuchel 2003), so further work is needed.

Insulation (Peripheral Changes in Blood Flow, Redistributed Body Fat, Hair, Feathers)

There has been a great deal of discussion about which came first, insulation or increased heat production. One argument is that insulation must have come first, because otherwise any

increase in heat production could not lead to higher T_b , and so the benefit could not be selected for. Alternatively, it is argued that insulation could not have come first because an ectotherm with insulation would be compromised in its capacity to raise T_b in the ectothermic way—by basking. Cowles's (1958) famous report of an experiment with an insulating mink jacket seems to make this point well. However, such arguments refer to external insulation, fur or feathers, and may not apply to internal insulation such as layers of fat. We note that an internal fat layer could serve quite well for insulation and, by way of variable blood flow in the skin, could either be effective in providing insulation or be bypassed, depending on need, by opening up peripheral blood flow. We have discussed above the capacity of reptiles for sophisticated control over peripheral blood flow in response to prevailing need, and changes to blood flow could bypass an internal insulating fatty layer, or reinstate it, in a putative protoendotherm.

There is a logical step that can be made from the reptiles in this case. Reptiles are typically capital rather than income breeders (in the sense of Bonnet et al. 1998) and store fat in conspicuous, lobed fat bodies within the peritoneal cavity in anticipation of reproduction. A redistribution of the fat bodies could provide effective, and bypassable, insulation.

Echidnas are also capital breeders to a substantial extent. Body mass may commonly change by 20%–30% seasonally with fat buildup during the summer and loss during hibernation and, particularly, in the posthibernation reproductive season (Grigg et al. 1992a). They store a substantial amount of this fat subcutaneously, up to 2–3 cm in thickness, where it can function for insulation. Despite this thick insulatory layer, Dawson et al. (1978) and Schmidt-Nielsen et al. (1966) described large changes in thermal conductance in both *Zaglossus* and *Tachyglossus* that can, presumably, be ascribed to changes in peripheral blood flow.

Thus, the situation in echidnas suggests that a protoendotherm lacking external insulation but having a layer of subcutaneous body fat and reptile-like capacities for controlling peripheral blood flow could, unlike Cowles's jacketed lizards, bask effectively and function ectothermically but also have a much reduced thermal conductance more typical of a mammal or bird. Heat produced by either incremental (and selected for) increases in resting metabolic rate or specific thermogenic mechanisms in skeletal muscle or elsewhere could have been retained by an internal layer of body fat. That is to say, mechanisms for heat production could have preceded the evolution of external insulatory devices. This is important because it offers a solution to the difficulty referred to by McNab (1978, p. 19) “that small endotherms cannot be directly derived from small ectotherms because of the requirement of the simultaneous change of thermal conductance and the rate of metabolism.”

The Evolutionary Pathways

In this review we have proposed that the first endotherms were facultatively endothermic and that short-beaked echidnas provide a useful model for a putative protoendotherm, albeit an advanced one because it is a facultative ectotherm rather than a facultative endotherm. As different mammalian lineages evolved to fill different niches, basic facultative endothermy was modified in different ways, not only leading to obligate endothermy in many cases but also, commonly, being retained to various extents by modern heterotherms.

Benefits of having a high T_b must include thermal niche expansion and generally increased metabolic efficiency and higher aerobic capacity, perhaps particularly for reproduction. Brooding pythons present a good example where the mechanism for producing warmth has apparently been the result of direct selection, the benefits being accelerated development of the embryos and an expanded geographic distribution, despite the energetic cost to the brooding female. It is interesting that energy optimization apparently favors resumption of an ectothermic lifestyle once brooding is complete. One of the dominant issues accounting for the type of heterothermy/homeothermy a mammal or bird displays must be dictated by the management of energy rather than temperature regulation per se. The work of Schmid (1996), Ortmann et al. (1996), and Dausmann et al. (2000) provides excellent examples of the way in which the pattern of T_b expresses the interplay between energy availability, ambient temperatures, facultative ectothermy, and energy savings. Other factors will also be important; for example, hibernation in echidnas may provide security from predation for a significant part of the year (Grigg and Beard 2000), and body size will be a very influential factor on energy management and, thus, on the expressed pattern of T_b (Geiser 2004). An additional aspect of energy management may be an increased life span. Hibernation in mild climates may stretch a life span over more breeding seasons, thus increasing potential lifetime reproductive output (Grigg and Beard 2000).

However, because of the high selective value of functions and structures that have a direct impact on reproduction, regardless of cost (peacock feathers and champagne being good examples), we agree with Farmer (2000) and Koteja (2000) that reproductive outcomes will have been of primary importance. It is noteworthy that the only time we see homeothermy in echidnas is while they are incubating an egg and shortly afterward. Also, as pointed out by Farmer (2000) and Koteja (2000), parental care requires sustained vigorous activity. The energetic requirements of development (egg production, incubation/gestation), nutrition (lactation/egg provisioning and parental foraging), and protection of young could be primary selective forces for body temperatures affording higher metabolic rates in both birds and mammals.

Table 2 is an attempt to portray schematically how, by stepwise acquisition of physiological and behavioral mechanisms,

Table 2: An example of stepwise acquisition of or change in emphasis on physiological and behavioral mechanisms by which the diverse patterns shown by endotherms may have arisen from ectothermy

	Mechanism	Pattern
1	Control over emergence, sun basking, control over shuttling, control over peripheral blood flow, shelter seeking at day's end, or tolerance for wide range in T_b , little heat produced by maintenance of gradients across leaky cell membranes. (Lizard-like, 20 g to ca. 20 kg.)	Morning warm-up, warm and stable T_b for much of the day, cooling to ambient temperature overnight and on days when emergence does not occur (e.g., poor weather, seasonal retreat). In many, including nocturnal reptiles, "constitutional eurythermy."
2a	As 1, plus internal insulation, shelter-seeking late in evening when T_b falls below chosen level. (No known model?)	As above, plus T_b maintained warm well into the evening, active season extended.
2b	As 1, plus large body size. (Crocodiles, to 1,000 kg.)	Daily cycles in T_b decrease as size increases, but without endothermic heat production; even the largest extant reptiles show marked seasonal T_b cycles and are not inertial homeotherms.
2c	As 1, plus facultative thermogenesis by muscular contractions (locomotion or shivering), behavior interleaved with basking if opportunity presents, increase in oxygen consumption if T_a falls. (Boid pythons.)	T_b raised substantially by either "shivering" or basking, to warm eggs. When not brooding, python resumes ectothermic behavior and pattern.
3	As 1, and 2a and/or 2c, plus modest increase in resting MR from thermogenesis in leakier cell membranes, perhaps some regulatory NST, maybe no need to seek shelter during the night in warm seasons. (No known model? Early protoendotherm.)	T_b able to be maintained overnight, but lowered T_b often dictated by energetic considerations. Active season extended, more energy for reproductive activities.
4a	Cool climate: As 1–3, plus significant resting MR (and regulatory NST?); no need to seek shelter in active season, energetics favors seeking a retreat in cool season (facultative hibernation/torpor). (Echidna-like, except above snowline; cynodonts?)	T_b warm and stable throughout day, regular/occasional torpor, active season extended further, facultative winter hibernation.
4b	Warm climate: As 1–3, 4a. Energetic balance favors year round activity (no hibernation/torpor). (Echidna in warm climate? Cynodonts?)	As 4a except climate too warm for torpor/hibernation to be effective for energy savings.
4c	Cold climate: As 1–3, 4a. Energetics demands seeking a retreat in winter (obligate hibernation). ("Classic" hibernators, echidnas above snowline, small to medium eutherian and marsupial torpidators/hibernators)	As 4a except T_b warm and stable T_b throughout day and night during the active season, entry to prolonged hibernation in winter to cope with cold/food unavailability.
5	Various climates: As 1–3, 4a–4c plus significant regulatory NST heat production; energetic balance mitigates against abandonment of endothermy at any time of the year and favours homeothermic endothermy (body size very relevant). "Constitutional eurythermy" lost. (All the mammals and birds that are regarded as "typical endotherms.")	T_b essentially stable day and night and throughout the year.

Note. The putative mechanisms (shown in the "Mechanism" column) are cumulative, underpinning the observed patterns of T_b (shown in the "Pattern" column). Extant or hypothetical animal models are shown in the left column. Mechanisms 2a, 2b, and 2c and 4a, 4b, and 4c represent alternates. Note that the table is meant to be indicative rather than comprehensive, particularly to illustrate an approach in which the acquisition of a particular mechanism leads to a change in the pattern exhibited and how different sets of different circumstances may lead to different outcomes (modified from Grigg and Beard 2000).

the diverse patterns shown by endotherms could have arisen stepwise from the basic ectothermic reptilian template. The model incorporates a stage or stages of facultative endothermy in which heat-production mechanisms are selected to augment the heat gained by insulation and implemented selectively according to need. Facultative endotherms may thus have the energetic benefits of both ectothermy and endothermy, and

some may show torpor and/or hibernation. We have argued that hibernation by echidnas in mild climates may be a strategy for economizing on energy requirements and expenditure by adopting periodically a cool/cold T_b , even though there is no immediate or looming food shortage (Grigg and Beard 2000). In this context, echidnas and many other heterothermic mammals and birds are facultative ectotherms. Referring to echidnas,

we envisage that facultative endothermy/ectothermy may have been important stages in the evolution of widespread homeothermy endothermy. In some mammals in particular this capacity for ectothermy has become more finely tuned and exaggerated to cope with habitats that became thoroughly hostile in the winter, resulting in obligate hibernators, such as arctic ground squirrels. In many other mammals, however, and in most of the birds, energy-optimization-related selection pressures, often dictated by the energetic costs of reproduction, apparently favored abandonment of the capacity for short- or long-term torpors, the loss of the capacity for constitutional eurythermy, and the evolution of a pattern of homeothermic endothermy.

We think this is a parsimonious model. It recognizes that mammalian and avian endotherms display very diverse thermal patterns. It describes the evolution of this diversity, recognizes that the evolution of endothermy and the evolution of homeothermy are not the same thing, and proposes that the second step, where it occurs, follows the first. It explains how avian and mammalian endothermy, in all of their diversities, could have arisen from reptilian ectothermy with most of the increments being quantitative rather than qualitative. It acknowledges that the step to endothermy may have been made a number of times, and it could accommodate a step back to full-time ectothermy, as proposed for crocodiles (Seymour et al. 2004). It is a model that accommodates diversity and that recognizes that there need not be only one specific, detailed model, but that different expressions of extent may have been achieved by different selection pressures in different groups in response to different circumstances, and at different times.

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