

Proceedings of the Satellite Symposium for the Australian Physiological and Pharmacological Society: The Evolution of Physiological Processes

EVOLUTION OF DAILY TORPOR AND HIBERNATION IN BIRDS AND MAMMALS: IMPORTANCE OF BODY SIZE

Fritz Geiser

Zoology, School of Biological Sciences, University of New England, Armidale, New South Wales, Australia

SUMMARY

1. The evolution of hibernation and daily torpor in mammals and birds remains a controversial subject. The original view was that use of torpor reflects a primitive thermoregulation, as it occurs in ancestral groups of mammals.

2. This view is no longer widely supported. However, the interpretation of a polyphyletic derivation of torpor also has been challenged because of the astonishing similarity of torpor patterns among various orders and even the two classes.

3. A recent argument is that mutations required for torpor and hibernation are unlikely to occur simultaneously and that torpor must be plesiomorphic (ancestral), although it is not functionally primitive. Homeothermy is interpreted as a loss of the ability to enter torpor in those groups that could survive without the requirement of heterothermic periods for energy conservation.

4. Interestingly, while torpor in mammals occurs in the phylogenetically old groups, lending support to the hypothesis of an ancestral derivation of torpor, the opposite is the case for birds. Modern bird groups and ancestral mammal groups contain mainly small species that often rely on fluctuating food supply, whereas modern mammalian orders and ancient bird orders contain the largest species with low energy requirements for maintenance and thermoregulation.

5. It is, therefore, possible that not phylogenetic position but size and diet determine the occurrence of heterothermy. Moreover, because endothermy and torpor in birds has apparently evolved separately from that in mammals and because it is possible that daily torpor and hibernation represent two distinct torpor patterns that evolved separately, a convergent evolution of torpor in endotherms cannot be excluded.

Key words: birds, body mass, daily torpor, diet, endothermy, evolution, hibernation, mammals.

INTRODUCTION

Torpor is characterized by substantial reductions of body temperature (T_b) metabolic rate (MR) and other body functions that occur periodically in many small (< 10 kg) mammals and birds from the arctic to the tropics.^{1–3} Although the reduction of MR and T_b during torpor in these 'heterothermic endotherms' may appear to be reminiscent of that in ectotherms, there are two major features that clearly distinguish them from the latter. The first of these is that T_b during torpor is regulated at, or above, a species-specific set point by a proportional increase of MR.⁴ The second difference is that heterothermic endotherms can rewarm themselves from the low torpor T_b by using endogenous heat production, while ectotherms must rely on uptake of external heat.

Most heterothermic endotherms that are able to reduce MR substantially below the basal MR (BMR) show one of two distinct patterns of torpor. The first, shallow daily torpor in the 'daily heterotherms' lasts, on average, for several hours, the mean minimum T_b (determined by the set point for T_b that is metabolically defended during torpor) is approximately 17°C, although there is a large variation among species. The MR during daily torpor is, on average, reduced to approximately 30% of the BMR³ and often to less than 10% of the resting MR during cold exposure.⁵ The reduction of MR in these species appears to be largely caused by the initial decrease of heat production for normothermic thermoregulation during early torpor entry and, for reduction of MR below the BMR, temperature effects caused by the fall of T_b .^{6–9} Daily torpor has been observed in many and diverse small mammal and bird species^{1–3,10–12} (Fig. 1).

The second common pattern, deep and prolonged torpor observed in the 'hibernators', is characterized by much longer bouts of torpor that, on average, last approximately 1–3 weeks and the mean minimum T_b is approximately 6°C. The MR during hibernation is, on average, reduced to 5% of the BMR.³ However, in small species, MR may be as low as 1% of BMR and a fraction of 1% when compared with the resting MR during cold exposure.^{3,5,13} The reduction of MR in hibernators appears to also be caused by the initial decrease of heat production for normothermic thermoregulation because the set point for T_b is lowered during torpor entry¹⁴ and, for reduction of MR below the BMR, a physiological inhibition of MR in addition to the temperature effects of the lowered T_b .^{6,13,15} Hibernation is known to occur in several mammalian orders and one species of bird, the poorwill (Strigiformes;¹⁶ Fig. 1). Species displaying deep and prolonged torpor at low ambient temperatures

Correspondence: F Geiser, Zoology, School of Biological Sciences, University of New England, Armidale, NSW 2351, Australia. Email: <fgeiser@metz.une.edu.au>

Presented at the Australian Physiological and Pharmacological Society Satellite Symposium on the Evolution of Physiological Processes.

Received 2 April 1998; revision 6 May 1998; accepted 19 May 1998.

(T_a) may display short torpor lasting for less than a day at high T_a or at the beginning of the hibernation season. However, physiologically, this appears to be a short bout of hibernation with a MR well below that during daily torpor, even at the same T_b ,^{5,6,13} and, thus, should not be equated with daily torpor. In contrast with hibernators, the daily heterotherms show daily torpor exclusively both at low and high T_a and often throughout the year.¹⁷⁻¹⁹

A third less common pattern of torpor has been observed in a few carnivores (e.g. bears, badgers) that are bigger than most other heterothermic endotherms. However, their T_b is much higher (around 28–30°C) than in most other heterotherms and their physiological responses appear to differ from those in the small heterotherms. Moreover, many bird species display 'nocturnal hypothermia', characterized by a fall of T_b at night by up to approximately 5°C and a reduction of MR to approximately BMR.^{11,20} Avian nocturnal hypothermia will not be considered in the present paper.

Because torpor appears to be at least a partial reversion to some ectothermic state, its evolution and its position in the evolution of endothermy, in general, have attracted much attention from researchers. The original view was that torpor, as it occurs in 'primitive' mammals, such as the monotremes and marsupials (which were then viewed as 'poor thermoregulators'), is both functionally and phylogenetically a primitive trait.^{21,22} As comparative data accumulated and thermoregulatory capabilities of many heterothermic animals were found to be similar to those of the homeotherms, this

view was no longer widely supported. Torpor was, and still is, seen by many as a sophisticated adaptation to the environment of particular endothermic groups or species. It was proposed that torpor is polyphyletic and evolved independently in many mammalian taxa and birds when environmental conditions required a reduction of the high endothermic metabolism for survival.²³⁻²⁵ More recently, the interpretation of a polyphyletic derivation of torpor has been challenged. Augee and Gooden²⁶ argue that convergent evolution of a complex phenomenon, such as hibernation, seems unlikely. They point out that the parsimonious explanation is that hibernation in mammals is a plesiomorphic (ancestral) trait, but that it is not functionally primitive.²⁶ If this interpretation is correct, hibernation in mammals has evolved only once and, therefore, must have been modified in species displaying daily torpor or lost in strictly homeothermic species. Similarly, Malan²⁷ argues that the genes underlying hibernation must be primitive because it is unlikely that several mutations required for hibernation occur simultaneously. He proposes that genes for hibernation and torpor were common to all ancestors of mammals and, possibly, birds and were lost later in some homeothermic orders. He also points out that some physiological traits, such as hypometabolism, are even found in invertebrates, suggesting that some of the genes required for heterothermy in endotherms may predate chordate evolution.²⁷

A comparison of the evolution of birds and mammals from the reptiles and the distribution of heterothermic species among orders may help resolve the likely derivation of torpor. It is widely accepted that both mammals and birds arose from two distinct reptilian lines that originated from the stem reptiles, the cotylosaurs, around 300 million years ago. One group, the synapsids, gave rise to the pelycosaurs, the therapsids and, finally, to the mammals approximately 220 million years ago. The mammals initially appear to have split into two branches, one leading to the Monotremata (Prototheria) and the other to the Marsupialia (Metatheria) and Placentalia (Eutheria) approximately 180 million years ago.²⁸ The marsupials and placentals were then separated into two groups approximately 120 million years ago,^{28,29} resulting in a total of three extant mammalian subclasses. The other group, the diapsids, gave rise to the birds, most likely via bipedal saurischian dinosaurs approximately 200 million years ago. Extant groups of birds arose approximately 50 million years ago and can be divided into the phylogenetically older eoaves (flightless birds, megapodes and relatives, fowl and goose relatives) and the more modern neoaves, the rest of the flying birds.³⁰

Heterothermy appears to be more widely used in mammals than in birds and the distribution of heterothermic orders differs between the two classes (Fig. 1). The tree of mammalian orders clearly shows that, in mammals, torpor is restricted to the more ancestral groups. Ten or 11 of the 25 mammalian orders of this taxonomy are heterothermic, including the two orders (bats, rodents) that make up approximately 65% of all mammalian species. Echidnas, members of the most primitive group of mammals, the egg-laying Monotremata, are known to hibernate.³¹ Similarly, three or four orders of the Marsupialia, the Didelphiformes (South American opossums and relatives), the Dasyuromorphia (Australian insectivorous/carnivorous marsupials) and the Diprotodontia (Australian possums and pygmy-possums), are known to undergo daily torpor and hibernation and the marsupial mole (Notoryctemorphia) also appears to be heterothermic.^{32,33} In placental mammals, heterothermy has been observed in the rodents, the elephant shrews (Macroscelidea; BG Lovegrove, pers. comm., 1997), the primates, the bats (both Mega- and

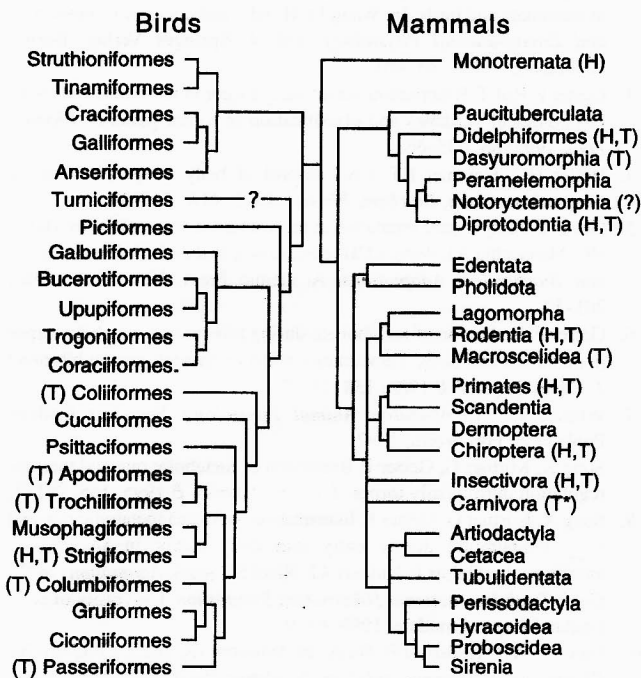


Fig. 1 A phylogenetic tree of mammalian and avian orders. The bird tree is based on Sibley and Ahlquist³⁰ and the mammal tree is based on information derived from the Tree of Life Homepage (November 1997; <<http://ag.arizona.edu/tree/phylogeny.html>>) for the placentals and the marsupials and monotremes based on Archer²⁸ and Szalay.²⁹ H, the group that contains species that have been observed in deep and prolonged torpor (hibernation); T, the group that contains species that have been observed to enter daily torpor exclusively; T*, shallow torpor of carnivores; ?, a high degree of uncertainty. Information on the torpor patterns of orders was taken from various references;^{3,11,33,36,37} for the Macroscelidea, the information was provided by BG Lovegrove (University of Natal, South Africa; pers. comm., 1997).

Microchiroptera), the insectivores and, as mentioned earlier, in the carnivores with their very shallow torpor.^{1,3,34} Presently, there is no evidence on torpor in the more derived mammals (Artiodactyla to Sirenia; Fig. 1). On the surface, this pattern appears to support the original hypothesis and those advanced by Augee and Gooden²⁶ and Malan²⁷ that heterothermy is an ancestral trait.

In contrast with mammals, the evolutionary tree of bird orders shows exactly the opposite distribution of heterothermic orders. All ancestral bird groups appear to be homeothermic. Heterothermy in birds appears to be restricted to the more modern groups. Six of 23 avian orders that are known to include heterothermic species are the Coliiformes (mousebirds), the Apodiformes (swifts), the Trochiliformes (hummingbirds), the Strigiformes (nightjar relatives), the Columbiformes (pigeons) and the Passeriformes (perching songbirds).^{10-12,16,35}

Thus, while the occurrence of torpor in mammalian orders may point towards an ancestral derivation of torpor, the opposite is the case for birds. This suggests that evolution of torpor in birds and mammals differs, pointing towards a separate derivation of torpor in the two classes. It also suggests that the phylogenetic position of heterothermic mammals may have led researchers to wrong conclusions. Ancestral mammals are those that contain small species with a high energy expenditure during normothermia. Moreover, many of these orders eat food that becomes seasonally unavailable. Heterothermic birds, in contrast, occur in the modern groups apparently because they are small and rely on food that can fluctuate.

Therefore, it appears that size and diet may provide a more satisfactory answer for the use of heterothermy in both birds and mammals than phylogeny. But, of course, this does not refute the argument that torpor is monophyletic. It is still possible that the ability to enter torpor was lost in those groups that grew to a large enough size. By reducing relative surface area they would have reduced energy costs for thermoregulation and their low mass-specific MR would have allowed them to survive for prolonged periods without food, even when homeothermic, or would have permitted them to specialize on low-quality food that was available all year round.

The other question that has to be resolved with respect to evolution of torpor is whether daily torpor and hibernation are only a variation of a theme or represent two different physiological adaptations that arose independently. In the past, it was often assumed that daily torpor represents the ancestral form of torpor that evolved to cope with daily fluctuation of ambient temperature and that hibernation is a more sophisticated form of torpor that arose from daily torpor in species occupying habitats with strong seasonal climates. However, when physiological variables (such as the minimum MR, the extent of reduction of MR below the BMR, duration of torpor bouts and the minimum T_b) of species using the two torpor patterns are compared, it is striking how they fall into two clearly distinct groups.³ This clear separation could be used to argue that the two patterns evolved separately and diverged very early in the evolution of endotherms. If the two patterns did evolve independently for a long time, one would, however, predict that only one pattern of torpor occurs within one order or class. As this is not the case and both patterns of torpor occur within certain orders of both classes, a more recent derivation according to ecological and physiological requirements appears more likely.

In conclusion, the similarity of torpor patterns in avian and mammalian taxa lends some support to the argument that torpor is plesiomorphic. However, convergent evolution can be deceptive and it is

possible that we may have been unable to recognize important differences among groups because they are concealed among the vast amount of available information. Because torpor occurs in modern bird orders, whereas in mammals it is restricted to ancestral orders, it seems likely that heterothermy evolved separately in the two classes and, thus, is polyphyletic. It is obvious that many questions remain unanswered, but detailed information from other avian and mammalian orders, together with information from molecular biology, may help resolve the argument.

ACKNOWLEDGEMENTS

This work was supported by the Australian Research Council. I thank Barry Lovegrove (University of Natal, South Africa) for useful discussion and advice on the avian and mammalian tree, Louise Streeting (University of New England, Armidale, NSW, Australia) for help with the illustration and Gerhard Körtner and Bronwyn McAllan (University of New England, Armidale, NSW, Australia) for constructive comments on the manuscript.

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