

S22-5 Evolutionary and ecological determinants of avian torpor: a conceptual model

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Abstract We constructed a generalized, conceptual model that attempts to predict the occurrence of avian torpor. A recent hypothesis suggests that endotherm heterothermy is monophyletic, and predicts that torpor should be more widespread in phylogenetically older taxa. Once phylogeny is accounted for, the most important determinant of avian torpor is body mass (M_b). We used an existing model of endotherm torpor to predict the relationship between M_b and minimum body temperature (T_b) during torpor. The available data show that the lower limit of torpor T_b is determined by the M_b -dependent costs of re-warming following a torpor bout. In addition to phylogeny and M_b , the relationship between the relative energetic benefits and potential ecological costs of torpor is likely to be an important determinant of torpor. We constructed a model which predicts that torpor should be more prevalent in species near the extremes of the avian metabolic continuum. Available data provide tentative support for this prediction. In addition to such generalized factors as phylogeny and M_b , specific aspects of the ecology of individual species need to be considered when predicting the occurrence of avian torpor.

Key words Body size, Ecology, Evolution, Metabolic rate, Torpor, Phylogeny

1 Introduction

Recent evidence suggests that avian torpor is more common, and occurs in a wider variety of ecological contexts, than previously thought. For example, torpor occurs routinely under natural conditions in several members of the Caprimulgidae and their relatives (Brigham, 1992; Brigham et al., 2000; Körtner et al., 2000). Evidence also exists that torpor is not necessarily confined to periods of energy shortage. In hummingbirds, its use is determined by a suite of proximate factors, including seasonal variation in the propensity for torpor, the perceived availability of food, and temporal variation in assimilation efficiency (Hiebert, 1991). Collectively, these observations suggest that the contribution of the capacity for torpor to avian fitness has been underestimated.

Facultative hypothermic responses have been investigated in 95 avian species, and approximately 30% apparently involve torpor (McKechnie and Lovegrove, 2002). The limited data set available makes it difficult to identify generalized evolutionary and ecological determinants of avian torpor. Here, we present a conceptual model for generating hypotheses concerning the occurrence or absence of torpor in particular species. Specifically, we argue that the occurrence of avian torpor can be predicted by (1) phylogeny, (2) body mass (M_b) constraints, (3) trade-offs between energetic benefits and potential ecological costs, and (4) specific ecological factors. We test these predictions where available data permit.

2 Phylogeny

The evolutionary origins of torpor remain controversial (Geiser, 1998). Malan (1996) has argued that hibernation and torpor in endotherms represent a release of an inhibition of the primitive tendency towards wide-amplitude T_b (body temperature) cycling, which comprised a hypothesized intermediate step in the transition from ectothermy to endothermy. His hypothesis concerning the ancestral nature of heterothermy provides a potential starting point for a model of the evolutionary determinants of avian torpor. If this hypothesis is correct, then torpor should be more prevalent in phylogenetically older taxa, once other factors are controlled for. Although insufficient data are currently available to test this prediction, torpor does appear to be more common in phylogenetically older taxa. In particular, it is more common in the Coliiformes, Trochiliformes and Strigiformes than in the Passeriformes, the most derived avian order (McKechnie and Lovegrove, 2002). Malan's (1996) view of torpor as a plesiomorphic, monophyletic trait may well explain its absence in many of the passerines investigated, even those permanently resident in Arctic and sub-Arctic regions. *A priori*, the absence of torpor in these species is surprising, as they routinely face low ambient temperatures combined with low food availability and short photoperiod (Reinertsen, 1996).

3 Body size

The potential energetic benefits of torpor are con-

strained by the mass-dependent relative cost of re-warming following a hypothermic bout. Prothero and Jürgens (1986) showed that the relationship between M_b (body temperature) and the time in torpor for which total energy savings during the entry and maintenance phases are equal to the costs of re-warming during the arousal phase is given by the equation:

$$W^{1-b} = \frac{1}{\left(\frac{24s}{1-\alpha}\right)\left(\frac{1}{a}\right) - \left(\frac{1}{2C_0}\right)} \left(\frac{t_{fc}}{T_b - T_a}\right)$$

(A24 in Prothero and Jürgens, 1986) where $W = M_b$ = body mass in kg; s = specific heat in kcal/(kg.°C); C_0 = coefficient relating cooling rate during the entry phase to M_b (°C. h⁻¹.kg^{1-b}); t_{fc} = time spent fully cooled in hours, i.e duration of maintenance phase; T_b = body temperature (°C); T_a = ambient temperature (°C); $\alpha = 10/[(T_b - T_a).Q_{10}]$ in °C⁻¹; a and b are the intercept and coefficient respectively of the equation relating resting metabolic rate (RMR) to W (M_b), i. e. $RMR = aW^b$ in kcal.day⁻¹. This equation can then used to calculate the critical M_b (i.e., the M_b at which the net energy savings equal zero) by setting the right-hand side of equation A24 to Q , such that:

$$W_c^{1-b} = Q \quad (\text{A22 in Prothero and Jürgens, 1986})$$

or

$$W_c = 10^{(\log Q)^{1-b}} \quad (\text{A23 in Prothero and Jürgens, 1986}).$$

These authors assumed that during torpor, $T_b = T_a$. The assumption is not critical since Q_{10} values, rather than temperature gradients ($T_b - T_a$), were used to calculate reductions in metabolic rate, and the model still operates if T_b is maintained above T_a during torpor. A second assumption was that the decrease in T_b during the entry phase occurred linearly. Although this is not the case, the authors showed, using empirical data for a hummingbird, that the model is adequate. Prothero and Jürgens (1986) used the model to calculate critical M_b s for varying bout lengths, but it can also be used to calculate critical M_b s for various torpor T_b s for a specific bout length. We assumed $s = 0.932$ kcal/(kg.°C) (specific heat of tissues; Withers, 1992), $C_0 = -0.519$ (scaling exponent for avian rest-phase thermal conductance; Schleucher and Withers, 2001), $Q_{10} = 2.5$, and normothermic $T_b = 38.5^\circ\text{C}$ (mean avian rest-phase T_b ; Prinzinger et al., 1991). For a and b , we used values from a conventional least-squares linear regression of field metabolic rate (FMR) on M_b for 81 bird species (Tieleman and Williams, 2000). We then calculated critical M_b s for a range of T_b s during torpor (Fig. 1).

A comparison of the plots generated by the Prothero and Jürgens (1986) model with the observed relationship between avian M_b and minimum hypothermic T_b (torpor and

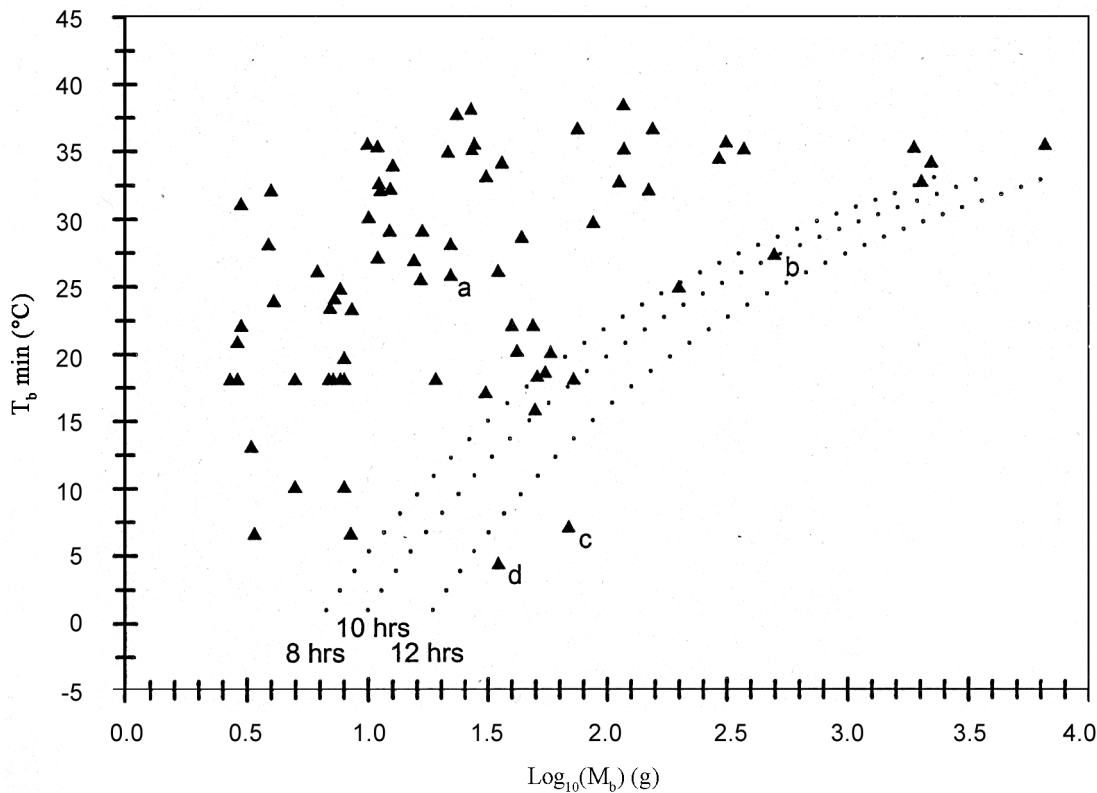


Fig. 1 Relationship between minimum body temperature during avian facultative hypothermia (T_b hypo) and \log_{10} body mass (M_b) The dotted lines indicate the minimum T_b at which a facultative hypothermic response will result in a net energy saving for a given bout length (indicated), and were calculated using Prothero and Jürgens' (1986) energetic model for daily torpor. Data for (a) *Delichon urbica* (Prinzinger and Siedle, 1988), (b) *Podargus strigoides* (Körtner et al., 2000), (c) *Caprimulgus europaeus* (Peiponen, 1966) and (d) *Phalaenoptilus nuttallii* (Brigham, 1992) are indicated by respective lower case letters.

rest-phase hypothermia) in 74 bird species (Fig. 1) suggests that the lower boundary of this relationship is determined by M_b -dependent constraints on re-warming. The only data that lie outside the theoretical boundaries plotted in Fig. 1 are those for *Phalaenoptilus nuttallii* and *Caprimulgus europaeus*. In *C. europaeus*, a minimum T_b of ca. 7°C was recorded during a bout lasting approximately 16 hours (Fig. 6 in Peiponen, 1966). In *P. nuttallii*, a minimum T_b of 4.3°C occurred during a bout of 8–10 hours (R.M. Brigham, pers. comm.).

Fig. 1 also reveals that a large component of variation in observed torpor T_b cannot be attributed to body size alone. Much of this variation may reflect phylogenetic variation in the capacity for torpor. The Prothero and Jürgens (1986) model allows the observed minimum torpor T_b to be compared with the critical value expected on the basis of M_b and bout length. By predicting critical T_b , and thus the maximum depression of T_b that will result in a net energy saving, the model provides a scale on which the hypothermic responses of a particular species can be assessed. For instance, a minimum T_b of 27°C in a 500 g tawny frogmouth (Körtner et al., 2000; symbol b in Fig. 1) is close to the critical T_b for a species of such size. In contrast, a minimum T_b of 25.7°C in a 22 g house martin (Prinzinger and Siedle, 1988; symbol a in Fig. 1) is considerably higher than critical T_b . The extent of T_b reduction as a percentage of the predicted maximum will be useful when comparing the extent to which facultative hypothermia has evolved as an energy-saving mechanism in closely related species. It should be noted that the Prothero and Jürgens (1986) model assumes that all of the energy required for arousal is derived from endogenous sources, such as shivering and non-shivering thermogenesis. The potential importance of solar radiation in reducing the costs of re-warming following avian torpor bouts deserves closer attention (see Brigham et al., this symposium).

4 Trade-off between energetic benefits and ecological costs

Species that possess the capacity for torpor by virtue of their phylogenetic position and M_b are likely to use torpor only if it confers direct fitness benefits. Presumably, the use of torpor is adaptive when the energetic benefits exceed the potential ecological costs. An understanding of the factors that determine these costs and benefits will facilitate the identification of species likely to use torpor.

The major energetic benefit of torpor is a reduction in rest-phase energy expenditure (Reinertsen, 1996). The relative benefits of torpor are hence likely to be correlated with other energetic traits that determine energy requirements in birds. Adaptive variation in such traits may be useful in identifying species in which the energetic benefits of torpor are relatively high. One such energetic trait exhibiting adaptive variation is basal metabolic rate (BMR). For instance, birds inhabiting desert habitats characterized by erratic rainfall and low primary production typically pos-

sess lower BMRs than species living in more predictable environments (Tieleman and Williams, 2000).

The adaptive variation in avian BMR implies that species near the lower end of the metabolic continuum, those with low relative BMR, have undergone strong selection for reduced energy requirements. Hence, the capacity for reducing energy requirements by means of torpor is likely to be similarly adaptive for these species. Data for both mammalian and avian heterotherms supports the hypothesized association between low BMR and torpor (Lovegrove, 1996; McNab, 1988). In contrast, species at the upper end of the metabolic continuum possess high relative BMRs and elevated energy requirements. In these species, the capacity for torpor is likely to be adaptive when the ability to meet metabolic requirements is limited by intake rates. For instance, McWhorter and Martinez del Rio (2000) found that intake rates of broad-tailed hummingbirds (*Selasphorus platycercus*) were limited by their digestive physiology.

The energetic benefits of torpor are presumably greatest at the extremes of the avian metabolic continuum. On the other hand, the potential ecological costs of torpor are presumably related to an increased risk of predation (Reinertsen, 1996; McKechnie and Lovegrove, 2002). Hence, potential ecological costs are independent of relative metabolic rate and constant across the metabolic continuum. A model of the relative energetic benefits and potential ecological costs of torpor (Fig. 2a) predicts that torpor should be more prevalent at the extremes of the metabolic continuum. In species at the extremes, the likelihood that the energetic benefits of torpor exceed the potential ecological costs is highest (Fig. 2a). The model also predicts that this effect should be more pronounced in species for which the potential ecological costs of torpor are high.

To test the prediction that torpor should be more prevalent at the extremes of the avian metabolic continuum, we obtained measures of BMR for 420 avian species from the literature. We calculated a conventional least-squares linear regression of \log_{10} BMR on $\log_{10} M_b$ (\log_{10} BMR = $0.667 \log_{10} M_b + 0.838$), and then calculated a \log_{10} BMR residual for each species. These residuals were approximately normally distributed. Of the 420 species, 35 are known to exhibit torpor (*sensu* Reinertsen, 1996; $T_b < 30^\circ\text{C}$). BMR and torpor T_b data are available on request from the corresponding author. The frequency distribution of the \log_{10} BMR residuals of these 35 species differed significantly ($\chi^2 = 68.934$; $df = 24$; $P \ll 0.05$) from the overall distribution. A frequency distribution of the proportion of species known to exhibit torpor (Fig. 2b) reveals that torpor is indeed more prevalent in species near the extremes of the avian metabolic continuum.

5 Ecological factors

We have argued that generalized factors, namely phylogeny, body size, and energetic traits such as BMR, can be used to generate hypotheses concerning the occur-

rence of avian torpor. However, both the relative energetic benefits that a bird derives and the potential ecological costs that it incurs by using torpor are determined by a suite of ecological factors. Any attempt to predict the occurrence of torpor in a particular species needs to take into account specific aspects of its ecology and behavior. Here we assess a specific example in attempting to identify the ecological determinants affecting the relative costs and benefits of torpor.

Schleucher (1994, 2001) investigated hypothermic responses in two small (ca. 40 g) doves, *Oena capensis* and *Geopelia cuneata*, and the relatively large (200 g) fruit-dove *Drepanoptila holosericea*. Both *O. capensis* and *G. cuneata* exhibited shallow hypothermia in response to food deprivation, with minimum T_b s of 35.3°C and 34.4°C respectively (Schleucher, 1994, 2001). In contrast, *D. holosericea* exhibited torpor (minimum T_b = 24.8°C) during *ad libitum* feeding at T_a s between 12°C and 27°C (Schleucher, 2001). *A priori*, the two smaller, desert

granivores might seem more likely candidates for torpor than a larger, rainforest frugivore. However, *O. capensis* and *G. cuneata* are nomadic, continental species (Baptista et al., 1997), and are presumably able to avoid areas of low food availability. Moreover, both these species have several potential nocturnal mammalian predators (Nowak and Paradiso, 1983). In contrast, *D. holosericea* is a non-migratory species restricted to New Caledonia (Baptista et al., 1997). In the Australasian zoogeographical region, the El Niño Southern Oscillation (ENSO) causes unpredictable, severe droughts (Stone et al., 1996; Philander, 1983). A sedentary, frugivorous species such as *D. holosericea* is likely to encounter large fluctuations in fruit availability associated with ENSO events (Van Schaik, 1986). We argue that *D. holosericea* experiences stronger selection for reduced energy requirements than *O. capensis* or *G. cuneata*. Moreover, there are no mammalian predators on New Caledonia (Nowak and Paradiso, 1983), and *D. holosericea* presumably has virtually zero risk of nocturnal predation.

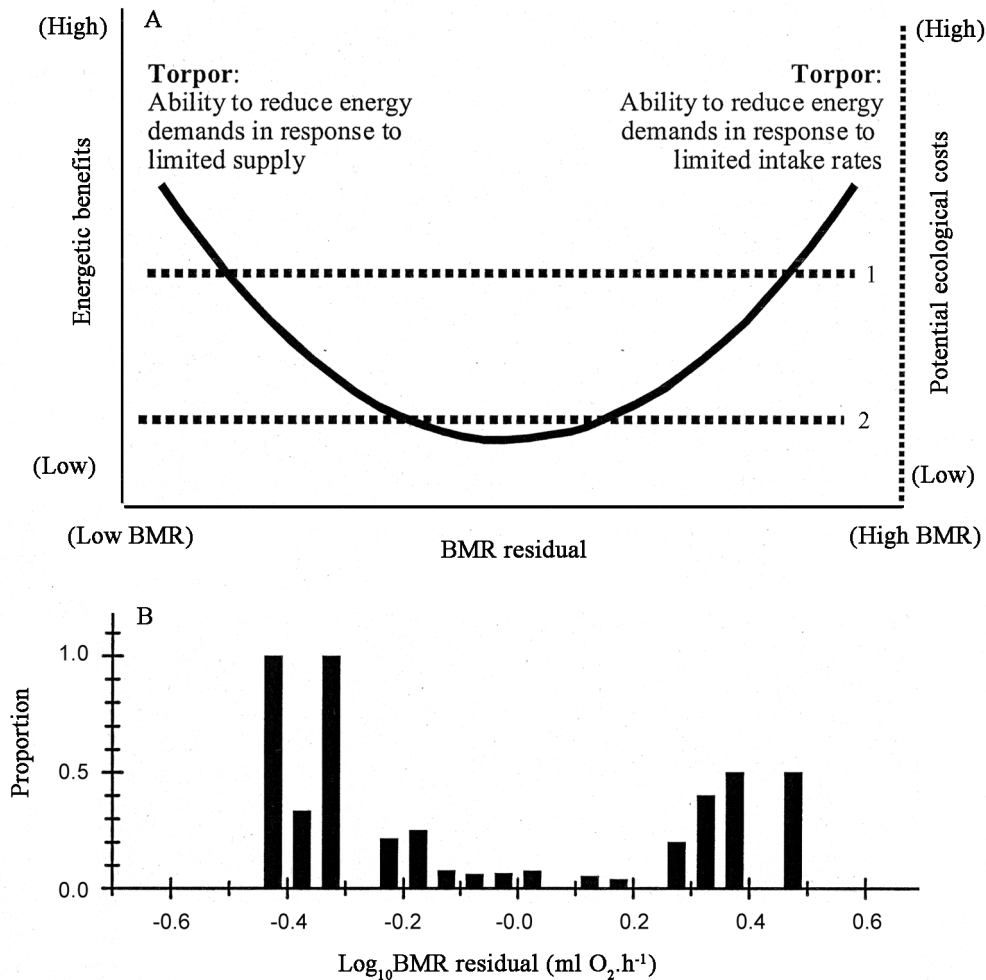


Fig. 2 A model of the relative energetic benefits and potential ecological costs of avian torpor

(A) The energetic benefits of torpor (solid line) are greatest at the extremes of the metabolic continuum. Dotted line 1 indicates a taxon in which the potential ecological costs of torpor are high (e.g., a large, non-cryptic species easily located by predators). Dotted line 2 indicates a taxon in which the potential ecological costs of torpor are low (e.g., small, cryptic species). The capacity for torpor should be adaptive when the energetic benefits are greater than the potential ecological costs, i.e. when the solid line is above the dotted line. (B) A frequency distribution of the proportion of species known to use torpor which supports this prediction.

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