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The Energetics of the Rewarming Phase of Avian Torpor

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Abstract. Avian rewarming rates are related to body mass by \( \log R = 0.436 - 0.634 \log M_b \), where \( R \) is rewarming rate (°C min\(^{-1}\)) and \( M_b \) is body mass (g). Predicted avian rewarming rates are lower than those for mammals at all but the smallest \( M_b \)s (< 5 g). The energy required to rewarm from torpor (\( E_{\text{rewarm}} \)) can be estimated using a simple biophysical model. The model predicts that \( E_{\text{rewarm}} \) increases linearly with \( M_b \) and that the slope of this relationship increases with decreasing torpor body temperature.

Introduction
In the last decade, it has become clear that daily torpor is considerably more common in birds than was previously thought (McKechnie and Lovegrove, 2002). Integrating data on the use of torpor with other aspects of a species' ecology requires an understanding of the energetic benefits and potential ecological costs. One major constraint on the energetic benefits associated with torpor is the energy required to rewarm to normothermic body temperature (Prorhoro and Jürgens, 1986). Metabolic heat production during rewarming (or arousal) can be considerable. In hummingbirds, for instance, metabolic rates during rewarming from torpor can be comparable to those achieved during hovering flight (Bech et al., in press). In an effort to better understand how biophysical constraints may limit the potential benefits of avian torpor, we investigated the energetics of the rewarming phase. Specifically, we asked two questions. First, how do avian rewarming rates scale with body size, and are they similar to those observed in mammals? Second, how does the cost of rewarming relate to body size and to physiological parameters of torpor such as body temperature?

Because of the paucity of empirical data, we constructed a model to address the latter question.

**Materials and Methods**

**Rewarming Rates**

We obtained rewarming rates for 13 species from the literature (Table 1). When authors did not report rewarming rates, we calculated them from traces of body temperature ($T_b$). For $T_b$ traces recorded in free-ranging birds, we calculated rewarming rates only when air temperature ($T_a$) was relatively stable. All body masses (g) and rewarming rates (°C min⁻¹) were log₁₀-transformed prior to analysis by least-squares linear regression.

**Energetic Cost of Rewarming**

*Table 1. Avian rewarming rates.*

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (g)</th>
<th>Rewarming rate (°C min⁻¹)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Archilochus alexandri</em></td>
<td>4.0</td>
<td>1.254</td>
<td>Lasiewski and Lasiewski, 1967</td>
</tr>
<tr>
<td><em>Anazilia versicolor</em></td>
<td>4.1</td>
<td>0.887</td>
<td>Bech et al., 1997</td>
</tr>
<tr>
<td><em>Eugenes fulgens</em></td>
<td>6.8</td>
<td>1.121</td>
<td>Lasiewski and Lasiewski, 1967</td>
</tr>
<tr>
<td><em>Melanotrichillus fuscus</em></td>
<td>7.7</td>
<td>0.457</td>
<td>Bech et al., 1997</td>
</tr>
<tr>
<td><em>Lampornis clemenciae</em></td>
<td>8.5</td>
<td>0.834</td>
<td>Lasiewski and Lasiewski, 1967</td>
</tr>
<tr>
<td><em>Eupetomena macroura</em></td>
<td>8.6</td>
<td>0.614</td>
<td>Bech et al., 1997</td>
</tr>
<tr>
<td><em>Patagona gigas</em></td>
<td>21.0</td>
<td>0.614</td>
<td>Lasiewski et al., 1967</td>
</tr>
<tr>
<td><em>Aeronautes saxatilis</em></td>
<td>31.0</td>
<td>0.370</td>
<td>Bartholomew et al., 1957</td>
</tr>
<tr>
<td><em>Colius colius</em></td>
<td>35.1</td>
<td>0.210</td>
<td>McKechnie and Lovegrove, 2001a</td>
</tr>
<tr>
<td><em>Phalacropterus nutalli</em></td>
<td>40.0</td>
<td>0.429</td>
<td>G. A. Bartholomew and R. C. Lasiewski (unpubl. data, cited in Lasiewski et al., 1967)</td>
</tr>
<tr>
<td><em>Aegotheles cristatus</em></td>
<td>48.2</td>
<td>0.143</td>
<td>Brigham et al., 2000</td>
</tr>
<tr>
<td><em>Colius striatus</em></td>
<td>51.0</td>
<td>0.219</td>
<td>McKechnie and Lovegrove, 2001b</td>
</tr>
<tr>
<td><em>Podargus strigoides</em></td>
<td>452.0</td>
<td>0.055</td>
<td>Köttner et al., 2001</td>
</tr>
</tbody>
</table>

The energy required to rewarm from torpor ($E_{rewarm}$) comprises two components: first, the energy required to raise the animal's tissues from torpor body temperature ($T_{torpor}$) to normothermic rest-phase body temperature ($T_{norm}$), and second,
the energy required to balance the heat lost to the environment during the rewarming process. Hence,

$$E_{\text{rewarm}} = s(T_{\text{norm}} - T_{\text{torpor}})M_b + \int_{t_1}^{t_2} Q$$  \hspace{1cm} (1)

where $s$ is the specific heat of animal tissues (3.43 J g$^{-1} \cdot$C$^{-1}$), $M_b$ is body mass, $Q$ is the rate of heat loss to the environment, and $t_1$ and $t_2$ are times corresponding to the start and end of rewarming respectively. The duration of the rewarming phase ($D_{\text{rewarm}}$) is calculated as

$$D_{\text{rewarm}} = \frac{T_{\text{norm}} - T_{\text{torpor}}}{R}$$  \hspace{1cm} (2)

where $R$ is the rewarming rate. To simplify the calculation of the second term of equation (1), we assumed that rewarming occurs linearly, so that

$$E_{\text{rewarm}} = s(T_{\text{norm}} - T_{\text{torpor}})M_b + D_{\text{rewarm}} \left( \frac{TMR + \frac{RMR - TMR}{2}}{2} \right)$$  \hspace{1cm} (3)

where TMR is the metabolic rate during steady-state torpor (i.e., the maintenance phase) and RMR is the normothermic resting metabolic rate.

To generate generalized predictions, we estimated RMR using predicted thermal conductance (Schleucher and Withers, 2001) and predicted basal metabolic rate (BMR; McKechnie and Wolf, 2004). We assumed that $T_{\text{norm}} = 38.5^\circ$C (Prinzinger et al., 1991), and that $T_{a} = 0^\circ$C. We used $T_{\text{torpor}}$ setpoints that were higher than $T_{a}$. Hence, we calculated TMR as $TMR = TMR_{\text{reg}} + C(T_{\text{reg}} - T_a)$, where $T_{\text{reg}}$ is the $T_a$ below which a $T_{\text{torpor}}$ setpoint is defended (typically 1–2$^\circ$C below the $T_{\text{torpor}}$ setpoint), $TMR_{\text{reg}}$ is the torpor metabolic rate at $T_a = T_{\text{reg}}$ (calculated as a $Q_{\text{btm}}$-mediated temperature-dependent decrease in BMR), and $C$ is thermal conductance. We assumed that thermal conductance during torpor was the same as during normothermy. The model is available as a spreadsheet from AEM.

**Results**

**Rewarming Rates**

Rewarming rate was strongly and negatively related to $M_b$ (Fig. 1). The slope of this relationship did not change significantly ($t = 0.069$, df = 21, P > 0.05) when we excluded *P. strigoides*, which is almost nine times heavier than the next
Fig. 1. The relationship between rewarming rate and body mass in birds. The solid line is a least-squares linear regression fitted to the data [log R = 0.436 – 0.634 log M_b; r^2 = 0.87, where R is rewarming rate (°C min^-1) and M_b is body mass (g)], and the dotted line is the relationship for mammalian daily heterotherms (log R = 0.237 – 0.349 log M_b; Geiser and Baudinette, 1990).

largest species. In addition, the rewarming rate observed in P. strigoides may have been affected by solar radiation (Körntner et al., 2001). The slope of our equation for avian rewarming rates is significantly greater than the slope of Geiser and Baudinette's (1990) equation for mammalian daily heterotherms (t = 2.811, df = 36, P < 0.05).

Energetic Cost of Rewarming

To validate our model for the energetic cost of rewarming, we compared predicted values of E_{rewarm} to those observed in a hummingbird (Selaphorus rufus; Fig. 2) and an elephant shrew (Elephantulus roseti; Fig. 2). Our model yielded reasonable predictions of E_{rewarm} in E. roseti at 10° C ≤ T_a ≤ 25° C, but underestimated E_{rewarm} at T_a = 5° C (Fig. 2). However, replacing the single allometrically
Fig. 2. The energetic cost of rewarming from torpor ($E_{\text{rewarm}}$) in a hummingbird (upper graph; Selasphorus rufus; data from Hiebert, 1990) and an elephant shrew (lower graph; Elephantulus rozeti; data from Lovegrove et al., 2001). In each graph, the solid line is the relationship between $E_{\text{rewarm}}$ and air temperature ($T_a$) predicted by our model, and the dashed line is the relationship between $E_{\text{rewarm}}$ and air temperature predicted by Prothero and Jürgens (1986) and Humphries et al. (2002). The dotted line in the lower graph is predicted $E_{\text{rewarm}}$ based on the relationship between rewarming rate and $T_a$ observed by Lovegrove et al. (2001), rather than a single allometrically predicted value.
predicted rewarming rate (Geiser and Baudinette, 1990) with Lovegrove et al.'s (2001) observed relationship between \( T_a \) and rewarming rate improved the accuracy of predicted \( E_{\text{rewarm}} \) at \( 5^\circ \text{C} \leq T_a \leq 10^\circ \text{C} \) (Fig. 2).

Our model predicts that, for a given \( T_{\text{torpor}} \), \( E_{\text{rewarm}} \) increases linearly with \( M_b \) (Fig. 3). The slope of the relationship between \( E_{\text{rewarm}} \) and \( M_b \) is directly related to the extent of body temperature reduction. As \( T_{\text{torpor}} \) decreases, and hence \( T_{\text{norm}} - T_{\text{torpor}} \) increases, \( E_{\text{rewarm}} \) increases more rapidly with increasing \( M_b \) (Fig. 3).

**Discussion**

**Rewarming Rates**

Our analysis reveals that the relationship between avian rewarming rate and body size differs from that of mammals (Fig. 1). Since thermal conductance is ca. 35% higher in mammals than in birds (Aschoff, 1981), the differences in rewarming rates likely reflect differences in the rate of heat production, rather

*Fig. 3. The predicted relationship for birds between the energetic cost of rewarming (\( E_{\text{rewarm}} \)), torpor body temperature, and body mass at an air temperature of 0°C.*
than differences in heat loss. In birds, thermoregulatory heat production predominantly involves shivering thermogenesis in the skeletal muscles (Dawson and Whitlow, 2000). Although avian nonshivering thermogenesis has recently been reported, and may be involved in rewarming in hummingbirds, brown adipose tissue is not thought to be present in birds (reviewed by Bicudo et al., 2002). Hence, the differences in rewarming rates may reflect physiological differences in the efficiency of thermogenesis or differences in the scaling of the sources of thermogenesis.

**Energetic Cost of Rewarming**

The energetic cost of rewarming from torpor can be estimated using a simple biophysical model (Fig. 2). The model can be used to generate generalized predictions of $E_{\text{rewarm}}$ using allometrically predicted BMR, thermal conductance, and rewarming rate but can also accurately predict $E_{\text{rewarm}}$ in particular species by incorporating species-specific deviations from allometrically expected values (Fig. 2).

Our approach to modeling $E_{\text{rewarm}}$ is more biologically realistic than previous models (Prothero and Jürgens, 1986; Humphries et al., 2002). These models did not account for heat loss during the rewarming process and can seriously underestimate $E_{\text{rewarm}}$ (Fig. 2). Moreover, they make the unrealistic prediction that $E_{\text{rewarm}}$ is constant at $T_s$ below the setpoint $T_{\text{torpor}}$.

Our model predicts that $E_{\text{rewarm}}$ increases linearly with body mass for any $T_{\text{torpor}}$. However, when $E_{\text{rewarm}}$ is expressed as a fraction of the predicted energy expenditure for an entire torpor bout ($E_{\text{torpor}}$: A. E. McKechnie and B. O. Wolf, unpubl. data), $F_{\text{rewarm}}/E_{\text{torpor}}$ increases with body mass following a three-parameter power function, confirming that rewarming from torpor is much more energetically costly, in relative terms, for larger birds. For instance, during a 12-hour torpor bout at $T_s = 0^\circ$ C and with $T_{\text{torpor}} = 18^\circ$ C, $E_{\text{rewarm}}$ represents 11% of $E_{\text{torpor}}$ in a 5 g bird, but 73% of $E_{\text{torpor}}$ in a 500 g bird.

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References


