Regulation of Oxygen Consumption and Body Temperature during Torpor in a Hummingbird, Eulampis jugularis

Abstract. *The West Indian hummingbird,* Eulampis jugularis, *maintained its body temperature in torpor at 18° to 20°C over an ambient temperature range of 2.5° to 18°C. At ambient temperatures below 18°C oxygen consumption during torpor increased linearly with decreasing temperature. Thermal conductances were the same for resting and torpid* Eulampis *regulating their body temperatures at 40° and 18°C, respectively.*

Most birds and mammals regulate their oxygen consumption and body temperature within closely defined limits. A few species, however, periodically reduce their body temperature and also reduce their oxygen consumption (*1–3*). Their lethargy and sluggishness during these periods has led to the use of the word "torpor" to describe the state, regardless of whether it occurs seasonally, as in hibernators and estivators, or daily, as in some small mammals and birds (*1–3*).

During an investigation of the physiology of a West Indian hummingbird, *Eulampis jugularis,* we found that this species regulates its oxygen consumption and body temperature during torpor. Such regulation has not previously been observed in birds, and these findings have implications for theories concerning the physiological control and functional significance of torpor.

Five males and four females were collected on Dominica, British West Indies (*4*). The average weights at the beginning of the experiments were 8.8 g for males and 7.8 g for females. Field weights for these species averaged 9.9 ± 0.7 g (S.D.) ($N = 11$) for males and 7.9 ± 0.4 g ($N = 28$) for females. The birds were fed sugar water, vitamins, and *Drosophila* and were kept at a photoperiod of 12½ hours light, 11½ hours dark, at about 23°C.

Oxygen consumption was measured in an open-flow system at ambient temperatures from 2.5° to 37°C. The metabolism chamber was placed in a temperature-controlled room (± 1.0°C) and consisted of a 4.9-liter glass jar fitted with a wire mesh floor above a layer of mineral oil. The air flow rate was adjusted from 150 to 550 ml/min. Lower flow rates were used while birds were in torpor to increase the accuracy of the measurements. Before the air entered the chamber, it was passed through a pressure regulator, desiccant, and a calibrated flowmeter (0 to 860 ml, ± 2 percent). Air temperature was equilibrated with chamber temperature by passing the air through copper coils in the environmental room. Effluent air was dried and passed through a paramagnetic oxygen analyzer (Beckman F-3, accuracy ± 0.2 percent O_2) which continuously recorded oxygen concentration. Oxygen consumption values were corrected to standard temperature and pressure.

The oxygen consumption of a bird placed in the darkened chamber reached a stable, resting level after 3 to 5 hours. If the bird entered torpor during this period, an additional 2 to 4 hours were allowed for a steady-state level of oxygen consumption to be reached. All oxygen consumption values represent stable values of at least 1 hour. Birds normally entered torpor after 3 to 5 hours, and it was unnecessary to employ prolonged food deprivation to induce torpor. At the termination of an experiment, body temperature was measured with a 36-gauge copper-constantan thermocouple (± 0.1°C) inserted 1.0 to 1.5 cm into the cloaca. If a bird entered torpor, body temperature was recorded as it aroused; normally a torpid bird was held by the wing tips in a gloved hand while body temperature was recorded. There was a short time delay (up to 1 to 2 minutes) between termination of an experiment and the first measurement of body temperature. Since body temperatures could increase slightly during this time, these measurements were extrapolated to the time that arousal was initiated. Also, to insure that the birds were capable of emerging from torpor without our handling them, several individuals were allowed to arouse spontaneously in the dark or after the lights were turned on.

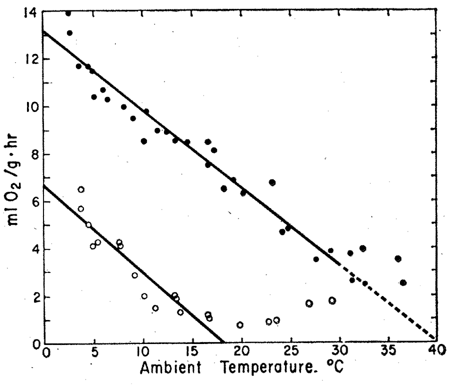

Fig. 1. Relation between oxygen consumption and ambient temperature in *Eulampis jugularis.* Solid circles are for resting birds; open circles signify birds in torpor. Each point represents a single determination.

Oxygen consumption of nontorpid birds increased as ambient temperature decreased below 30°C (Fig. 1, solid circles). The least squares regression equation for this increase was:

$$O_2\ (\text{ml g}^{-1}\ \text{hr}^{-1}) = 13.056 - 0.326(T_A);\quad S_{yx} = \pm 0.679,\ N = 23$$

where T_A is ambient temperature.

Body temperatures remained constant while the birds were not in torpor (Fig. 2, solid circles). The least squares regression equation for body temperature (T_B) as a function of ambient temperature was:

$$T_B = 39.258 + 0.051(T_A);\quad S_{yx} = \pm 1.252,\ N = 18$$

The slope of this regression was not significantly different from zero ($.1 > P > .05$).

Oxygen consumption in torpor was divided into two distinct phases (Fig. 1, open circles). From an ambient temperature of 30° to 18°C, oxygen consumption decreased with decreasing ambient temperature. The Q_{10} between 18° and 30°C for individual measurements varied from 1.5 to 5.6. Below 18°C, oxygen consumption in torpor increased with decreasing ambient temperature. This increase was described by the following least squares regression equation:

$$O_2\ (\text{ml g}^{-1}\ \text{hr}^{-1}) = 6.655 - 0.367\ (T_A);\quad S_{yx} = \pm 0.606,\ N = 15$$

Body temperature measurements during torpor also revealed two distinct phases in relation to ambient temperature (Fig. 2, open circles). Body temperatures decreased with decreasing ambient temperature from 30° to 18°C, but below 18°C, body temperature increased slightly from 18° to 20°C. The least squares regression equation for body temperature as a function of ambient temperature below 18°C was:

$$T_B = 20.903 - 0.204(T_A);\quad S_{yx} = \pm 0.516,\ N = 9$$

The slope of this line was significantly different from zero ($P < .01$).

For an organism to maintain a constant body temperature, heat loss must equal heat production. Thermal conductance is the reciprocal of insulation and provides a measure of the resistance to heat flow provided by the plumage and surface tissues (*2*, *5*, *6*). Since thermal conductance will influence heat loss, it is of interest to determine if this parameter changes when both oxygen consumption and body temperature are drastically altered during torpor. Thermal conductances were calculated for *Eulampis* at rest and in torpor from the following equation:

$$\text{Thermal conductance} = \frac{\text{Heat loss}}{T_B - T_A}$$

Heat production was assumed to be equal to heat loss, and a caloric equivalent of 4.8 cal/ml of O_2 was assumed for calculation of heat production from oxygen consumption data. Heat loss due to evaporation at low ambient temperatures was assumed to be negligible.

The thermal conductance for nontorpid *Eulampis* was 1.55 ± 0.22 (S.D.) cal/g hr °C and the thermal conductance for *Eulampis* that entered torpor below an ambient temperature of 18°C was 1.43 ± 0.29 cal/g hr °C. These values are not statistically different ($.3 > P > .2$). Also, the values for thermal conductance for resting and torpid *Eulampis* are similar to empirically predicted values for an 8- to 9-g bird, 1.41 to 1.33 cal/g hr °C, derived from the equation of Lasiewski *et al.* (*2*); and values of 1.51 to 1.42 cal/g hr °C, derived from the equation of Herreid and Kessel (*6*). It appears, therefore, that there is no change in thermal conductance in *Eulampis* while oxygen consumption and body temperature are regulated during torpor.

The striking feature in torpid *Eulampis* is the thermostatic control of oxygen consumption and regulation of body temperature at ambient temperatures below 18°C. An ambient temperature of 18°C appears crucial for reactivation of some control mechanism in *Eulampis*. Between ambient temperatures of 18° and 30°C oxygen consumption and body temperature in torpid *Eulampis* are related to ambient temperature in a manner similar to other torpid hummingbirds (*7*) and small mammals (*8*).

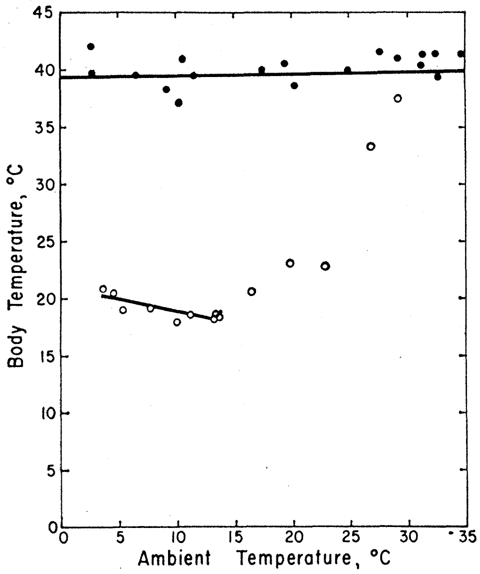

Fig. 2. Relation between body temperature and ambient temperature in *Eulampis*. Symbols as in Fig. 1.

This type of regulation has not been observed in other birds. Several species of hummingbirds enter torpor below an ambient temperature of 15°C, but do not emerge (*7*). Bartholomew, Howell, and Cade (*9*) induced torpor in an Anna hummingbird (*Calypte anna*) at an ambient temperature of 2°C, and this bird emerged from torpor, but they did not observe a regulation of body temperature. Similar observations have been made on the poorwill (*Phalaenoptillus nuttallii*) (*9*, *10*). Phenomena somewhat similar to that seen in *Eulampis* have been observed in a few species of mammals. Some hamsters (*Mesocricetus auratus*) increase oxygen consumption below ambient temperatures of 2.2° to 3.6°C (*11*), and some *Perognathus californicus* pocket mice increase their oxygen consumption at ambient temperatures below 15°C (*8*).

The regulation of oxygen consumption during torpor in *Eulampis* raises interesting questions concerning the evolution and possible adaptive significance of such a phenomenon. Much has been said about the adaptive significance of torpor for conserving energy in small birds and mammals (*1*, *3*). Regulation of oxygen consumption during torpor would certainly place an upper limit on energy conservation for *Eulampis*. The maximum savings in oxygen consumption amounts to 6.4 ml of O_2 per gram per hour. This is about half the metabolic expenditure of nontorpid *Eulampis* at an ambient temperature of 0°C and is approximately a 90 percent energy savings at an ambient temperature of 18°C. Although *Eulampis* will save energy by entering torpor, the regulation of oxygen consumption does not appear to be designed for maximum energy conservation. Such a regulation could, however, prevent *Eulampis* from reaching a level of oxygen consumption or body temperature from which it could not emerge. A number of species of birds and mammals fail to emerge when they enter torpor below a certain ambient temperature (*12*).

A possible further selective advantage of regulating body temperature during torpor could relate to the time required for arousal, which is a function of body temperature during torpor and the rate of increase of body temperature from torpor. Presumably, a bird should take longer to arouse from torpor at a low body temperature than from a high body temperature. Predation, competition for food, and other ecological factors might place a selective advantage on minimizing arousal time. Regulation of oxygen consumption and body temperature during torpor, therefore, could represent an evolutionary compromise between energy conservation and time for arousal.

F. Reed Hainsworth
Larry L. Wolf

Department of Zoology,
Syracuse University,
Syracuse, New York 13210

References and Notes

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12. These include hamsters [$T_A = 2.2°$ to 3.6°C (*11*)], several hummingbirds [$T_A = 15°C$ (*7*)], the cactus mouse [*Perognathus eremicus*, $T_A = 5°C$, R. E. MacMillen, *Amer. Zool.* **4**, 305 (1964)], some *Perognathus californicus* [$T_A = 15°C$ (*8*)], the brown bat [*Myotis lucifugus*, $T_A = 3°C$, M. Menaker, *J. Cell. Comp. Physiol.* **59**, 163 (1962)], the eastern chipmunk [*Tamias striatus lysteri*, $T_A = 16°C$, A. E. Woodward and J. M. Condrin, *Physiol. Zool.* **18**, 162 (1945)], and a number of cricetid rodents [$T_A = 13°$ to 19°C, J. Hudson, in *Mammalian Hibernation*, K. C. Fisher *et al.*, Eds. (Elsevier, New York, 1967), vol. 3].
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