NOCTURNAL HYPOTHERMIA IN ROSY FINCHES[1]

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Most species of small birds reduce their overnight energy expenditure by lowering body temperature (T_b) a few degrees while roosting. Nocturnal hypothermia sufficient to induce torpor is relatively uncommon in birds, but is known to occur in hummingbirds, swifts, caprimulgids, sunbirds, colies, anis, and manakins (see review by Bartholomew, Vleck, and Bucher 1983). Moderate overnight reductions of T_b have been reported for a few passerine species in the family Paridae, such as Black-capped Chickadees, *Parus atricapillus*, Siberian Tits, *Parus cinctus*, and Willow Tits, *Parus montanus* (Steen 1958, Haftorn 1972, Chaplin 1976, Reinertsen and Haftorn 1983). However, most temperate-zone passerines do not appear to lower T_b by more than about 2°C at night unless stressed by severe depletion of energy reserves (Steen 1958, Biebach 1977, Reinertsen and Haftorn 1986).

Small birds living at high altitudes face the compound physiological challenge of low ambient temperature and low partial pressure of oxygen. Under these conditions, nocturnal hypothermia could be an important mechanism for reducing requirements for gas exchange, as well as for conserving limited energy reserves. Although data on T_b are available for montane sunbirds (Cheke 1971), I am aware of no previous studies on nocturnal T_b in temperate-zone passerines native to high altitude. In this study, I measured core body temperatures in Sierra Nevada Rosy Finches (*Leucosticte arctoa*, subfamily Carduelinae), which are native to elevations above 3,500 m in eastern California, and examined the effect of reduced food availability on their nocturnal thermoregulation.

MATERIALS AND METHODS

ANIMALS AND STUDY SITES

Rosy Finches were captured by mist net during midsummer in the White Mountains of eastern California (4,200 m elevation) and by Potter trap during late winter in the Sierra Nevada near Bishop, California (2,500 m). In both seasons, birds were captured in good condition near abundant natural food sources or feeding stations. The birds were weighed at the time of capture and transferred to individual holding cages (40 cm × 40 cm × 40 cm) constructed of wood and nylon mesh, where they remained for the duration of the experiments (about 1 week). Measurements were made dur-

ing summer at the University of California's White Mountain Research Station (WMRS) Barcroft Laboratory (3,800 m), and during winter at the WMRS Bishop Laboratory (1,200 m).

BODY TEMPERATURE

Mini-Mitter Model X telemeters (mass 1.5 g) were surgically implanted in the body cavity of freshly captured birds. Prior to insertion, the telemeters were calibrated in a water bath to an accuracy of 0.1°C, at 2° intervals from 35°C to 45°C. Calibration temperatures were measured with a Bailey BAT-12 thermocouple amplifier calibrated against a platinum resistance thermometer traceable to the U.S. Bureau of Standards.

Rosy Finches were lightly anesthetized during the procedure with approximately 75% N_2O in O_2, delivered continuously through a small mask at a flow rate of 150–200 ml min^{-1}. A 1-cm incision was first made through the mid-lateral abdominal wall. The telemeter was then inserted into the peritoneal cavity, and the incision closed with silk sutures. The birds were allowed to recover indoors for 2 days following surgery, and experiments were then performed for three to five consecutive nights. For measurements of T_b, the holding cages were placed in a sheltered outdoor area under natural conditions of ambient temperature and photoperiod (ca. 11 hr in winter and 13 hr in summer). Food and water were provided ad libitum, except for a limited number of experiments in which food was removed 4–6 hr before roosting. Telemeters were removed and recalibrated upon completion of the experiments, and birds were subsequently released following recovery.

Telemeter signals were received by a standard AM transistor radio from antenna wire woven through the cage mesh and secured underneath the bird's perch. The radio output and ambient temperature in the cage (measured by thermocouple) were recorded by a portable computer (Radio Shack Model 100), via an analog-digital converter (ADC-1, Remote Measurement Systems). A simple opto-isolator circuit was connected between the radio and the A-D converter to eliminate feedback from the computer to the radio, and external interference was reduced by shielding the cage and radio with grounded aluminum screens. Telemeter and thermocouple data were recorded simultaneously from two birds each night, at 5- or 10-min intervals, using a program that averaged the telemeter pulse rates over each interval.

CALCULATIONS

Calibration curves were generated by plotting the pulse rates for each telemeter against temperature (°C), and fitting the data by computer with second order poly-

TABLE 1. Nocturnal body temperatures (T_b) of Rosy Finches measured in summer and late winter. Values are $\bar{x} \pm$ SD with sample sizes in parentheses. T_a is ambient temperature.

	Body mass (g)	T_b (°C)	T_a (°C)
Summer (3,800 m)			
Fed ad libitum	25.3 ± 2.0	39.1 ± 0.4	6.2 ± 1.9
	(4)	(4)	(4)
Fasted	23.1 ± 2.2	37.8 ± 0.7	5.8 ± 0.9
	(3)	(3)	(3)
Winter (1,200 m)			
Fed ad libitum	23.5 ± 1.6	38.9 ± 0.9	3.3 ± 0.3
	(5)	(5)	(5)
Fasted	21.5 ± 0.8	37.5 ± 1.3	0.7 ± 3.3
	(4)	(4)	(4)

nomial equations. The final calibration was used in the analysis whenever possible. Body temperatures (T_b) were plotted in real time and minimum nocturnal T_b's were determined as the lowest level maintained for at least 30 min. The effect of nutritional status on T_b was evaluated by a Wilcoxon's two-way test on pooled data for summer and winter birds. All data are presented as $\bar{x}$ ± SD.

RESULTS

Rosy Finches recovered quickly from the surgery, and were often eating within 1 hr of completion of the procedure. Resting ventilatory frequency, measured by body plethysmography (see Clemens 1988), increased markedly after insertion of telemeters. This presumably resulted from a reduction in abdominal air-sac volume due to the presence of the telemeter in the body cavity.

Minimum nocturnal body temperatures of birds in summer and late winter were very similar (Table 1). The combined mean nocturnal T_b of summer and winter birds was 39.0 ± 0.7°C ($n = 9$), which was about 2°C below daytime resting levels of 41.0–41.5°C. The temporal pattern of nocturnal hypothermia was variable both between and within individuals (Fig. 1). The minimum T_b usually occurred between 02:00 and 04:00, but was maintained in some cases for up to 6 hr. Noc-
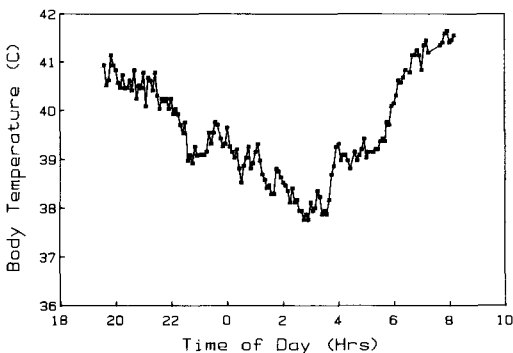

FIGURE 1. A typical recording of nocturnal body temperature in a Rosy Finch (mass = 24.2 g) measured in late winter ($T_a = 3$°C). Sunset—18:30; sunrise—07:00.

turnal T_b of both summer and winter birds was significantly lower in individuals fasted for 4–6 hr prior to roosting, than in birds fed ad libitum ($P < 0.01$). The combined mean T_b of the fasted birds was 37.6 ± 1.0°C ($n = 7$). Minimum ambient temperatures (T_a) for both summer and winter measurements averaged around 3°C (range = -4 to $+8$°C).

DISCUSSION

Daily cycles of body temperature are virtually universal in birds and mammals (see review by Aschoff 1970). Among temperate-zone passerines, substantial and consistent nocturnal hypothermia has been documented only for a few species of parids that overwinter at high latitudes. Wintering Willow Tits, for example, typically regulate nocturnal T_b's at 5–6°C below daytime resting levels, and may reduce T_b by as much as 12°C under conditions of low T_a and depleted nutritional reserves (Reinertsen and Haftorn 1984). By comparison, the nocturnal reductions of T_b in Rosy Finches were much less pronounced, and more similar to the pattern found in another member of the cardueline subfamily, the Common Redpoll, *Acanthis flammea*. In this species, nocturnal T_b averages only about 1°C below daytime levels (41°C) for individuals fed ad libitum, but can decrease by as much as 8°C in fasted individuals roosting at T_a's below -20°C (Reinertsen and Haftorn 1986). At more moderate T_a's (0–5°C), nocturnal T_b falls by about 5–6°C in fasted redpolls, compared to an average decline of about 3°C in the fasted Rosy Finches of this study. This difference between the two cardueline species is probably associated with a difference in body mass. Rosy Finches (24 g) are about 70% larger than Common Redpolls, and can presumably survive longer on internal energy stores without major reductions in T_b. However, under more extreme conditions of low T_a or prolonged fasting than those examined in this study, Rosy Finches might show greater T_b reductions. For example, a minimum T_b of 35.6°C was recorded from one fasted individual whose preroosting body mass had fallen about 3 g below its initial value. Unfortunately, the data for Rosy Finches were not sufficient to establish a significant correlation between preroosting body mass and the depth of hypothermia or duration of the minimum T_b period.

Cardueline finches and parids are conspicuously successful among the small birds that overwinter in cold boreal habitats. The marked difference between these two taxa in the occurrence and extent of nocturnal hypothermia may be explained in part by differences in their feeding strategies (Reinertsen and Haftorn 1986). In contrast to the relatively sedentary wintering parids, carduelines such as Common Redpolls and Rosy Finches are nomadic during winter and can utilize a wide variety of patchy and ephemeral food resources. Furthermore, some species of carduelines can sustain dramatic increases in metabolic rate for several hours under extreme cold stress, and remain normothermic at ambient temperatures below $-60°C$ (Dawson and Carey 1976, Dawson et al. 1983). This suggests that carduelines have evolved an energy-intensive overwintering strategy, in which high mobility and metabolic scope are of paramount importance.

Given that the thermal conductance of Rosy Finches is constant between $-10°C$ and $+20°C$ (Clemens 1988), the total amount of energy saved per unit time should also be constant for a given reduction of T_b over this T_a range. In Rosy Finches, a 3°C decrease in T_b would result in a reduction in standard metabolic rate (SMR) of about 54 mW, or about 7% of the SMR at 0°C. This in turn would confer an energy saving of about 1.5 kJ over the course of an 8-hr roosting period. While this represents only a small energy gain, it could be important when nutritional reserves are severely limited.

While nocturnal hypothermia is traditionally viewed within the framework of animal energetics, the physiological implications of reduced T_b are manifold. For example, it has been suggested that moderate hypothermia may be advantageous to blood oxygen transport in small birds at high altitudes, due to the effect of temperature on the O_2 affinity of avian blood (Maginniss 1985). While increases in O_2 affinity with reduced T_b could improve O_2 transport in species with relatively low affinity blood, an equivalent change could impair oxygen delivery in species with high affinity blood. Since the blood O_2 affinity of Rosy Finches is relatively high at 41°C (Clemens, unpubl.), nocturnal hypothermia of more than a few degrees could severely compromise O_2 transport under conditions of high O_2 demand (e.g., thermoregulation at very low ambient temperatures). It is likely that large changes in T_b cause a decline in the functional efficacy of a wide range of physiological processes in homeothermic animals. Therefore, limited nocturnal hypothermia of the kind seen in Rosy Finches probably represents an evolutionary compromise between the need for energy conservation and the requirements for maintaining adequate physiological function.

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