Short Communications and Commentaries

The Auk 112(4):1034-1036, 1995

Maximum Metabolic Rate, Thermal Insulation and Aerobic Scope in a Small-sized Chilean Hummingbird (*Sephanoides sephanoides*)

M. Victoria López-Calleja and Francisco Bozinovic
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

Maximal rates of energy metabolism (MMR) for thermoregulation may influence the survival of birds by setting the limit for cold tolerance (Rosenmann and Morrison 1974, Bozinovic 1992) and affect geographical distributional limits (Bozinovic and Rosenmann 1989, Peterson et al. 1990, Bozinovic et al. 1994). Bennett and Ruben (1979) and Bennett (1991) suggested that MMR is correlated with minimum or basal rates of metabolism (BMR) in different taxa. The range between BMR and MMR represents the aerobic scope. Animals with a "power strategy" (Gnaiger 1987) or higher mass-independent metabolic rates (MR) and aerobic scopes could have higher rates of energy intake and processing, and comparatively higher-elevated MR at rest than those with "frugal strategies" (Szarski 1983, Karasov 1990).

In small endotherms like hummingbirds, MR is higher than expected from the general allometric trends (McNab 1992). According to Bennett (1991), higher rates of aerobic metabolism may have been selected for thermoregulatory reasons.

Our objective is to describe and compare the maximum and basal metabolic rates for thermoregulation, as well as the aerobic scope of the small-sized hummingbird *Sephanoides sephanoides* (sometimes referred to as *S. galeritus*) inhabiting the Mediterranean environments of central Chile. Also, the indirect estimation of the thermal role of feathers in a small species in reference to similar-sized endotherms was of basic interest. In order to eliminate potential methodological distortions, we restricted our analysis to information published by investigators who used methods similar to our own.

Methods.—We used 23 animals, all adult males, with a mean body mass (m_b) of 5.74 ± SD of 0.72 g captured with mist nets in central Chile, about 80 km east of Santiago (33°15'S, 71°11'W), during the winter (July to August 1994). Hummingbirds were individually maintained in cages with a 0.75 M sugar solution, fruit flies, and water *ad libitum*. Measurements were conducted during the second week after capture. Ambient temperature (T_a) in the animal's room was maintained constant at 25°C and the photoperiod was L:D of 12:12. Metabolic rate was measured at different T_a (range 5°-35°C) in dark metabolic chambers using a closed computerized manometric respirometer (Morrison 1951). Carbon dioxide and water in the metabolic chamber were absorbed with barium hydroxide and calcium chloride. Ambient temperatures were controlled (±0.1°C) in a thermoregulated water bath where the metabolic chambers were submerged. Resting MMR for thermoregulation was measured with mixtures of 20% O_2 and 80% He, a fourfold more conductive medium than air that greatly facilitates heat transfer and elicits maximum thermogenic resting metabolism (Rosenmann and Morrison 1974). After approximately 1 h in which MR was measured, metabolic chambers were flushed with six times their volume of the He-O_2 mixture, while MR was continuously monitored. Birds were removed when their MR declined, and body temperature (T_b) was immediately measured. All animals removed exhibited hypothermia, which indicated that MMR had been attained. To avoid damage, T_b was measured under the plumage in the axila with Cu-constantan thermocouples connected to a digital BAT-12 thermometer (Krüger et al. 1982). Minimal thermal conductance (*C*) was calculated from the slope of the regression between MR and T_a curve below the thermoneutral zone. BMR was estimated within the thermoneutral zone from the mean values of MR when an animal's heat production showed independence of T_a. The equations of Aschoff and Pohl (1970) for BMR of $4.01m_b^{-0.266}$ (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), and of Lasiewski et al. (1967) for C of $0.848m_b^{-0.508}$ (mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) were taken as standard references for birds.

Results and discussion.—The minimal euthermic response of *S. sephanoides* to T_a between 5° and 35°C is shown in Figure 1. The lower limit of the thermoneutral zone is 28°C. The mean BMR of 3.17 ± 0.58 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ is equivalent to 125.8% of the expected rate according to Aschoff and Pohl (1970). Prinzinger et al. (1992) documented a much higher than expected BMR for this species. However, these authors assumed a BMR at T_a of 22°C. We observed that at this T_a animals were below the thermoneutral zone because we found the same magnitude of MR at 22°C than those authors. T_b measured in the axilla of the euthermic hummingbirds was 36.5 ± 1.72°C. Below a T_a of 28°C the increase of MR in air with decreasing

T_a is described by the equation:

$$\text{MR (in air)} = (14.616 \pm 0.515) - (0.397 \pm 0.027)T_a \ (\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) \quad (1)$$

$(r = -0.936, P < 0.001, n = 31)$.

The slope is a measure of minimal thermal conductance and is 147.5% of the expected value of Lasiewski et al. (1967). After the shift from air to He-O_2, MR increased well above resting levels in air (Fig. 1) and is described by the equation:

$$\text{MR (in He)} = (34.071 \pm 2.776) - (0.866 \pm 0.146)T_a \ (\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) \quad (2)$$

$(r = -0.925, P < 0.001, n = 8)$.

The substitutions of the enclosed air in feathers by the more conductive He-O_2 facilitate heat transfer to the environment. A ratio C_{He}/C_{air} of 2.18 (i.e. 0.866/0.397) was observed, reflecting an increase of C in He as compared to C in air (Fig. 1). Slopes or C values were significantly different (ANCOVA, $t = 5.365$, df $= 34$, $P < 0.001$). MMR was 26.51 ± 0.65 (mL $O_2 \cdot g^{-1} \cdot h^{-1}$) and was obtained at a T_a of 10°C (Fig. 1). According to Rosenmann and Morrison (1974), the ratio MMR/C_{air} provides an estimate of the maximum temperature differential tolerable, and also is related to limits of distribution of animals (Bozinovic and Rosenmann 1989). In this case, we obtained a value of 66.7°C. By extrapolation of C in air to MMR, the lower lethal ambient temperature (T_{LL}) at which animals attain its maximal instantaneous MR was approximately −30°C (Fig. 1). The ratio MMR/BMR or metabolic expansivity was 8.4×. The ratio MMR/BMR$_{expected}$ was 10.5×, and the aerobic scope (MMR − BMR) was 23.3 mL $O_2 \cdot g^{-1} \cdot h^{-1}$.

We also observed torpor below thermoneutrality at a T_a of 15°, 17.5°, 20° and 25°C, with MR values among 0.6 to 1.1 mL $O_2 \cdot g^{-1} \cdot h^{-1}$. During torpor, T_b varied below 19.3° to 30°C depending on T_a. The regression curve between T_a and T_b during torpor was:

$$T_b\ (°\text{C}) = (7.534 \pm 1.885) + (0.833 \pm 0.109)T_a \quad (r = 0.967, P < 0.002, n = 4). \quad (3)$$

In spite of the fact that BMR was higher than predicted based on body mass, it was between the range of values documented for Trochilidae (McNab 1988). The quotient C_{He}/C_{air} of 2.2 is similar to the ratio 2.6 found in a three-times larger passerine (*Acanthys flammea*) by Rosenmann and Morrison (1974). Thus, thermal insulation of feathers in small birds seems to be more effective than that supplied by hairs in mammals of similar size (Rosenmann and Morrison 1974). The MMR/BMR quotient is between the range reported for rodents (4-9×) by Rosenmann and Morrison (1974) and Bozinovic et al. (1990), and within the same range of values documented for passerines with an m_b ranging from 17 to 20 g (i.e. 5.5× for the Rufous-collared Sparrow [*Zonotrichia capensis*; Novoa et al. 1990] and 6.6× for the Dark-eyed Junco [*Junco hyemalis*; Swanson 1990]). Nevertheless, the ratio MMR/BMR$_{expected}$ is some of the higher documented for endotherms (see Rosenmann and Morrison 1974). The value of T_{ll} of *S. sephanoides* was higher than the −75°C documented for the Common Redpoll (*Carduelus flammea*) by Rosenmann and Morrison (1974), but similar to T_{ll} of −31.8° and −33.6°C reported by Novoa et al. (1990) for two populations of Rufous-collared Sparrows from low and high altitude in central Chile. The aerobic scope (MMR − BMR) of *S. sephanoides* is higher than the documented for authors cited above (i.e. for Common Redpoll, 18.1 mL $O_2 \cdot g^{-1} \cdot h^{-1}$; for House Sparrow, 12.9 mL $O_2 \cdot g^{-1} \cdot h^{-1}$; for Rufous-collared Sparrow, 13.5 mL $O_2 \cdot g^{-1} \cdot h^{-1}$; and for Dark-eyed Junco, 19.3 mL $O_2 \cdot g^{-1} \cdot h^{-1}$).

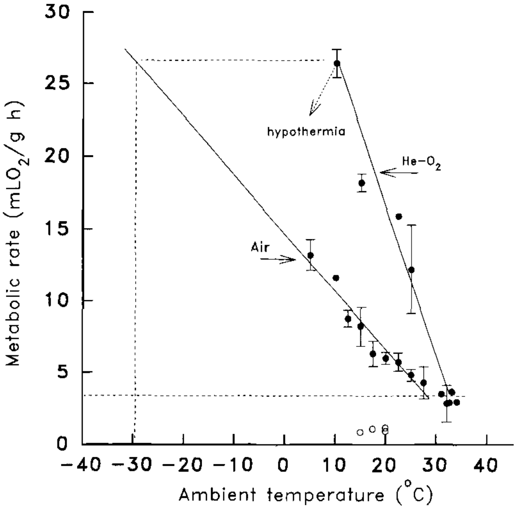

Fig. 1. Relationship between metabolic rate and ambient temperature of *Sephanoides sephanoides* in air and in He-O_2. Upper and lower dotted lines indicate maximum and basal metabolic rate, respectively. Vertical dotted line from intercept between maximum metabolic rate and MR in air indicates extrapolated ambient temperature for maximum metabolic rate. MR during torpor is indicated with open circles. Whiskers indicate ±1 SD.

Finally, *S. sephanoides* exhibited some of the highest-reported MMR for thermoregulation and aerobic scopes. McNab (1992) pointed out that comparative increments in MR appear to be an adjustment or even a cost to allow continuous endothermy in small endotherms. Thus, *S. sephanoides* energetics may be mainly related to its small body mass, but also to its life modes, including their foraging strategies as well as their spatial and temporal patterns of distribution. To test this hypothesis, more information is needed concerning the scaling of thermoregulatory MMR and aerobic scope in hummingbirds and birds differing in body mass and from different habitats.

Acknowledgments.—We thank M. Rosenmann for comments on an early version of the manuscript. A. Sazo provided valuable help during experiments. Research was funded by Fondo Nacional de Ciencia y Tecnología 1950394 to F.B. and was conducted during the graduate program of M.V.L-C.

LITERATURE CITED

ASCHOFF, J., AND H. POHL. 1970. Rhythmic variation in energy metabolism. Fed. Proc. 29:1541-11552.

BENNETT, A. F. 1991. The evolution of activity capacity. J. Exp. Biol. 160:1-23.

BENNETT, A. F., AND J. A. RUBEN. 1979. Endothermy and activity in vertebrates. Science 206:649-654.

BOZINOVIC, F. 1992. Scaling of basal and maximum metabolic rate in rodents and the aerobic capacity model for the evolution of endothermy. Physiol. Zool. 65:921-932.

BOZINOVIC. F., AND M. ROSENMANN. 1989. Maximum metabolic rate of rodent: Physiological and ecological consequences on distributional limits. Funct. Ecol. 3:173-181.

BOZINOVIC, F., F. F. NOVOA, AND C. VELOSO. 1990. Seasonal changes in energy expenditure and digestive tract of *Abrothrix andinus* (Cricetidae) in the Andes range. Physiol. Zool. 63:1216-1231.

BOZINOVIC, F., M. ROSENMANN, F. F. NOVOA, AND R. G. MEDEL. 1994. Mediterranean-type climatic adaptation in the physiological ecology of rodent species. Pages 347-362 *in* Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia (M. T. Kalin-Arroyo, P. H. Zedler, and M. D. Fox, Eds.). Springer-Verlag, New York.

GNAIGER, E. 1987. Optimum efficiencies of energy transformation in anoxic metabolism. The strategies of power and economy. Pages 7-36 *in* Evolutionary physiological ecology (P. Calow, Ed.). Cambridge Univ. Press, Cambridge.

KARASOV, W. H. 1990. Digestion in birds: Chemical and physiological determinants and ecological implications. Pages 391-415 *in* Avian foraging: Theory, methodology, and implications (M. L. Morrison, C. J. Ralph, and J. R. Jehl, Eds.). Stud. Avian Biol. 13.

KRÜGER, K., R. PRINZINGER, AND K. L. SCHUCHMANN. 1982. Torpor and metabolism in hummingbirds. Comp. Biochem. Physiol. A Comp. Physiol. 73: 679-689.

LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797-813.

MCNAB, B. K. 1988. Food habits and the basal rate of metabolism in birds. Oecologia 77:343-349.

MCNAB, B. K. 1992. The comparative energetics of rigid endothermy: The Arvicolidae. J. Zool. Lond. 227:585-606.

MORRISON, P. R. 1951. An automatic manometric respirometer. Rev. Sci. Instrum. 22:264-267.

NOVOA, F. F., F. BOZINOVIC, AND M. ROSENMANN. 1990. Maximum metabolic rate and temperature regulation in the Rufous-collared Sparrow, *Zonotrichia capensis*, from central Chile. Comp. Biochem Physiol. A Comp. Physiol. 95:181-183.

PETERSON, C. C., K. A. NAGY, AND J. DIAMOND. 1990. Sustained metabolic scope. Proc. Natl. Acad. Sci. USA 87:2324-2328.

PRINZINGER, R., T. SCHÄFER, AND K. L. SCHUCHMANN. 1992. Energy metabolism, respiratory quotient and breathing parameters in two convergent small bird species: The Fork-tailed Sunbird *Aethopyga christinae* (Nectariniidae) and the Chilean hummingbird *Sephanoides sephanoides* (Trochilidae). J. Therm. Biol. 17:71-79.

ROSENMANN, M., AND P. R. MORRISON. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O_2. Am. J. Physiol. 226:490-495.

SWANSON, D. L. 1990. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). Auk 107:561-566.

SZARSKI, H. 1983. Cell size and the concept of wasteful and frugal evolutionary strategies. J. Theor. Biol. 105:201-209.

Received 5 October 1994, accepted 24 July 1995.