The Auk 118(3):781–785, 2001

Standard and Comparative Energetics of a Small Avian Herbivore (*Phytotoma rara*)

ENRICO L. REZENDE, M. VICTORIA LÓPEZ-CALLEJA, AND FRANCISCO BOZINOVIC[1]
Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT.—We studied the standard and comparative energetics of the Rufous-tailed Plancutter (*Phytotoma rara*), one of the smallest avian herbivores. The Rufous-tailed Plancutter had basal metabolic rate (BMR) values that so far are the highest mass-independent values observed in avian herbivores. Probably the BMR values attained by *P. rara* reflect its geographic distribution in temperate environments. Using a comparative analysis, we observed that herbivorous birds from temperate geographic areas tend to have higher BMR than tropical ones.

The level of energy expenditure of endotherms is a function of body mass (m_b) as well as of food habits, climate, phylogeny, and activity, among other factors (McNab 1986). Ecological factors, such as climate and food habits, appear to be the most important features in determining mass-independent energy expenditure at both intra- and interspecific levels (McNab 1988a, Veloso and Bozinovic 1993, Haim 1987; but see Geluso and Hayes 1999). Nevertheless, despite of the great amount of literature relating those features in mammals (see McNab 1986, 1988a for reviews), relatively few studies were carried out in birds. Independently of food habits, it has been described that basal metabolic rates (BMR) scales to body mass as it does in mammals, although birds have higher mass-independent BMR than mammals (McNab 1988b).

However, the maintenance of positive energy balance in small herbivorous endotherms in spite of highly fibrous diets seems to be inconsistent with allometric rules (Demment and Van Soest 1985, Foley and Cork 1992). In fact, McNab (1988b) showed that relatively few bird species show herbivory when compared with mammals. That author postulated that differences observed in BMR between those classes could be partially explained by that differential occurrence of herbivorous species. Nevertheless, almost no studies have been carried out in small (<150 g) avian herbivores, and the few available were conducted with tropical species (Bosque et al. 1999). Here we studied the energetics of the Rufous-tailed Plantcutter (*Phytotoma rara*). *Phytotoma rara* is one of three species of South American Phytotomidae, and it is among the smallest species of avian herbivores (m_b = 42 g) (Ziwiler and Farner 1972). Field and laboratory observations showed out that *P. rara* prefers leaves over fruits and insects, being that during winter its diet is composed almost 100% of vegetative tissues (Jaksic and Feinsinger 1991, López-Calleja and Bozinovic 1999). In addition, López-Calleja and Bozinovic (2000) reported that under both natural and experimental conditions, *P. rara* preferred monocotyledons to dicotyledons and young over mature plants.

The study of *P. rara*'s standard and comparative energetics is particularly interesting, because of 1) the cost of continuous endothermy is higher at small body sizes, 2) this species feeds on an energetically diluted diet (López-Calleja and Bozinovic 2000), and 3) is one of the few small herbivorous birds with temperate geographic distribution. In fact, among Phytotomidae, *P. rara* is the species with the southernmost distribution, from Vallenar (28°34'S, 70°45'W) to Chiloé (42°25'S, 73°46'W), Chile (López-Calleja and Bozinovic 1999). Therefore, our objective was to determine the standard BMR, maximum metabolic rate (MMR), thermal conductance (C), body temperature (T_b), maximum and minimum thermal differential (ΔT_M and ΔT_m, respectively), and comparative energetics (BMR and geographic distribution of other herbivorous birds) of this species.

Methods.—We used 21 adults averaged 41.6 ± 2.5 g (SD) captured with mist nets in central Chile, ~130 km west of Curicó (72°02'W, 34°78'S) during 1996 and 1997. Birds were maintained in an outdoor aviary, with water and food (lettuce and blackberries) *ad libitum*.

Measurements of metabolic rate (MR) were conducted for 2 h during the second week after capture through oxygen-consumption records. Measurements were carried out at different ambient temperatures (T_a) in a range of 5–35°C in dark metabolic chambers by using a computerized closed-circuit automatic system based on Morrison (1951). Some individuals were randomly run more than one at different T_a. Between measurements birds rested for 2 days. 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 in six individuals with mixtures of 20% O_2 and 80% He (a fourfold more conductive medium than air) which greatly facilitates heat transfer and elicits maximum

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[1] Address correspondence to this author. E-mail: fbozinov@genes.bio.puc.cl

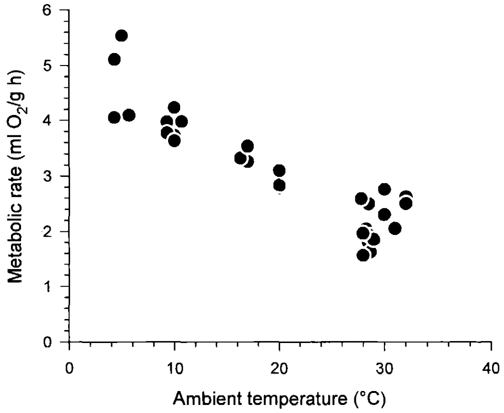

FIG. 1. Metabolic rate of *Phytotoma rara* as a function of ambient temperature.

thermogenic resting metabolism (Rosenmann and Morrison 1974). After ~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 T_b was immediately measured with Cu-constantan thermocouples and a Digi-Sense electronic thermometer. All animals removed exhibited hypothermia ($T_b < 35$°C), which indicated that MMR had been attained. On the other hand, BMR was estimated within the thermoneutral zone in postabsorptive individuals during their period of inactivity using the mean values of MR when oxygen consumption showed independence of T_a. The lower limit of the thermoneutral zone was determined through the equation: T_b − (BMR/C) (see Bozinovic and Rosenmann 1989).

As an attempt to compare the energetic of *P. rara* with other largely herbivorous species, data of m_b and BMR were collected from the literature (Appendix). Log-log transformed data were used to determine the allometric relationship between BMR and m_b. We used the latest allometric curve of BMR for all birds described in literature (Reynolds and Lee 1996): BMR = 7.01 $m_b^{-0.330}$ (mLO_2 g^{-1} h^{-1}) and the transformed equations of Lasiewski et al. (1967): C = 0.848 $m_b^{-0.508}$ (mLO_2 g^{-1} h^{-1} °C^{-1}) as standard references for birds. On the other hand, MMR values of *P. rara* were compared with the transformed equation of Hinds et al. (1993) for birds: MMR = 46.68 $m_b^{-0.374}$ (mLO_2 g^{-1} h^{-1}). Statistical analyses were performed using STATISTICA (1997) statistical package for Windows 95. Data were adjusted by using linear regression. Comparisons between expected and observed values were carried out using Student *t*-test for dependent samples or Wilcoxon matched pairs test, while an analysis of covariance (ANCOVA) was used to determine differences between the allometric slopes of BMR.

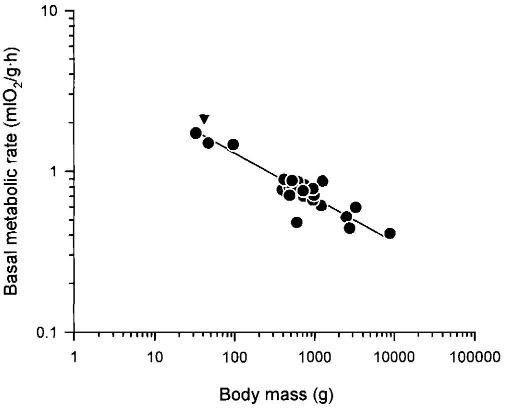

FIG. 2. Double logarithmic relationships between BMR and body mass for 21 avian herbivores from the literature (black circles) together with our data obtained for *P. rara* (black triangle). The line represents the regression obtained with these values, with the equation: BMR = 4.95 $m_b^{-0.286}$.

Results.—Average T_b in *P. rara* was 40.2 ± 0.9°C (n = 26), and the lower limit of the thermoneutral zone is 22°C. The mean BMR of 2.47 ± 0.30 mLO_2 g^{-1} h^{-1} is significantly higher than the expected rate (2.07 mLO_2 g^{-1} h^{-1}), according to Reynolds and Lee (1996) (Wilcoxon, Z = 2.37, P = 0.02), equivalent to a 121.3% higher. On the other hand, C was 0.135 ± 0.013 mL O_2 g^{-1} h^{-1} °C^{-1}, equivalent to 105.2% of the expected value based on m_b (t = −1.93, df = 15, P = 0.07), see Figure 1.

The mean value of MMR of *P. rara* was 11.69 ± 2.31 mL O_2 g^{-1} h^{-1} (n = 6), quite similar to the expected value of 11.59 mL O_2 g^{-1} h^{-1}, according to Hinds et al. (1993). The ratio MMR/BMR was 4.73, which is in the same range of values reported by Hinds et al. (1993) in other species of bird species. In addition, the aerobic scope of *P. rara* (MMR − BMR) was 9.22 mL O_2 g^{-1} h^{-1}. According to Rosenmann and Morrison (1974), the ratio MMR/C provides an estimate of the maximum temperature differential tolerable or ΔT_M, and also is related to the limits of distribution of animals (Bozinovic and Rosenmann 1989). We obtained a value of ΔT_M = 85.8°C. The lower lethal ambient temperature ($T_{LL} = T_b$ − MMR/C) at which animals attain its maximal instantaneous MR was approximately −43°C.

The allometric relationship for the 21 species of avian herbivores was BMR (mL O_2 g^{-1} h^{-1}) = 4.95 $m_b^{-0.286}$ (Fig. 2). The log-transformed curve of Reynolds and Lee (1996) was significantly different of the one described above (ANCOVA, F = 4.157, df = 22 and 1, P = 0.05).

Discussion.—*Phytotoma rara* had BMR values that are so far the highest observed in avian herbivores (Appendix). Therefore, the high-fiber contents of

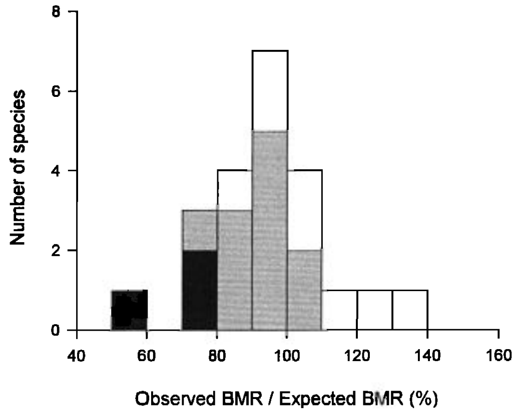

FIG. 3. Variations of BMR in respect to species' latitudinal location. Expected BMR based on body mass were calculated with the equation of Reynolds and Lee (1996): 7.01 $m_b^{-0.330}$. Black bars represent tropical species, gray bars represent temperate, species and white bars represent species with cool to cold ranges of distribution.

plant material together with a short digestive tract (Ziwiler and Farner 1972, López-Calleja 2000) does not seem to restrict high rates of energy acquisition necessary to maintain such metabolic expenditure (Bozinovic 1993). *Phytotoma rara* exhibits active food selection, fast passage rates, an effective physical breakdown of cell walls, as well as constant and high activities of digestive enzymes (López-Calleja and Bozinovic 1999, Meynard et al. 1999). According to López-Calleja and Bozinovic (2000) those functional traits make available the highly nutritious cell contents to the small herbivore without the energy costs of anatomical structures for bacterial fermentation or slow digesta passage rates of herbivorous birds which rely extensively on fermentation of cells walls. Those are possible crucial adaptations in the evolution of herbivory in small birds, allowing the maintenance of the observed high BMR. In contrast, smaller tropical arboreal folivores such as saltators and mousebirds exhibited low BMR although they are able to process plant material (Bosque et al. 1999), but it is not known to what extent they are able to digest cell walls or extract solubles from leaves. In short, as pointed out by Veloso and Bozinovic (1993), the interaction between diet quality and digestive physiology might influence BMR because digestive processing might limit rates of energy acquisition, thus setting an upper limit to the energy budget.

In regards to the allometric relation observed for avian herbivores, we found a significant difference between the slopes of our curve and the one described by Reynolds and Lee (1996). Climatic conditions of birds' habitats may explain that pattern. That relationship is noticeable when we consider deviations of observed with respect to the expected BMR values. We observed that birds from temperate geographic areas tend to have higher BMR, whereas tropical birds show lower values (Fig. 3).

In summary, the Rufous-tailed Plantcutter is able to maintain high metabolic rates despite of the poor quality of its diet, suggesting that there are no constraints on herbivory due to body size and environmental temperatures in the ranges we analyzed.

Acknowledgments.—We thank M. Rosenmann for all the laboratory facilities he gave us to carry out this work and A. Sazo for taking care of the animals. This study was supported by Fondo Nacional de Ciencia y Tecnología (FONDECYT) grant No. 1980959 to F. Bozinovic and 2970002 to M.V. López-Calleja.

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Received 29 November 1999, accepted 23 January 2001.
Associate Editor: C. Bosque

APPENDIX. Basal metabolic rate (BMR) and body mass (m_b) in herbivorous birds.

Species	m_b (g)	BMR (mL/O_2 /g h)	References
Anatidae			
Anas platyrhyncos	741	0.82	Daan et al. (1990)
Anas gibberifrons	391	0.77	McNab (1994)
Anas rhynchotis	480	0.80	McNab (1994)
Anas aucklandica chlorotis	529	0.79	McNab (1994)
Anas castaneas	944.1	0.78	Hinds et al. (1993)
Anser anser	3250	0.60	Kendeigh et al. (1977)
Aythya fuligula	611	0.86	Daan et al. (1990)
Anas penelope	723	0.70	Kendeigh et al. (1977)
Tadorna variegata	1199	0.61	McNab (1994)
Cygnus buccinator	8880	0.41	Benedict and Fox (1927)
Branta bernicla	1253	0.87	Daan et al. (1990)
Ralidae			
Crex crex	96	1.47	Kendeigh et al. (1977)
Fulica atra	412	0.89	Kendeigh et al. (1977)
Gallinula tenebrosa	519	0.87	McNab (1994)
Gallinula mortierii	944	0.66	McNab (1994)
Porphyrio porphyrio	973	0.71	McNab (1994)
Porphyrio mantelli	2764	0.44	McNab (1994)
Cuculidae			
Opisthocomus hoazin	598	0.48	Grajal A. (1991)
Tetraonidae			
Centrocerus urophasianus	2500	0.52	Vehrencamp et al. (1989)
Emberezidae			
Saltator coerulescens	47	1.49	Bosque et al. (1990)
Saltator orenocensis	32.7	1.72	Bosque et al. (1990)
Phytotomidae			
Phytotoma rara	41.6	2.47	this study

The Auk 118(3):785–789, 2001

Function and Temporal Variation in Use of Ossuaries by Bearded Vultures (*Gypaetus barbatus*) During the Nestling Period

ANTONI MARGALIDA[1] AND JOAN BERTRAN

Group of Study and Protection of the Bearded Vulture, Apdo. 43, E-25520 El Pont de Suert (Lleida), Spain

ABSTRACT.—We analyze the use and functionality of ossuaries by the Bearded Vulture (*Gypaetus barbatus*) in the Pyrenees during the nestling period. In 71% of cases, the ossuary was used to prepare food for chicks, in 11% for storing food, and only in 18% for preparing the adults' own food. Pairs used an average of two ossuaries at a mean distance from the nest of 789 m (SE ± 377). The average time dedicate to breaking bone was 5.3 min (SE ± 4.2) and 4.5 throws (SE ± 5.8) for each session in the ossuarie (n = 86). The temporal variation found in the use of the ossuaries, with maximum frequencies between 31–90 days of age of chicks, may be due to a possible qualitative variation in chicks' diets. Ossuaries are also used to store food, this being a differentiating and advantageous trait with respect to feeding behavior developed by other meat scavengers.

Bearded Vultures (*Gypaetus barbatus*) feed mainly on the carcasses of medium-sized domestic and wild ungulates (Hiraldo et al. 1979). Although most of the

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[1] E-mail: margalida@gauss.entorno.es