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Nonconformance of Standard Metabolic Rate with Body Mass in Hawaiian Honeycreepers

R.E. MacMillen
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717 USA

Summary. Among four species of Hawaiian Honeycreepers, three from Hawaii (*Vestiaria coccinea,* 15.0 g; *Himatione sanguinea,* 12.9 g; *Loxops virens,* 10.7 g) and one from Kauai (*Loxops parva,* 7.9 g), standard metabolic rate (in ml $O_2/g \cdot h$) was positively related to body mass, the opposite of that predicted by conventional endothermic allometry. SMR of *V. coccinea* conformed to the predicted value, but in the remaining species was progressively reduced below expected levels as body mass decreased. All four species occur predominantly in *Metrosideros collina* forests, where their preferred food is the nectar of its blooms. At least on Hawaii and during periods of moderate bloom the species are aligned along a dominance hierarchy, with the largest species most dominant and most successful at nectar exploitation. I believe that nonconformancy of SMR with body mass in the smaller species reflects an energy-conserving measure, the degree of which is dictated by social position and relative success in nectar exploitation.

Introduction

In an earlier study of metabolic rate and thermoregulation of the Hawaiian Honeycreepers *Loxops virens* and *L. parva* I observed (MacMillen 1974) that the standard metabolic rate (SMR, expressed in ml $O_2/g \cdot h$) of the former (mean body mass, 15.3 g) exceeded that of the latter (mean body mass, 7.9 g); this is the reverse of what is expected from conventional allometric considerations (Aschoff and Pohl 1970). Weathers (1979) has recently shown that high latitude birds tend to have higher than expected SMRs, while low latitude birds show the converse, and invokes thermal influences. *L. virens* and *L. parva* are sympatric on the tropical island of Kauai where latitudinal and thermal influences are the same for each; clearly selective forces other than thermal influences must be operating to determine the metabolic performances of these species. In addition, since both species are shade foragers (Eddinger 1970), it is doubtful that deviations from their expected metabolic performances can be attributed to differences in foraging sites (shade vs. sun) as has been postulated recently for tropical birds (Weathers 1979).

During the course of a study on the foraging behavior and energetics of three species of Honeycreepers on the island of Hawaii (Carpenter and MacMillen 1976a, b; MacMillen and Carpenter 1977, 1980), and realizing the extent of metabolic divergence among congeneric and sympatric *Loxops* species, it became apparent that metabolic rates of all study species would have to be measured in order to determine to what extent they deviated from conventional allometric expectations and to provide realistic estimates of the energetic costs of foraging. Herein I report and comment on the metabolic performances of the Honeycreepers Iiwi (*Vestiaria coccinea,* 15.0 g), Apapane (*Himatione sanguinea,* 12.9 g), and Amakihi (*Loxops virens,* 10.7 g), all sympatric in native forests on the island of Hawaii, and compare these performances with that of the Anianiau (*L. parva,* 7.9 g), which is confined to the island of Kauai and where it co-occurs with the other three species; all four species are closely related, belonging to the passerine family Drepanididae (=Drepaniidae; Amadon 1950).

Materials and Methods

The individuals of *V. coccinea, H. sanguinea* and *L. virens* employed in this study were all collected at elevations between 1,350 and 1,850 m on the Keauhou Ranch, Kau District, Hawaii, on the east flank of the volcano Mauna Loa. They were captured in mature stands of ohia *(Metrosideros collina)*-koa *(Acacia koa)*- tree fern *(Cibotium glaucum)* montane forest (Mueller-Dombois and Fosberg 1974). Since earlier I had determined that these birds could not be kept in good health in captivity for more than a few days, all birds were captured in mist nets one day, held overnight in small cages, with metabolic measurements ensuing the next day; they then were released that same day or the following morning at the site of capture. While in captivity, except while measurements were being made, the birds were subjected to natural photo- and thermoperiods and provided ad libitum a 20% sucrose solution for food and water; this corresponds with the concentration of their preferred natural food source, the nectar of ohia flowers (*Metrosideros collina;* Carpenter 1976).

Metabolic measurements and housing of the birds were in a temporary laboratory established at a cottage in the residence compound, Hawaii Volcanoes National Park, elevation 1,225 m. Measurements of oxygen consumption (corrected to STP) were made in an open-airflow system similar to that described in MacMillen (1974) except that outside air was pumped into the system with a Bell and Gossett Oil-less air compressor. Oxygen consumption was determined with a Beckman E-2 paramagnetic oxygen analyzer, with birds held individually in 3.5-l respirometer chambers, placed within a darkened constant-temperature cabinet. Airflow through the chambers was maintained at 800 ml/min, and measurements were made over a temperature range of about 10 to 35° C. Each bird was maintained at the measurement temperature for an hour prior to measurement; all measurements were confined to the subsequent half-hour and were made at 5-min intervals. The two lowest measurements at each temperature for each bird were accepted as representative metabolic rates. Birds were weighed prior to and after each one-half-h episode and the weight for calculation of oxygen consumption was interpolated, assuming constant weight loss. All measurements were made while the birds were postabsorptive, during the daylight hours, but in darkness, conforming to Aschoff and Pohl's (1970) active (α) requirements. Measure-

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ments on *V. coccinea* and *H. sanguinea* were made during July and August 1973; those on *L. virens* were made during July and August 1974, and are independent of those reported in MacMillen (1974) for hand-reared birds.

The comparative values for *L. parva* were collected in the same manner during July and August 1971, except they were from hand-reared, captive birds maintained and measured in Honolulu, HI, at an elevation near sea level as reported in MacMillen (1974). The *L. parva* specimens were collected in Kokee State Park, Kauai by C.R. Eddinger.

Results

Although the three species of wild-caught Honeycreepers were treated in the conventional manner for achieving measurements of SMR during the active phase of their circadian cycle (Aschoff and Pohl 1970), all showed greater than usual variability in measurements at each temperature. In Fig. 1 are seen values for oxygen consumption in *L. virens*, which are representive of the variability observed in all three species. Nevertheless mean standard metabolic rate of these birds at T_a between 29.2 and 33.7° C ($\bar{X}=31.1°$ C) was not significantly different (Mann-Whitney U-test, $P>0.05$) from mean SMR determined in very quiescent hand-reared birds of the same species at $T_a=29.9$ to 30.6° C (MacMillen 1974); these values are $3.47 \pm$ SD 1.08 ml O_2/g·h and 3.54 ± 0.38 ml O_2/g·h, respectively. Thus in spite of the degree of variability I conclude that the SMRs reported herein for the wild-caught birds are accurate and representative of the species studied.

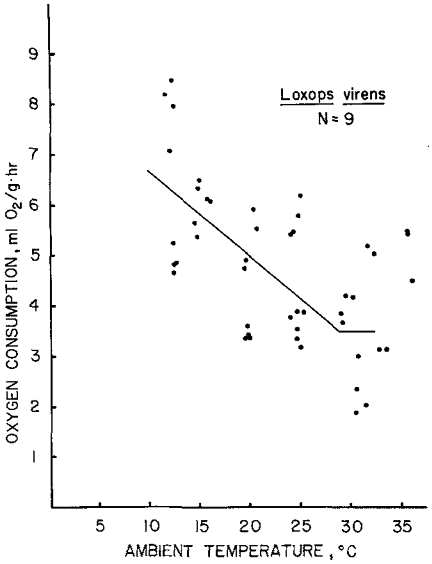

Fig. 1. The relationship between consumption and ambient temperature in *Loxops virens* from the island of Hawaii. The diagonal line is fitted to the data below thermal neutrality by the method of least squares (see Table 1 for equation); the horizontal line represents mean standard metabolic rate

The mean values of SMR for all four Honeycreeper species, together with their regression equations relating metabolic rate to T_a below thermal neutrality are indicated in Table 1. The double logarithmic relationship between SMR and body mass in the four Honeycreeper species is shown in Fig. 2; it is represented by a positive regression line described by the equation $SMR=2.35\ W^{0.139}$, where SMR is in ml O_2/g·h and W is body mass in g (this line however does not statistically deviate in slope from zero; $F=1.016$, d.f.$=1,44$). This figure also shows the negative line connecting the SMR values predicted for passerine birds of these masses and in the α metabolic phase as described by the equation $M=140.9\ W^{0.704}$ (Aschoff and Pohl 1970); where M is SMR in kcal/day and W is mass in kg (SMR was converted from kcal/day to ml O_2/g·h by assuming 4.8 cal = 1 ml O_2). In addition to the slopes of the curve being very different, only the SMR value predicted for the largest Honeycreeper *(V. coccinea)* falls within the 95% confidence limits of the empirically-derived regression line for Honeycreepers (Fig. 2).

While SMR varies in an unconventional manner (according to Aschoff and Pohl 1970) with body mass, there is no parallel variation in body temperature. Regressing body temperature on body mass results in a relationship not statistically different from zero ($T_b=0.399$–0.698 W; $F=0.778$, d.f.$=1,12$) and with little or no correlation ($r=0.247$, $N=14$). Thus the observed reduction in SMR in the smaller species cannot be attributed to reduced body temperatures.

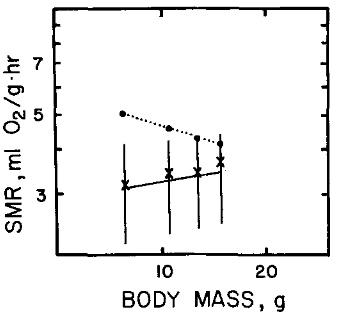

Fig. 2. The relationship between standard metabolic rate *(SMR)* and body mass in four species of Hawaiian Honeycreepers. The diagonal solid line is derived from the empirical data and is described by the regression equation $SMR=2.35\ W^{0.139}$ (SMR in ml O_2/g·h, W in g); X represents mean SMR for each species and the vertical solid lines encompass the 95% confidence limits around the regression line. The dotted line connects the predicted SMRs of all four species based on Aschoff and Pohl's (1970) equation $SMR=140.9\ W^{0.704}$ (SMR in Kcal/day, W in kg)

Table 1. Metabolic performances of three Honeycreeper species from Hawaii, and one *(L. parva)* from Kauai. Metabolic rates (M or SMR) are expressed in ml O_2/g·h; mean values are followed by standard deviations

Species	Below thermal neutrality		Within thermal neutrality			
	Regression equation, *r*	No. birds (No. measurements)	$\bar{X}$ SMR (ml/g·h)	$\bar{X}$ Mass (g)	$\bar{X}$ T_a (° C)	No. birds
Vestiaria coccinea	$M=7.077-0.138\ T_a$, $r=0.487$	7 (30)	3.71 ± 1.39	15.0 ± 1.9	24.9 ± 0.3	6
Himatione sanguinea	$M=6.415-0.122\ T_a$, $r=0.542$	8 (40)	3.46 ± 1.42	12.9 ± 1.5	25.1 ± 0.5	7
Loxops virens	$M=8.376-0.169\ T_a$, $r=0.582$	9 (32)	3.47 ± 1.08	10.7 ± 1.4	31.1 ± 1.5	6
Loxops parva	$M=10.544-0.219\ T_a$, $r=0.920$	4 (24)	3.22 ± 0.20	7.9 ± 0.6	32.4 ± 0.4	4

Table 2. Observed and predicted standard metabolic rates (after Aschoff and Pohl 1970) and daily energy expenditures (after MacMillen and Carpenter 1977) in four species of Hawaiian Honeycreepers

Species	SMR, Kcal/day		Daily Energy Expenditure, Kcal/day[a]		
	Observed	Predicted	Observed	Predicted	Predicted/Observed × 100
Vestiaria coccinea	6.4	7.3	14.08	16.06	114.1
Himatione sanguinea	5.1	6.6	11.22	14.52	129.4
Loxops virens	4.3	5.8	9.46	12.76	134.9
Loxops parva	2.9	4.7	6.38	10.34	162.1

[a] Daily Energy Expenditure = SMR × 2.2, as demonstrated in *Vestiaria coccinea* by MacMillen and Carpenter, 1977

Discussion

The dogma that for birds weight-relative standard metabolic rate varies negatively with body mass and/or whole-animal metabolic rate varies positively with body mass is so ingrained in the literature (Brody and Proctor 1932; Kleiber 1932, 1947; Benedict 1938; Brody 1945; Scholander et al. 1950; King and Farner 1961; Lasiewski and Dawson 1967; Aschoff and Pohl 1970), that it has been almost heretical to suggest outherwise. This is in spite of the common acknowledgment that energy availability and/or the thermal enviroment can exert powerful selective influences on organisms, particularly on those such as endotherms with inherently high rates of energy exchange. Recently, however, Dawson and Bennett (1973) have shown that desert-dwelling doves and pigeons have SMRs that are uniformly depressed below those predicted for their sizes and those measured in non-desert doves and pigeons. Still more recently, Weathers (1979) has shown that SMR of birds correlate broadly with climate of origin, with high latitude birds having higher than predicted SMRs, and low latitude birds more typically having SMRs depressed below the predicted values. Both of these studies attribute manipulations of metabolic performance to alterations in rates of heat production consistent with environmentally-induced conditions of radiant heat load (deserts and/or low latitudes) and excessive heat loss (high latitudes).

Equally plausible to me is the possibility that birds may deviate from predicted levels of metabolic performance if their food supply is periodically precarious, by possessing a depressed metabolism. Such an adaptation is not nearly as extreme as torpor (it involves no lowering in body temperature) yet theoretically is an alternative energetic means of dealing with periods of temporarily depressed food resources. An ideal avian group in which to examine this possiblility is a single taxon in which the member species are aligned along a gradient of food availability. Such a gradient likely would exist if some member species relied primarily on nectar, a renewable resource whose abundance is fixed in time and space, while others were chiefly insectivorous and used resources whose abundances fluctuated in a more stochastic manner. The drepanidid Honeycreepers studied herein meet these criteria for, although all four species seem to prefer to use *Metrosideros* nectar when it is readily available, during times of lesser abundance they exploit nectar with differential success. *Vestiaria coccinea* and *Himatione sanguinea* are highly nectarivorous while *Loxops virens* and *L. parva* employ nectar when readily available, but spend considerable time gleaning for insects amongst leaves, twigs and branches (Baldwin 1953; Eddinger 1970; personal observation). In addition, on Hawaii during the nonbreeding season when this study was made, and during periods of moderate nectar availability, *V. coccinea, H. sanguinea,* and *L. virens* are aligned along a pronounced linear dominance hierarchy with the highly territorial *V. coccinea* dominant over *H. sanguinea* and *L. virens,* and with *H. sanguinea* dominant over *L. virens* (Carpenter and MacMillen 1976b and in prep.; J.J. Hatch, pers. comm.). This dominance hierarchy also extends across a gradient of decreasing size. Although we have not observed the interspecific social status of *L. parva* on Kauai, its reported feeding habits (Eddinger 1970) and smallest size infer social subordinacy.

The dominance hierarchy is inconspicuous or lacking during periods of maximal *Metrosideros* bloom, but becomes pregressively more conspicuous as the bloom lessens. During periods of modest to poor bloom on Hawaii nectar exploitation is dominated first by *V. coccinea* and then by *H. sanguinea; Loxops virens* is nearly exluded from access to nectar, spending most of its foraging time seeking insects. I believe the same applies on Kauai, and that *L. parva* is pushed even further off the nectar-exploitation scale. Thus I look upon the Honeycreepers' progressive reduction from predicted metabolic rate as an energy-conserving measure related to the relative availability and exploitability of nectar as the prefered food.

Such empirically-derived deviations from expected metabolic values emphasize further the danger of relying exclusively on allometric predictions in time-energy studies or related preoccupations in ecological energetics. For example in these Honeycreepers if the 2.2 increment for daily energy expenditure (DEE) is multiplied by SMR (after MacMillen and Carpenter 1977) the DEE based on predicted SMR deviates progressively and substantially with decreases in body mass from the observed values (Table 2). Clearly exclusive use of the predicted values would result in gross overestimates of the energy exchanges of the smaller species within this avian taxon.

I conclude that energy availability and predictability can serve as a powerful selective force not only in moulding interspecific foraging and social behavior, but also in influencing energetic performance. These influences must be reckoned with in studies of ecological energetics.

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