

# BIOENERGETICS OF HAWAIIAN HONEYCREEPERS: THE AMAKIHI (*LOXOPS VIRENS*) AND THE ANIANIAU (*L. PARVA*)<sup>1</sup>

RICHARD E. MACMILLEN

Department of Population and Environmental Biology  
University of California  
Irvine, California 92664

Insular biotas have attracted considerable biological attention and have been very important in the formulation of evolutionary thought and theory. Since Charles Darwin's visit to the Galápagos Islands and his description of the Galápagos Finches, insular land birds have played very prominent roles in evolutionary biology, largely based upon detailed morphological and taxonomic analyses.

Yet virtually no attention has been paid to assessments of the functional attributes of terrestrial birds inhabiting oceanic islands. Ideal candidates for studies of adaptive physiology of an island avifauna are the endemic Hawaiian Honeycreepers (Passeriformes: Drepanididae) which exhibit among their "numerous species the most striking example of adaptive radiation from an assumed single ancestral species of any bird family in the world" (Berger 1970). This study undertakes to examine certain bioenergetic characteristics of two congeneric species of Hawaiian Honeycreepers, the Amakihi (*Loxops virens*) and the Anianiau (*L. parva*). Measurements of oxygen consumption, thermoregulation, and evaporative water loss were made in order to provide data to reveal magnitudes of physiological divergence or conformance in comparison with continental passerines.

## MATERIALS AND METHODS

The Family Drepanididae is divided into two divergent subfamilies: Drepanidinae and Psittirostrinae. *Loxops* is the most primitive genus of the latter subfamily (Amadon 1950). The Amakihi (*Loxops virens*) is the second most common living Honeycreeper, occurring on all of the main islands. Its broad climatic distribution suggests that it may be the most adaptable of the surviving species of Honeycreepers (Berger 1970). The Amakihi is insectivorous and nectivorous, and also drinks the juices from fruits (Baldwin 1953). Of the six *L. virens* employed in this study (mean initial weight:  $19.2 \pm$  SD 4.0 g), three were *L. v. virens* (mean initial weight: 16.8 g, range: 13.1–21.1 g) collected during the last week of January 1968 in the Kaoho Game Management Area on the Island of Hawaii, at an elevation of about 2226 m. This is an area of mamani-naio (*Sophora chrysophylla-Myoporum sandwicense*) forest, a dry, open parkland on the

southern and western slopes of Mauna Kea. The three *L. v. stejnegeri* (mean initial weight: 21.6 g, range: 19.0–23.6 g) were collected on 17 May 1969 in Kokee State Park on the Island of Kauai at elevations between 1067 and 1220 m. This habitat is an ohia-koa (*Metrosideros collina-Acacia kauaiensis*) rainforest, with a mean annual rainfall of about 216 cm (Eddinger 1970).

The Anianiau (*L. parva*) is endemic only to Kauai where it is fairly common in the Kokee and Alakai Swamp regions of the island. Its food consists chiefly of insects and nectar (Berger 1972). Of four *L. parva* employed in this study (mean initial weight,  $9.0 \pm$  SD 1.0 g), some were collected in June 1969 and some in June 1970 in Kokee State Park, at the same locality as that of the Kauai Amakihi. All of the birds were collected as nestlings and then brought to the University of Hawaii, Honolulu, for hand-rearing. After fledging, the birds were provided a diet of Gerber's high protein baby cereal, Deca Vi Sol babies vitamin drops, egg yolks, wheat germ, honey-water, papayas, oranges, grapefruit, apples, fly larvae, fly pupae, and autolyzed brewer's yeast fraction (see Eddinger 1969). Except while measurements were being made, the birds were housed in large indoor aviaries, under conditions of usual room temperature ( $T_a = 21\text{--}27^\circ\text{C}$ ) and humidity (RH = 40–60%), and subjected to approximately natural photoperiod. At the time of this study (July and August 1971), the birds were between 12 and 42 months of age, and all appeared to be in optimal states of health. Since there is little sexual dimorphism in either species, no attempt was made to distinguish between the sexes.

Body temperature ( $T_b$ ) was measured to the nearest  $0.1^\circ\text{C}$  in each individual at the end of each measurement of oxygen consumption and after at least 1.5-hr exposure to a given ambient temperature ( $T_a$ ).  $T_b$  was measured either with a copper-constantan thermocouple ensheathed in plastic tubing and attached to a Leeds and Northrup portable potentiometer or with a small-animal thermister attached to a Y.S.I. Telethermometer. For  $T_b$  measurements, the temperature probe was inserted manually into the cloaca to a depth of at least 2 cm, and the measurement made usually within 15 sec after initial handling of the bird.

Ambient temperature was monitored to the nearest  $0.1^\circ\text{C}$  with Y.S.I. temperature probes inserted through air-tight ports into the respirometer chambers which, in turn, were contained within an insulated constant temperature cabinet equipped with refrigeration and heating units and blowers;  $T_a$  inside the respirometer chambers could be controlled to within  $\pm 0.2^\circ\text{C}$  of the desired setting.  $T_a$  was measured for each individual within 30 sec of each measurement of oxygen consumption.

Measurements of oxygen consumption were obtained

<sup>1</sup> Contribution No. 12, Island Ecosystems IRP/IBP Hawaii.

alternately from each of two birds placed in air-tight 3.5-liter respirometer chambers placed within the darkened constant temperature cabinet. The chambers were constructed of clear-glass, wide-mouthed specimen jars, equipped with ports for the introduction and removal of air and  $T_a$  thermister probes. The birds rested on hardware-cloth platforms about 8 cm above the bottoms of the chambers which were covered with mineral oil to a depth of 2 cm to prevent evaporation from excreta. Air which had been dried by passage through indicating Drierite was metered to the respirometer chambers at flow rates of 800  $\text{cm}^3/\text{min}$  and 600  $\text{cm}^3/\text{min}$  for *L. virens* and *L. parva*, respectively. Samples of air flowing from the chambers ( $\text{CO}_2$  not removed) were then delivered to a Beckman Model E2 paramagnetic oxygen analyzer for measurements of oxygen consumption. All measurements of oxygen consumption were made on post-absorptive birds held in the dark after at least 1-hr exposure to a given  $T_a$ , and during their usual diurnal period of activity (between 10:00 and 17:00). Measurements on each bird and at each  $T_a$  were made over a 0.5-hr period at 5 min intervals. Each bird was measured at no more than three  $T_a$  settings on a given day, and several days followed between measurements of an individual. The two lowest measurements for each bird at each  $T_a$  were used for calculations of oxygen consumption. Rates of oxygen consumption were corrected to S.T.P. but were not corrected to allow for expired  $\text{CO}_2$ . Each bird was weighed to the nearest 0.1 g before being placed in, and after removal from, the respirometer chambers. Weights at the times of measurements of oxygen consumption were interpolated.

Evaporative water loss (EWL) was measured gravimetrically and simultaneously with the 0.5-hr measurements of oxygen consumption by passage of air effluent from the respirometer chambers through 150-mm desiccating tubes filled with small-mesh calcium chloride; this air was then delivered to the oxygen analyzer. An additional desiccating tube was used as a control to measure water vapor in the air being delivered to the respirometer chambers.

All tests of statistical significance between mean values employed the statistic  $\bar{X} \pm t_{0.05} \text{ SE}$  (Simpson et al. 1960:166). Unless otherwise noted, all means hereafter are expressed  $\pm$  one standard deviation.

## RESULTS

### BODY TEMPERATURE

Body temperature data for *L. virens* and *L. parva* and over a  $T_a$  range of 10–40°C are summarized in figure 1. In general, the relationships between  $T_b$  and  $T_a$  for both species are sigmoid in nature, with a slight reduction in  $T_b$  at low  $T_a$  and an increase in  $T_b$  at high  $T_a$ . Polynomial regression analyses were conducted on the data indicated in figure 1 for both species. For *L. virens* the best fit of the data (F-test,  $P < 0.001$ ) is described by the third-degree quadratic equation  $T_b = 34.51418 + 0.91066 T_a - 0.04346 T_a^2 + 0.00065 T_a^3$ . A biologically consistent and statistically significant (F-test,  $P < 0.005 > 0.001$ ) fit of the data for *L. parva* is described by the third-degree quadratic equation  $T_b = 32.09711 +$

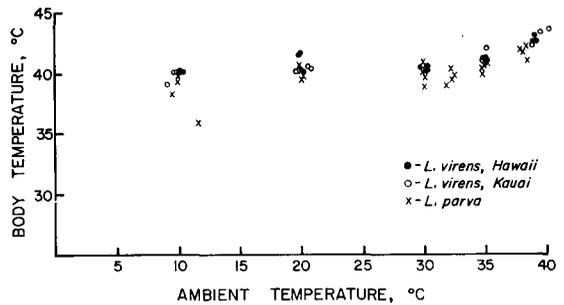


FIGURE 1. The relationship between body temperature and ambient temperature in *Loxops virens* from Hawaii (●) and Kauai (○), and in *L. parva* (X).

$1.00983 T_a - 0.04433 T_a^2 + 0.00064 T_a^3$ . It is interesting to note, however, that a second-degree quadratic and a linear equation provide equally good or even better fits (F-test,  $P < 0.005 > 0.001$ ,  $P < 0.001$ , respectively), in spite of the intuitively sigmoid nature of the data (fig. 1). Representative body temperatures of the two species as predicted by the third-degree equations above are indicated in table 1, with those of *L. virens* consistently but slightly higher than those of *L. parva*. In these analyses of body temperature data, no attempt was made to distinguish between the two island races of *L. virens*.

### OXYGEN CONSUMPTION

The relationship between rates of oxygen consumption and  $T_a$  in *L. virens* is indicated in figure 2. At  $T_a < 35^\circ\text{C}$ , both Hawaii and Kauai *L. virens* showed similar responses in oxygen consumption; a line fitted by the method of least squares to these data below  $T_a = 35^\circ\text{C}$  is described by the equation  $M$  (Metabolism in  $\text{cm}^3 \text{O}_2/\text{g}$  per hr) =  $6.710 - 0.108 T_a \pm 1.196$ . A polynomial regression analysis was conducted on the entire array of data in figure 2 for *L. virens*. The best fit of the data (F-test,  $P < 0.001$ ) is described by the second-degree quadratic equation  $M = 8.29713 - 0.30552 T_a + 0.00501 T_a^2$ . When both races are treated collectively, thermal neutrality appears to extend between  $T_a = 30$  and  $35^\circ\text{C}$ . The collective mean standard

TABLE 1. Predicted body temperatures of *Loxops virens* and *L. parva* at several different ambient temperatures.

Species	$T_a$ , °C				
	10	20	30	35	38
<i>L. virens</i> , $T_b$ °C	39.9	40.5	40.3	41.0	42.0
<i>L. parva</i> , $T_b$ °C	38.4	39.7	39.8	40.6	41.6

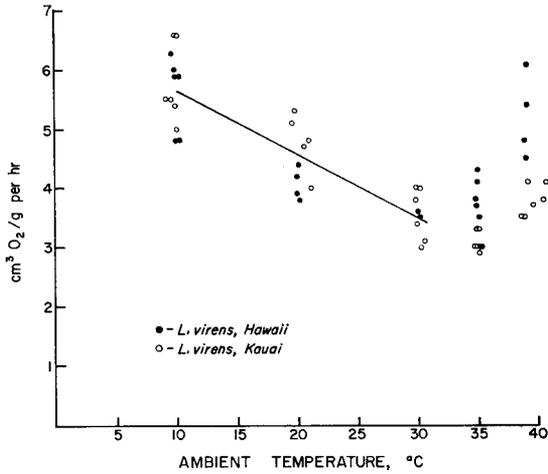


FIGURE 2. The relationship between oxygen consumption and ambient temperature in *Loxops virens*. The diagonal line is fitted to the data below thermal neutrality by the method of least squares.

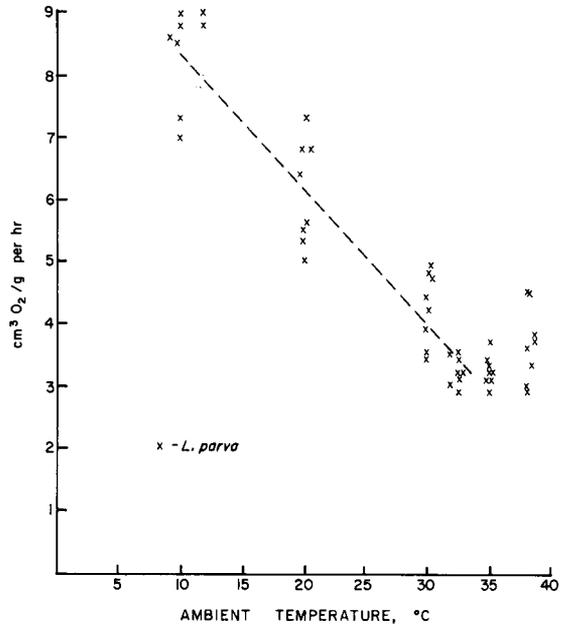


FIGURE 3. The relationship between oxygen consumption and ambient temperature in *Loxops parva*. The diagonal line is fitted to the data below thermal neutrality by the method of least squares.

metabolic rate at  $T_a = 30^\circ\text{C}$  is  $3.54 \pm 0.38$   $\text{cm}^3 \text{O}_2/\text{g per hr}$ , and that at  $T_a = 35^\circ\text{C}$  is  $3.41 \pm 0.34$   $\text{cm}^3 \text{O}_2/\text{g per hr}$ ; these means are not statistically different. When the two races of *L. virens* are examined separately at  $T_a = 35^\circ\text{C}$  and above, although the sample sizes are insufficiently large for certain verification, intraspecific differences are apparent: at  $T_a = 35^\circ\text{C}$ , the three birds from Hawaii appear to be slightly above the upper critical temperature with a mean rate of oxygen consumption of  $3.73 \pm 0.45$   $\text{cm}^3 \text{O}_2/\text{g per hr}$ , while the three Kauai birds are still in thermal neutrality with a mean of  $3.09 \pm 0.17$   $\text{cm}^3 \text{O}_2/\text{g per hr}$ . At  $T_a = 39\text{--}40^\circ\text{C}$ , the increase

in oxygen consumption of the Hawaii race is much more pronounced than that of the Kauai race, with no overlap in the ranges.

The rates of oxygen consumption as a function of  $T_a$  in *L. parva* are summarized in figure 3. A line fitted by the method of least squares to the data below thermal neutrality is described by the equation  $M = 10.544 - 0.219 T_a \pm 1.991$ . A polynomial regression analysis was conducted on the entire array

TABLE 2. Mean ( $\pm$  SE) rates of evaporative water loss (EWL), heat dissipation (EWL/MHP  $\times$  100),<sup>a</sup> and thermal conductance (C) in *Loxops virens* and *L. parva*, and  $T_a$  and humidities when measured.

Species	$\bar{X} T_a$ , °C	No. animals	Evaporative water loss		Heat dissipation % <sup>a</sup>	C $\text{cm}^3 \text{O}_2 (\text{g hr } ^\circ\text{C})^{-1}$	Atmospheric humidity	
			% Body wt./day	Mg $\text{H}_2\text{O}/\text{cm}^3 \text{O}_2$			% RH	WVP, <sup>b</sup> mm Hg
<i>L. virens</i>	9.8	6	9.1 $\pm$ 1.3	0.6 $\pm$ 0.1	7.7 $\pm$ 1.2	.189 $\pm$ .006	16.3	1.5
<i>L. parva</i>	9.9	3	8.3 $\pm$ 2.0	0.4 $\pm$ 0.1	4.8 $\pm$ 1.0	.302 $\pm$ .019	8.9	0.8
<i>L. virens</i>	20.3	6	10.1 $\pm$ 1.2	0.8 $\pm$ 0.1	9.9 $\pm$ 0.9	.220 $\pm$ .009	9.3	1.6
<i>L. parva</i>	20.0	4	12.9 $\pm$ 2.3	0.8 $\pm$ 0.1	9.3 $\pm$ 1.2	.305 $\pm$ .016	7.2	1.2
<i>L. virens</i>	30.1	6	17.8 $\pm$ 3.3	1.6 $\pm$ 0.2	18.7 $\pm$ 2.4	.348 $\pm$ .012	8.1	2.4
<i>L. parva</i>	30.2	4	20.7 $\pm$ 5.5	1.9 $\pm$ 0.4	22.3 $\pm$ 5.2	.412 $\pm$ .036	6.3	1.8
<i>L. parva</i>	32.4	4	17.8 $\pm$ 3.2	2.0 $\pm$ 0.3	23.6 $\pm$ 4.1	.442 $\pm$ .012	4.8	1.7
<i>L. virens</i>	35.1	6	25.1 $\pm$ 3.7	2.8 $\pm$ 0.4	33.3 $\pm$ 4.4	.551 $\pm$ .024	8.2	3.3
<i>L. parva</i>	35.0	4	25.8 $\pm$ 3.8	2.9 $\pm$ 0.5	35.3 $\pm$ 5.6	.594 $\pm$ .019	6.0	2.4
<i>L. virens</i>	39.4	5	59.8 $\pm$ 10.0	4.9 $\pm$ 0.4	59.2 $\pm$ 4.5	1.228 $\pm$ .066	15.0	7.8
<i>L. parva</i>	38.2	4	45.9 $\pm$ 3.7	4.4 $\pm$ 0.4	53.3 $\pm$ 4.7	1.098 $\pm$ .117	8.8	4.2

<sup>a</sup> Calculated assuming 1  $\text{cm}^3 \text{O}_2$  yields 4.8 cal and 1 mg  $\text{H}_2\text{O}$  dissipates 0.58 cal; MHP = metabolic heat production.

<sup>b</sup> WVP = water vapor pressure.

All standard error calculations are based on one observation per animal except those for thermal conductance, based on two observations per animal.

of data in figure 2 for *L. parva*. The best fit of the data (F-test,  $P < 0.001$ ) is described by the second-degree quadratic equation  $M = 12.49182 - 0.45178 T_a + 0.00552 T_a^2$ . Thermal neutrality appears to be rather sharply delineated, extending between about  $T_a = 31$  and  $36^\circ\text{C}$ . The standard metabolic rate measured at  $\bar{X} T_a = 32.4$  and  $35.0^\circ\text{C}$  was  $3.22 \pm 0.20$  and  $3.23 \pm 0.24 \text{ cm}^3 \text{ O}_2/\text{g per hr}$ , respectively. This rate of *L. parva* (mean body weight = 7.9–8.0 g) is not statistically different from the standard metabolic rate of *L. virens* (mean body weight = 15.3 g), in spite of nearly a twofold difference in body weight.

#### EVAPORATIVE WATER LOSS

Rates of evaporative water loss (EWL) expressed both as functions of body weight and of oxygen consumption and for both *L. virens* and *L. parva* are indicated in table 2. Expressed in both ways there is a direct relationship between EWL and  $T_a$ ; EWL increases precipitously at  $T_a > 35^\circ\text{C}$ . At no  $T_a$  at which measurements of both species were made was there a significant difference between mean EWL of the two species. Assuming that  $1 \text{ cm}^3 \text{ O}_2$  consumed yields 4.8 cal and that  $1 \text{ mg H}_2\text{O}$  evaporated dissipates 0.58 cal, EWL data can be used to express efficiency in heat dissipation. Such an expression is included in table 2 and indicates that at the highest  $T_a$  employed in this study only about 59% of the heat produced by metabolism was dissipated by evaporative cooling in *L. virens* (at  $T_a = 39.4^\circ\text{C}$ ) and 54% of the metabolic heat production was dissipated evaporatively by *L. parva* (at  $T_a = 38.2^\circ\text{C}$ ). Also included in table 2 are estimates of atmospheric humidities of the respirometer chambers at each  $T_a$  at which oxygen consumption,  $T_b$ , and EWL were measured. Relative humidity was calculated after the method proposed by Lasiewski et al. (1966), and water vapor pressure (WVP) was determined from the calculated values of relative humidity.

#### THERMAL CONDUCTANCE (C)

The mean values of thermal conductance or heat transfer coefficient (Gagge 1969), calculated from the relationship  $C = M/(T_b - T_a)$  (where  $M$  is metabolism in  $\text{cm}^3 \text{ O}_2/\text{g per hr}$ ), for the two species at each  $T_a$  for which measurements are available are summarized in table 2. In *L. virens*, conductance was directly related to  $T_a$  with the mean value calculated for each  $T_a$  significantly lower ( $t$ -test) than that for the next higher  $T_a$ , even below thermal neutrality. In *L. parva*, the

mean conductance below thermal neutrality (at  $T_a = 10$  and  $20^\circ\text{C}$ ) was virtually constant [at  $0.302$  and  $0.305 \text{ cm}^3 \text{ O}_2 (\text{g hr } ^\circ\text{C})^{-1}$ , respectively] and significantly higher than in *L. virens*. At  $T_a = 30^\circ\text{C}$  and higher, mean conductance values at each  $T_a$  for which measurements were available were not significantly different between the two species, increasing directly with temperature. The greatest increase in thermal conductance, an approximate doubling for both species, was between  $T_a$  of 35 and  $38\text{--}39^\circ\text{C}$ .

#### TOLERANCE TO HIGH $T_a$

Assuming that *L. virens* could readily withstand  $T_a$  equivalent to their usual  $T_b$  (about  $40^\circ\text{C}$ ), six birds were each placed in respirometer chambers for measurements at about that  $T_a$ . Four of the birds died either during exposure (one bird) or after exposure (three birds) to the experimental  $T_a$  ( $\bar{X} = 39.6^\circ\text{C}$ , range:  $39.0\text{--}40.4^\circ\text{C}$ ). The mean  $T_b$  of the three that expired, immediately following the 1.5-hr period of exposure at high  $T_a$ , was  $43.1^\circ\text{C}$  (range:  $42.5\text{--}43.6^\circ\text{C}$ ); all died within 36 hr following exposure. All of the birds that expired were observed panting vigorously with beaks open while exposed to the high  $T_a$ . The two birds that survived were at  $T_a = 38.9$  and  $39.1^\circ\text{C}$ ; their  $T_b$  after 1.5-hr exposure to high  $T_a$  were  $42.2$  and  $43.0^\circ\text{C}$ , respectively. Of these two, the one with the lower  $T_b$  was not observed to be panting, while that with the higher  $T_b$  panted vigorously. No differences in temperature tolerance were noted between the races of *L. virens* as two birds of each race perished and one survived.

After the inadvertent experience of *L. virens* with lethal  $T_a$ , much greater caution was taken in exposing *L. parva* to high  $T_a$ . The four birds were exposed for 1.5 hr to  $\bar{X} T_a = 38.3^\circ\text{C}$  (range:  $38.0\text{--}38.5^\circ\text{C}$ ). All survived, none was observed panting, and the mean  $T_b$  immediately after exposure to high  $T_a$  was  $41.7^\circ\text{C}$  (range:  $41.0\text{--}42.1^\circ\text{C}$ ). No attempt was made to expose them to higher  $T_a$ .

#### DISCUSSION

The two island races of the Amakihi (*Loxops virens*) are considered separately in the Results section; because of small sample sizes and few apparent differences, they will be considered collectively for purposes of this discussion. When compared with bioenergetic variables expected for passerine birds of comparable size, those measured in the Amakihi (*L. virens*) and the Anianiau (*L. parva*)

TABLE 3. Comparisons of mean observed and expected (for passerine birds) bioenergetic parameters of *Loxops virens* and *L. parva*.

	<i>L. virens</i>		<i>L. parva</i>	
	Observed	Expected	Observed	Expected
Standard metabolism, cm <sup>3</sup> O <sub>2</sub> /g per hr <sup>a</sup>				
T <sub>a</sub> = 35.0°C, wt. = 15.3 g	3.41	3.55		
T <sub>a</sub> = 32.4°C, wt. = 7.9 g			3.22	4.26
T <sub>a</sub> = 35.0°C, wt. = 8.0 g			3.23	4.25
Standard metabolism, cm <sup>3</sup> O <sub>2</sub> /g per hr <sup>b</sup>				
T <sub>a</sub> = 35.0°C, wt. = 15.3 g	3.41	3.54		
T <sub>a</sub> = 32.4°C, wt. = 7.9 g			3.22	4.23
T <sub>a</sub> = 35.0°C, wt. = 8.0 g			3.23	4.22
Standard metabolism, cm <sup>3</sup> O <sub>2</sub> /g per hr <sup>c</sup>				
T <sub>a</sub> = 35.0°C, wt. = 15.3 g	3.41	4.22		
T <sub>a</sub> = 32.4°C, wt. = 7.9 g			3.22	5.13
T <sub>a</sub> = 35.0°C, wt. = 8.0 g			3.23	5.12
Thermal conductance, cm <sup>3</sup> O <sub>2</sub> (g hr °C) <sup>-1</sup> <sup>d</sup>				
T <sub>a</sub> = 9.9°C, wt. = 18.7 g	0.189	0.191		
T <sub>a</sub> = 20.4°C, wt. = 17.9 g	0.220	0.196		
T <sub>a</sub> = 10.4°C, wt. = 8.8 g			0.302	0.281
T <sub>a</sub> = 20.1°C, wt. = 8.5 g			0.305	0.286
Evaporative water loss, g H <sub>2</sub> O/day <sup>e</sup>				
T <sub>a</sub> = 20.3°C, wt. = 18.2 g	1.84	2.93		
T <sub>a</sub> = 30.1°C, wt. = 16.2 g	2.85	2.86		
T <sub>a</sub> = 20.0°C, wt. = 8.5 g			1.08	2.49
T <sub>a</sub> = 30.2°C, wt. = 8.0 g			1.64	2.46

<sup>a</sup> Calculated from the relationship  $M = 129W^{0.724}$  ( $M$  in Kcal/day,  $W$  in Kg) after Lasiewski and Dawson (1967), and assuming 1 cm<sup>3</sup> O<sub>2</sub> yields 4.8 cal.

<sup>b</sup> Calculated from the relationship  $M = 132W^{0.730}$  ( $M$  in Kcal/day,  $W$  in Kg), equation (12) for  $\alpha$ -values from Aschoff and Pohl (1970) and derived from data of Lasiewski and Dawson (1967); assumes 1 cm<sup>3</sup> O<sub>2</sub> yields 4.8 cal.

<sup>c</sup> Calculated from the relationship  $M = 140.9W^{0.704}$  ( $M$  in Kcal/day,  $W$  in Kg), equation (6) for  $\alpha$ -values from Aschoff and Pohl (1970); assumes 1 cm<sup>3</sup> O<sub>2</sub> yields 4.8 cal.

<sup>d</sup> Calculated from the relationship  $C = 0.848W^{-0.508}$  [ $C$  in cm<sup>3</sup> O<sub>2</sub> (g hr °C)<sup>-1</sup>,  $W$  in g] after Lasiewski et al. (1967).

<sup>e</sup> Calculated from the relationship  $E = 1.563W^{0.217}$  ( $E$  in g/day,  $W$  in g) after Crawford and Lasiewski (1968); expected  $E$  at T<sub>a</sub> = 25°C.

range from the expected to the unexpected (table 3).

For predictive purposes Lasiewski and Dawson (1967) thoroughly documented the size-related differences in standard metabolism between passerine (higher values) and nonpasserine birds (lower values). More recently, Aschoff and Pohl (1970) have extended this comparison to demonstrate that the level of standard metabolism of postabsorptive birds measured under darkened conditions may be higher during the normal period of activity and lower during the normal period of inactivity. For diurnally active passerines, Aschoff and Pohl (1970) give two equations for calculating expected rates of standard metabolism ( $\alpha$ -values): (1) equation (12) derived from the appropriate data from Lasiewski and Dawson (1967); and (2) equation (6) derived independently by Aschoff and Pohl (1970) (see table 3 for these equations). Within the size range of the birds

employed in this study, predictive values obtained from Aschoff and Pohl's (1970) equation (12) are virtually identical to those obtained from Lasiewski and Dawson's (1967) original equation; in fact, the former values are actually slightly lower than the latter, but differ by no more than 0.03 cm<sup>3</sup> O<sub>2</sub>/g per hr (table 3). The predictive values obtained from Aschoff and Pohl's (1970) independently derived equation (6) are invariably much higher (by 19–21%) than those obtained from the former two equations. The expected values of standard metabolism predicted by all three equations are represented in table 3. Because of known similarities in methodology, however, the values which are thought best to reflect valid comparisons for the purposes of this study are the nearly identical ones obtained either directly or indirectly from the data of Lasiewski and Dawson (1967); these values are cited in the discussion below and in figure 4.

*Loxops virens* conforms rather closely to the expected passerine patterns with a standard metabolic rate ( $3.41 \text{ cm}^3 \text{ O}_2/\text{g}$  per hr) which is 96% of the predicted levels ( $3.54$  to  $3.55 \text{ cm}^3 \text{ O}_2/\text{g}$  per hr); with thermal conductance below thermal neutrality which is 99 and 112% of the expected levels at  $T_a = 9.9$  and  $20.4^\circ\text{C}$ , respectively; and with rates of evaporative water loss which at  $T_a = 20.3^\circ\text{C}$  is 63% of that predicted (at  $T_a = 25^\circ\text{C}$ ) but at  $T_a = 30.1^\circ\text{C}$  is nearly identical to that predicted at  $T_a = 25^\circ\text{C}$  (table 3). Rather surprising is the demonstration in *L. virens* that thermal conductance below thermal neutrality is not constant but is directly related to  $T_a$  (tables 2 and 3). *L. parva*, however, deviates rather drastically from the patterns predictable for passerine birds of its size: standard metabolic rate at  $T_a = 32.4$  and  $35^\circ\text{C}$  is only 76–77% of the expected; thermal conductance below thermal neutrality is constant, and at  $T_a = 10.4$  and  $20.1^\circ\text{C}$  is 108 and 107% of the expected, respectively; and evaporative water loss at  $T_a = 20.0$  and  $30.2^\circ\text{C}$  is reduced to 43 and 67%, respectively, of that predicted at  $T_a = 25^\circ\text{C}$  (table 3).

It is not unexpected to find bioenergetic variables which differ from predicted levels since the latter are derived from equations which ignore the variability upon which they were originally based. It was unexpected, however, to find in two sympatric (at least on Kauai), congeneric passerines, even though they are isolated insular species, one which conforms rather closely to expected values and one which deviates rather drastically. Physiological divergence of such magnitude within a single genus would seemingly preclude the possibility of establishing phylogenetic patterns in bioenergetic phenomena, at least within the drepanidid subfamily Psittirostrinae.

The intragenetic bioenergetic differences between *L. virens* and *L. parva* are summarized diagrammatically in figure 4. Particularly impressive are the differences in slope of the lines fitted to the values for oxygen consumption below thermal neutrality; when extrapolated to the abscissa (zero metabolism), these lines for *L. virens* and *L. parva* intersect the abscissa at  $T_a$  of  $62.4$  and  $48.1^\circ\text{C}$ , respectively, indicating that neither bird conforms to the Newtonian (Fourier's) model of homeothermy (see Scholander et al. 1950; Kleiber 1972). That which conforms the least is *L. virens* with a resultant inconstant thermal conductance below thermal neutrality (tables 2 and 3). Such inconstancy of

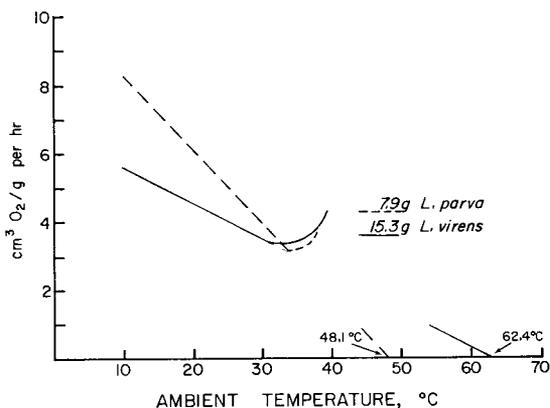


FIGURE 4. Summary of the relationship between oxygen consumption and ambient temperature in *Loxops virens* (solid line) and *L. parva* (dashed line). The diagonal lines are fitted to the data below thermal neutrality by the method of least squares; the numbers with arrows indicate the temperatures at which these lines, when extrapolated to zero metabolism, intersect the abscissa. The lines above the lower critical temperature connect the means measured at the various temperatures. The horizontal lines indicate standard metabolic rates predicted for passerine birds with the mean body weights of *L. virens* (15.3 g) and *L. parva* (7.9 to 8.0 g), and from the equation derived by Lasiewski and Dawson (1967) and from equation (12) from Aschoff and Pohl (1970).

thermal conductance may well be of ecological importance, for nocturnal temperatures in the high forests where these birds live are often below  $10^\circ\text{C}$ , and may drop this low in any month of the year (Berger 1972; Eddinger 1970); thus under conditions of low  $T_a$  and with minimal thermal conductance, energetic costs would also be minimal. The slope of the line relating oxygen consumption to  $T_a$  for *L. parva* is also less steep than might be anticipated (fig. 4), although thermal conductance was constant at  $T_a$  of  $10$  and  $20^\circ\text{C}$ , and higher than predicted for a bird of its size (table 2). This reduction in slope (and therefore in oxygen consumption at lower  $T_a$ ) was apparently accomplished by a reduction in  $T_b$  at lower  $T_a$ : mean  $T_b$  at  $T_a$  of  $10.3^\circ\text{C}$  was  $38.3^\circ\text{C}$ , while that at  $T_a$  of  $20.0^\circ\text{C}$  was  $40^\circ\text{C}$  (fig. 1). Thus both *L. virens* and *L. parva* possess differing thermoregulatory capacities which result in energetic savings at lower  $T_a$  ( $10^\circ\text{C}$ ), typical of that encountered in their forest habitats at night.

Another striking intragenetic difference between *L. virens* and *L. parva*, which is revealed in figure 4 and table 3, is the conformance to passerine levels of standard metabolism in the former, and the 24% reduction below the expected passerine level in

the latter. Thus, although *L. parva* weighs about 52% as much as *L. virens*, both have nearly identical energy demands while in thermal neutrality ( $T_a$  of about 31–36°C), with that of the former (3.2 cm<sup>3</sup> O<sub>2</sub>/g per hr) actually slightly lower than that of the latter (3.4 cm<sup>3</sup> O<sub>2</sub>/g per hr).

The most surprising bioenergetic phenomenon found in the Honeycreepers was the apparent complete lack of tolerance to high  $T_a$  in *L. virens*, and its inability to control  $T_b$  below lethal levels, even at only moderately high  $T_a$ . Four of six *L. virens* which had been exposed to  $T_a$  between 38.9 and 40.4°C for 1.5 hr perished within 36 hr after exposure; this  $T_a$  range was equal to or lower than the usual  $T_b$  at cooler temperatures. Moderate hyperthermia (mean  $T_b$  of 42.9, range: 42.2–43.6°C) occurred, but  $T_b$  never reached 44°C, which is readily tolerated by other passerines (Lasiewski et al. 1966; Dawson and Hudson 1970). Lasiewski et al. (1966) caution investigators to employ high flow rates (and low atmospheric humidities) in respirometry at high  $T_a$  for otherwise the high atmospheric humidities resulting within the respirometer chambers preclude sufficient evaporative cooling for heat dissipation. At the flow rate employed in this study (800 cm<sup>3</sup>/min) and at the  $T_a$  ( $\bar{X}$  of 39.4°C) which proved lethal, the mean atmospheric humidity (15% RH or 7.8 mm Hg, table 2) was well within or below the range at which the passerines cited by Lasiewski et al. (1966) were able to dissipate by evaporative cooling all of the heat produced metabolically. At the mean  $T_a$  (39.4°C) which proved fatal to four of six *L. virens*, only 59.2% of the heat produced metabolically was dissipated by evaporative cooling (table 2). Thus it would appear that not only does *L. virens* lack the tolerances to  $T_b$  of about 44°C, seemingly characteristic of many passerines, but also it lacks the apparent avian characteristic (Lasiewski et al. 1966) of dissipating metabolic heat through evaporative cooling under conditions of high  $T_a$  and low atmospheric humidity. The absence of this characteristic is not altogether surprising, however, for the highest  $T_a$  recorded in the 4-year period 1966–69 at or near the collecting localities on Kauai and Hawaii are 26.7 and 31.1°C, respectively (Berger 1972; Eddinger 1970). Thus it is doubtful that ambient temperatures for these high forest birds, even though they occur within the tropics, ever exceed thermal neutrality. One can but speculate whether these absences of heat tolerances and heat-dissipating mechanisms

are primitive or derived characteristics, but they are certainly atypical of the usual avian condition.

Since great care was taken to avoid lethal temperatures with *L. parva*, nothing substantive can be said about its high temperature tolerance, except there is no reason to believe, either physiologically or ecologically, that it would differ from that of *L. virens*.

## SUMMARY

Bioenergetically, the congeneric Hawaiian Honeycreepers *Loxops virens* and *L. parva* are quite distinct from each other. *Loxops virens* has a higher  $T_b$ , lower and inconstant thermal conductance, and a standard metabolic rate (3.41 cm<sup>3</sup> O<sub>2</sub>/g per hr) that is 96% of that predicted for passerines. In *L. parva*, only about half the size of *L. virens*, standard metabolism (3.22 cm<sup>3</sup> O<sub>2</sub>/g per hr) is lower than in the latter and is reduced to 76–77% of the predicted passerine level. Neither bird conforms to the Newtonian (Fourier's) model of homeothermy, as *L. virens* has an inconstant thermal conductance below thermal neutrality, while in *L. parva* thermal conductance is constant but  $T_b$  is reduced at low  $T_a$ .

Evaporative water loss is rather comparable in both species, conforming closely to expected passerine levels in *L. virens* but considerably reduced below these levels in *L. parva*. Under conditions of high  $T_a$ , both species become hyperthermic and increase evaporative water loss, but insufficiently to dissipate by evaporation the heat that is produced metabolically, even under conditions of low atmospheric humidity. In four of six *L. virens*,  $T_a$  of about 39–40°C and  $T_b$  of 42.5–43.6°C proved fatal; *L. parva* was not exposed to such high  $T_a$ . High temperature tolerances apparently are lacking in these species, but they inhabit high forests where such temperatures are seldom encountered.

## ACKNOWLEDGMENTS

This study was supported by NSF Grant GB-23230, Island Ecosystems IRP/IBP Hawaii; thanks are due also to the Primo Foundation. My special gratitude goes to S. K. Hong and G. C. Whittow, Department of Physiology, School of Medicine, University of Hawaii, for use of facilities and cooperation. The birds employed in this study were generously provided and maintained by A. J. Berger and C. R. Eddinger, Department of Zoology, University of Hawaii. K. W. Bridges, Department of Botany, University of Hawaii, aided in data computation.

## LITERATURE CITED

- AMADON, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist. 95:151–262.

- ASCHOFF, J., AND H. POHL. 1970. Der ruheumsatz von vögeln als funktion der tageszeit und der körpergrösse. *J. Ornithol.* 111:38-47.
- BALDWIN, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves, Drepaniidae). *Univ. Calif. Publ. Zool.* 52:285-398.
- BERGER, A. J. 1970. The present status of the birds of Hawaii. *Pacific Sci.* 24:29-42.
- BERGER, A. J. 1972. Hawaiian birdlife. University Press, Honolulu, Hawaii.
- CRAWFORD, E. C., JR., AND R. C. LASIEWSKI. 1968. Oxygen consumption and respiratory evaporation of the emu and rhea. *Condor* 70:333-339.
- DAWSON, W. R., AND J. W. HUDSON. 1970. Birds. In G. C. Whittow [ed.] *Comparative physiology of thermoregulation* Vol. I: Invertebrates and nonmammalian vertebrates. Academic Press, New York.
- EDDINGER, C. R. 1969. Experiences with hand-raising passerine birds in Hawaii. *Avicult. Mag.* 75:12-14.
- EDDINGER, C. R. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepaniidae). Ph.D. Dissertation, Univ. Hawaii.
- GAGGE, A. P. 1969. Proposed standard system of symbols for thermal physiology. *J. Appl. Physiol.* 27:439-445.
- KLEIBER, M. 1972. A new Newton's law of cooling? *Science* 178:1283-1285.
- LASIEWSKI, R. C., A. L. ACOSTA, AND M. H. BERNSTEIN. 1966. Evaporative water loss in birds—I. Characteristics of the open flow method of determination and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* 19:445-457.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the giant hummingbird, *Patagonia gigas*. *Comp. Biochem. Physiol.* 23:797-813.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* 99:237-258.
- SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. *Quantitative zoology*. Harcourt, Brace & World, Inc., New York.

Accepted for publication 30 July 1973.