ENERGETIC RELATIONSHIPS OF A VERY SMALL PASSERINE BIRD

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The paucity of information on the energetic relationships of smaller homeotherms and the recent examination of the weight-metabolism relationships of birds (King and Farner, 1961) indicate the need of additional information concerning the energy metabolism of small birds. Accordingly, this study was undertaken to investigate the effects of environmental temperature on the oxygen consumption and evaporative water loss of the Black-rumped Waxbill (*Estrilda troglodytes*), which weighs only 6 or 7 grams.

The Black-rumped Waxbill is found over a wide area in Africa, ranging from Senegal to Ethiopia. Apparently, this ploceid occurs in a variety of habitats. Mackworth-Praed and Grant (1955:1022) state it to be "locally common in swampy places at low levels and along the banks of streams." On the other hand, Bannerman (1949:339) notes that "it is the only Waxbill which is found in the dry country nearing the desert, but even there it has a very restricted range."

Note.—While this manuscript was being prepared, we learned that Cade, Tobin, and Gold of Syracuse University had also completed a study on the physiology of *Estrilda troglodytes*. However, since the two parallel studies stress different aspects of the physiology of these small birds, and differ in methodology, both teams decided jointly to proceed with their respective plans for publication.

MATERIALS AND METHODS

The 22 Black-rumped Waxbills used in this study were obtained from a commercial source but had been captured originally in the wild. In the laboratory, they were maintained during the months of April and May, 1963, on a natural photoperiod for latitude 42° N, at temperatures of 21° to 27° C. A commercial seed mixture for finches, and gravel, cuttle bone, and water were always available, except during experiments.

On nights prior to an experiment, the bird selected for study was isolated from the flock and held in a cage containing water but no food. The next morning, the post-absorptive bird was weighed and placed on a perch in a one-gallon chamber. This chamber was fitted with exit and entry ports for air, and the bottom of the chamber was covered with mineral oil to a depth of 2 centimeters to entrap feces as they were voided. The bird was separated from the mineral oil by a floor of one-half inch mesh hardware cloth. The chamber with the bird was placed in a darkened temperature cabinet, in which the temperature was controlled within 0.5°C. of the desired level.

Dried air was circulated through the chamber at 122 to 152 cc. air/min., and oxygen consumption was monitored with a Beckman G–2 paramagnetic oxygen analyzer used in conjunction with a recording potentiometer. When the record of the oxygen analysis indicated that metabolism had reached a stable minimal level (generally 2 to 3 hours after the bird was placed in a darkened chamber), a lightweight drying tube, filled with fresh indicating Drierite (anhydrous $CaSO_4$), was placed in the air line connected to the exit port of the chamber. It was possible to obtain simultaneous measurements of oxygen consumption and evaporative water loss over a wide range of ambient temperatures by analyzing the air for the amount of oxygen removed by the bird and weighing the tube plus Drierite to the nearest milligram before and after the measurement period.

Temperatures inside the chamber were monitored with a copper-constantan thermocouple connected to a Brown recording potentiometer. The bird was weighed after each experiment, and all oxygen consumption values were corrected to standard conditions of temperature and pressure.

Heart and breathing rates were measured while the birds were immobilized in flannel jackets. Two electrodes fashioned from fine, stainless steel insect pins were inserted in the pectoral musculature and the leads from these electrodes were connected to a high gain preamplifier, which was used with a Sanborn recording oscillograph. This treatment did not seem to disturb the birds greatly, and they remained alert and unharmed throughout the measurements.

RESULTS

The relationship between ambient temperature and the oxygen consumption of postabsorptive Black-rumped Waxbills resting in the dark is illustrated in figure 1. Standard metabolic values ranged from 3.5 to 3.9 cc. O_2/gm./hr., or the equivalent of 2.5 to 2.7 kcal./day. The limits of the zone of thermal neutrality are not well defined,
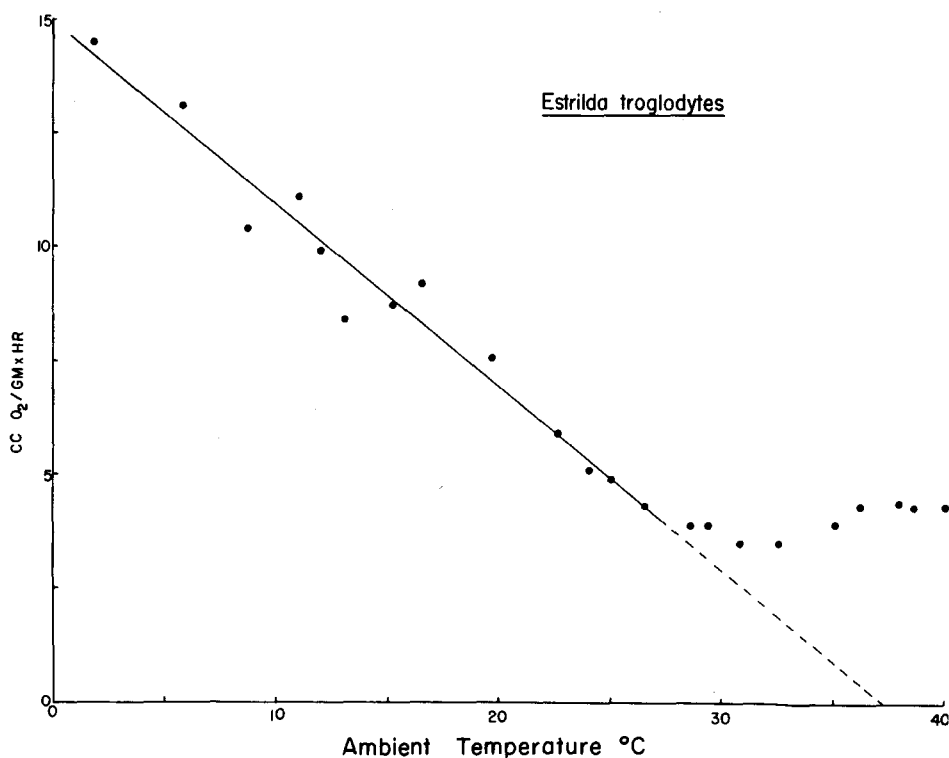

Fig. 1. The relation between ambient temperature and the oxygen consumption of postabsorptive Black-rumped Waxbills (*Estrilda troglodytes*) resting in the dark. Each point represents an individual bird; the regression line was fitted by the least-squares method.

because of a curvilinear relationship in the area of the lower critical temperature and an ill-defined upper critical temperature. On the basis of the available data on oxygen consumption and evaporative water loss, we estimate that the thermoneutral zone extends from approximately 28° to 35° C. The straight regression line, fitted to the data below the lower critical temperature, has a slope of 0.40 cc. O_2 (gm./hr./°C.)$^{-1}$, and extrapolates to a temperature of 37°C. at zero metabolism.

The amount of water lost through evaporation in *E. troglodytes* increases slowly with increasing temperature, as shown in figure 2, with values ranging from 1.6(?) to
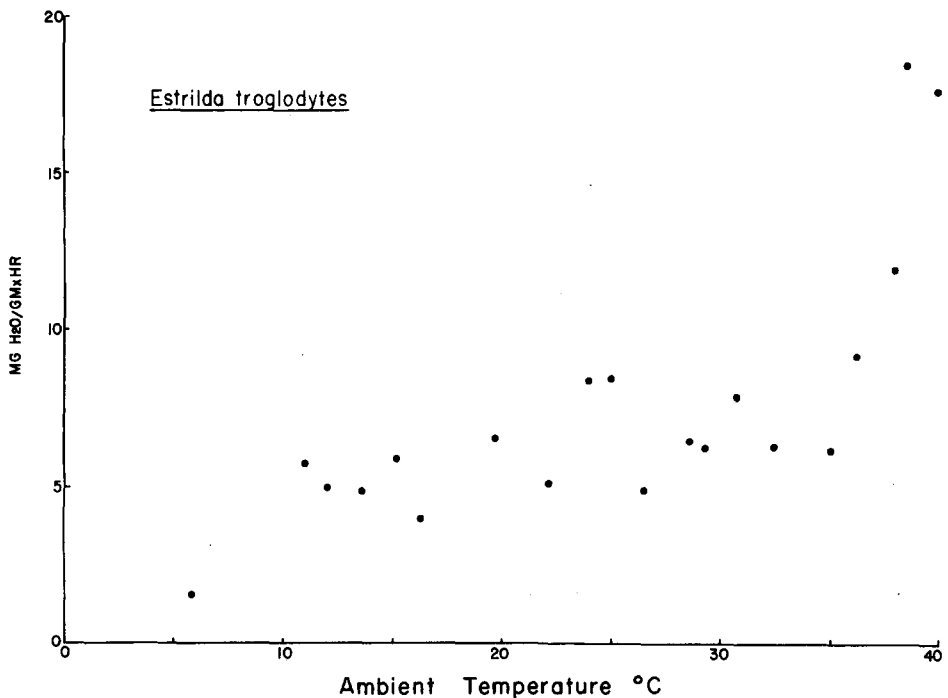
Fig. 2. The relation between ambient temperature and evaporative water loss of postabsorptive *Estrilda troglodytes* resting in the dark.

18.4 mg. H_2O/gm./hr. at temperatures of 5.8° and 38.6° C., respectively. Between 10° and 35° C., evaporative water loss increases only slightly. Above 35° C., evaporative water loss increases markedly, with maximum values being equivalent to a water loss of 44 per cent of the body weight per 24 hours. During measurements of evaporative water loss, the relative humidity in the chamber varied between 12.3 and 45.1 per cent (table 1).

TABLE 1

REPRESENTATIVE RELATIVE HUMIDITIES IN CHAMBER DURING MEASUREMENTS OF
EVAPORATIVE WATER LOSS AND OXYGEN CONSUMPTION IN THE
BLACK-RUMPED WAXBILL

Ambient temperature (° C.)	Relative humidity (per cent)
5.8	18.6
13.0	45.1
19.7	30.8
25.0	24.2
35.0	12.3
40.0	28.2
29.3	16.0

Heart rates of Black-rumped Waxbills confined in flannel jackets at ambient temperatures between 28° and 35° C. ranged from 500 to 540 heartbeats per minute in resting individuals to maximum recorded values as high as 1020 heartbeats per minute

in a frightened bird. Breathing rates for resting birds at these temperatures were 135 to 140 breaths per minute.

Waxbills appear to have little resistance to cold in comparison to other, larger passerines. Three of these birds died after only two hours in the dark at temperatures of 1.8°, 6°, and 9° C.

DISCUSSION

STANDARD METABOLIC RATE

The relation between body size and metabolic rate has been of recurrent interest to students of energetics. Brody and Proctor (1932) described a relationship between the body weight of birds and their metabolism, which may be expressed as: log Metabolism (kcal./day) = log 89 + 0.64 log Weight (kg.). King and Farner (1961) reanalyzed the available data on metabolism in birds and found that the equation log Metabolism (kcal./day) = log 74.3 + 0.744 log Weight (kg.) describes the metabolism of birds weighing more than 125 gm. more satisfactorily than the Brody-Proctor equation, although they noted that their equation "does not adequately describe the metabolic intensity of the smaller birds." The weight-regression coefficient of 0.744 in the King-Farner equation is similar to that found in mammals (0.756) by Kleiber (1947).
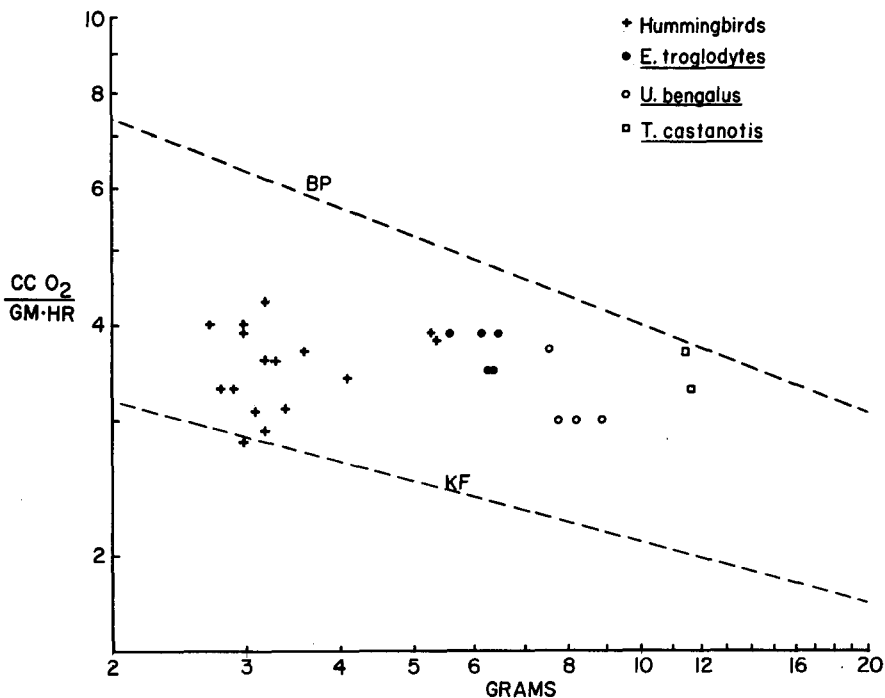

Fig. 3. Oxygen consumption in small birds as a function of body weight. Lines BP and KF represent values predicted for small birds on the basis of the Brody-Proctor equation and the King-Farner equation, respectively (assuming that 1 cc. O_2 consumed is equivalent to 4.8 cal.). Values shown here were obtained from: six species of hummingbirds (Lasiewski, 1963); Black-rumped Waxbill, *Estrilda troglodytes* (present study); Red-cheeked Cordon Bleu, *Uraeginthus bengalus* (Lasiewski, Moberly, and Hubbard, MS); Zebra Finch, *Taeniopygia castanotis* (Calder, MS; Cade, Tobin, and Gold, pers. comm.).

The standard metabolic values for *E. troglodytes* of 3.5 to 3.9 cc. O_2/gm./hr. lie between the values predicted for birds of this size range (mean weight, 6.1 gm.) by the equations (fig. 3). Metabolic values for the Red-cheeked Cordon Bleu, *Uraeginthus bengalus* (Lasiewski, Moberly and Hubbard, unpublished observations), Zebra Finch, *Taeniopygia castanotis* (Calder, MS; Cade, Tobin, and Gold, personal communication), and seven species of hummingbirds (Lasiewski, 1963) also lie between the values predicted by the two equations. The values for hummingbirds are relatively close to the line representing the King-Farner equation, while those for the Zebra Finch are close to that of the Brody-Proctor equation. There is an increasing amount of evidence suggesting that the King-Farner equation may adequately describe the metabolism of nonpasserine birds weighing less than 125 gm. A weight regression coefficient of 0.7 has been noted among passerines by Dawson (Lasiewski, *op. cit.*), although the weight-metabolism relationship for passerines has a higher y intercept than that for nonpasserine birds. It may be that the passerine birds are operating at a higher metabolic level than nonpasserines of the same weight range. More data from nonpasserines weighing less than 100 gm. are needed before any definite conclusions can be drawn.

King and Farner noted that much of the data for the metabolism of small birds had been obtained during the day, while data for large birds were taken at night. Because of the diurnal cycle of body temperature in birds, they restricted their analysis to data obtained at night. We measured the metabolism of a Black-rumped Waxbill all night at a temperature of 32.6° C., and the minimal level of metabolism at night (3.6 cc. O_2/gm./hr., 3:13 a.m.) is indistinguishable from our equilibrium values obtained from postabsorptive birds during the day. A similar relationship was found in hummingbirds (Lasiewski, *op. cit.*). If the conditions required for standard metabolic levels are carefully met, it seems probable that values obtained from small birds during the day can validly be compared to those obtained at night. This seems particularly true when one is able to monitor oxygen consumption or carbon dioxide production continuously and select a period when the bird is obviously at complete rest. Black-rumped Waxbills which were fed before being placed in the metabolic chamber took as long as seven hours to reach minimal stable levels of oxygen consumption.

OXYGEN CONSUMPTION VERSUS AMBIENT TEMPERATURE

The estimated thermoneutral zone for this species (28° to 35° C.) is somewhat arbitrary for reasons cited previously. A lower critical temperature of 28° C. is in agreement with comparable values for hummingbirds (Lasiewski, 1963) and shrews (Morrison, Ryser, and Dawe, 1959), the smallest homeotherms studied. However, it is somewhat lower than would be predicted on the basis of data on several passerines of somewhat larger size. Even so, it indicates very limited resistance to low temperatures in *E. troglodytes*. It is unlikely that this species ever encounters extremely cold weather in nature, since its distribution is limited to the lower altitudes in equatorial regions.

Thermal conductance in homeotherms is inversely related to body weight (Lasiewski, *op. cit.*), as shown in figure 4. High thermal conductance values are indicative of high heat loss and relatively poor insulation. At temperatures below the zone of thermal neutrality, smaller homeotherms are forced to expend more energy per unit weight than larger ones to maintain a constant body temperature. The value of 0.40 cc. O_2 (gm./hr./ °C.)$^{-1}$ for thermal conductance of *E. troglodytes* is among the highest recorded to date, being surpassed only by those of hummingbirds and shrews. This value is in close agreement with what would be predicted on the basis of weight-conductance relationships of other birds and mammals, as are the recently obtained conductance values for the Cali-

fornia pocket mouse, *Perognathus californicus* (Tucker, MS), and the Zebra Finch (Calder, MS; Cade, Tobin, and Gold, personal communication), also shown in figure 4.

EVAPORATIVE WATER LOSS

The amount of water lost through evaporation in the Black-rumped Waxbill increases sharply at temperatures above 35° C. with a 2.5-fold difference between water loss in the zone of thermal neutrality and maximum recorded values. Over the temperature ranges studied, water loss in *E. troglodytes* is intermediate between that reported for the Cardinal, *Richmondena cardinalis* (Dawson, 1958), and for six species of hummingbirds (Lasiewski, in press). Water loss through evaporation appears to be somewhat lower in the Black-rumped Waxbill than would be predicted for a bird of this size on the basis of the water loss-body weight curve obtained by Bartholomew and Dawson (1953). The differences are probably due in large part to the conditions under which measurements were made. The values for *E. troglodytes* are for postabsorptive birds at rest in the dark, obtained with air flows of 122 to 152 cc. air/min. Those obtained by Bartholomew and Dawson were from birds that were not necessarily postabsorptive,
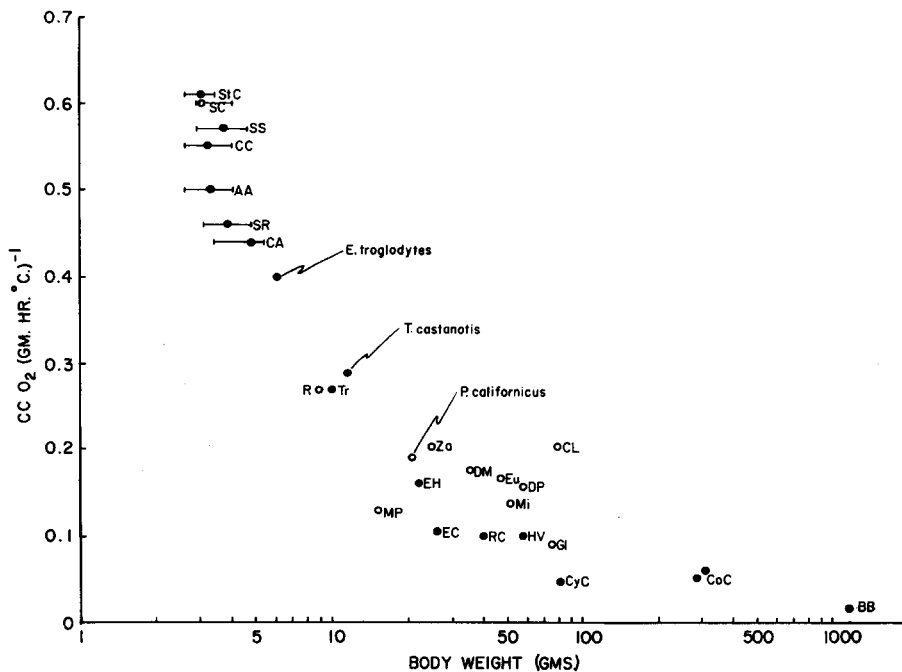

Fig. 4. The relation between thermal conductance and body weight in representative smaller birds and mammals (modified from Lasiewski, 1963). Recently available values were obtained from the following sources: Black-rumped Waxbill and Zebra Finch (see legend for fig. 3); California pocket mouse, *Perognathus californicus* (Tucker, MS). Shaded circles represent birds; unshaded circles represent mammals. Initials represent the following animals: *Stellula calliope* (StC), *Sorex cinereus* (SC), *Calypte costae* (CC), *Archilochus alexandri* (AA), *Selasphorus sasin* (SS), *Selasphorus rufus* (SR), *Calypte anna* (CA), *Reithrodontomys megalotis* (R), *Troglodytes aedon* (Tr), *Microdipodops pallidus* (MP), *Emberiza hortulana* (EH), *Zapus* (Za), *Emberiza citrinella* (EC), *Dipodomys merriami* (DM), *Richmondena cardinalis* (RC), *Eutamias* (Eu), *Microtus* (Mi), *Dipodomys panamintinus* (DP), *Hesperiphona vespertina* (HV), *Glaucomys* (Gl), *Citellus leucurus* (CL), *Cyanocitta cristata* (CyC), *Corvus caurinus* (CoC), *Branta bernicla* (BB).

and air flow was maintained at 350 cc./min. Increased flow rate decreases the relative humidity of the air in the chamber, thereby increasing the amount of water lost by a bird. Due to the differences in techniques, our evaporative water loss values are not strictly comparable to those obtained by Bartholomew and Dawson. They are, however, indicative of the amount of water lost through evaporation by Black-rumped Waxbills resting in the dark, in a postabsorptive state.

DISSIPATION OF METABOLIC HEAT

By obtaining simultaneous measurements of oxygen consumption and evaporative water loss, it is possible to estimate the amount of metabolic heat that is dissipated by evaporation. The relationship between heat produced, heat dissipated and ambient temperature is shown in figure 5. It is almost identical in form with that shown for the
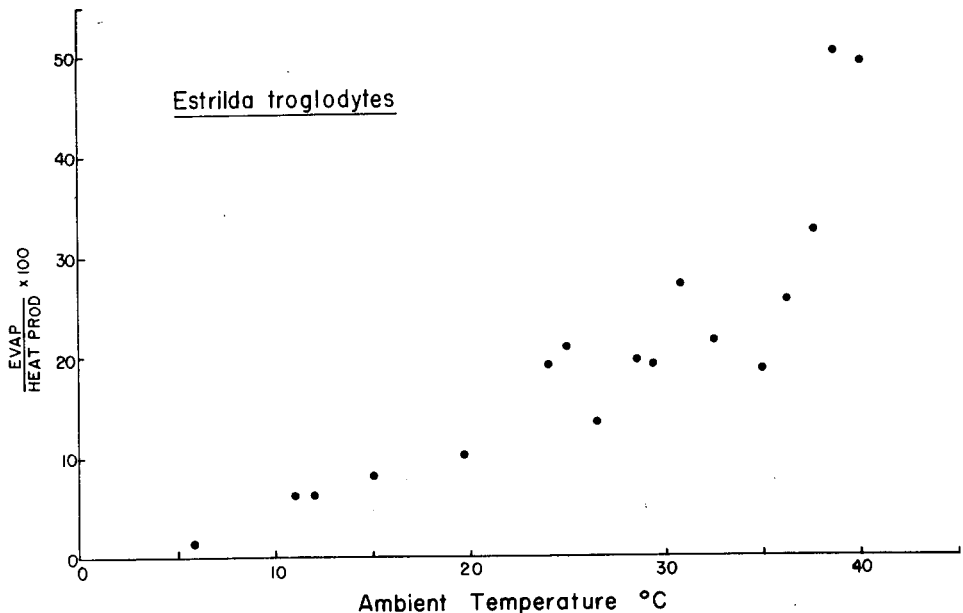

Fig. 5. The relation between heat produced through metabolism and heat dissipated through evaporative water loss, as a function of ambient temperature, in *Estrilda troglodytes*. Calculations are based on the assumption that 1 cc. O_2 consumed represents the production of 4.8 calories, and 1 mg. of H_2O evaporated represents the dissipation of 0.58 calories.

Cardinal by Dawson (1958). *Estrilda troglodytes* is unable to dissipate more than half of the heat produced by metabolism through the process of evaporative cooling in the temperature interval studied. Most species of birds studied to date are unable to dissipate, through evaporative cooling, more than 50 per cent of the metabolic heat produced, where heat loss by conduction, convection, and radiation is restricted (see King and Farner, 1961:263). Therefore most birds are forced to evade high temperatures or undergo a rise in body temperature.

HEART AND BREATHING RATES

Heart and breathing rates of 500 to 540 per minute and 135 to 140 per minute, respectively, for *E. troglodytes* at temperatures within the zone of thermal neutrality are in the same general range as values for a shrew (Morrison, *et al.*, 1959), humming-

birds (Odum, 1941; Lasiewski, in press), and other small birds (Odum, 1941, 1945). Yapp (1962) has suggested that the upper limit of heart action in small birds is around 1000 beats/min., on the basis of available information. The maximum recorded value for the Black-rumped Waxbill is 1020 beats/min., which represents a two-fold increase over resting levels and is consistent with this suggestion. Among birds, only humming-birds have higher heart rates than this, with the maximum recorded values being 1200 beats/min. for the Costa Hummingbird, *Calypte costae* (Lasiewski, in press), and 1260 beats/min. for the Black-chinned Hummingbird, *Archilochus alexandri* (Lasiewski, unpublished observations). This again represents a two-fold difference between resting and maximum levels of pulse rate. Since standard and flight metabolism in *Calypte costae* differ by a factor of ten (Lasiewski, 1963), hummingbirds must either increase heart rate further than 1200/min. during flight, increase systolic output (stroke volume), or most probably, increase both. More data are needed to clarify this point.

ACKNOWLEDGMENTS

SUMMARY

The oxygen consumption of postabsorptive Black-rumped Waxbills (*Estrilda troglodytes*) ranged from 3.5 to 3.9 cc. O_2/gm./hr. in the zone of thermal neutrality (approximately 28° to 35° C.), to 14.5 cc. O_2/gm./hr. at 1.8° C. The thermal conductance value of 0.40 cc. O_2 (gm./hr./°C.)$^{-1}$ is among the highest recorded to date, as would be expected for a bird this small (average postabsorptive weight, 6.1 gm.). Evaporative water loss increased with increasing ambient temperatures, with values ranging from 1.6(?) to 18.4 mg. H_2O/gm./hr. at temperatures of 5.8 to 38.6° C., respectively. Maximum recorded water loss values were equivalent to a loss of 44 per cent of the body weight per 24 hours. The Black-rumped Waxbill is unable to dissipate more than 50 per cent of its metabolic heat through evaporative cooling in the temperature interval studied. Heart rates of 500 to 540 beats per minute, and breathing rates of 135 to 140 breaths per minute, in the thermoneutral zone, are consistent with similar measurements from other small birds and mammals.

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