METABOLISM AND SURVIVAL TIME OF THE RED-WINGED BLACKBIRD*

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THIS study was undertaken to determine quantitatively the relationship between metabolic rate of the Red-winged Blackbird (*Agelaius phoeniceus*) and its survival time during periods when an external source of energy is unavailable. The relationship between the metabolic rate and the reserve energy supply determines the survival time of birds in different ecological or physiological conditions.

PROCEDURE

The birds used in this study were captured by the use of mist nests during the last 2 weeks of June in the State College, Pennsylvania area. The birds were maintained in the laboratory in large indoor cages (6 feet × 6 feet × 3 feet) at a photoperiod of 15 hours and at an environmental temperature of between 24 and 30 C. All birds were maintained in the laboratory for at least 2 weeks prior to being tested in the respiration chamber.

The respiration chamber used to determine the metabolic rates was an open-circuit system used by Haldane (1892). Tests by Kendeigh (1939) using measured amounts of CO_2 and moisture, showed that the gaseous output of a bird could be measured in this type of apparatus with an error of less than one per cent. Tests on the apparatus used in these experiments using measured amounts of CO_2 and moisture gave an accuracy within 0.7 per cent, which compares closely with Kendeigh's results. The basic design of the apparatus was the same as Kendeigh (1939) except four tubes instead of two were used to remove the CO_2 and water vapor from the incoming air. The respiration chamber for measuring metabolism of resting birds was constructed from a one-gallon, wide-mouth jar with a metal top and rubber gasket. The chamber for measuring roosting metabolism was a black, one-gallon, wide-mouth jar. For measuring the metabolic rate of active birds, the respiration chamber was constructed from a 12-gallon rectangular aquarium covered with heavy plastic sealed with one-inch adhesive tape. The birds were observed periodically during the tests and were found to be in an active condition. Air flow through all systems was maintained with a small air pump (75 cu. inch capacity) connected in reverse to pull air through the system. Air flow through all the systems was not measured exactly, however preliminary tests on the apparatus indicated that the air flow approximated 530 cc/min.

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Three hours before being placed in the respiration chamber, the bird was removed from a large indoor cage and placed in a small holding cage with water but no food. A study by Stevenson (1933) showed that 57 small passerine birds of different species quickly entered a postabsorptive state after being fasted. Feces from ingested grain that had been stained for identification was eliminated within 2.5 hours. Previous investigators have found that small passerine bird enter a postabsorptive state after a fast of about 2 hours (Kendeigh, 1944; Salt, 1952; Dawson, 1954; and Wallgren, 1954). Thus, the 3-hour fasting period was deemed sufficiently long enough to insure a condition of fat metabolism. Immediately before the start of each test, the bird was removed from the holding cage, weighed to the nearest milligram, and placed in the respiration chamber. The air pump was then connected and the system allowed to come to equilibrium for 15 minutes, after which the previously weighed (150 mm high × 18 mm diameter) drying tubes (weighed to ± one milligram) were connected into the system.

Each bird was tested for 3 hours; after this time it was removed from the respiration chamber and immediately weighed to ± one milligram. If feces were voided during the test these were also weighed in order to calculate the actual weight loss of the bird. The glass drying tubes were then weighed to find the grams of CO_2 (absorbed by soda lime) and water vapor produced (absorbed by $CaCl_2$). Oxygen consumption was calculated from the difference between the sum of CO_2 and water vapor produced and the loss of weight of the bird. The respiratory quotient was then calculated from the grams of CO_2 produced and the grams of O_2 consumed as described by Brody (1945:334). The temperature ranged between 24 and 30 C in both the fasting and metabolic chambers. The soda lime and $CaCl_2$ were changed after each test to assure the maximum possible absorption of CO_2 and water vapor.

The metabolism while roosting may be the basal metabolism for the Red-winged Blackbird. However, the bird may not be at complete rest during the fasting period and in the chamber. For this reason, "roosting metabolism" is used throughout this paper in place of "basal metabolism." A roosting condition refers to a bird sitting quietly in a dark chamber. Resting metabolism refers to the metabolic rate of a bird at rest the majority of the time in a lighted chamber, but the bird may be active for short intervals.

To determine survival time four birds were fasted until death in the chamber for measuring roosting metabolism and also in the chamber for measuring active metabolism. The following data were recorded: initial weight, weight at death, and the survival time. The birds were checked every 4 hours until midnight and then again at 8:00 AM.

TABLE 1

OXYGEN CONSUMPTION AND BODY WEIGHT OF RED-WINGED BLACKBIRDS IN ROOSTING, RESTING, AND ACTIVE CONDITIONS

Metabolic condition	No. of determinations	Mean cc O_2/g/hr	SE*	Mean weight	Weight range
Roosting	12	2.90	0.896	53.143	38.603–65.252
Resting	11	6.31	1.83	54.171	39.260–63.680
Active	10	12.46	2.08	53.657	38.181–62.197

* Standard error.

The total body fat of 14 birds was determined by the following procedure. The birds were minced and then dried to a moisture-free basis. The moisture-free birds were then extracted in petroleum ether for 24 hours. The total body fat was calculated as the difference in weight between the moisture-free birds before and after ether extraction. The total body fat was then expressed as a percentage of the live weight.

RESULTS

A total of 11 birds (9 males and 2 females) was used for the measurement of resting metabolism (Table 1). The mean rate of oxygen consumption for a resting bird was 6.31 ± 1.83 cc O_2/g–hr. The metabolism for 12 roosting birds (10 males and 2 females) was 2.90 ± 0.896 cc O_2/g–hr and was significantly lower than the rate for resting birds ($P < 0.01$). The mean rate of oxygen consumption for 10 active birds (9 males and 1 female) was 12.46 ± 2.08 cc O_2/g–hr and was significantly higher than the rate for resting birds ($P < 0.001$) and for roosting birds ($P < 0.001$).

SURVIVAL TIME

The length of time an animal can survive under conditions of total fasting can be predicted if the body weight and the metabolic rate of the animal are known. The energy available to the bird is equal to $0.7W$, where $W =$ weight in grams and 0.7 is derived from the proportion of the initial weight of the bird remaining at death. The energy available is derived from the following equation:

$$\frac{1\text{ g fat}}{9\text{ kcal}} = \frac{0.08W}{X} \qquad [X = 0.7W].$$

In this equation $W =$ weight in grams, $X =$ kcal and 0.08 is equal to the proportion of the live weight of the bird which is fat. The fat content of

TABLE 2

CALCULATED AND OBSERVED SURVIVAL TIME OF BIRDS UNDER ROOSTING CONDITIONS

Initial weight (g)	Weight at death (g)	Percentage of initial weight at death	Observed survival time (days)	Calculated survival time (days)
57	37	64.9	5.0	2.89
57	38	66.7	4.0	2.86
58	40	69.0	4.0	2.94
56	45	80.4	3.0	2.84
Mean		70.3	4.0	2.88
			chi-square = 3.50	

14 birds, determined by ether extraction of total body fat, varied from 9.3 to 7.8 per cent, with a mean of 7.9 ± 0.94 per cent of the live weight. The metabolic rate (*M*) was calculated from the grams of CO_2 produced per 24 hours at any given RQ (Brody, 1945:334). For calculation of the metabolic rate in kcal/bird–day, a thermal equivalent of 3.325 kcal per gram of CO_2 at an *RQ* of 0.722 was used (Brody, 1945:310). The survival time under any given condition can be calculated from the formula $S = F/M$, where S is the survival time (days), F is the kcal of energy available to the bird ($0.7W$), and M the metabolic rate under any given condition.

The roosting Red-winged Blackbird had a mean metabolic rate of 13.8 ± 0.042 kcal/bird–day, and the mean metabolic rate for an active bird was 40.9 ± 0.98 kcal/bird–day (measured for 3 hours). The mean calculated survival time for four birds under roosting conditions was 2.88 days, and was not significantly different from the mean observed survival time of 4.0 days ($P > 0.80$) (Table 2). The mean calculated survival time in an active condition was 0.86 days and was significantly lower than the observed survival time of 2.81 days ($P < 0.01$) (Table 3).

The metabolic rate can also be calculated from the formula $S = F/M$ if the survival time and available reserve energy are known. The mean calculated metabolic rate for birds fasting until death in a roosting condition was 10.2 kcal/bird–day and was not significantly different from the observed metabolic rate for roosting birds of 13.8 kcal/bird–day ($P > 0.75$). The metabolic rate was also calculated by theoretical equation of $M = 70W^{3/4}$ stated by Kleiber (1947, 1961). The theoretical metabolic rate, calculated by the preceding equation, of 11.8 kcal/bird–day was not significantly different from the observed metabolic rate of 13.8 kcal/bird–day ($P > 0.80$).

The weight of fat required for a bird to survive for 4 days in a roosting

TABLE 3

CALCULATED AND OBSERVED SURVIVAL TIME OF BIRDS UNDER ACTIVE CONDITIONS

Initial weight (g)	Weight at death (g)	Percentage of initial weight at death	Observed survival time (days)	Calculated survival time (days)
59	40	66.7	3.75	1.01
49	38	77.6	2.50	0.84
55	43	78.2	2.50	0.94
37*	26	70.3	2.50	0.64
Mean		73.5	2.81	0.86
			chi-square = 18.71	

* Female.

condition was 6.3 g (calculated from $S = F/M$) and was not significantly different from the 4.5 g calculated by the $0.7W$ method ($P > 0.50$). These results indicate that the survival time of birds in a roosting state may be calculated if the body weight and the metabolic rate of the bird are known. The mean metabolic rate, calculated from $S = F/M$, of birds in the chamber for measuring active metabolism was 14.7 kcal/bird–day and was significantly lower than the observed metabolic rate of 40.9 kcal/bird–day ($P < 0.001$). These data indicate that the birds probably did not remain in an active condition until death.

DISCUSSION

The mean metabolic rate of 2.90 cc O_2/g–hr for roosting birds compares closely with previous work. Dawson (1954) recorded an average oxygen consumption of 2.80 cc/g–hr for the Abert Towhee (*Pipilo aberti*) and of 2.85 cc/g–hr for the Brown Towhee (*Pipilo fuscus*). The oxygen consumption reported for the Cardinal (*Richmondena cardinalis*) was 2.60 cc O_2/g–hr at a temperature range of 24–33 or 34 C (Dawson, 1958). A metabolic rate of 2.5 cc O_2/g–hr for the Evening Grosbeak (*Hesperiphona vespertina*) at a temperature range of 20–31 C was reported by Dawson and Tordoff (1959). A metabolic rate of 3.1 cc O_2/g–hr for the Red Crossbill (*Loxia curvirostra sitkensis*) and 2.8 cc O_2/g–hr for the White-winged Crossbill (*Loxia leucoptera*) was reported by Dawson and Tordoff (1964).

The range in cc O_2/g–hr of roosting birds was not so great as that of resting birds, probably because the birds settled down almost at once after being placed in the black chamber (Table 1). Inactivity in the respiration chamber probably accounted for the small range of values. Results from the clear chamber were more erratic than those from the black chamber, probably because some birds struggled, while others sat in the chamber with little or no movement at all. These results indicate that the metabolic rate of roosting birds is a better measure of basal metabolism than is the metabolic rate of resting birds.

Previous studies have shown that the metabolic rate of active animals is higher than the basal level. Pearson (1947) found that two species of bats, *Eptesicus fuscus* and *Myotis lucifugus,* had active rates of 17 or 18 times their basal level. Pearson (1950, 1954) found that the average active rate for a flying Anna's Hummingbird at 24 C was 68 cc O_2/g–hr; only a 5.5 increase over the basal rate for this species. Pearson also stated that the hovering hummingbird consumes oxygen at a much faster rate than that recorded for any other vertebrates. Lasiewski (1962) stated that the average metabolic rate of a flying hummingbird is 42 cc O_2/g–hr and this value is probably more representative of the flight metabolism of hummingbirds than the previously reported values. The mean increase of resting above the roosting rate was 2.24 cc O_2/g–hr and the mean increase of active above roosting was 4.30 cc O_2/g–hr. The increase in the metabolic rate during periods of activity influences the rate of utilization of reserve energy supply (fat). The relationship between the metabolic rate and reserve energy supply determines the survival time of the organism under any given ecological or physiological condition.

In 12 tests in the black chamber, the mean respiratory quotient was 0.722, which indicates that the metabolism of these birds in the roosting state was probably at the expense of fat reserves. This figure of 0.722 agrees with the 0.73 found for the House Wren by Kendeigh (1939) and Riddle et. al. (1932) for pigeons older than 22 days. The fact that a metabolic rate of 13.8 kcal/bird–day was not significantly different from the calculated basal rate of 11.8 kcal/bird–day based on Kleiber's weight-relative formula ($M = 70W^{3/4}$) lends support for the suggestion that the metabolic rate of a roosting bird may be the basal rate for the Red-winged Blackbird. A respiratory quotient of 0.722 indicates that fats make up 95.6% of the oxidized material burned by the body (Brody, 1945:310). As suggested above, this respiratory quotient indicates that the metabolic rate of a roosting bird may be the basal metabolic rate for the Red-winged Blackbird.

Odum and Perkinson (1951) determined the total body lipids of 86 individual White-throated Sparrows (*Zonotrichia albicollis*) collected at four different seasons, viz., postmigration (October–November), midwinter (January–February), molting period (March–April), and premigration (April–May). The average total body lipids in percentage of body weight were: postmigration, 6.88 per cent; midwinter, 12.05 per cent; molt, 6.25 per cent; and premigration, 16.66 per cent. The mean total body fat was

8.39 per cent of the total body weight during the postmigration, midwinter, and molt periods. This figure compares with mean lipid content of 7.9 per cent of the body weight determined for 14 Red-winged Blackbirds. Further investigation is required to determine if the method described in this study for determining the reserve energy supply of birds during the period of rapid deposition of fat prior to vernal migration is useful. However, since the lipid content of birds is variable throughout the year, the $0.7W$ method may be sufficient to estimate the reserve energy supply and total body fat of birds in the different seasons.

The reserve energy available to animals is dependent on the body weight (Morrison, 1960). The basal metabolic rate of animals is also dependent on the body weight and increases with approximately the 0.73 power of the body weight (Brody, 1945). The weight relationship to the basal metabolic rate and available energy is also the formula for metabolic body size, $W^{3/4}$, as described by Kleiber (1932, 1947, 1961). The energy available to a 50-gram bird if $0.7W$ is used for determination in 35 kcal, and the energy available is 37.5 if $0.75W$ is used for the calculation of available energy. The difference of 2.5 kcal probably is not significant in the prediction of the survival time of an animal. The survival time of an individual bird is determined by the reserve energy supply and metabolic rate. The survival time of birds is further influenced by changes in the environmental and/or internal physiological mechanisms. The interaction between metabolic rate and utilization or deposition of reserve may be a factor in regulating the various phases in the life history of the species.

SUMMARY

The oxygen consumption of the Red-winged Blackbird was determined for roosting, resting, and active birds. The mean metabolic rate for a roosting Red-winged Blackbird was 2.90 ± 0.896 cc O_2/g–hr; the mean rate for a resting bird was 6.31 ± 1.83 cc O_2/g–hr; and the mean rate for an active bird was 12.46 ± 2.08 cc O_2/g–hr. The metabolic rate for roosting birds was significantly lower than the metabolic rates for resting and active birds. The respiratory quotient for roosting birds after fasting for 6 hours was 0.722, which indicates fat metabolism.

The reserve energy available to a bird is dependent on the body weight and is calculated by multiplying 0.7 by the body weight. The survival time can be calculated from the body weight and the metabolic rate of a bird under any given condition. The calculated survival time of birds in a roosting state was not statistically different from the observed.

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