

ENERGY AND NUTRIENT REQUIREMENTS OF THE RED-WINGED BLACKBIRD

FRED J. BRENNER

VARIOUS factors in the environment affect the existence energy requirements of birds and variation in the existence energy requirements of a particular species may influence various phases of its life history. This study investigated the relationship of environmental changes to the existence energy requirements and hence the nutritional requirements of the Red-winged Blackbird (*Agelaius phoeniceus*). The existence energy of a population represents the energy metabolized when the birds maintain a constant weight; thus the energy is used for standard metabolism, heat regulation, food assimilation, and securing food and water. Net energy (productive energy) is that energy metabolized beyond that required for existence. By taking into account all losses in metabolism, net energy is that portion of the metabolized energy that appears as product (fat, egg production, etc.).

Breeding birds arrive in central Pennsylvania in mid-March when the photoperiod is between 12 and 13 hours and the average daily air temperature is between 5 and 7 C. The photoperiod during the breeding season in May and June is between 14 and 15 hours, and the average air temperature is 17 C (mean of 70 years). After the breeding season, in July, the birds leave the breeding grounds and are joined by birds from other areas, including migrants. Red-winged Blackbirds depart from central Pennsylvania in October and November when the photoperiod is between 10 and 11 hours and the average air temperature is between 5 and 8 C (Brenner, 1964). However, it has not been determined whether the birds observed in October and November are summer residents, migrants, or both.

METHODS

The birds were captured in mist nets near State College, Pennsylvania, and in Florida. The birds, confined in the laboratory for 2 or 3 weeks before the start of experiments, were housed in groups of four or five in large artificially lighted cages (6 ft × 6 ft × 3 ft). Eight separate measurements of the existence energy requirements and body weights of 10 birds (two groups of five) were made per month during March, April, and May. During this time the photoperiod was increasing and environmental temperatures averaged between 21 and 25 C. Eight individual measurements per month (July–August and October–November) were made of the existence energy requirements and body weight of eight birds (two groups of four) at a decreasing photoperiod and temperature. The existence energy requirements and body weight of

eight birds (two groups of four) held at 10 hours of light was determined from 32 separate measurements (eight measurements per month). These measurements were made to determine whether decreasing temperature alone influenced the existence energy requirements of birds. These two experiments were undertaken simultaneously. The windows were open in the laboratory in an attempt to subject the birds to fluctuations in environmental temperature. The ambient temperature in the laboratory was determined from the temperature recorded every 2 hours by a continuous 7-day recording thermograph.

The method of measuring food consumption and excrement loss, described by Kendeigh (1949) and also employed by Seibert (1949), Davis (1955), and West (1960), was followed. Two foods were used: high protein poultry laying pellets and cracked corn. All birds were fed ad libitum. In order to minimize diurnal differences, the birds were fed and weighed at approximately the same time each day. The birds were supplied a weighed amount of food and at the end of 5 days the uneaten food and the excrement were collected, dried, and weighed. The excrement was saved for caloric determination and chemical analysis. The caloric content of the feed and excrement was determined in a plain oxygen bomb calorimeter. The nutrient content of the two types of food was determined by standard biochemical methods as described by Maynard and Loosi (1962).

The existence energy was determined by subtracting the caloric content of the excreta from the caloric content of the food consumed (gross energy). The coefficient of metabolizable dry matter was calculated from the food intake (dry weight) minus the dry weight of the excreta divided by the food intake. The coefficient of metabolism of the various nutrients was then multiplied by the grams of the nutrient in the food per 100 g in order to determine the grams of nutrients metabolized per 100 g of food intake.

The reserve energy supply (fat) was determined by the following method described by Brenner and Malin (1965). The reserve energy available to a bird was calculated from the following equation:

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

In this equation W = weight in grams, X = kcal, and 0.08 is the proportion of the live weight which is fat.

RESULTS

The decrease in the existence energy requirements of the birds from month to month in the spring (Table 1) was not significant ($P > 0.08$). The difference of 2.4 kcal in the existence energy requirements while feeding on the two types of food was not significant ($P > 0.50$). The mean existence

TABLE 1
EXISTENCE ENERGY REQUIREMENTS OF RED-WINGED BLACKBIRDS DURING AN INCREASING PHOTOPERIOD**

Month	Photo- period	Temp. C	Existence Energy Requirements							
			Pellets*				Corn*			
			kcal/bird-day		kcal/g-day		kcal/bird-day		kcal/g-day	
Mean	SE	Mean	SE	Mean	SE	Mean	SE			
March	12	21	29.4	0.19	0.60	0.009	27.6	0.38	0.59	0.067
April	13	25	25.7	0.28	0.52	0.046	21.6	0.35	0.48	0.063
May	14	23	22.5	0.36	0.60	0.042	21.2	0.18	0.47	0.008
Mean			25.9	-	0.54	-	23.5	-	0.51	-

* Five birds in each group.

** Ten measurements/month.

energy requirements of the birds on the two different foods was 24.8 kcal/bird-day.

The existence energy requirements of Red-winged Blackbirds increased from month to month in the autumn ($P < 0.05$) (Table 2). The existence energy requirements increased from a mean of 25.8 kcal/bird-day at 15 hours of light and 21 C to a mean of 45.5 kcal/bird-day at 9 hours of light and 11 C. The gross energy intake and excrement energy loss also increased as the photoperiod and temperature decreased ($P < 0.05$). However, the variation in photoperiod and temperature did not influence significantly the efficiency of metabolism by the birds ($P > 0.08$). Therefore, it may be assumed that the increase in the existence energy resulted from hyperphagia and not from a change in the efficiency of metabolism by the birds. The existence energy requirements of birds at a 14-15-hour photoperiod and 21 C (July and August) did not vary significantly from birds held at an increasing photoperiod and 23 C ($P > 0.50$). The difference in the existence energy requirements between the two types of food was not significant (Table 2) ($P > 0.70$).

TABLE 2
EXISTENCE ENERGY REQUIREMENTS OF BIRDS AT A DECREASING PHOTOPERIOD AND TEMPERATURE**

Month	Photo- period	Temp. C	Existence Energy Requirements							
			Pellets*				Corn*			
			kcal/bird-day		kcal/g-day		kcal/bird-day		kcal/g-day	
Mean	SE	Mean	SE	Mean	SE	Mean	SE			
July	15	21	26.3	0.45	0.44	0.066	25.2	0.34	0.46	0.023
August	14	21	30.2	0.90	0.51	0.057	23.9	0.19	0.44	0.090
October	12	17	40.4	0.26	0.68	0.039	35.4	0.34	0.65	0.066
November	9	11	45.2	1.08	0.74	0.083	45.7	0.39	0.88	0.058

** Eight measurements/month.

* Four birds in each group.

TABLE 3
EXISTENCE ENERGY REQUIREMENTS OF BIRDS AT A CONSTANT 10-HOUR PHOTOPERIOD AND
DECREASING TEMPERATURE**

Month	Photo- period	Temp. C	Existence Energy Requirements							
			Pellets*				Corn*			
			kcal/bird-day		kcal/g-day		kcal/bird-day		kcal/g-day	
Mean	SE	Mean	SE	Mean	SE	Mean	SE			
July	10	21	37.0	0.89	0.64	0.055	35.1	0.55	0.59	0.083
August	10	21	34.1	0.40	0.54	0.063	36.9	0.15	0.64	0.022
October	10	17	43.9	0.18	0.75	0.024	40.0	0.56	0.75	0.084
November	10	11	44.7	0.87	0.79	0.057	41.0	0.67	0.78	0.065

** Eight measurements/month.

* Four birds per group.

The existence energy requirements of the control birds held at 10 hours of light for 16 weeks increased during the last 8 weeks of the experiment ($P < 0.01$) (Table 3). The mean existence energy requirements increased from 35.5 to 40.4 kcal/bird-day during the latter half of the experimental period when the temperature decreased. The existence energy requirements of birds held at a 10-hour photoperiod and 21 C were significantly higher than the existence energy requirements of birds on the 12- to 14-hour photoperiod and 23 C ($P < 0.05$). The birds held at these photoperiods did not appear to be molting. However, nightly unrest may have occurred in either population (it was not measured). If nightly unrest did occur, this may account for the difference in the energy metabolized by the different populations. The existence energy requirements of the control birds were also significantly higher than those for birds held at 14-15 hours of light and 21 C ($P < 0.05$); however, at photoperiods between 9 and 12 hours of light and at temperatures between 11 and 17 C the existence energy requirements did not vary significantly from those of the birds held at a 10-hour photoperiod at the same temperature ($P > 0.050$). During periods of decreasing temperatures and low photoperiods both groups of birds increased their existence energy requirements above that required for birds during periods of an increasing photoperiod and constant temperature ($P < 0.001$).

The existence energy requirements of the birds in all three groups were also analyzed in terms of the energy required per gram of body weight in order to standardize the results. The existence energy requirements of birds in terms of kcal/g-day also increased when the temperature decreased (Tables 2 and 3). The body weight of the birds in the three groups did not vary significantly with temperature and hence the energy reserve (fat) of the birds which is related to the body weight did not vary (Fig. 1). Therefore, the energy intake was only sufficient to maintain the daily metabolic processes.

The theoretical existence energy requirements may be calculated by the

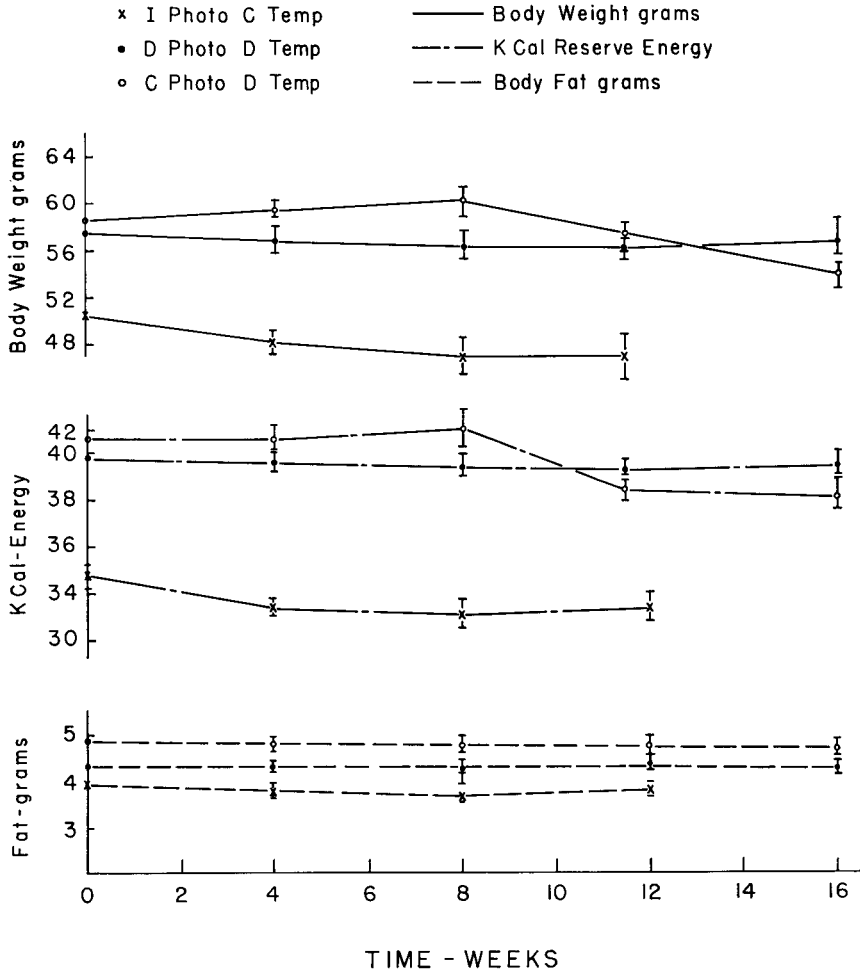


FIG. 1. Body weight, reserve energy supply, and estimated body fat of experimental birds under three different environmental conditions.

following formula modified from Maynard and Loosi (1962): $EE_{kcal} = 140 W^{.75}$ where EE_{kcal} is the existence energy requirements and W is the body weight. This formula may only be used to calculate the existence energy requirements of birds within the thermoneutral zone for the particular species. The mean existence energy requirements of 30.4 kcal/bird-day for Red-winged Blackbirds in all three groups at a mean environmental temperature of 22 C did not vary significantly from the theoretical value of 28.1 kcal/bird-day ($P > 0.40$); however, when the temperature decreased the

TABLE 4
METABOLIZABLE COEFFICIENTS OF NUTRIENTS, TOTAL METABOLIZABLE NUTRIENTS, AND METABOLIZABLE DRY MATTER UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

Nutrient	Food	Environmental Condition					
		Decreasing photoperiod and temperature ¹		10-Hour photoperiod and decreasing temperature ²		Increasing photoperiod constant temperature ³	
		Mean	SE	Mean	SE	Mean	SE
Ether extract (fat)	Corn	92.44	0.238	91.04	0.243	90.30	1.240
	pellets	92.93	0.905	92.80	0.740	90.52	0.220
Crude fiber	Corn	56.92	3.500	69.06	2.300	54.21	3.240
	pellets	77.51	0.900	71.11	1.100	76.67	0.984
Ash	Corn	69.54	2.200	72.89	2.510	70.01	2.470
	pellets	62.85	3.570	72.45	3.210	62.01	3.320
Crude protein	Corn	59.88	0.800	59.31	0.764	72.54	0.977
	pellets	30.65	1.930	31.38	1.810	34.07	0.970
Nitrogen-free extract (carbohydrate)	Corn	94.13	0.241	94.36	2.410	94.21	1.410
	pellets	76.24	0.433	68.12	0.521	72.31	0.620
Energy	Corn	90.50	0.699	92.10	0.899	88.50	1.650
	pellets	70.20	1.600	72.60	1.710	66.00	1.910
Dry matter	Corn	90.50	3.270	89.90	3.410	90.40	0.570
	pellets	65.10	0.887	61.00	0.921	62.50	1.040

¹ Eight birds; ² Eight birds; ³ 10 birds.

observed existence energy requirements were significantly higher than the theoretical value ($P < 0.001$).

The metabolizable coefficient of the various nutrients and energy did not vary with the different environmental conditions (Table 4), therefore, the grams of nutrients metabolized per 100 g of food remained the same regardless of the environmental condition (Table 5). The grams of carbohydrate (nitrogen-free extract) metabolized per 100 g of food intake was the only nutrient that was significantly different between the two foods. These data further illustrate that the nutritional requirements of the birds did not vary with the different environmental conditions.

DISCUSSION

The existence energy requirements of Red-winged Blackbirds increase in response to decreasing temperature and the gross energy intake of the birds also increased at the same time. Therefore, the increase in the energy metabolized by the birds was due to hyperphagia and not to an increase in the efficiency of metabolism by the birds. The total metabolizable nutrients

TABLE 5
GRAMS OF NUTRIENTS METABOLIZED PER 100 GRAMS OF FOOD INTAKE

Nutrient	Food	Environmental Condition					
		Decreasing photoperiod and temperature ¹		10-Hour photoperiod and decreasing temperature ²		Increasing photoperiod constant temperature ³	
		Mean	SE	Mean	SE	Mean	SE
Ether extract (fat)	Corn	2.63	0.018	2.59	0.016	3.44	0.073
	pellets	2.51	0.071	2.51	0.059	3.54	0.026
Crude fiber	Corn	2.28	0.142	2.76	0.122	2.71	0.131
	pellets	1.88	0.056	1.73	0.041	1.88	0.048
Ash	Corn	0.765	0.006	0.802	0.010	0.770	0.008
	pellets	1.54	0.150	2.07	0.125	1.77	0.141
Crude protein	Corn	6.76	0.140	6.70	0.131	5.25	0.093
	pellets	7.60	0.480	7.85	0.386	6.31	0.390
Nitrogen-free extract (carbohydrate)	Corn	69.49	3.09	76.21	2.79	78.10	2.87
	pellets	57.63	3.26	48.84	3.13	52.46	3.21
Total met. nutrients	Corn	92.17	0.742	92.13	0.721	90.27	0.732
	pellets	64.88	0.795	63.00	0.631	65.96	0.784

¹ Eight birds; ² Eight birds; ³ 10 birds.

and the metabolizable dry matter did not change under the different environmental conditions. This coefficient of metabolizable dry matter (corn) of 90.5 per cent is the same as the 90.4 per cent for grain stated by Stevenson (1933) for 57 small passerine birds of different species.

The effect of photoperiod and temperature on the existence energy requirements of the Red-winged Blackbird may influence various phases of its life history. It appears that during the breeding season in central Pennsylvania the increasing environmental temperature results in a decrease in the existence energy requirements of the breeding population. Thus, it may be postulated that during the breeding season in May and June when the existence energy requirements are low the time required for feeding may be reduced, and therefore, the individuals may spend more time in defense of territory, caring for young, and other breeding activities.

At lowered temperatures, which normally occur during shorter photoperiods of the winter, the existence energy requirements are increased, and therefore, the birds have less feeding time available during a period of increased energy expenditure. Thus, it appears that migration serves as a survival factor in that it lowers the existence energy requirements due to the warmer environmental temperature of the winter range as well as providing an increased

feeding period in the lower latitude. Low environmental temperature is correlated with the high existence energy requirements of birds. The birds held at a constant 10-hour photoperiod maintained a constant body weight while their existence energy requirements increased as the temperature decreased, indicating that the birds were ingesting only sufficient energy to maintain life. Temperature has a greater influence than photoperiod on the existence energy requirements of the species, because of the increased energy required for thermoregulation at low temperatures.

Most Red-winged Blackbird roosts occur in the eastern United States from Virginia south to northern Florida (Meanley and Webb, 1960). These birds are exposed to a photoperiod between 10 and 11 hours of daylight during the winter months. The existence energy requirements of birds at 11 C and 10 hours of light was 42.8 kcal/bird-day compared with 45.2 kcal/bird-day for 9-hour photoperiod which occurs in central Pennsylvania during the winter months. The birds migrating south in response to photoperiod would conserve only 2.5 kcal/bird-day at an environmental temperature of 11 C.

The Red-winged Blackbird inhabits the southern United States during the months of November, December, January, and February. The average temperature during these months for the six states where winter roosts of Red-winged Blackbirds occur ranged between 5 and 18 C (mean 10 C). The average temperature during these months for central Pennsylvania varied between 4 C and -3 C (mean 0.7) during the period from 1887 to 1956. The data presented here indicate that the energy requirements of birds increase with decreasing temperature. The results of this study further illustrate that at a low environmental temperature the existence energy requirements of Red-winged Blackbirds was significantly higher than the theoretical value of 28.1 kcal/bird-day, indicating that the experimental and control birds may have been exposed to environmental temperatures below their range of thermal neutrality. Siebert (1949) stated that migratory birds cannot metabolize energy fast enough during cold weather at short photoperiods to maintain life. Individual Starlings (*Sturnus vulgaris*) increased their metabolic rate under roosting conditions from 2.86 cc O₂/g-hr at 24 to 30 C to 5.83 cc O₂/g-hr at 2-4 C and the survival time decreased from 3 days to 1 day. However, when Starlings were grouped at 2-4 C, survival time increased from 1 to 3 days. The metabolic rate was also lower for birds grouped at 2-4 C than for birds roosting singly, indicating less heat loss per bird (Brenner, 1965). The increase in temperature in the wintering area plus the flocking behavior of the birds probably aids the Red-winged Blackbird in surviving inclement winter weather. The effect of light and temperature on the energy requirements probably influences the development of fall migration.

SUMMARY

The existence energy requirement of the Red-winged Blackbird was determined under different environmental conditions. The birds were fed two foods: high protein poultry laying pellets and cracked corn. The mean existence energy requirement of birds under an increasing photoperiod at an environmental temperature between 21 and 25 C was 24.9 kcal/bird-day.

The existence energy requirements increased from 25.8 kcal/bird-day at 21 C and 15 hours of light to 45.5 kcal/bird-day at 11 C and 9 hours of light. The existence energy requirements of birds held at a 10-hour photoperiod for 16 weeks also increased as the temperature decreased. There was no difference in the total metabolizable nutrients and metabolizable dry matter available to the birds under the different environmental conditions.

The effect of environmental temperature and photoperiod on the existence energy requirements in regard to the survival of the species and migration is discussed. The environmental temperature probably has a greater influence on the existence energy requirements of birds than has photoperiod.

ACKNOWLEDGMENTS

The author thanks Dr. Ted Long and the Department of Animal Industry and Nutrition of the Pennsylvania State University for the use of equipment and for assistance in the chemical analysis of food and excreta; Dr. S. Charles Kendeigh for his helpful suggestions and criticisms in the preparation of this paper, and the United States Fish and Wildlife Service for supplying birds for this study.

LITERATURE CITED

- BRENNER, F. J.
1964 The rainfall to reproduction in Red-winged Blackbird populations. Unpubl. Ph.D. thesis, Pennsylvania State University.
- BRENNER, F. J., AND W. F. MALIN
1965 Oxygen consumption and survival time of the Red-winged Blackbird. *Wilson Bull.*, 77:282-289.
- BRENNER, F. J.
1965 Metabolism and survival time of Starlings at various temperatures. *Wilson Bull.*, 77:388-395.
- DAVIS, E. A.
1955 Seasonal changes in the energy balance of the English Sparrow. *Auk*, 72: 385-411.
- KENDEIGH, S. C.
1949 Effect of temperature and season on the energy resources of the English Sparrow. *Auk*, 66:113-127.
- MAYNARD, L. A., AND J. K. LOOSI
1962 Animal nutrition. McGraw-Hill Book Co., Inc., New York.
- MEANLEY, B., AND J. S. WEBB
1960 Distribution on winter blackbird roosts east of the Appalachians. Wildlife Leaflet 428. Bureau of Sport Fisheries and Wildlife, Fish and Wildlife Service. Washington, D.C.

SIEBERT, H. C.

1949 Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. *Auk*, 66:128-153.

STEVENSON, J.

1933 Experiments on the digestion of food by birds. *Wilson Bull.*, 45:155-167.

WEST, G. C.

1960 Seasonal variation in the energy balance of the Tree Sparrow in relation to migration: *Auk*, 77:306-329.

DEPARTMENT OF ZOOLOGY, THE PENNSYLVANIA STATE UNIVERSITY, UNIVERSITY PARK, PENNSYLVANIA. (CURRENT ADDRESS: BIOLOGY DEPARTMENT, THIEL COLLEGE, GREENVILLE, PENNSYLVANIA.) 19 FEBRUARY 1965

NEW LIFE MEMBER

A recent addition to the list of Life Members of the Wilson Ornithological Society is Dr. John T. Emlen, Professor of Zoology at the University of Wisconsin. A graduate of Haverford College, and holder of a doctorate from Cornell University, Dr. Emlen is one of the country's distinguished ornithologists. He is the author of over 100 scientific papers and his research interests have taken him to all parts of the United States, as well as to Africa to study the gorilla, and to the Antarctic to investigate the navigational abilities of penguins. In addition to his own work he has trained a number of students who are becoming prominent scientists in their own right. A member of the BOU, the Deutsche Ornithologische Gesellschaft, the AAAS, and the Cooper Society (past president of the northern division), Dr. Emlen has also been honored by election to the office of Vice President of the AOU. From 1956 to 1958 he served as President of the Wilson Society. He has three sons, all of whom are students of biology, and besides



his professional work finds time to devote to conservation matters, as well as photography and biophilately.