

THE AUK

A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 66

APRIL, 1949

No. 2

EFFECT OF TEMPERATURE AND SEASON ON ENERGY RESOURCES OF THE ENGLISH SPARROW

BY S. CHARLES KENDEIGH

INTRODUCTION

In order better to understand the underlying causes regulating the distribution, migration, abundance, reproduction, and other aspects of bird behavior, a series of researches has been undertaken to determine the manner in which the energy balance of the bird is affected by environmental factors. An early study (Kendeigh, 1934) outlined the problem and some of the environmental factors that are involved. A relation of size and number of eggs per set to temperature and energy resources was demonstrated in 1941. In 1944, the rate of energy outgo for standard metabolism was shown to vary inversely with temperature as a straight line between $+ 37^{\circ}$ and $- 40^{\circ}$ C. In 1945, measurement was made, over the same wide range of temperature, of the extent and ability of birds to utilize the energy reserve in their bodies for postponing death from starvation.

The present study is concerned with measurement of the rate of energy intake at these same temperatures and an analysis of the energy resources of the bird throughout the year. There have been many detailed studies of the energy values of different kinds and amounts of food for chickens and other domestic animals and on the energy resources of these animals (Brody, 1945). Only an occasional study, however, treats of the influence of temperature on the utilization of food energy (Kleiber and Dougherty, 1934). Larguier des Bancels in 1902 and Lapique and Lapique in two papers in 1909 demonstrated in a few species of wild birds a decrease in gross energy intake with a rise in temperature. There are other references scattered in the literature on the weight consumption of food at different temperatures (especially Rörig, 1905: 24-34). Most of the work on the

food of wild birds has dealt with the identification of the items consumed.

Dr. Tom S. Hamilton, Department of Animal Science, University of Illinois, kindly had made in his laboratory for the present study the caloric determinations of bird food and excrement and also read and commented on the manuscript.

PROCEDURE

English sparrows, *Passer domesticus*, were placed consecutively at different temperatures under controlled laboratory conditions for a total of several weeks. The birds were captured and all experiments run between the middle of November and early in March to represent the birds in the winter phase of the yearly cycle. The responses of birds during the summer period, when breeding and molt are in process, would likely be quite different.

The food supplied the birds was the University of Illinois chick mash No. 393 containing the following ingredients: 49 parts ground corn, 10 parts ground oats, 15 parts bran, 10 parts middlings, 5 parts alfalfa meal, 5 parts meat scraps, 5 parts soy bean oil meal, and 1 part salt. This mixture contained 15 per cent protein, a moisture content of 13 per cent, and an energy value of 4.40 large calories per gram of dry weight. The diet contained all known essential food elements; the birds consumed it readily and appeared to do well on it. Caloric determinations of unused food remaining in the dishes at the end of experimental periods were not significantly different from those of fresh food, indicating that the birds did not discriminate appreciably in their selection of food from the mixed diet available to them.

Weighed amounts of food were given the birds at intervals of three or four days. The food was offered in a fresh condition without drying, although the dry weight was calculated. At the end of a feeding period, the food tray was removed, excrement separated, and the food dried at 100° C. to determine the *gross energy* consumed. All weights were measured to one-tenth gram.

The excreta were separated by hand from the unused food, dried at 100° C., and their caloric value determined. This caloric wastage subtracted from the gross energy gives the *metabolizable energy* of the food consumed (= available energy of Kleiber and Daugherty, 1934: 713). No correction could be made for the slight loss of energy due to fermentation of undigested food and energy utilization by bacteria in the large intestine.

The birds were confined in small cages of hardware cloth, measuring 5 by 10 by 10.5 inches, with the greatest dimension being the height.

The small size of the cages prevented much activity. These cages were closely fitted into metal trays having a depth of four inches. Single sheets of newspapers were also placed in the trays to catch grain particles tossed or kicked out by the birds. Water was supplied at temperatures above freezing, and snow or frost was taken from the refrigeration plates at lower temperatures.

Various degrees of temperature were maintained through use of a special constant-temperature unit for extreme temperatures and constant-temperature rooms for the medium temperatures. The photoperiod was maintained at 10 hours of light per day in all experiments by means of two 100-watt light bulbs connected with an automatic time switch which turned the lights on at 7:00 a. m. and off at 5:00 p. m., Central Standard Time. The birds were in absolute darkness when the artificial lights were off, and there was no feeding during these hours.

Preliminary experiments were performed during the winter of 1944-45 and 61 experiments during the winter of 1945-46. Some experiments were unsuccessful due to mortality, intrusion of mice, or other difficulties so that 54 successful measurements of food absorption were obtained at various temperatures on five male and nine female birds. The total number of days of feeding by individual birds involved in getting these measurements is 850. The same bird was used at all temperatures as far as possible, so that individual differences in food absorption at the various temperatures were largely eliminated. Because careful attention showed there were no sexual differences in food absorption or excrement eliminated, all data are combined as of equal value. The number of records obtained at extremely low temperatures was few, as the birds had to be acclimated step by step or mortality resulted.

Each bird was kept at each temperature level until successive measurements over three- or four-day intervals gave similar results in amount of food consumed and in maintenance of weight. In this way it was certain that the birds had become adjusted to the temperature, were feeding and behaving normally, and had established an existence level or balance of energy ingo and outgo. Data obtained before this balance was reached were not used. The average daily change in weight was ± 0.07 gram. This variation is so small that it may be accounted for by the amount of food and unvoided excrement that happened to be in the bird at the time of its weighing.

ENERGY INTAKE

From Table 1 it is apparent that the amount of food ingested,

TABLE 1
EXPERIMENTAL DATA ON FOOD CONSUMPTION BY ENGLISH SPARROWS

Tem- per- ature (°C.)	Number of birds	Total days feed- ing	Average weight of birds (grams)	Average weight change per day (grams)	Food intake		Excrement loss		Metabolizable energy	
					Cal. per bird per day	Standard deviation	Cal. per bird per day	Standard deviation	Cal. per bird per day	Standard deviation
-31	3	24	24.3	-0.03	39.60	±0.44	6.41	±0.59	33.19	±0.50
-25	3	36	24.2	+0.07	35.20	0.27	5.79	0.26	29.41	0.91
-13	6	100	24.7	-0.06	31.24	0.84	4.96	0.19	26.28	0.89
-4	6	81	23.1	+0.18	26.40	3.11	3.77	0.26	22.63	2.58
+10	12	208	24.3	+0.06	25.96	3.74	3.26	1.32	22.70	3.07
+24	12	194	23.1	-0.02	18.04	1.87	2.01	0.07	16.03	1.64
+34	12	207	22.9	-0.10	16.28	2.68	1.90	0.59	14.38	2.34

gross energy, increased with a drop in air temperature. Figure 1 shows that this increase was a linear one. As Kleiber and Daugherty (1934: 709-711) found with baby chicks, there appears to be no limit to the birds' appetite with decreasing temperatures.

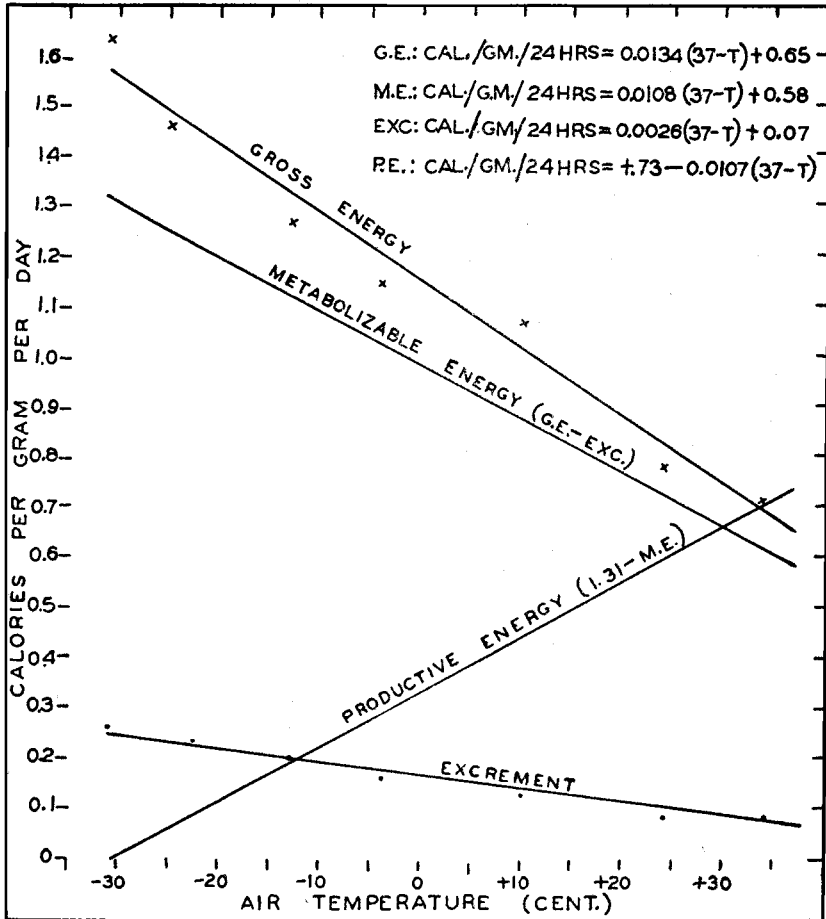


FIGURE 1. Energy intake of English sparrows at various temperatures.

The amount of energy lost in the excrement also increased with decreasing temperatures (Fig. 1). This would be expected from the larger amount of food ingested and from the increased rate of metabolism in the body generally. In addition, the percentage of energy intake that was lost in the excrement varied from 11.1 at 24° C. to

16.4 at -25° C. (Table 1), which indicated a less efficient digestion and a less complete utilization of food energy at the lower temperatures. It is well known for other animals that the completeness of digestion and absorption decreases as the mass of food ingested increases (Brody, 1945: 79-86).

The caloric value of the dried excrement varied slightly with temperature and inversely with the total excrement voided. Three separate determinations at each temperature of $+33^{\circ}$, $+10^{\circ}$, and -15° C. in 1946 gave figures of 4.20, 3.98, and 3.87 calories per gram, respectively. This decrease in caloric value of the excrement at lower temperatures was also found in two sets of determinations made in 1945 when a slightly different type of food was used. The excrement includes both unabsorbed food energy from the large intestine and unmetabolized energy excreted by the kidneys. Differences in the proportion of waste energy from the two sources may account for the change in the caloric value of the excrement at different temperatures.

The metabolizable energy, or the energy absorbed, increased as a straight line with decreasing temperatures (Fig. 1). This rate of increase (0.0108 cal./gm./degree C.) was significantly less than the rate of increase in gross energy (0.0134 cal./gm./degree C.), not only for statistical reasons, but also because of the lower percentage of digestion that occurs at lower temperatures. Kleiber and Daugherty (1934: 717) showed that the relationship between increase in metabolizable or available energy and drop in temperature was a curve. Actually, a straight line may be drawn with equal accuracy through their data which only cover a range from 40° to 21° C.

EFFECT OF WEIGHT

The average weight of all birds used in the experiments was 23.8 grams. There was no consistent difference in the average weight of birds at different air temperatures, although the birds at the highest temperature actually averaged the least in weight (Table 1). Thirteen to 17 measurements were made, at each temperature of -25° , -15° , $+10^{\circ}$, 22° , and 33° C., of the bird's weight in early morning before feeding commenced and in late afternoon after the last feeding had occurred. The average differences in these weights at the above temperatures were 1.76, 1.76, 1.08, 1.40, and 1.30 grams, respectively. Except for the low value of 1.08 grams at $+10^{\circ}$ C., there was evident a greater daily rhythm in weight correlated with the greater energy exchanges at lower temperatures. The food assimilation during the daylight period was sufficient to offset the energy requirements for the

entire 24 hours so that the average weight was maintained fairly constant throughout the experimental period.

Coefficients of correlation at -13° , $+10^{\circ}$, 24° , and 34° C. gave an average of -0.39 ± 0.26 between weights of individual birds and calories of metabolizable energy *per gram* per day. At -4° C. the correlation was positive, but only six records were available at this temperature. Although the negative correlation has low statistical reliability, it was in the direction expected, as the additional weight was largely inert fat and water.

The correlation between weight of bird and calories *per bird* per day averaged $+0.46 \pm 0.20$, except at -13° C. where a negative correlation was again based on only six records. This positive correlation indicated that, in addition to a larger amount of fat and water, heavier birds have also a greater rate of total energy exchange.

Calories per bird per day were plotted against individual bird weights at each temperature, and straight lines were drawn to the best fit of the data. No correlation between the two factors was evident at -13° C. At -4° , $+10^{\circ}$, $+24^{\circ}$, and $+34^{\circ}$ C. the slope of the lines indicated that per gram increase in weight there was an increase of 1.2, 0.5, 0.6, and 0.6 cal./bird/day. The average of these four values was 0.7 calories. In converting calories per gram per day into calories per bird per day, therefore, the following formula applies:
$$\text{cal./bird/day} = \text{cal./gm./day} \times [23.8 + 0.7 (\text{grams weight} - 23.8)].$$

EXISTENCE AND PRODUCTIVE ENERGY

Existence energy is the composite of energy requirements involved in maintaining standard or basal metabolism, in chemical heat regulation, in securing food and drink (economic maintenance) and in the heat increment or "specific dynamic action" of digestion and assimilation. *Productive energy* (economic production) is here defined as that portion of the metabolizable food intake over and above the energy requirements of existence at a minimum level of activity. Productive energy is not to be confused with net energy as used by Brody (1945: 34) who defined it as the metabolizable energy of food minus the heat increment of feeding, and which is available both for other factors in existence metabolism and for productive activities. It agrees, however, with net energy as used by Kleiber and Daugherty (1934: 703-704). Productive energy is of importance to the bird as this is the energy utilized for such activities as growth, locomotion, migration, reproduction, molt, and fat deposition.

In the present experiments, the birds maintained a constant weight that averaged about 5.4 grams less than they maintain under free

natural conditions out-of-doors (Baldwin and Kendeigh, 1938: 436-437). The exact reasons for the decrease in weight of birds brought indoors are not known but are doubtless related to close confinement in inside cages. The birds were free to move around in their small cages, but frequent observations indicated that movements were confined for the most part to those associated with feeding. Since no obvious work was performed except that of existence and since existence was held at a weight level just above that of starvation (Kendeigh, 1945: 220), it appeared that there was no appreciable productive energy involved and that the metabolizable energy in these experiments was equivalent to existence energy.

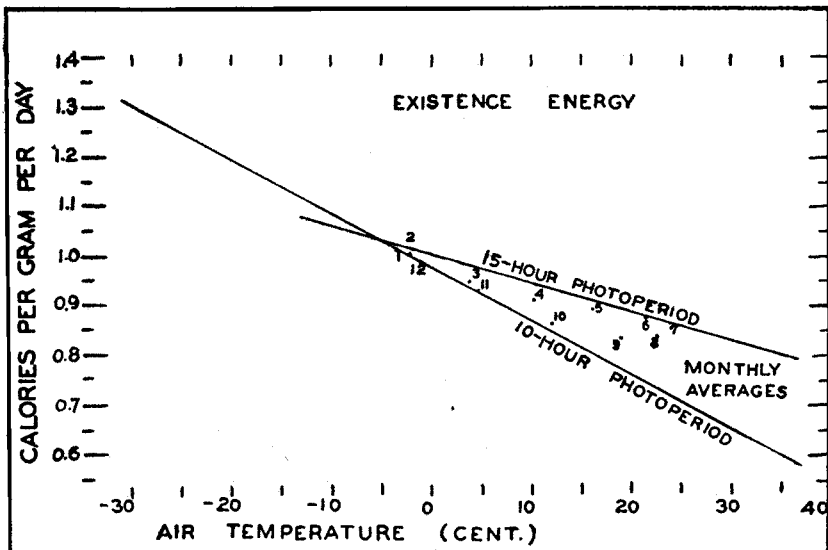


FIGURE 2. Energy requirements for existence of English sparrows at two photoperiods with monthly averages for Champaign, Illinois. Data for the 15-hour photoperiod are from Seibert (1949: 134).

It would be useful to know the maximum rate of food absorption of which the bird is capable. Under the stimulus of low air temperatures, existence energy at -31°C . becomes 114 per cent greater than at $+34^{\circ}\text{C}$. However, at temperatures below -20°C ., as mentioned above, a readjustment or acclimation of the energy balance appears necessary. At these extreme low temperatures, the rate of energy intake may be approaching, if not actually reaching, a maximum in the vicinity of 1.31 cal./gm./day. If this "maximum" energy intake could also be attained at higher temperatures, when demands for

purposes other than heat production required it, the productive energy would be the difference between the potential energy intake (1.31 cal./gm./day) and the energy required for existence (Fig. 1).

A factor, other than temperature, that is very important in affecting the energy resources of birds is the daily photoperiod (Fig. 2). Seibert (1949) has measured the energy intake for existence of English sparrows in a photoperiod of 15 hours of light per day. Comparisons can be made with the energy intake under the 10-hour photoperiod here reported. Energy utilization in terms of calories per gram per day generally was found to be greater under a 15-hour than a 10-hour photoperiod, but as temperatures dropped the difference between the two photoperiods diminished until it disappeared altogether below -5° C. Since birds have a higher rate of standard metabolism during the wakeful, light period and since they are also more active during the daylight period when they do all their feeding, a greater energy utilization during the long photoperiods would be expected.

SEASONAL CHANGES

Knowing the effect of air temperature and photoperiod upon the energy balance, it is possible to calculate what changes may occur in this balance from month to month under natural conditions out-of-doors (Table 2). Using the mean monthly temperature and photoperiod at Champaign, Illinois, corresponding calories per gram per day were interpolated in Figure 2. In order to use the formula above for converting these values to calories per bird per day, the average monthly weights of adult English sparrows living freely out-of-doors were taken from Figure 3, using the mean temperature of each month as the reference point. In this figure, the curve showing the relation between the average daily weight and air temperature is based on a similar curve given in Baldwin and Kendeigh (1938: 455) and on additional data obtained since that paper was published. Separate curves are given for young and adult birds since young birds, hatched during the summer, do not reach the weight of adult birds until autumn or winter. There are only scattered weights for adult birds during the warmer months, so the curve for adult birds is in part calculated from average differences between weights of adults and young during the summer season. Adult males tend to weigh slightly more than adult females during the autumn and winter, but this difference disappears during the breeding season, and the curve given is an average for the two sexes. It was necessary to determine monthly bird weights in this manner because a sufficient number of actual bird weights have not been taken during all months. Where

comparison was possible, calculated monthly weights agreed closely with weights of adult birds actually measured. The existence energy of adult birds was thus calculated and plotted for each month of the year (Fig. 4).

TABLE 2
VARIATIONS IN MONTHLY ENVIRONMENTAL CONDITIONS AND ENERGY BALANCE
OF ENGLISH SPARROWS AT CHAMPAIGN, ILLINOIS

Month	Mean tem- pera- ture (°C.)	Mean photo- period (hours, minutes)	Actual bird weight, grams	Effec- tive bird weight, ¹ grams	Existence energy		Cal./bird/day	
					Cal./ gm./ day	Cal./ bird/ day	Poten- tial energy	Produc- tive energy
January	-3.0	9 44	29.0	27.4	1.007	27.59	35.89	8.30
February	-2.0	10 41	28.9	27.4	1.002	27.45	35.89	8.44
March	+4.0	11 56	28.3	27.0	0.950	25.65	35.37	9.72
April	10.3	13 15	27.7	26.5	0.912	24.17	34.72	10.55
May	16.3	14 20	27.3	26.3	0.893	23.49	34.45	10.96
June	21.6	14 54	27.2	26.2	0.876	22.95	34.32	11.37
July	24.1	14 40	27.1	26.1	0.853	22.26	34.19	11.93
August	22.8	13 43	27.2	26.2	0.832	21.80	34.32	12.52
September	19.0	12 27	27.2	26.2	0.832	21.80	34.32	12.52
October	12.2	11 10	27.5	26.4	0.867	22.89	34.58	11.69
November	4.8	10 2	28.2	26.9	0.928	24.96	35.24	10.28
December	-0.9	9 27	28.8	27.3	0.982	26.81	35.76	8.95

¹ Effective bird weight = 0.7 (actual weight - 23.8) + 23.8 (see p. 119)

To calculate the maximum potential energy intake of birds each month, the value of 1.31 was substituted in the above formula for calories per gram per day. It remains to be demonstrated experimentally, however, that birds are capable of the same potential energy intake during the summer as under the stimulus of extreme cold in winter. The productive energy each month is simply the difference between the potential intake and the amount required for existence.

The curves of existence energy and productive energy are inverse to each other, and the potential energy intake is lower in summer than in winter, when calculated on the basis of lower summer weights of the birds (Fig. 4). Energy for existence is greatest in January when 77 per cent of the potential intake is used for this purpose. During August and September, temperatures are high and the photoperiod has shortened appreciably; thus, the energy cost of existence is at its lowest for the year. At this time it equals 64 per cent of the potential rate of energy intake. Energy requirements for existence increase more rapidly in the autumn than they decrease in the spring, since temperatures fall rapidly and the greater economy of energy during short, compared to long, photoperiods becomes lost. The difference between the minimum summer existence requirements and the winter

maximum is 5.79 cal./bird/day. This may represent the approximate increase of energy required for the bird's tolerance of mid-winter cold.

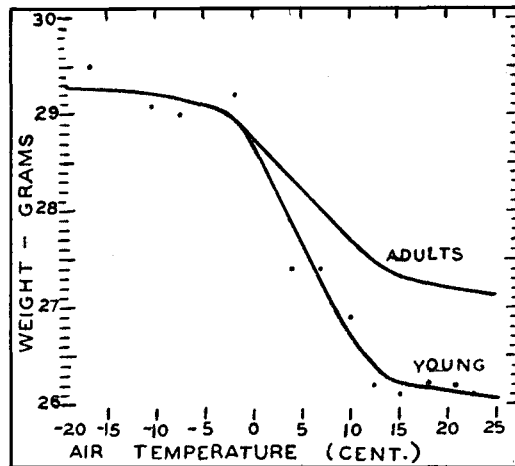


FIGURE 3. Correlation of variations in weight with temperature in English sparrows.

During the mid-winter month of January, the productive energy is 8.30 calories. Minimum existence requirements were determined in these experiments with the birds in small cages where they were hampered in movement and where food was abundantly available for the taking. Under free existence out-of-doors, food must be searched for, and this is often difficult during the winter. Furthermore, the birds seek out roosts at night, must be ever alert for enemies, and have social contacts with one another in flocks, all of which require energy and are involved in maintaining free existence. A surplus of energy is a safeguard also against the demands of short periods of extreme cold when temperatures fall far below the monthly mean. It may well be that the largest part of this productive energy during the winter is used up by the energy cost of living a free existence out-of-doors.

Productive energy increases from the mid-winter low of 8.30 in January to a maximum in August and September of 12.52 cal./bird/day, providing certain modifying factors balance each other. During the summer, food is abundant and easy to find, and it would seem that the energy cost of a free existence would be less. However, by summer the bird's plumage has become worn and thin and it is known that at comparable air temperatures the bird's resting metabolism is higher than during the winter (Kendeigh, 1934: 331-336). Although during

the summer the bird is not subject to the energy drain of severe cold, it is occasionally exposed to excessive heat. Protection is afforded by the evaporation of moisture from the respiratory system, which begins to increase noticeably at temperatures above 25° C. and becomes excessive above 35° C. (Kendeigh, 1944: 9). The evaporation of this

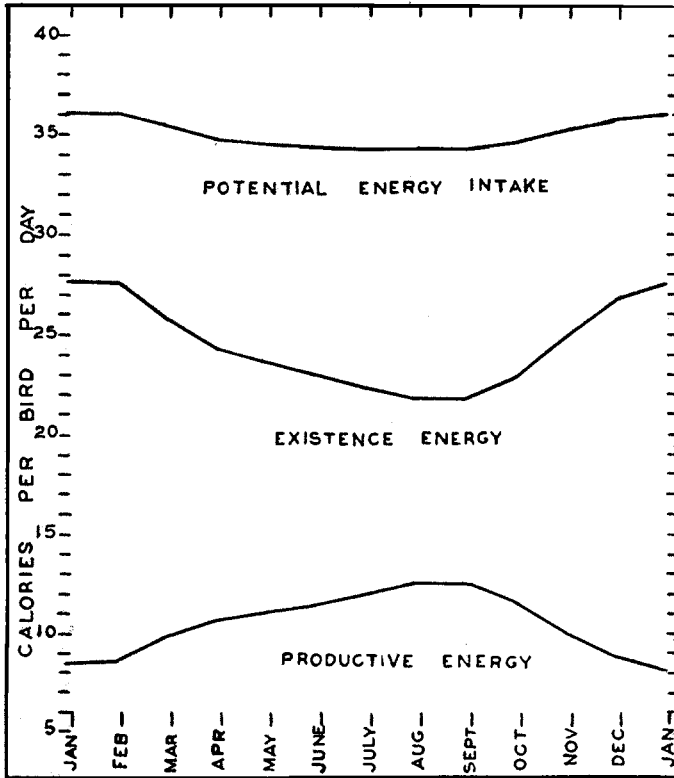


FIGURE 4. Variations in the energy balance of English sparrows throughout the year.

water utilizes energy from the bird, and this, together with the higher resting metabolism, may balance the greater ease in procuring food and shelter. Perhaps the increase of 4.22 cal./bird/day from winter to summer may be considered as the energy available for carrying on reproduction and molt. Nesting activities begin in March and are in full sway in April. During August and September, when potential productive energy is greatest, most birds are through nesting and are undergoing molt and renewal of feathers. All these activities are completed before the curve of productive energy starts to drop

rapidly in the autumn and before the winter regime begins. These theoretical calculations should be checked by actual measurements during each season of the year.

DISCUSSION

The present analysis of the energy balance in the English sparrow is based upon data obtained from their consumption of one kind of diet. The type of food consumed, its protein content, and its balance of essential elements and vitamins may affect the efficiency of its utilization as energy (Hamilton, 1939). The diet given the birds in these experiments, however, is similar to what they get normally out-of-doors, and one would not expect much dissimilarity in its energy utilization. According to Kalmbach (1940: 12, 23-24), 96.6 per cent of their natural food is mixed grain, grass and weed seeds, and fruit, in which cracked corn, picked up around barns and poultry yards, predominates, followed by oats, wheat, various sorghums, barley, buckwheat, and rice. The remainder of their food (3.4 per cent) is insects, which varies from a mere trace in their diet in January to 11.6 per cent in May.

Birds make the most efficient use of their productive energy by the spacing of their major activities so that they do not occur simultaneously or seriously overlap. In the yearly cycle of activities for birds, in general, occur spring migration, competition for territory (male), nest-building, egg-laying (female), incubation (mostly female), feeding of young, molting of feathers, fall migration, and tolerance of winter cold. One activity does not ordinarily begin until the previous one is completed, except that resistance to cold persists to a lessened extent in the spring after nesting begins. Severe weather during the spring will cause delay or a temporary inhibition of nesting activities.

The English sparrow is a permanent resident species, and it is probable that its curve of energy resources is representative of other species of permanent residents as well, although this should be tested. One would expect differences, both in the annual rhythm in energy requirements for existence and in productive energy, in migrant species that leave the region to breed further north or which breed in the region and winter farther south. With some species that go north to nest, Wolfson (1945: 109-121) has found a deposition of fat just before migration begins. At this time, the drain on energy resources for tolerating winter conditions is decreasing, and the energy demands of reproduction have not yet begun; thus, the unused productive energy that accumulates is simply stored in the body. In permanent, resident species, the productive energy is used, as soon as it occurs, in

initiating reproductive activities, and thus there is none available for storage as fat. Spring migration in migrant species may very well wait until this productive energy becomes available and may conceivably be induced by this change in the energy balance. The problem then is why certain species initiate reproductive activities when this productive energy becomes available and other species migrate instead. These different behavior patterns must have evolved over a long period of time in order to furnish each species the best relationship between seasonal physiological and environmental changes.

Seasonal variations in energy exchanges of birds in the tropics should be less pronounced and those in arctic regions more pronounced than those in temperate regions, but acclimatization may have modified their adjustments in various ways. Climatic factors other than temperature and photoperiod, especially rainfall which would affect the food supply, may modify the seasonal rhythm. Doubtless there are also taxonomic differences, as each species may work out its own adjustments based on its peculiar physiological potentialities.

CONCLUSIONS

1. Gross energy intake and metabolizable energy intake of English sparrows, on a voluntary diet just sufficient to give continual maintenance of weight in a photoperiod of 10 hours of light per day, increase as straight lines between $+ 34^{\circ}$ and $- 31^{\circ}$ C.

2. The increase in rate of metabolizable energy intake (0.0108 cal./gm./degree C.) with decreasing temperature does not keep pace with the increase in gross energy intake (0.0134 cal./gm./degree C.). This is due in part to an increasing percentage of energy loss in the excrement from the large intestine and kidneys.

3. Preliminary calculations indicate that birds during midwinter, living at liberty under natural conditions, have a potential, metabolizable energy intake of 35.89 cal./bird/day, of which 21.80 calories are equivalent to the minimum existence requirement under the most favorable summer conditions, 5.79 calories represent the increased energy cost of resistance to the winter cold, and the remainder (8.30 calories) is productive energy which is divided between the cost of maintaining a free existence and other miscellaneous activities.

4. During spring and summer, under free, natural conditions there may be small decrease in the potential energy intake and a larger decrease in energy required for existence. As a consequence, productive energy may rise to 12.52 cal./bird/day, an increase of 4.22 calories

over midwinter. This additional energy makes possible such other activities as migration, reproduction, molt, and fat deposition.

5. The initiation of migration, reproduction, molt, and other activities requiring considerable expenditures of energy may be conditioned by the availability of productive energy over and above that required for existence.

LITERATURE CITED

- BALDWIN, S. PRENTISS AND S. CHARLES KENDEIGH. 1938. Variations in the weight of birds. *Auk*, 55: 416-467.
- BRODY, SAMUEL. 1945. Bioenergetics and growth. (Reinhold Publ. Corp., New York), pp. i-xii + 1-1023.
- HAMILTON, TOM S. 1939. The heat increments of diets balanced and unbalanced with respect to protein. *Journ. Nutrition*, 17: 583-599.
- KALMBACH, E. R. 1940. Economic status of the English sparrow in the United States. U. S. Dept. Agr., Tech. Bull. 711: 1-66.
- KENDEIGH, S. CHARLES. 1934. The role of environment in the life of birds. *Ecol. Monog.*, 4: 299-417.
- KENDEIGH, S. CHARLES. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. *Ecology*, 22: 237-248.
- KENDEIGH, S. CHARLES. 1944. Effect of air temperature on the rate of energy metabolism in the English Sparrow. *Journ. Exp. Zool.*, 96: 1-16.
- KENDEIGH, S. CHARLES. 1945. Resistance to hunger in birds. *Journ. Wildl. Manag.*, 9: 217-226.
- KLEIBER, M. AND J. E. DOUGHERTY. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. *Journ. Gen. Physiol.*, 17: 701-726.
- LAPICQUE, LOUIS AND MARCELLE LAPICQUE. 1909. Consommations alimentaires d'oiseaux de grandeurs diverses en fonction de la température extérieure. *Compte Rendu Soc. Biol.*, 66: 289-292.
- LAPICQUE, LOUIS AND MARCELLE LAPICQUE. 1909a. Consommations alimentaires des petit oiseaux aux températures élevées. *Compte Rendu Soc. Biol.*, 67: 337-339.
- LARGUIER DES BANCELS, JEAN. 1902. De l'influence de la température extérieure sur la ration d'entretien chez l'oiseau. *Compte Rendu Soc. Biol.*, 54: 162-164.
- RÖRIG, G. 1905. Studien über die wirtschaftliche Bedeutung der insektenfressenden Vogel. *Arb. Biol. reichsanstalt Land- und Forstwirtschaft (Biol. Abteil. f. Land- und Forstwirtschaft am Kais. Gesundheits, Berlin)*, 4: 1-50.
- RUBNER, MAX. 1910. Über Kompensation und Summation von funktionellen Leistungen des Körpers. *Sitz. Ber. der Königlich Preuss. Akad. Wiss.*, 1910: 316-324.
- SEIBERT, HENRI C. 1949. Differences between migrant and nonmigrant birds in food and water intake at various temperatures and photoperiods. *Auk*, 66: 128-153.
- WOLFSON, ALBERT. 1945. The role of the pituitary, fat deposition, and body weight in bird migration. *Condor*, 47: 95-127.
- Department of Zoology and Physiology, University of Illinois,
Champaign, October 21, 1948.*