# SEASONAL VARIATION IN THE ENERGY BALANCE OF THE TREE SPARROW IN RELATION TO MIGRATION*

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THE present distribution of birds implies favorable adaptation to specific niches. Permanent residents are adjusted to changing seasonal conditions in a single locality, while migrant species are adjusted to winter and summer environments in different localities. Migratory birds may attain a more nearly uniform environment than if they were to stay in one locality throughout the year. Studies on the House Sparrow, *Passer domesticus* (Kendeigh, 1949; Seibert, 1949; Davis, 1955), have shown how a resident species adjusts to seasonal changes in temperature and photoperiod. Seibert (1949) emphasized the importance of photoperiod, because he believed that migratory birds cannot metabolize energy at a rate sufficient to tolerate the low, northern, winter temperatures on the short photoperiods. Lincoln (1950) suggested that birds migrate north in the spring primarily to avoid overcrowded conditions in the south; but such migrants also would secure longer photoperiods in the north and avoid the extreme high temperatures of southern latitudes. Since Tree Sparrows, *Spizella arborea,* have been successfully kept outdoors throughout the summer in Illinois, several hundred miles south of their breeding range (Weise, 1956), an investigation was undertaken to trace the annual cycle of certain physiological changes in this species to determine whether migration is necessary to maintain a favorable energy condition throughout the year.

## METHODS

### *Effect of Constant Temperature*

To establish rates of energy intake at different temperatures and photoperiods, experiments under constant conditions were carried out in Champaign, Illinois, during 1956–1959 inclusive, and at Fort Churchill, in northern Manitoba, during the summers of 1956 and 1957.

Illinois birds were caught from large flocks with traps or mist nets from November through March. Churchill birds were trapped on their nests from 28 June to 17 July at the height of the nesting season. Sex was determined by autopsy at the end of the experiments. Birds

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captured during the first winter were placed in large cages or in large aviaries. There was a 50 per cent mortality within the first two weeks, apparently due either to the inability of some birds to locate food or to the less-aggressive birds being kept from food by their more-dominant cagemates. All birds captured later were placed in small, individual experimental cages measuring 6 x 10 x 10 inches and made of one-half-inch-mesh hardware cloth. Mortality decreased to 27 per cent. Once they were adjusted to captivity and food, birds not currently being used in experiments could be transferred, in groups of four, into the large cages outdoors, with only occasional mortality.

Methods of measuring food consumption and excrement loss, initiated by Kendeigh (1949) and subsequently employed by Seibert (1949) and Davis (1955), were followed. Metabolized energy was obtained by subtracting the caloric energy of the excreta from that of food consumption *(gross energy intake)*. This difference represents *existence energy,* when birds maintain constant weight and the only energy demands are for standard metabolism, chemical heat regulation, specific dynamic action of food assimilation, and the securing of food and water. *Productive energy* is the energy metabolized beyond that required for existence. The potential productive energy at each temperature may be calculated by subtracting existence energy from the maximum amount of energy that can be metabolized at that temperature.

Coarsely ground food, University of Illinois baby chick mash No. 521, used by previous investigators and in the present study, was ground in a mill so that all particles would pass through one-sixteenth-inch-mesh window screening. Reduction in particle size facilitated sorting of excrement from unused food and insured against selection by the birds of specific components in the mixture.

Prior to experimentation, birds were confined in individual experimental cages for from one week to 10 days. In addition, from three to five days were allowed for birds to adjust to experimental temperatures. Metabolic data were collected only in the periods that birds maintained relatively constant weight; fluctuations of as much as 0.5 grams were allowed, since eating or voiding before weighing could change the weight by that amount. In order to minimize diurnal differences in weight, birds were always weighed at the same time of the day.

Birds were weighed and checked for fat and molt condition every three to five days. Fat classes are adapted from Weise (1956):

| | | |
|---|---|---|
| Class 1 | No visible fat. | No fat visible in the furcular depression or on the abdomen. |
| Class 2 | Little fat. | Fat lining the furcular depression, none on the abdomen. |
| Class 3 | Medium fat. | Fat filling the furcular depression, visible fat in the abdomen between the intestinal folds. |
| Class 4 | Heavy fat. | Furcular depression bulging with fat; peritoneal fat filling in between the intestinal folds. |
| Class 5 | Very heavy fat. | Furcular depression bulging with fat; abdominal region bulging with peritoneal and subcutaneous fat. |

An index of molt was obtained by use of the following scale: 0–2, little molt; 3–6, moderate molt; 7–9, heavy molt; 10–25, very heavy molt. Sheathed feathers on the body were added to those on the cage floor to give the total molt value where one molt unit was assigned for each primary, secondary or retrix; one unit for every five trunk feathers; and one unit for every 10 small head, neck, or throat feathers.

The cages were cleaned at the end of each three- to five-day metabolic run. All remaining food and excrement were placed in a drying oven at 83° to 100° C for from three to six days. The dried food and excrement were emptied into the sieve of window screening. A light rubbing of the contents with the palm of the hand usually was sufficient to effect complete separation of food from excrement. Any persistent food particles in the sieve were removed by hand. The dry weights of food and excrement were recorded to the nearest hundredth gram on a triple-beam balance immediately after sorting. The sorting and weighing process lasted two minutes or less per sample, hence there was little or no resorption of moisture.

The caloric value for each 100-pound bag of food measured in a Parr adiabatic oxygen bomb calorimeter varied between 4.437 and 4.449 kcal. per gram dry weight. Moisture in the food varied from 10.2 to 16.6 per cent water. Values used in the calculations were those of the particular batch of food being used. The amount of food given the birds varied with the temperature from 50 grams wet weight at 39° C to 100 grams wet weight at —30° C for three-day intervals. Water was available ad libitum; snow or frost was provided at temperatures below freezing.

Three large cabinets, one small refrigerator unit, one kitchen refrigerator, and a specially constructed "hot box," all thermostatically controlled, provided the necessary range of temperatures. The first four units were utilized in Illinois, the latter two at Churchill. Humidity varied from 23 to 33 per cent in the high-temperature cabinet, from 73 to 85 per cent in the medium-temperature cabinet, from 70 to 87 per cent in the low-temperature cabinet, and from 74 to 76 per cent in the small refrigerator unit. The kitchen refrigerator had a high relative humidity; the "hot box" was extremely dry. No attempt was made to regulate humidity, since the effect of air moisture on temperature regulation and metabolism is probably important only at much higher humidities at high temperatures (Salt, 1952; Wallgren, 1954).

Air movement in the medium-temperature cabinet was measured with an anemotherm. Measurements taken with a probe inside the experimental cages averaged 21.3 feet per minute. No corrections have been made for the effect of air movement. There was no forced-air movement in the high- or low-temperature cabinets, and only a slight air flow in the small unit, kitchen refrigerator, and "hot box."

Light was regulated by automatic time switches to correspond with the amount of time birds were observed to be active. Birds at Churchill were active for 19 hours each day during June (2:30 A.M. to 9:30 P.M.), but the time between sunrise and sunset is only 18.01 hours. Astronomical twilight lasts 5:31 hours. Hence birds are active for only one hour or 18.2 per cent of the astronomical twilight period (approximately 67 per cent of civil twilight). Assuming that the same relative amount of the astronomical twilight period is utilized in all months, the effective photoperiod consists of the average number of hours between sunrise and sunset per month plus 18.2 per cent of the monthly mean astronomical twilight period. Therefore, the 10-hour photoperiod, regulated from 7 A.M. to 5 P.M., corresponds with the minimum effective winter photoperiod in Illinois. Fifteen-hour photoperiod (6 A.M. to 11 P.M.) represents the average effective summer photoperiod in Illinois, 19-hour photoperiod (2:30 A.M. to 9:30 P.M.), the maximum effective summer photoperiod at Churchill.

Birds were only rarely shifted from one photoperiod to another, and in these cases, the photoperiod was changed gradually over at least three days. The amount of light varied from 65 lux (6.0 foot-candles) in the high-temperature cabinet to 74 lux (6.8 foot-candles) in the small unit, 110 lux (10.2 foot-candles) in the medium-temperature cabinet and 112 lux (10.3 foot-candles) in the low-temperature cabinet. The kitchen refrigerator contained one 100-watt incandescent bulb; the "hot box" had two 40-watt fluorescent lamps.

Burger (1949) states that 10 foot-candles (108 lux) is sufficient light for normal winter sperm production in House Sparrows. It is well known that birds may be normally active under natural conditions at much lower intensities. Light measurements were made with a Weston Illumination Meter model No. 603, using a viscor filter that records the various wave lengths in proportion to the reception of the human and probably also bird eye (Walls, 1942: 497–504).

### *Effect of Fluctuating Temperatures*

As a control for constant condition experiments, 36 birds were kept outdoors for varying lengths of time in Illinois and at Churchill. Birds were placed in small, individual experimental cages, provided with food and drink, and in all ways treated like the birds under constant conditions. Birds were weighed, checked for molt and fat, the cages cleaned, and metabolism measured every three to six days from February to

August 1956, and February to April 1958, in Illinois, and during late July and August of 1956, and August 1957, in Churchill.

Illinois birds were kept in an aviary protected from precipitation and except in the early morning hours shielded from direct sunlight. The cages were partially protected from the wind by the walls of a building on the north and west and by vines that covered the aviary in the summer. All temperatures were obtained in summary form from the Urbana weather station, located about 100 yards from the aviary.

During the summer of 1956, Churchill birds were kept on a shelf in an otherwise abandoned building, 12 x 18 x 10 feet. Windows on all sides were fitted with screens; but due to high winds, it was necessary to cover many of the windows on the north, east, and west sides with translucent plastic screening. Daily temperatures were recorded with a maximum-minimum thermometer and averaged slightly higher than at the Fort Churchill weather station, about one-quarter mile distant. In 1957, a wooden shelter, 6 x 4 x 6 feet, was constructed on the roof of the Defence Research Northern Laboratory building. Birds were kept on a shelf and protected on all sides but the south. An overhanging roof prevented rain from entering the cages. Temperatures recorded with a maximum-minimum thermometer did not differ from those at the weather station.

Air temperature fluctuated from —14° to +26° C during the course of the measurements in Illinois. The photoperiod rose from 11:12 in February to a maximum of 15:39 in June, then fell to 14:23 in August.

Statistical procedures are taken from Ostle (1954) and Snedecor (1956). Unless otherwise indicated, a probability level of 0.01 was required for comparisons to be considered significant.

## RESULTS

### *Effect of Constant Temperature*

*Weight.* Body weights declined after capture, but increased to their original level before experimentation. There were no significant differences in weights of experimental birds one to three weeks before starting their first experimental run and average monthly weights of birds shot in the field and weighed a few hours after death (Table 1). Due to the large individual variation in minimal weight, minor variations in average weight and fat classes from temperature to temperature or between photoperiods are not significant (Table 2). Minimal weight is the lowest, not the average, body weight that a bird maintained for at least two days while at a fat class of 1.

TABLE 1

WEIGHTS OF TREE SPARROWS CAPTURED ALIVE AND WEIGHED ONE TO THREE WEEKS BEFORE EXPERIMENTATION COMPARED WITH WEIGHTS AND FAT CLASSES OF WILD BIRDS THAT WERE SHOT

| | | | *Captured* | | | *Shot* | |
|---|---|---|---|---|---|---|---|
| *Month* | *Sex* | *No. of birds* | *Av. wt. (gms.)* | *Sex* | *No. of birds* | *Av. wt. (gms.)* | *Av. fat class* |
| Nov. | M | 4 | 19.2 | M | 7 | 17.8 | |
| | F | 1 | 18.2 | F | 7 | 16.8 | |
| | M+F | 5 | 18.9 | M+F | 14 | 17.3 | 2.9 |
| Dec. | M | 3 | 19.3 | M | 10 | 19.2 | |
| | F | 3 | 17.3 | F | 7 | 17.7 | |
| | M+F | 6 | 18.3 | M+F | 17 | 18.6 | 2.8 |
| Jan. | M | 9 | 19.4 | M | 5 | 19.5 | |
| | F | 5 | 17.4 | F | 4 | 18.3 | |
| | M+F | 16 | 18.6 | M+F | 9 | 18.9 | 3.3 |
| Feb. | M | 11 | 19.2 | M | 16 | 20.1 | |
| | F | 11 | 17.9 | F | 10 | 18.8 | |
| | M+F | 23 | 18.5 | M+F | 26 | 19.6 | 3.8 |
| Mar. | M | 1 | 20.6 | M | 9 | 19.6 | |
| | F | — | — | F | 4 | 19.3 | |
| | M+F | 1 | 20.6 | M+F | 13 | 19.5 | 3.6 |
| June | M | — | — | M | 19 | 18.7 | |
| | F | 1 | 17.7 | F | 20 | 19.3 | |
| | M+F | 1 | 17.7 | M+F | 39 | 18.9 | 2.9 |
| July | M | 7 | 16.7 | M | 14 | 18.6 | |
| | F | 9 | 17.9 | F | 3 | 17.2 | |
| | M+F | 16 | 17.4 | M+F | 17 | 18.4 | 2.1 |
| Aug. | M | — | — | M | 4 | 18.7 | |
| | F | — | — | F | 1 | 15.5 | |
| | M+F | — | — | M+F | 5 | 18.1 | 1.6 |

Summer birds kept in captivity in Illinois were fatter than either winter birds or summer birds at Churchill. Experiments in 1958 at 15 and 19 hours in Illinois were carried out during the summer, and therefore these two photoperiods had birds of higher weights than did the 10-hour winter group (Table 2). All 1959 birds were placed at 10 hours and —4° C immediately upon capture in December. Experiments were conducted from January to May.

As temperature was lowered toward —30° C, fat decreased slowly until a minimum fat class of 1 was reached at the lowest temperature (Tables 2 and 3). Because birds with heavier minimal weights were by chance used at lower temperatures, the mean experimental weights did not decline as would be expected. However, the per cent difference between the average minimal weight and the average experimental

TABLE 2

BODY WEIGHTS, FAT CLASSES AND MOLT VALUES OF TREE SPARROWS UNDER CONSTANT CONDITIONS

| *Temp. (° C)* | *No. birds* | *Minimal wt. gms. ± S.E.* | *Av. wt. gms. ± S.E.* | *Per cent diff.* | *Fat class* | *Molt units* |
|---|---|---|---|---|---|---|
| 10-hour photoperiod (1956–1958) | | | | | | |
| −29.6 | 4 | 17.2 ± 0.46 | 18.5 ± 0.69 | 7.0 | 1.0 | 0.5 |
| −24.2 | 5 | 16.8 ± 0.30 | 17.9 ± 0.53 | 6.1 | 1.0 | 0.8 |
| −22.0 | 10 | 16.8 ± 0.44 | 18.5 ± 0.51 | 9.2 | 1.6 | 0.1 |
| −15.0 | 12 | 17.0 ± 0.39 | 18.7 ± 0.40 | 9.1 | 1.6 | 0 |
| −4.0 | 12 | 17.2 ± 0.29 | 18.8 ± 0.43 | 8.5 | 2.8 | 0 |
| +4.0 | 11 | 16.7 ± 0.34 | 18.7 ± 0.54 | 10.7 | 1.6 | 0 |
| +18.7 | 3 | 16.8 | 19.0 ± 0.95 | 11.6 | — | — |
| +30.0 | 11 | 16.0 ± 0.31 | 18.9 ± 0.48 | 15.3 | 2.2 | 0.4 |
| +35.0 | 6 | 15.5 ± 0.31 | 18.8 ± 0.59 | 17.6 | 3.2 | 0 |
| +37.0 | 7 | 15.3 ± 0.33 | 17.3 ± 0.57 | 11.6 | 2.9 | 0 |
| +38.0 | 6 | 15.5 ± 0.31 | 16.4 ± 0.37 | 5.5 | 2.6 | 0.3 |
| +39.0 | 6 | 15.5 ± 0.31 | 15.8 ± 0.34 | 1.9 | 2.2 | 0.3 |
| (1959) | | | | | | |
| −4.0 | 10 | — | 18.5 ± 0.39 | — | 1.9 | 0 |
| 15-hour photoperiod (1956–1958) | | | | | | |
| −27.6 | 7 | 16.2 ± 0.35 | 19.1 ± 0.74 | 15.2 | 1.7 | 0 |
| −15.0 | 9 | 16.8 ± 0.37 | 20.7 ± 0.71 | 18.8 | 3.0 | 0 |
| +4.0 | 11 | 17.2 ± 0.17 | 19.9 ± 0.50 | 13.6 | 3.0 | 0.1 |
| +30.0 | 8 | 17.4 ± 0.19 | 21.1 ± 0.74 | 17.5 | 4.1 | 0.1 |
| +37.0 | 6 | 15.5 ± 0.31 | 16.9 ± 0.49 | 8.3 | 3.7 | 0.1 |
| +39.5 | 6 | 15.5 ± 0.31 | 16.1 ± 0.52 | 3.7 | 3.4 | 0.9 |
| (1959) | | | | | | |
| −4.0 | 10 | — | 18.7 ± 0.39 | — | 2.8 | 0 |
| −4.0 | 6 | — | 17.8 ± 0.68 | — | 1.4 | 20.8 |
| 19-hour photoperiod (Illinois) (1956–1958) | | | | | | |
| −29.0 | 4 | 17.2 ± 0.19 | 19.3 ± 0.43 | 10.9 | 1.0 | 0.8 |
| −25.0 | 3 | 17.9 ± 0.45 | 18.6 ± 1.34 | 9.1 | 1.5 | 0 |
| −15.0 | 11 | 17.1 ± 0.17 | 19.0 ± 0.60 | 10.0 | 1.6 | 0 |
| +8.0 | 8 | 16.7 ± 0.43 | 20.1 ± 0.74 | 16.9 | 3.2 | 0.3 |
| +30.0 | 10 | 16.6 ± 0.35 | 22.1 ± 0.71 | 24.9 | 4.9 | 0.1 |
| (1959) | | | | | | |
| −4.0 | 10 | — | 20.2 ± 0.74 | — | 1.2 | 0 |
| −4.0 | 9 | — | 18.0 ± 0.63 | — | 2.0 | 4.9 |
| 19-hour photoperiod (Churchill) (1956–1957) | | | | | | |
| +7.8 | 13 | 15.8 ± 0.29 | 18.3 ± 0.34 | 13.7 | 1.1 | 5.1 |
| +32.1 | 13 | 15.8 ± 0.29 | 17.2 ± 0.35 | 8.1 | 1.1 | 3.3 |

TABLE 3

FAT CLASSES OF INDIVIDUAL TREE SPARROWS MAINTAINED INDOORS AT DIFFERENT CONSTANT TEMPERATURES

| *Temp. (° C)* | *Band number of bird*<br>*04054* | *04074* | *04045* | *04056* | *04050* | *04066* |
|---|---|---|---|---|---|---|
| —30 | 1 (Mar.)* | 1 (Mar.) | 1 (Feb.) | — | — | — |
| —24 | 1 (Mar.) | 1 (Mar.) | — | — | — | — |
| —22 | 1 (Feb.) | 1 (Mar.) | — | 2 (Mar.) | 2 (Mar.) | — |
| —15 | 2 (Feb.) | — | 2 (Jan.) | 2 (Feb.) | 1 (Jan.) | — |
| —4 | — | 2 (Feb.) | 3 (Dec.) | — | — | — |
| +4 | 2 (Jan.) | — | 2 (Dec.) | 2 (Jan.) | — | — |
| +8 | — | 5 (June) | 4 (June) | 4 (June) | 2 (June) | 3 (June) |
| +30 | — | — | 5 (May) | 5 (May) | 3 (May) | 5 (May) |
| +35 | — | — | — | — | — | 4 (Feb.) |
| +37 | — | — | — | — | 1 | 3 (Mar.) |
| +38 | — | — | — | — | — | 3 (Mar.) |
| +39 | — | — | — | — | — | 3 (Apr.) |

* Month of observation.

weight of birds at 10 and 19 hours decreased at lower temperatures (Table 4). Because vernally fattened birds were brought in from outdoors and placed immediately at low temperatures, this decrease did not occur at 15 hours.

Although male Tree Sparrows weigh more than females (Table 1), their energy requirements showed no significant differences. Therefore, all data for both sexes are combined in the following analyses.

Heavier birds require more energy than lighter at temperatures from —15° to —30° C, but not at 30° C (Table 4). This is apparently due to the added adipose tissue in heavier birds, since at —15° and —25° to —30° C there is a significant increase in metabolism and no significant difference in minimal weights. Odum and Perkinson (1951) have also shown that in White-throated Sparrows, *Zonotrichia albicollis,* lean weights remained approximately the same at all seasons, and seasonal changes in weight were the result of fat deposition and utilization. The metabolism of adipose tissue (exclusive of brown fat) is considerably below that of other body tissues (Shapiro and Wirtheimer, 1956); thus the extra energy utilization of heavier birds appears to be correlated with the added amount of fat.

The calories metabolized per gram mean body weight were not significantly different within each temperature range (Table 4). Therefore, expression of energy values in terms of the whole bird is justified only when the bird's average experimental weights are approximately the same at each temperature condition.

### TABLE 4

### RELATION OF BODY WEIGHT TO METABOLISM OF TREE SPARROWS UNDER CONSTANT CONDITIONS

| *Av. exp. wt.* | *No. of birds* | *Minimal wt. (gms.) mean ± S.E.* | *P* | *Metabolized energy* kcal./bird/day ± S.E. | *P* | *kcal./gm. av. wt./day ± S.E.* | *P* |
|---|---|---|---|---|---|---|---|
| *−25° to −30°C* | | | | | | | |
| 18.0 | 17 | 16.6 ± 0.21 | >0.2 | 26.89 ± 0.67 | >0.001 | 1.50 ± 0.05 | >0.2 |
| 20.6 | 6 | 17.3 ± 0.19 | | 34.23 ± 0.87 | | 1.64 ± 0.04 | |
| *−15°C* | | | | | | | |
| 16.4 | 4 | 15.6 ± 0.48 | >0.05 | 22.38 ± 0.99 | >0.1 | 1.36 ± 0.06 | >0.9 |
| 18.9 | 21 | 17.2 ± 0.23 | >0.5<br>>0.2 | 25.49 ± 0.58 | >0.05<br>>0.01 | 1.35 ± 0.04 | >0.3<br>>0.05 |
| 22.2 | 7 | 16.9 ± 0.26 | | 28.53 ± 0.86 | | 1.28 ± 0.02 | |
| *+30°C* | | | | | | | |
| 18.4 | 17 | 16.1 ± 0.27 | >0.5 | 10.77 ± 0.32 | >0.5 | 0.57 ± 0.02 | >0.2 |
| 23.0 | 12 | 17.2 ± 0.18 | | 11.28 ± 0.55 | | 0.49 ± 0.03 | |

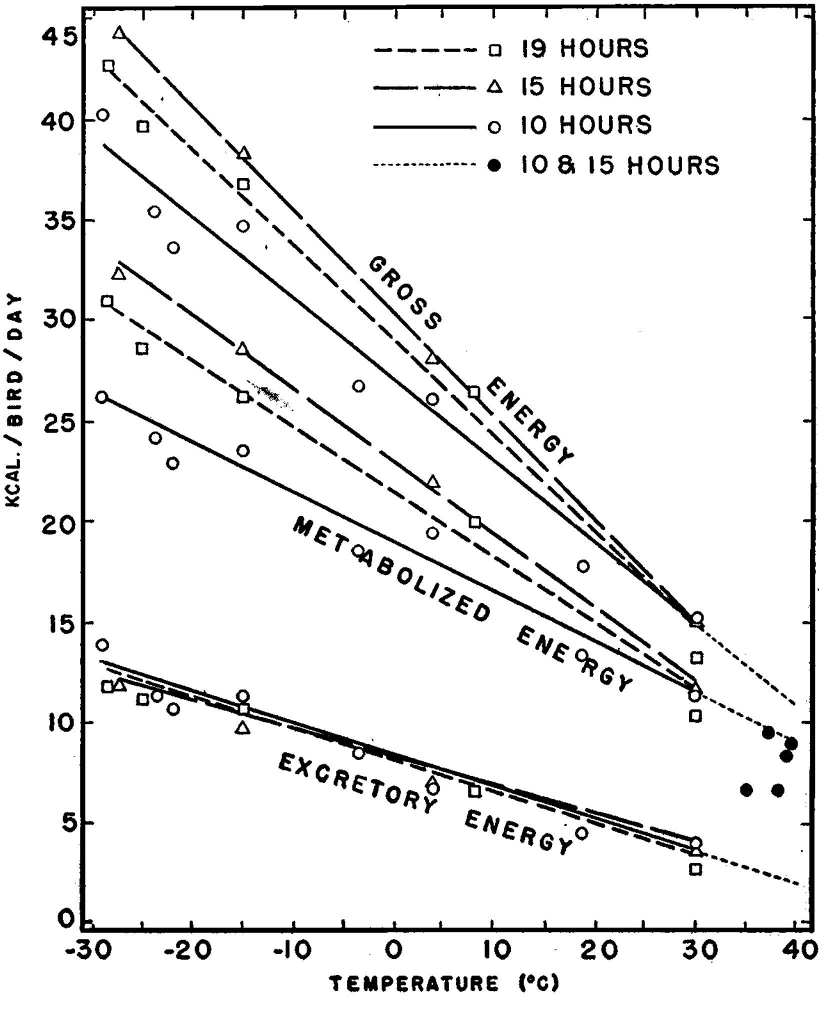

**Figure 1.** Energy balance of Tree Sparrows at 10-, 15- and 19-hour photoperiods under constant conditions. The following formulae apply: gross energy in kcal./bird/day: 10 hours, 28.73-0.406T° C; 15 hours, 30.19-0.507T° C; 19 hours, 28.68-0.428T° C. Excretory energy: 10 hours, 8.02-0.159T° C; 15 hours, 7.62-0.141T° C; 19 hours, 7.61-0.152T° C. Metabolized energy: 10 hours, 18.57-0.247T° C; 15 hours, 22.57-0.366T° C; 19 hours, 21.07-0.330T° C. Lines between 30° and 39.5° C are extensions of regression lines for the 10-hour photoperiod.

*Gross energy intake.* Like earlier investigators (Kleiber and Dougherty, 1934; Kendeigh, 1949; Seibert, 1949; Davis, 1955; Steen, 1957), I found (Figure 1) that food intake increases with decreasing temperature below the point or zone of thermoneutrality.

*Excretory energy.* Energy lost in the excrement is a combination of intestinal and renal wastes. Kendeigh (1949: 118) found that the energy per gram excrement in House Sparrows increased with lower

TABLE 5

METABOLIZED ENERGY OF TREE SPARROWS UNDER CONSTANT CONDITIONS

| *Temp. (° C)* | *Month of experiment* | *No. of birds* | *Total days feeding* | *Metabolized energy kcal./bird/day ± S.E.* |
|---|---|---|---|---|
| 10-hour photoperiod (1956–1958) | | | | |
| −29.6 | Mar. | 4 | 21 | 26.22 ± 1.07 |
| −24.2 | Mar. | 5 | 17 | 24.19 ± 0.69 |
| −22.0 | Mar. | 10 | 60 | 22.91 ± 0.36 |
| −15.0 | Jan., Feb. | 12 | 91 | 23.55 ± 0.74 |
| −4.0 | Dec. | 12 | 80 | 18.52 ± 0.95 |
| +4.0 | Dec. | 11 | 112 | 19.33 ± 0.80 |
| +18.7 | Apr. | 3 | 39 | 13.12 ± 1.10 |
| +30.0 | Dec., Feb. | 11 | 90 | 11.14 ± 0.50 |
| (1959) | | | | |
| −4.0 | Jan. | 10 | 90 | 18.58 ± 0.29 |
| 15-hour photoperiod (1956–1958) | | | | |
| −27.6 | July | 7 | 49 | 32.59 ± 1.30 |
| −15.0 | July | 9 | 93 | 28.35 ± 0.55 |
| +4.0 | May, June | 11 | 107 | 20.84 ± 0.60 |
| +30.0 | May | 8 | 77 | 11.67 ± 0.35 |
| (1959) | | | | |
| −4.0 | Jan. | 10 | 90 | 20.46 ± 0.59 |
| −4.0 | May | 6 | 54 | 24.55 ± 0.75 |
| 19-hour photoperiod (Illinois) (1956–1958) | | | | |
| −29.0 | June | 4 | 29 | 30.79 ± 1.33 |
| −25.0 | June | 3 | 12 | 28.49 ± 1.85 |
| −15.0 | May | 11 | 93 | 26.13 ± 0.66 |
| +8.0 | June | 8 | 76 | 19.94 ± 0.36 |
| +30.0 | May | 10 | 92 | 10.25 ± 0.53 |
| (1959) | | | | |
| −4.0 | Apr. | 10 | 90 | 23.59 ± 0.34 |
| −4.0 | May | 9 | 81 | 24.88 ± 0.73 |
| 19-hour photoperiod (Churchill) (1956–1957) | | | | |
| +7.8 | July, Aug. | 13 | 133 | 21.01 ± 1.38 |
| +32.1 | July, Aug. | 13 | 113 | 13.11 ± 0.48 |

temperatures. Seibert (1949: 135) showed that the least amount of energy per gram excrement in the Junco, *Junco hyemalis,* White-throated Sparrow, and House Sparrow was produced at 22° C. Davis (1955: 393), however, concluded that, in 46 House Sparrows, there was "no direct relationship between temperature and per gram fecal energy." In the present study, involving 136 calorimetric determinations of 59 birds at 10- and 19-hour photoperiods and from —29.6° to +39° C, no significant variation of calories per gram excrement with temperature could be demonstrated. The average of all determinations was 3.735 kcal./gram.

Decreasing temperature caused increased energy loss in the excrement, but there were no significant differences between photoperiods (Figure 1).

*Metabolized energy.* The differences between photoperiods in the regression lines for the daily amount of metabolized energy were not statistically significant (Table 5 and Figure 1). Metabolized energy values at Churchill (Table 5) were high, since the birds were in molt (Table 2) and probably had moderate nocturnal activity. Other Tree Sparrows kept outdoors during the time the constant-temperature experiments were run showed nightly activity of three intervals out of 20 per hour for the five-hour night.

*Efficiency of food utilization.* The Tree Sparrow shows a steady rise in efficiency with temperature, best expressed with the 10-hour birds (65 per cent at —28°, 77 per cent at +37° C). The percentage of food digested likewise increases from short to long photoperiods (at 19 hours: 72 per cent at —29° C, 79 per cent at +35° C).

In studying winter-acclimated House Sparrows, both Seibert (1949) and Kendeigh (1949) showed steady increases in efficiency from low to high temperatures (84 per cent at —31°, 92 per cent at +34° C), and the 15-hour birds were more efficient than 10-hour birds. Davis (1955), in studying summer-acclimated birds, discovered an increase in efficiency only up to 18° C and a sudden drop above this (75 per cent at 0°, 88 per cent at 18°, 74 per cent at 26° C). Again the 15-hour birds were more efficient than the 10-hour group. He (p. 395) explained that this 18° C temperature approximated the environmental temperature (19.4° C) from May through October to which the birds were naturally adapted.

*Tolerance of low temperature.* The limit of tolerance to low temperature (when only 50 per cent of the birds were able to survive and maintain constant weights for a period of nine days) was determined for Tree Sparrows in Illinois. This limit for 10-hour winter birds (4 out of 9 survived) was —28° C; for summer birds —27.6° (5 out of 10) on 15-hour photoperiods and —25° C (3 out of 6) on 19-hour photoperiods. The statistically insignificant reduction in tolerance of the 19-hour birds is correlated with molt taking place at the time. Apparently, the heat released with nightly activity in the 15- and 19-hour birds did not extend the lower limit of temperature tolerance. There is no appreciable seasonal change in ability to tolerate low temperatures; the lower limit for the species lies near —28° C. These results are quite different from those for the permanent resident House Sparrow, where the lower limit of tolerance of —31° C in winter decreases to 0° C in the summer (Davis, 1955).

TABLE 6

Metabolism of Tree Sparrows at High Constant Temperatures during February and March (37° C Represents Averages of 10- and 15-Hour Photoperiod, 30°, 35°, 38°, 39° Are 10 Hours, 39.5° C Is 15 Hours)

| *Temp. (° C)* | *No. birds* | *Gross energy kcal./bird/day ± S.E.* | *Excretory energy kcal./bird/day ± S.E.* | *Metabolized energy kcal./bird/day ± S.E.* |
|---|---|---|---|---|
| 30.0 | 11 | 15.18 ± 0.65 | 4.03 ± 0.22 | 11.14 ± 0.50 |
| 35.0 | 6 | 9.06 ± 0.60 | 2.30 ± 0.22 | 6.76 ± 0.40 |
| 37.0 | 7 | 12.25 ± 0.50 | 2.96 ± 0.03 | 9.29 ± 0.42 |
| 38.0 | 6 | 8.78 ± 0.45 | 2.07 ± 0.15 | 6.72 ± 0.31 |
| 39.0 | 6 | 10.95 ± 0.70 | 2.57 ± 0.13 | 8.39 ± 0.54 |
| 39.5 | 6 | 12.04 ± 0.56 | 3.12 ± 0.19 | 8.92 ± 0.43 |

*Experiments at high air temperatures.* Exploratory experiments at high air temperatures, 35° to 39.5° C on 10- and 15-hour photoperiods, were run in order to determine upper lethal limits for Tree Sparrows. The same six birds were used in all experiments; one additional bird was used at 10 hours and 37° C. Although the birds used at high temperatures by chance had lower minimal weights, fat values and weights declined at high temperatures (Table 2). Molt did not increase but remained between 0 and 0.9 units at all temperatures.

Metabolism decreased abruptly between 30° and 35° C and then fluctuated to 39.5° C (Table 6 and Figure 1). Although a thermoneutral zone was not demonstrated, the critical temperature is assumed to be in the vicinity of 40° C.

Upper limits of tolerance were not determined. However, when the temperature in the cabinet accidentally rose to 45° C for about two hours, all five of the remaining birds survived the temperature shock. The following day the temperature rose to 47° C for one hour. Four birds were in heat shock; their breathing rates averaged 300/minute, even after the temperature in the cabinet had dropped to 40° C. These birds died, although they had been placed while alive at room temperature and given water. Weights taken immediately after death averaged 14.1 grams (1.1 grams below average minimal weights), indicating excessive water loss.

### *Effect of Fluctuating Temperature*

*Gross energy.* Gross energy (G.E.) intake decreased linearly with increasing temperature (G.E. = 25.89 kcal./bird/day — 0.254T° C). The slope of the line is not as steep as the gross energy line under constant temperature conditions. The two lines cross at about 9° C and diverge to become significantly different at both high and low temperatures (West, 1958).

*Excretory energy* (E.E.) Energy lost in the excrement decreased linearly with increasing temperature (E.E. = 6.84 kcal./bird/day — 0.088T° C). The rate is less than under constant conditions, but the difference is not significant. The food-utilization efficiency of outdoor birds is the same as that of birds under constant conditions on 19- and 15-hour photoperiods, and above that of 10-hour birds except at —4° C (West, 1958).

*Metabolized energy.* Metabolized energy (M.E.) decreased with increasing temperature (M.E. = 19.05 kcal./bird/day — 0.167T° C). The line for fluctuating temperature crosses the line for constant temperature at —4° C and then diverges at high and low temperatures, where the two lines are significantly different (West, 1958). Davis (1955) found that House Sparrows outdoors in the summer metabolize almost the same amount at all temperatures, with only a slight slope indicated. The metabolic rate is higher than would be expected with change from low to high temperatures and lower than expected with change in the reverse direction. The flatter slopes of birds under fluctuating conditions are as yet unexplained.

Birds kept outdoors at Churchill during late July and August showed considerable variation in metabolism in the temperature range from 10° to 22° C. As with Illinois birds, energy metabolism decreased with increasing temperature, but only the regression of gross energy intake was significant. The lack of significant changes in metabolized energy with temperature may be explained by variations in intensity of the postnuptial molt during August and in the amount of insulation furnished by the plumage.

*Plumage weight.* Feathers were weighed to determine if temperature had any effect on the density of the plumage. Summer Tree Sparrows collected in Churchill had 25 per cent lower plumage weights than Illinois winter birds, but birds retained in Illinois during the summer lost only 6 per cent of their heavier winter plumage (West, 1958). Kendeigh (1934) has shown that House Sparrows decrease the weight of their plumage by 29 per cent from the previous autumn to summer. These observations indicate that either differences occur in plumage wear or that wild birds molt more extensively in the spring than do caged birds. According to Dwight (1900), Weise (1956), and the present study, only a partial spring molt, involving the head and neck, occurs; but Baumgartner (1938) records a more extensive molt in birds shot in the spring at Ithaca, New York.

There is no significant difference in the plumage weights of Illinois winter birds maintained above 35° C and below —15° C, nor are there any differences between the plumage weights of either group and those of the outdoor winter controls (West, 1958).

## Discussion

It was originally supposed (Kendeigh, 1949) that the maximum metabolized energy value occurring at the lowest tolerated temperature could also be attained at higher air temperatures under other energy-demanding stresses than heat regulation and that productive energy would increase as a straight line from zero at the lower limit of tolerance to a maximum at the zone of thermoneutrality. This concept needs to be modified for the Tree Sparrow.

Although the regression lines for metabolized energy are not statistically different, it was suspected that this might be due to nightly unrest in the 15- and 19-hour birds. No recordings of either daytime or nocturnal activity had been made. It is well known (Eyster, 1954) that migratory birds become active at night when the photoperiod is increased either experimentally or in nature as in the spring. Since the experimental birds had been caged outdoors from their capture in February until 1 May, their gonads had fully developed when they were moved inside on 15-hour photoperiods, and there is every reason to believe that their nightly unrest was strong. This is doubtless the reason why their metabolized energy was above that of the 10-hour birds at all temperatures (Kendeigh, West, and Cox, MS).

The intermediate values for metabolized energy of the 19-hour birds are probably due to the shorter night period available for unrest. Birds were shifted back and forth between 15 and 19 hours, especially at the lower temperatures; therefore, they were probably active at both photoperiods.

At the lowest tolerated temperature (—28° C), birds that were presumably active at night on 15-hour photoperiods metabolized 32.82 kcal./bird/day, 7.34 kcal. more than those that were on 10-hour photoperiods, not active at night, and at an existence level at —28° C. This may still not be the maximum that the birds can metabolize at this temperature. The maximum energy utilization is at least as great as this at other temperatures, but, as yet, it has not been demonstrated that it could be greater for any extended period with the bird maintaining a constant weight.

In experiments at —4° C, birds that were active at night (44.0 units/night) metabolized 23.81 kcal./bird/day; birds that were molting heavily (20.8 units), 24.55 kcal.; and birds that were both somewhat active at night (1.8 units/night) and molting lightly (4.9 units) were able to metabolize 24.86 kcal./bird/day, an average of 5.86 kcal. more than those on an existence level at the same temperature. Again, these rates may not represent the maximum capability of the bird.

The ability to do work probably reaches a maximum at some temperature range between the lower limit of tolerance and the thermoneutral zone. In man, maximum work is possible between 4° and 18° C (Brody, 1945). In the House Wren, *Troglodytes aedon,* the largest eggs are produced at temperatures between 20° and 25° C (Kendeigh, 1941). The productivity of farm animals remains constant in environmental temperatures from the comfort zone (15°–21° C) to perhaps —18° C, while above 27° C, productivity is reduced (Brody, 1945). Maximum work of laboratory white mice occurs between 20° and 30° C (Hart, 1950).

At high air temperatures, the ability to work decreases rapidly. Milk production in cattle, growth of baby chicks (Brody, 1945), and work ability of man (Bedford, 1952) decline with increasing temperature. At the upper end of the thermoneutral zone, the ability to carry on work even over short periods of time is presumably reduced to zero, since the body temperature would be raised toward the lethal level.

It is postulated that the amount of energy available for activities other than existence, rather than increasing as a straight line to the critical temperature, increases with increasing temperature from —28° C to about 20°–25° C and then drops rapidly to zero at the critical temperature of about 40° C (Figure 2). Potential total energy intake appears

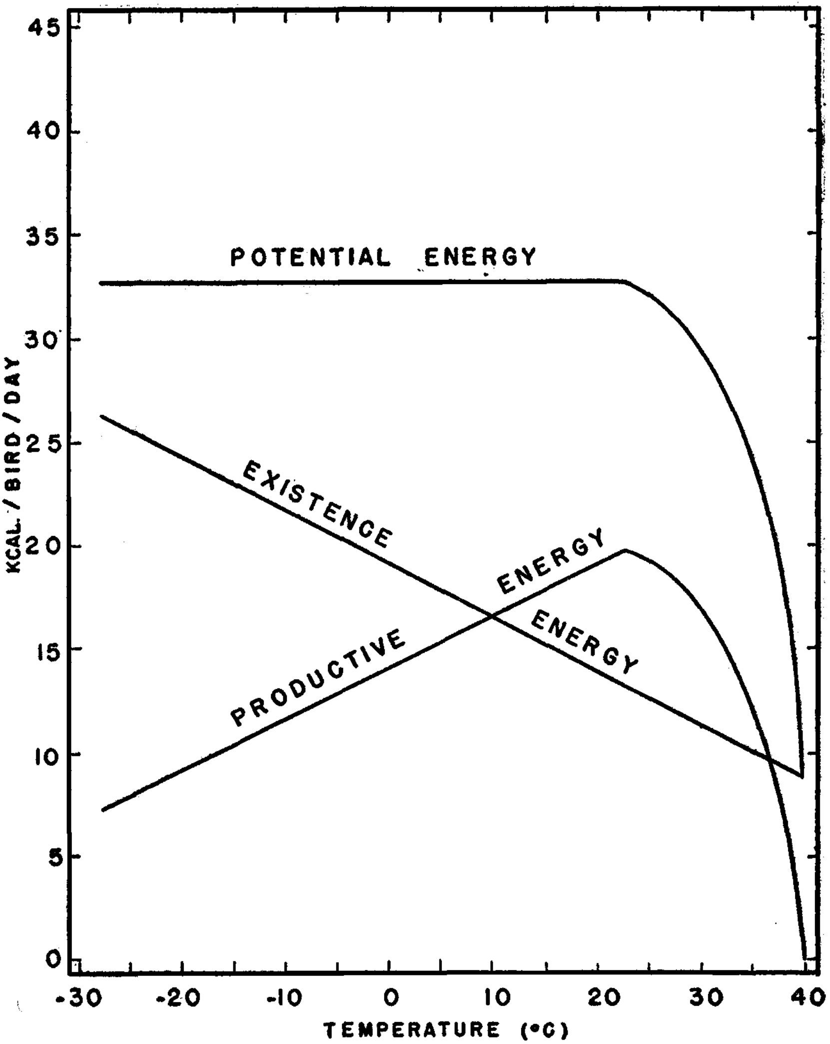

**Figure 2. Potential, existence, and productive energy of Tree Sparrows. Potential energy is based on the assumption that at least the maximum amount of metabolized energy could be metabolized at any temperature from —28° to 20°-25° C.**

to be a constant from —28° to about 20°–25° C; it decreases to the existence level at about 40° C (Figure 2).

Curves of existence energy throughout the year are constructed for the Tree Sparrow by substituting the mean temperatures of the appropriate months for Illinois and at Churchill in the formula for metabolized energy under constant conditions at 10-hour photoperiods (18.57 kcal./bird/day — 0.247T° C, Figure 3). Since birds are migrating during April, May, September, and October, they do not experience the mean monthly temperature at either locality, and lines have been drawn at intermediate levels.

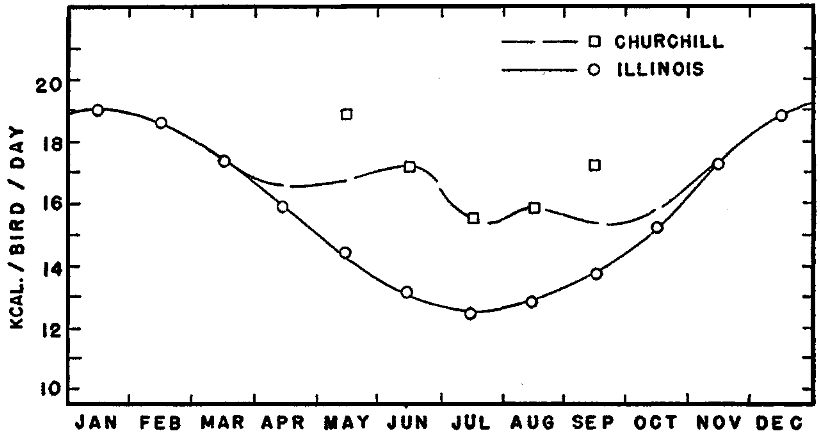

**Figure 3. Existence energy requirements of Tree Sparrows throughout the year. The solid line represents requirements for birds spending the year in Champaign, Illinois; the broken line is for birds migrating to Churchill.**

Due to the lower mean temperatures in summer, the daily existence energy requirements are greater at Churchill than they would be if birds remained in Illinois. However, the increased summer daylight in the north (19 compared with 15 hours in Illinois) cancels the effect of lower mean temperatures, so that the hourly rate at which existence energy must be accumulated is the same in both latitudes (0.85 kcal./bird/hour of daylight).

The following analyses of the amounts of energy required for activities other than existence, although preliminary and hypothetical, are made in order to form a more complete picture of the total annual energy needs of the Tree Sparrow.

From the first week in November when the Tree Sparrow arrives in Illinois until the middle of February, birds put on winter fat. The average weight of Tree Sparrows in November is 17.3 grams and in February 19.6 grams (Table 1). Assuming that the weight increase is

70 per cent fat (McGreal and Farner, 1956), this represents 15.21 kcal. of fat, an increase accumulated at the average rate of 0.17 kcal. per day. During March and early April, premigratory fat is deposited rapidly, so that in 30 days birds gain an average of 1.8 grams (Kendeigh, West, and Cox, MS). Since the per cent water content in storage fat decreases with increasing stores (McGreal and Farner, 1956), about 88 per cent of the weight gain is fat. This represents the accumulation of 14.97 kcal. of fat at the average rate of 0.50 kcal. per day.

At the same time, nightly unrest increases to its maximum. Birds at the peak of nocturnal activity metabolize 23.81 kcal./bird/day at —4° C. However, 18.55 kcal. is spent on existence, and 0.50 kcal. is deposited as fat. The cost of depositing one kcal. of fat is 1.67 kcal. beyond existence (Connell, 1959). The difference, 3.92 kcal., is the daily cost of maximal nightly unrest.

In preparation for each migratory flight, fat is deposited at an increasing rate until flight occurs, and then the fat stores are rapidly depleted (Wolfson, 1954). This pattern is repeated until the bird reaches its destination. The actual energy cost of a migratory flight was not obtained.

The energy required for reproductive activities in the summer may be estimated for the female during the incubation period. With the exception of the requirements for egg production, males and females probably have similar daily energy expenditures.

The average temperature of the eggs throughout the 24-hour day is 33.8° C in most songbirds (Huggins, 1941). The average body temperature of birds during the breeding season is 41.3° C (Baldwin and Kendeigh, 1932). There is thus a 7.5° C average difference between eggs and bird throughout the 24-hour period. Van't Hoff's law for biological functions states that the rate of a function increases two to three times with an increase of 10° C body temperature, $Q_{10}$ (Heilbrunn, 1943). This has not been determined for the Tree Sparrow, but assuming an increase of 2.5 times/10° C, the increase would be 2.0 times for the 7.5° C difference between egg and body temperature. Or, inversely, a drop of 7.5° C would reduce the rate of metabolism to one-half.

Assuming that the energy necessary to maintain one gram of egg at incubation temperature is equal to maintaining one gram of bird at the same body temperature, the following equation applies:

$$\frac{\dfrac{\text{Existence energy (kcal./bird/day)}}{\text{Bird wt. (grams)}} \times \text{Total weight of eggs (grams)}}{Q_{10}} = \text{Energy required for incubation (kcal./day).}$$

At Churchill, birds require an average of 16.15 kcal. per day for existence during the summer. The average body weight of birds in the summer is 18.7 grams (Table 1). Eggs weigh 2.12 grams each, and the average clutch size is 5 (Baumgartner, 1937).

Therefore:

$$\frac{\frac{16.15}{18.7} \times 5(2.12)}{2.0} = 4.58 \text{ kcal./day.}$$

In Illinois, with a mean summer temperature of 23.3° C, energy required for incubation would amount to only 3.63 kcal./day.

The complete postnuptial molt begins the first week in August and lasts into September. Caged Tree Sparrows undergoing a complete molt at —4° C metabolized 6.00 kcal./day above the existence level for over one week.

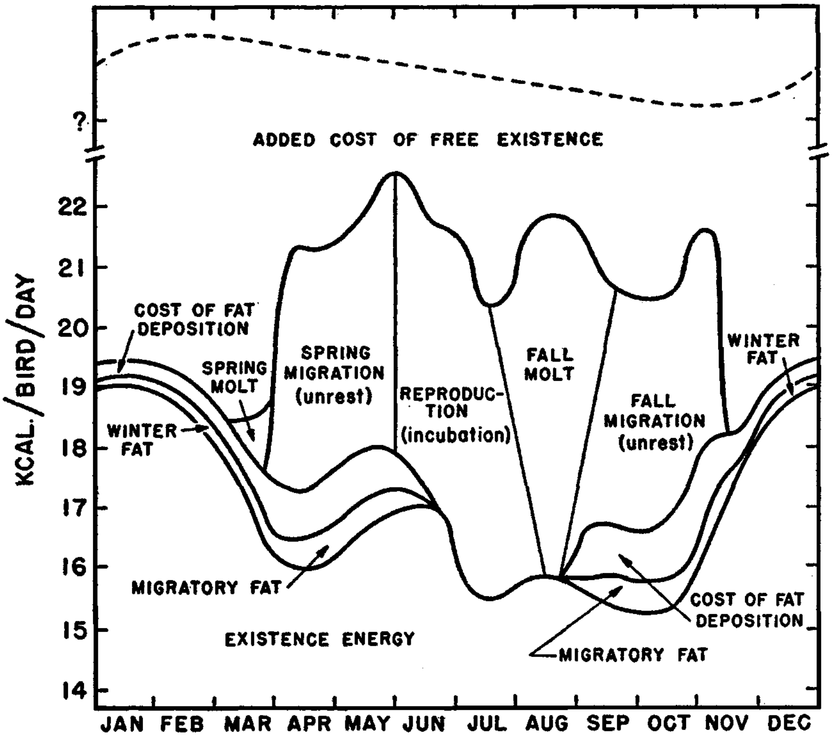

**Figure 4. Total energy requirements of Tree Sparrows throughout the year. The lowest curve is that of existence energy to which the energy required by various activities has been added.**

By adding the values for fat deposition, migratory unrest, reproduction, and molt to the average monthly existence requirements, the total energy expenditure of the Tree Sparrow can be plotted throughout the year (Figure 4).

The cost of living a free existence has not been measured but, due to greater difficulty in finding food, may well be more in the winter than in the summer. If this additional cost were added above the top curve in Figure 4, it might make the total energy intake more nearly the same throughout the year.

Tree Sparrows do not gain a more favorable energy balance by migrating northward each summer to breed, since the energy required for existence and incubation would be less in Illinois than at Churchill, and the energy requirement for migration would exist only for birds migrating to Churchill. The energy required for molting would be the same in the two localities. Undoubtedly factors other than energy balance are responsible for the northward migration of this species. These factors need to be investigated.

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## CONCLUSIONS

1. Under constant experimental conditions, an increase or decrease of temperature from 35° C results in a reduction of body weight due to the loss of body fat. Birds in wild natural conditions, however, show a weight and fat increase during the lower winter temperatures.
2. At experimental temperatures between —15° and —30° C, heavy birds metabolize more energy than light birds.

3. Gross energy intake per day increases linearly with decreasing temperature but at different rates on 10-, 15-, and 19-hour photoperiods.

4. The caloric value per gram of excrement does not vary significantly with photoperiod or temperature.

5. The amount of energy lost in the excrement per day increases linearly with decreasing temperature, with no significant difference among photoperiods. This increase is due to a greater volume of food digested at low temperatures.

6. Metabolized energy increases with decreasing temperature. Differences among photoperiods are explained by differences in night-time activity.

7. The efficiency of food utilization increased with temperature at all photoperiods. However, since digestion is more rapid on the short photoperiod, winter birds at 10 hours are less efficient than summer birds at 15 or 19 hours.

8. Metabolism is decreased above 30° C with no change of rate indicated between 35° and 39.5° C.

9. Energy metabolism of control birds under fluctuating outdoor temperatures in Illinois increases significantly with decreasing temperature, but at a slower rate than under constant conditions.

10. Churchill birds had a higher metabolic rate than Illinois birds at both high constant and fluctuating temperatures due to decreased feather insulation and onset of fall molt at the time of the experiments in July and August.

11. Nonmolting birds at Churchill during June and July have 25 per cent lighter plumages than in the winter in Illinois. Birds retained in captivity in Illinois during the summer lost only 6 per cent of their heavier winter plumage.

12. Short-term acclimation to low or high constant temperatures by altering plumage density does not occur in the Tree Sparrow.

13. The lower limit of temperature tolerance in the Tree Sparrow is the same throughout the year (—28° C).

14. The maximum observed daily capacity for metabolizing energy, such as occurs at the lowest tolerated temperature, is probably the same in all seasons (32.82 kcal./bird/day).

15. Energy required for existence under natural conditions is greatest during January in Illinois, the least in July at Churchill. If birds remained in Illinois during the summer, their existence energy requirement would be 26 per cent less than at Churchill.

16. The hourly rate at which existence energy must be accumulated is the same in summer at Churchill and Illinois.

17. The greatest amount of productive energy per day is potentially available during the summer. Therefore, energy-demanding activities such as migration, nesting, and molting are evenly spaced between April and October.

18. Since daily energy requirements become greater, the Tree Sparrow does not gain a more favorable energy balance by migrating north each spring. Factors other than energy relations are undoubtedly responsible for migration in this species.

## LITERATURE CITED

BALDWIN, S. P., and S. C. KENDEIGH. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist., **3:** x + 196.

BAUMGARTNER, A. M. 1937. Nesting habits of the Tree Sparrow at Churchill, Manitoba. Bird-Banding, **8** (3): 99–108.

BAUMGARTNER, A. M. 1938. Seasonal variation in the Tree Sparrow. Auk, **55** (4): 606–613.

BEDFORD, T. 1952. Heat and work. Research, **5:** 155.

BRODY, S. 1945. Bioenergetics and growth. Reinhold Publ. Corp., New York. xii + 1023.

BURGER, J. W. 1949. A review of experimental investigations on the seasonal reproduction in birds. Wilson Bull., **61** (4): 211–230.

CONNELL, C. E. 1959. Seasonal lipid levels in three population groups of an old field ecosystem. Ph.D. thesis, University of Georgia.

DAVIS, E. A. 1955. Seasonal changes in the energy balance of the English Sparrow. Auk, **72** (4): 385–411.

DWIGHT, J. J. 1900. The sequence of plumages and moults of the passerine birds of New York. Annals N.Y. Acad. Sci., **13** (1): 73–360.

EYSTER, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monographs, **24:** 1–28.

HART, J. S. 1950. Interrelations of daily metabolic cycle, activity, and environmental temperature of mice. Canadian J. Research, **28** (6): 293–307.

HEILBRUNN, L. V. 1943. An outline of general physiology. 2nd Ed. W. B. Saunders Co., Philadelphia. xii + 748.

HUGGINS, R. A. 1941. Egg temperatures of wild birds under natural conditions. Ecology, **22** (2): 148–157.

KENDEIGH, S. C. 1934. The role of environment in the life of birds. Ecol. Monog., **4:** 299–417.

KENDEIGH, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. Ecology, **22:** 237–248.

KENDEIGH, S. C. 1949. Effect of temperature and season on the energy resources of the English Sparrow. Auk, **66** (2): 113–127.

KENDEIGH, S. C., G. C. WEST, and G. W. COX. 1959. Annual stimulus for spring migration in birds. MS.

KLEIBER, M., and J. E. DOUGHERTY. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. Jour. Gen. Physiol., **17:** 701–726.

LINCOLN, F. C. 1950. Migration of birds. U.S. Gov. Printing Office, Washington, D.C. iii + 102.

MCGREAL, R. D., and D. S. FARNER. 1956. Premigratory fat deposition in the Gambel White-crowned Sparrow. Northwest Sci., **30:** 12–23.

ODUM, E. P., and J. D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds; seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., **24:** 216–230.

OSTLE, B. 1954. Statistics in research. Iowa State Coll. Press, Ames. xiv + 487.

SALT, G. W. 1952. The relation of metabolism to climate and distribution in three finches of the genus Carpodacus. Ecol. Monographs, **22:** 121–152.

SEIBERT, H. C. 1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk, **66** (2): 128–153.

SHAPIRO, B., and E. WERTHEIMER. 1956. The metabolic activity of adipose tissue —a review. Metabolism, **5:** 79–86.

SNEDECOR, G. W. 1956. Statistical methods. 5th Ed. Iowa State Coll. Press, Ames. xii + 534.

STEEN, J. 1957. Food intake and oxygen consumption in pigeons at low temperatures. Acta Physiol. Scand., **39** (1): 22–26.

WALLGREN, H. 1954. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. Acta Zool. Fenn., **84:** 1–110.

WALLS, G. L. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Inst. Sci. Bull. No. 19. xiv + 785.

WEISE, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, **37** (2): 274–287.

WEST, G. C. 1958. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. Ph.D. thesis, University of Illinois.

WOLFSON, A. 1954. Body weight and fat deposition in captive White-throated Sparrows in relation to the mechanics of migration. Wilson Bull., **66:** 112–118.

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