DIFFERENCES BETWEEN MIGRANT AND NON-MIGRANT BIRDS IN FOOD AND WATER INTAKE AT VARIOUS TEMPERATURES AND PHOTOPERIODS[1]

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INTRODUCTION

AN environmental factor in the life of birds that has recently received considerable attention is the photoperiod. Most of the research on the effect of changing light and dark periods has been directed at the reproductive cycle. The evidence now indicates rather definitely that increasing photoperiods cause an enlargement of avian gonads (Bissonnette, 1937; Rowan, 1938). However, birds undergo seasonal rhythms in physiological processes other than the activity of the gonads. Weights vary with the seasons. Molt occurs regularly in late summer or early autumn and, in some species, fat is deposited subcutaneously in the spring prior to migration. The regularity of these events presupposes that some seasonal environmental condition, occurring with but little variation year after year, must be responsible. The only known factor that meets this requirement is the length of day, that varies with the precision of the earth's revolution around the sun.

A common requirement for the outward manifestations of seasonal rhythms is energy. Recrudescence of the gonads, especially in the female, requires energy, as does molt and deposition of fat; the results of these activities are reflected in seasonal changes of weight. For practically all birds, except owls, feeding or energy consumption occurs only during the daylight hours, when enough must be ingested to furnish the bird with energy for the night. It, therefore, becomes logical to investigate the rôle that the photoperiod plays on the amount of food consumed. Since the energy balance of the body is affected by the temperature to which it is subjected, it becomes necessary to combine external temperature with photoperiod. By obtaining quantitative data on the energy intake under these two sets of variable conditions a better basis will be available for understanding the seasonal changes occurring in birds. Knowing under what conditions the bird is able to gain, lose, or merely maintain itself in its energy balance should supply a clue as to why certain rhythms in behavior occur when they do.

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REVIEW OF PREVIOUS STUDIES

If an energy balance is maintained, then energy intake must equal energy outgo, and factors affecting one would also affect the other. Although the heat production has been determined for many species of birds, very little research has been done on food consumption in terms of energy intake. Most of the latter has been concentrated on economic species such as the domestic fowl. The effect of photoperiod has scarcely been investigated.

Rörig (1905: 24–34) made an intensive investigation of food consumption of small wild birds and, although he amassed a wealth of data, the caloric value of the food was not determined. In many cases he grouped several species and calculated the amount of food eaten by the entire ensemble. One group of five species of tits and kinglets (three *Parus palustris*, three *P. caudatus*, one *P. coeruleus*, one *P. ater*, one *Regulus cristatus*), totalling 89 grams in weight, ate 18 per cent of their weight per day in dry food, and another group ate 26 per cent. Bluebirds, *Sialia sialis* (25 grams), ate 10 to 12 per cent; a blackbird, *Turdus iliacus* (57.5 grams), ate 10.1 per cent; and a starling, *Sturnus vulgaris* (79 grams), ate 8.0 per cent. He concluded that the smaller a bird was, the relatively more food it consumed. During the summer the amount of food consumed increased, the starling from 8.0 per cent of body weight in winter to 11.9 per cent in summer, *Sylvia cinerea* from 13.4 to 19.2 per cent, the bluebird from 12.4 to 17.7 per cent. This increase was attributed to longer days for food-energy ingestion and shorter nights for energy outgo.

Lapicque and Lapicque (1909 a, b) noted that food consumption decreased as the temperature rose. A change from 13° to 28° C. decreased the grams of food eaten per day from 26.0 to 16.0 in the pigeon, from 11.7 to 6.8 in a dove, and from 13.8 to 6.7 in *Geopelia*. An increase in temperature from 16° to 31° caused the bengali, *Uraeginthus bengalus*, to decrease consumption from 6.10 to 2.98 grams. These writers concluded that the latter bird would die from lack of food in the periods of short daylight of the northern winters, although no experimental proof was given. In a later paper, Lapicque (1911) claimed that the weaver, *Estrelda astrild*, died at 15° C. for lack of food but that light for two to three hours during the middle of the

night enabled it to live at 14° and even 13° C. The precise sensitivity of the bird to such a slight change in temperature is difficult to believe.

Schildmacher (1929) compared the food consumption of two species of weavers, *Ploceus cucullatus abyssinicus* (40 grams) and *Quelea quelea* (18 grams). At 18° C., the former ate 20 per cent of its body weight in food in 24 hours, and the latter 28 per cent. At 7°, the respective percentages were 28 and 33. The ratio of 20 to 28 per cent is 1 to 1.4 and that of 28 to 33 per cent, 1 to 1.18. In other words, the smaller bird did not eat as correspondingly increased amounts of food at the lower temperatures as did the larger. Schildmacher assumed this to indicate that *Ploceus* was better adapted to a lower temperature than *Quelea*. Such low temperatures are not met with in the latter's range.

Although turkey hens were stimulated earlier to sexual activity by the addition of white and red light than by blue, the food consumption was not similarly correlated. Under white light, they ate 69.85 pounds per bird per four weeks; under red, 59.74; under blue, 62.41; and with no additional light, 63.00 (Scott and Payne, 1937: 95). Total food consumption by turkeys was not increased by the addition of artificial lighting, nor was there any difference between birds in heated and non-heated pens, according to Wilcke (1939). However, birds in heated pens ate a considerably higher proportion of mash and much less grain than non-heated birds. Heywang (1945) found no increase in food consumption by pullets as a result of an increased artificial illumination. Beck (1930: 308–330) noted that chickens ate less food in semi-darkness and under green and blue lights.

METHODS

All birds in the experiments here reported were captured by sparrow traps from wild populations. The species used were English sparrow, *Passer domesticus*, slate-colored junco, *Junco hyemalis*, white-throated sparrow, *Zonotrichia albicollis*, blue jay, *Cyanocitta cristata*, and field sparrow, *Spizella pusilla*.

Each experiment started with three to five birds of one species. The individual birds were placed in cages, 10 by 10.5 by 5 inches, made of one-half inch mesh hardware cloth. The cages sat in tall, close-fitting, metal pans, and between the two there was inserted a doubled full-size sheet of newspaper to catch any feed that might escape the pan.

The time of year that these experiments were run was as follows: junco and English sparrow at 34° and 22° C., February 15 to June 13; junco at 10° and −13° C., July 3 to September 15; English spar-

row at −13° C., January 30 to March 30; white-throated sparrow at all temperatures, October 15 to December 12.

Experiments at 22° C. were run in basement rooms, well insulated from the out-of-doors, and fluctuations in temperature between night and day and summer and winter did not vary more than plus or minus two degrees. Experiments at higher temperatures were run in a constant temperature room and those at low temperatures were conducted in a refrigerator unit where the temperature control was accurate to 1° C. The door of the refrigerator was constructed of six panes of glass for insulation and to allow light to enter from the outside. Air temperatures were recorded by self-recording potentiometers using thermocouples. The accuracy of these instruments was checked every other week with thermometers in the temperature units. All the rooms were light-proof and each was illuminated by two 150-watt bulbs regulated by time clocks.

The feed used was a ground mixed chicken mash, the same as that used by Kendeigh (1949: 114), with a caloric value of 4.40 large calories per gram dry weight. This picture does not correspond precisely to the diet that wild birds of these species normally eat. It agrees best with what the English sparrow consumes (Kendeigh, 1949: 114). Experimental conditions make it necessary that the food be measured accurately and easily handled; it should not vary except for the occasional addition of cuttlefish bone and grit. It is doubtful that wild birds could obtain out of doors a more nutritious diet in terms of calories per gram.

A weighed amount of the food was placed in a glass bowl and put into the cage. The moisture content of the feed was determined to be 13 per cent, and this correction was applied to the weighed amount of feed originally given the bird. Water was made available in cups suspended from the side of the cage. After four to five days, the unused food was collected, the feces extracted, and both dried in an oven at 98° C. for over 48 hours and then weighed. The difference in dry weights was, therefore, the amount of food consumed for the period of observation.

The caloric value of the feed and of the feces was determined in a Parr adiabatic oxygen calorimeter.

From the gross energy consumed was subtracted the caloric value of the feces to give the metabolizable energy. The latter value was then divided by the total hours of light to which the bird had been exposed to give the rate of calories consumed per hour. The rate per day was obtained by multiplying the calories per hour by 10 or 15, depending on the length of the light period.

The birds were weighed each time the food was changed, and an attempt was made to do this at the same time each day to cancel variations in weight due to the daily rhythm. The average weight of the bird during the feeding period was the one used to compute calories per hour per gram of live weight.

The photoperiod was increased one-half hour every other day, alternating between morning and evening, beginning with 10 hours to which the birds were adjusted, until 15 hours were reached. This was maintained until at least four collections of feed had been made. Each collection period lasted four to five days. The photoperiod was then reduced to 10 hours at the same rate and collections made until a nearly constant rate of food consumption was obtained. The entire process extended over three months. However, in case of mortality, new birds when available were substituted directly at the current photoperiod without acclimation. It was soon found that birds adjusted themselves quickly to changes in temperature and day-length, so that the changes in photoperiod were increased to one-half hour every day in later experiments. All the juncos and five of seven white-throats used on the 10-hour photoperiod were among those previously used on the 15–hour photoperiod. Because of the time consumed in performing an experiment at one temperature, a single species was run at three, sometimes four, temperatures concurrently, and with the exception of one junco (at 10° C. and 34° C.) a different set of birds was used at each temperature.

Since activity on the part of the bird increases its energy requirements, care was taken to disturb the birds as little as possible. Because of the small size of the cages, activity was limited and confined mostly to feeding. It is unlikely that the birds fed at night. When the lights were turned off, the rooms were in absolute darkness. The cages were examined numerous times at night with a flashlight, and in no single instance was a bird discovered near its food supply. In a separate experiment, English sparrows that were weighed continuously on their perches during the night remained stationary for the entire period of darkness.

All data on the English sparrow at a 10-hour photoperiod were derived from experiments conducted by Kendeigh (1949).

GROSS ENERGY

Table 1 demonstrates that all three species increased the amount of food consumed as air temperatures dropped. The grams of food consumed per bird have not been incorporated in Table 1 but can be

readily calculated by dividing the caloric intake by 4.4 which is the number of calories per gram of dried feed.

Most data on food consumption by wild birds have been in terms of grams of food eaten in relation to body weight. Rörig's birds, most comparable to the junco in size, ate 18 per cent of their body weight per day during the winter (short day, but indoors at room temperature). Lapicque and Lapicque (1909a) calculated that the bengali, weighing approximately 15 grams, ate 18 per cent of its weight at 31° and 40.7 per cent at 16° C. Our juncos, averaging 19 grams, ate 17.2 per cent at 34° (average of both photoperiods) but only 22.4 per cent at 10° C. In no case was there a doubling in the amount consumed within the short temperature range of Lapicque's experiments. Our values for the larger sparrows at 22° were higher than those given by Rörig for a 25-gram bluebird. However, the sparrows were fed grain which contained more waste material than the dried animal food that was given the bluebird. Taber's results (1928), presumably taken during the summer at out-of-door temperatures, showed that the junco ate 13.5 per cent, the white-throat, 15.8, and the English sparrow, 11.9. In comparison, our birds ate 17.7, 17.6, and 20.2 per cent, respectively. These values are greater than those obtained by Taber, as would be expected from his method of computation which is subject to several errors. He made use of the differential in evening and morning weights of birds to calculate their food consumption. However, the evening weight is not necessarily the maximum weight attained by the bird. The gain in weight measures only the energy stored and not the energy expended in obtaining the food and in other activities. More food must be consumed than is indicated by the gain in weight. Furthermore, the loss in weight measures the amount of feces lost during the night or the amount of food the bird had in its digestive tract before it ceased feeding and metabolic loss of food reserve (fat) in the body, not the total food that passed through the digestive tract during the course of the day.

The hourly rate of food consumption was greater on a 10-hour day than on a 15-hour day. In only two cases, however, (the white-throat at 22° and the English sparrow at − 13° C.) was the increased hourly rate sufficient to enable the bird to eat more on a 10-hour day than on a 15-hour day. Rörig (1905: 29) also found that his birds ate more during the long summer days than during the winter.

ENERGY LOSS IN EXCREMENT

The excrement from birds consists of undigested food, digested but unabsorbed food, together with the nitrogenous wastes from the

TABLE 1

EXPERIMENTAL DATA ON ENERGY INTAKE IN BIRDS

Temperature (°C.)	Photoperiod (hours)	Number of birds	Total days feeding	Average weight of bird (grams)	Gross Energy Cal./bird/day	Gross Energy Cal./bird/hour	Energy of Excrement Cal./bird/day	Energy of Excrement Cal./bird/hour	Energy of Excrement Percent of food intake per day	Cal./bird/day	Cal./bird/hour	Metabolizable Energy Cal./kg./day	Metabolizable Energy Cal./sq. meter/day
							JUNCO						
34	10	4	50	18.6	12.61	1.26	1.96	0.20	15.5	10.64	1.06	599	1569
34	15	4	107	18.9	15.77	1.05	2.37	0.16	15.0	13.41	0.89	708	1880
22	10	2	51	18.5	14.92	1.49	1.21	0.12	8.1	13.72	1.37	752	1978
22	15	2	62	20.9	15.68	1.05	1.61	0.11	10.3	14.07	0.94	701	1932
10	10	2	36	18.9	18.43	1.84	2.47	0.25	13.4	15.95	1.60	841	2238
10	15	5	132	20.0	19.95	1.33	1.92	0.13	9.6	18.04	1.20	940	2532
-13	10	1	18	20.1	25.97	2.60	5.96	0.60	23.2	20.00	2.00	999	2717
-13	15	2	39	19.7	28.52	1.90	5.36	0.36	18.8	23.18	1.55	1274	3337
						WHITE-THROATED SPARROW							
34	10	3	53	23.7	15.68	1.57	2.08	0.21	13.3	13.61	1.36	579	1663
34	15	2	48	19.6	16.08	1.07	2.12	0.14	13.2	13.96	0.93	698	1889
22	10	3	60	27.7	20.68	2.07	2.74	0.27	13.3	17.94	1.79	652	1973
22	15	3	54	25.0	19.95	1.33	1.74	0.12	8.7	18.23	1.22	725	2114
-13	10	3	63	22.2	23.47	2.35	4.56	0.46	19.4	18.92	1.89	870	2427
-13	15	2	19	23.1	29.97	2.00	6.08	0.41	20.3	23.89	1.59	1036	2945
						ENGLISH SPARROW							
34	10	12	207	22.9	16.28	1.63	1.90	0.19	11.7	14.38	1.44	628	1782
34	15	2	60	24.1	20.07	1.34	1.59	0.11	7.7	18.45	1.23	787	2278
24	10	12	194	23.1	18.04	1.80	2.01	0.20	11.1	16.03	1.60	695	1978
22	15	3	87	24.1	23.99	1.60	2.16	0.14	9.0	21.83	1.46	902	2595
-13	10	6	100	24.7	31.24	3.12	4.96	0.50	15.9	26.28	2.63	1065	3100
-13	15	4	51	24.0	31.00	2.07	5.37	0.36	17.3	25.63	1.71	1068	3212
						BLUE JAY							
22	10	1	29	79.0	62.18	6.22	14.70	1.47	23.6	47.48	4.75	601	2580
22	15	1	20	80.7	54.10	3.61	14.10	0.94	26.0	40.00	2.67	495	2136
						FIELD SPARROW							
22	15	1	25	10.7	20.72	1.38	1.74	0.12	8.4	18.98	1.26	1775	3905

kidneys.   All references to excrement or feces in this paper refer to the products combined.

The total caloric value of the feces excreted divided by the daylight hours to which the birds were exposed was used to derive the calories lost per hour in the feces.   Daylight hours instead of the full 24 hours per day were used because this method gives results that are closer to the actual rate and because direct comparisons with the hourly rate of food consumption were desired.   Although birds voided excrement at night, the preponderance of defecation at night occurred shortly after the birds had ceased to feed, and the rate declined rapidly thereafter.   In the morning when the birds began feeding, the digestive tract was empty, and elimination of feces did not become regular until after feeding was well underway.   The loss of feces in the early night and the lack of it in the early morning are approximately equivalent.   Daily rates were obtained by multiplying the hourly rate obtained in this manner by the photoperiod to which the bird was exposed.

Decreasing temperatures generally increased the number of calories lost by way of the feces, except at 22° in the junco at both photoperiods and in the white-throat at 22° on the 15-hour day (Table 1). This increase was due largely to the greater amount of food consumed.

It is known from nutritional studies that the greater the quantity of food consumed per unit time, the less relative amount that is digested. The percentage of food intake that is excreted should, therefore, increase with a drop in temperature because of the greater amount of food that is eaten.   This was partially true; the highest percentages occurred at − 13° C. (Table 1), but the lowest percentages came as often at 22° as at 34° when the least food was consumed.

Calorimetric determinations of the feces from birds kept at different temperatures indicated a difference with temperature in the energy per dry weight of the feces excreted (Fig. 1).   In all species, the caloric value of the feces per unit weight was least at 22°.   Either the most efficient absorption occurred at this temperature or the feces contained a different ratio of the wastes from the intestine and kidney. At − 13°, the white-throat and junco had a lower percentage of wastage of consumed food than did the English sparrow.   At 34 to 37° C., the wastage of energy in all species was greater than at any other temperature.   At 37° C. the junco and white-throat had a greater wastage of energy than at any other temperature investigated.   This is presumably true for the English sparrow, although to a less extent, since at 34° C. its wastage was about equal to that at −13° C.

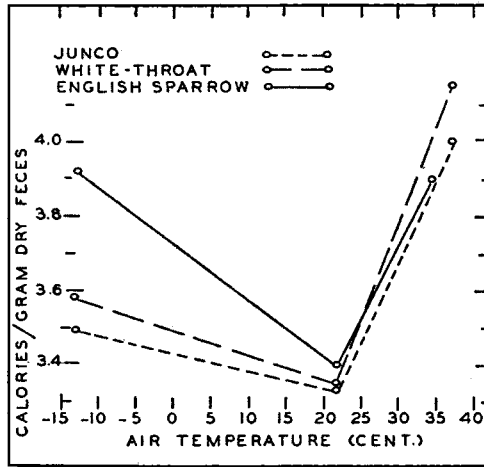If the voiding of excrement is computed for the same number of

FIGURE 1.—Calories per gram of dry feces excreted by junco, white-throated sparrow and English sparrow on a 12-hour day at various temperatures.
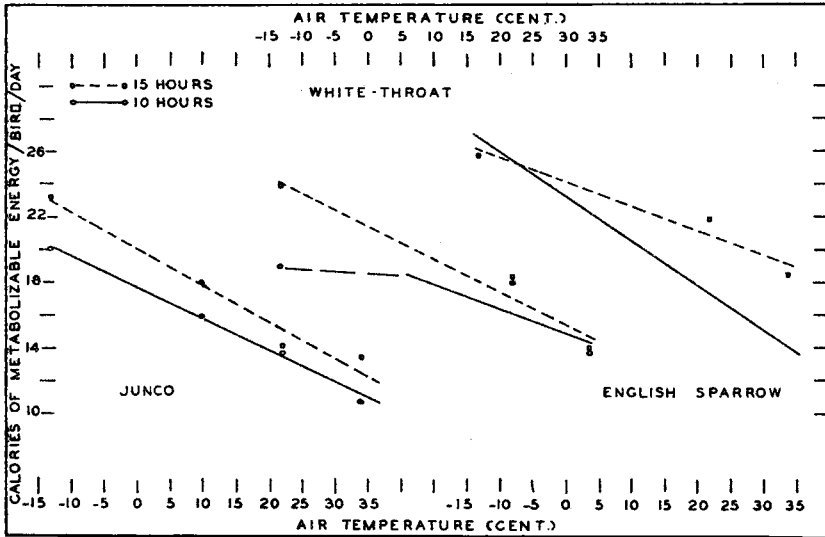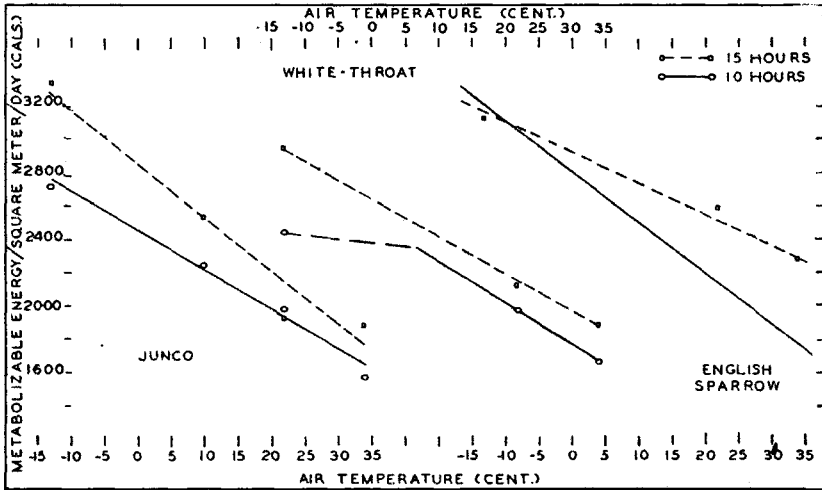

FIGURE 2.—Calories of metabolizable energy absorbed per bird per day by junco, white-throated sparrow and English sparrow on a 15- and 10-hour photoperiod at various temperatures.

hours as feeding took place, all birds at all temperatures excreted more per hour when on the 10-hour than on the 15-hour photoperiod (Table 1). This is what would be expected from the fact that the birds similarly ate more per hour on the shorter photoperiod.

However, in only six of 11 cases were more calories excreted per bird per day during the 15-hour photoperiod, in spite of the greater food consumption. This lack of increase in excrement loss indicates a more leisurely and complete digestion because the caloric food intake per hour was at a slower rate.

METABOLIZABLE ENERGY

Metabolizable energy is the food actually digested and absorbed by the bird. This energy must provide the bird with all its energy requirements for existence and productive activities. The latter would include movement, growth, molt, and reproduction.

Metabolizable energy intake increased with decreasing temperatures (Table 1). In all birds at each temperature the metabolizable energy absorption per hour was greater during the short than the long photoperiod, notwithstanding differences that occurred in the number of calories excreted. No birds, with the exception of the English sparrows at − 13° C. and the blue jay at 22°, were able to absorb as much during the 10 hours as during the 15 hours, in spite of the increased hourly rates of food absorbed during the short day.

Changes in temperature and photoperiod had varied effects on the three species, and these are shown in Figure 2 where the straight lines were fitted to the observed points by the least squares method. The junco responded by increasing its intake of metabolizable energy proportionally to the drop in temperature at both photoperiods, but at a slightly faster rate on the long day. The white-throat increased its intake on the 15-hour day at a slower rate than the junco. However, on the 10-hour day, at some point between 22° and − 13°, it was unable to increase further its intake proportionally with a drop in temperature, with the result that the straight line relationship no longer held. On the other hand, the English sparrow was able to maintain a rapid increase with drop in temperature when the day was 10 hours long but had a slower increase when it was 15 hours. At − 13° C. its energy intake on a 10-hour photoperiod equalled its intake on a 15-hour period. Since existence needs increase proportionally to a decrease in temperature (Kendeigh, 1949), any deviation from this relationship should give an indication of the bird's ability or inability to meet its requirements at that particular temperature.

Since the experimental birds were kept in small cages and left

relatively undisturbed, the need of productive energy was negligible. The energy utilized was presumably directed to existence which involved standard metabolism plus the energy increment of feeding and chemical heat regulation. Any energy intake in excess of these requirements would have been stored and reflected in an increase of weight. If a minimum level of energy intake was not maintained, existence would be possible only as long as reserve fats in the body were available for utilization. Any deviations in a strict balance between energy intake and outgo would be reflected in changes of body weight.

Figure 3.—Calories of metabolizable energy absorbed per square meter of surface per day by junco, white-throated sparrow and English sparrow on a 15- and a 10-hour photoperiod at various temperatures.

In a series of body weights determined from recently trapped birds, Baldwin and Kendeigh (1938: 437) found that juncos averaged between 18.9 and 23.2 grams during the fall and winter months. Under conditions of starvation, Kendeigh (1945: 223) found that juncos weighed 16.0 grams at − 14° C. and 14.9 grams at − 3° at the time of death. Since our birds weighed from 18.5 to 20.7 grams at all temperatures investigated, the conclusion is warranted that they were maintaining an energy balance well above that of minimum existence. On the 15-hour photoperiod, the weights of the junco did not vary significantly from 22° to − 13°. This indicated that the increase in food consumption was utilized for increased heat production. On the 10-hour photoperiod there was a gradual increase in weight from 18.5

grams at 22° to 18.9 grams at 10° to 20.0 grams at − 13°. The latter rise was 3.2 times the standard error. The conclusion would be that the birds were consuming more than necessary for existence and that this excess was being stored. However, the birds used at 10° C. were not the same individuals used at − 13°.

Data (Baldwin and Kendeigh, 1938: 436–437) showed that the average weight of white-throated sparrows varies from 25.1 grams to 29.4 grams from September to May. Death from starvation occurred at − 17° when the birds were down to 21.7 grams (Kendeigh, 1945: 223) and at − 1° when the weight was 20.2 grams. Our data show that the birds at 22° were well within the range of weights for free individuals out-of-doors. At − 13° there was a pronounced drop in weight of birds on the 10-hour photoperiod. The loss, from 27.7 grams to 22.2 grams, was 7.5 times the standard error. The latter weight was near the weight of birds dying from starvation at low temperatures. The birds were continuing to lose weight when the experiment was terminated. These results clearly indicate that a 10-hour photoperiod at a temperature of − 13° C. was causing difficulty in maintaining a prolonged energy balance, even though these birds were able to live precariously for 63 days. Such temperatures out-of-doors under natural conditions would be near, if not beyond, the environmental limits that the species could tolerate for any prolonged period. On the 15-hour day, there was a slight loss in weight, from 25 to 23.1 grams (1.7 times the standard error). Individual birds maintained a more or less constant weight throughout the experiment. The latter weight (23.1 grams), however, is only 1.4 grams greater than the weight at death from starvation at − 17°. These birds were existing at a level only slightly above the minimum, but, nevertheless, the longer photoperiod was of distinct advantage to the species.

Wild English sparrows weigh from 26 to 29 grams (Baldwin and Kendeigh, 1938: 436–437). At − 14° C. the birds die from starvation at a weight of 24.4 grams (Kendeigh, 1945: 223). Since the experimental birds used in these experiments averaged about this weight, it must be assumed that they were living at a bare existence level at all temperatures investigated.

On the other hand, as temperatures were increased from 22° to 34° C. the junco showed a significant (three times the standard error) loss in weight on the 15-hour photoperiod, but not on the 10. The white-throat lost considerable weight on both the 15- and 10-hour photoperiods (5.9 and 11.3 times the standard errors, respectively).

The English sparrow showed no significant change in weight at either photoperiod.

Kendeigh's survival data showed that juncos died at a weight of 14.6 grams at 35° C.   This weight is well below the minimum of our birds.   Tolerance of high temperature involves the problem of heat loss, with heat production reduced to a minimum.   Kendeigh (1944: 9, and 1945: 222) has shown that the shortened survival time at high temperatures is due to inability to attain or maintain the requisite high rate of water loss.   The slight drop in weight may be a result of the energy consumed in the active process of water elimination or the result of a faster decrease in feeding rate, rather than any increase in energy needs.

The extreme loss in weight by the white-throat showed that this species is less tolerant than the junco to a temperature of 34° C. Kendeigh's paper (1949) does not include data, that could be used for comparison, on the white-throated sparrows' resistance to hunger at 34°.

The English sparrow showed no significant weight change.   Kendeigh's English sparrows died at 34° at a final weight of 19.6 grams, a value below the weight of our birds.   This species showed a better adjustment to a high temperature than did the junco or white-throat.

To correct for the size of the bird, metabolizable energy utilization was calculated per kilogram of body weight (Table 1).   In spite of their body weights being nearly the same, the rate of absorption per kilogram was generally least in the white-throated sparrow and greatest in the English sparrow and junco.   Straight lines fitted to the observed points gave the following formulae, with y the calories per kilogram of weight per day and x the temperature in degrees centigrade.   The critical temperature of minimum rate of metabolism is 37° C. in the English sparrow (Kendeigh, 1944: 8).   The caloric value of metabolizable energy at that temperature is the basic rate to which is added the increased energy absorption at lower temperatures.   The figures in front of the parenthesis represent the increase in the number of calories for each degree of temperature below 37° C.

Junco   15 hours: $y = 13.0 (37 - x) + 596.7$
                 10 hours: $y = 8.2 (37 - x) + 603.5$
White-throat   15 hours: $y = 7.6 (37 - x) + 647.0$
                 10 hours: $y = 6.2 (37 - x) + 559.8$
English sparrow 15 hours: $y = 4.6 (37 - x) + 815.7$
                 10 hours: $y = 10.8 (37 - x) + 583.1$

The number of calories absorbed per kilogram at 37° was least in

the white-throat (559.8) on a 10-hour photoperiod. In the other species, whenever the value of 37° was low it was compensated by a more rapid rate of increase with drop in temperature.

Most students of bioenergetics maintain that heat production should be evaluated in terms of surface area rather than volume or weight. Therefore, metabolizable energy was determined in terms of one square meter of body surface, the latter being calculated by using Meeh's formula ($S = Kw^{2/3}$) and using a value of 10 for K. Various refinements of this formula have been proposed, but in view of the fact that a bird's body is covered with feathers and that the three species probably differ in the quality as well as the quantity of their insulating cover, these refinements appear unwarranted. The data are graphed in Figure 3.

The observed points were fitted to straight lines and the following formulae obtained, y being the calories of metabolizable energy per square meter of body surface and x the temperature in degrees centigrade.

Junco	15 hours	$y = 33.1 (37 - x) + 1634.1$
	10 hours	$y = 23.8 (37 - x) + 1560.2$
White-throat	15 hours	$y = 22.8 (37 - x) + 1799.0$
	10 hours	$y = 18.4 (37 - x) + 1603.9$
English sparrow	15 hours	$y = 19.1 (37 - x) + 2219.3$
	10 hours	$y = 31.3 (37 - x) + 1651.4$

In both the junco and white-throat, the rate of increase in energy absorption with drop in temperature was greater on the long day than on the short, but in the English sparrow the condition was reversed. These rates also demonstrate that the white-throat did not respond so rapidly to a drop in temperature while on a 10-hour photoperiod as did the other species. Kendeigh's data on the English sparrow (1949: 118) indicate a straight line relationship between energy absorption and temperature. The data on the juncos in this experiment, which were investigated at four temperatures, also point to a straight line as the best possible fit to the data. However, in the case of the white-throat on a 10-hour photoperiod, the birds failed to absorb any significantly greater amount of energy at − 13° C. than they did at 22°; consequently, they lost weight. Because of this reduced weight, metabolizable energy on a kilogram or square meter basis is correspondingly increased and the observed points approximate a straight line. The line in Figure 3 is drawn as being broken, however, to show that somewhere between 22° and − 13° the energy balance was upset and the relationship between food absorption and temperature was no longer truly linear (Fig. 2).

It would be expected that because of its smaller size the field spar-row would be the lightest eater, but it absorbed more metabolizable energy than the junco and the white-throat at comparable tempera-tures and photoperiods (Table 1). This large capacity for energy absorption is more markedly emphasized when the caloric intake is measured in relation to body weight and surface area. Wild field sparrows fluctuate between 11 and 13 grams in weight, being lightest in the summer months (Baldwin and Kendeigh, 1938: 436–437). Since this captive specimen averaged 10.7 grams, this great consump-tion maintained it at only a minimum existence level.

The weight of the blue jay varied between 79.0 and 80.7 grams, values well within the range for wild birds. Although restricted to a diet consisting mostly of grain, this bird survived in good health until the end of the experiment.

WATER CONSUMPTION

Quantitative data on water consumption by birds are scarce. Rubner (1897: 53) pointed out that pigeons died from thirst in four to five days but that those allowed water and no food lived for 12 days. Bennion and Warren (1933: 78) measured the mean daily water con-sumption of chickens at 21° and 27° C. and found it to be 224 grams; at 32° it increased 3.8 per cent, to 233 grams. Mitchell and Kelley (1933: 737–738, 740) calculated water needs of chickens for drinking as—the sum of the water vaporized, the water in the excreta and the water stored in the tissues, minus the water obtained from food. At 28° C., with due corrections for moisture in the food, water analysis of the gain, and metabolic water calculated from nutrients in the feed, it was found that a one-pound chicken needed 99 grams of water per day (9.04 milligrams per gram per hour) and a five-pound chicken, 223 grams of water (4.10 milligrams per gram per hour). On the basis of these data, Lippincott and Card (1946: 267) stated that the average water intake of laying hens was about 35 to 40 pounds per 100 hens per day. Large hens, laying at a high rate in hot weather, would require 50 to 60 pounds.

In our experiments on water consumption the same type of indi-vidual cages was used, as previously described for the feeding experi-ments. Instead of water cups, a small crystalline dish, 1¾ by 1⅛ inches, was placed in each cage. At the higher temperatures of 34° and 37° C., 20 cubic centimeters of distilled water were put into each dish with a delivery pipette, but only 10 cubic centimeters at the temperatures of 0° and 22° C. Each dish with water was weighed to within one milligram on an analytical balance before it was given to

the bird and again at the end of the experiment.   Two or three other dishes with equivalent amounts of water were set in near by positions but out of reach of the birds in order to measure evaporation.   The average amount of evaporation subtracted from the total lost in the experimental dishes gave the amount of water consumed by the birds. The dishes were removed from the cages after three to seven hours. As this was the only water available to the birds for the entire day, the total drunk divided by 24 gave the rate per hour.   In this case, the total day rather than just the daylight period was used to calculate

TABLE 2

CONSUMPTION OF DRINKING WATER BY THE JUNCO, WHITE-THROATED SPARROW
AND ENGLISH SPARROW ON A 12-HOUR PHOTOPERIOD

Temperature (° C.)	Number of observations	Period (hours)	Bird weight (grams)	Water drunk (grams)	24 hour period (mgm./gm./hr.)
		JUNCO			
0	8	4.70	18.0	1.88	4.4
23	5	4.83	16.1	2.57	6.6
34	5	6.02	16.7	2.90	7.2
37	7	4.93	17.0	3.62	8.9
		WHITE-THROATED SPARROW			
0	10	4.80	25.0	4.60	7.7
23	11	4.01	23.3	6.27	11.2
37	5	4.93	21.2	9.22	18.2
		ENGLISH SPARROW			
0	7	4.33	24.7	4.04	6.8
23	8	4.42	24.9	4.31	7.2
34	4	6.34	23.9	6.39	11.1
37	3	4.89	24.3	7.99	13.7

the rate per hour, in order to render the results comparable to the published data and since water is actually being lost continually in respiration.   Before readings were taken, two to three days were allowed for the bird to become acclimated to the restricted period of availability of water.   The failure of the birds to lose weight indicated that adjustment was complete and that sufficient water for their needs had been consumed.   The data on water consumption are given in Table 2.   There is no indication in the table that the birds consistently drank more water when it was available for a longer period.

As the temperature increased, the amount of water consumed per hour also increased.   The amount consumed, both absolutely and relatively, was greatest in the white-throat and least in the junco. Tests for significance of the rates of consumption among the species were made by using Student's method of analysis for small samples.

At 0° C., the white-throat and the English sparrow did not differ
significantly, whereas the difference between the white-throat and the
junco was highly significant.   Between the English sparrow and the
junco, the chance probability of the difference being as great or greater
than the one observed was 2 in 100, a chance sufficiently remote to be
considered significant.   At 23°, the difference between the English
sparrow and the junco was insignificant, but between the white-throat
and the other two species, the probability was 0.03.   At 37°, all
differences were significant, although between the white-throat and
the other two species, the probability of the difference was 0.05.

The white-throat consumed more drinking water than either the
English sparrow or the junco at all temperatures investigated; this
difference became increasingly greater with a rise in temperature.
From 0° to 37° C. its consumption increased 136 per cent.   Although
relative water consumption by the junco was the least of all, it in-
creased its daily intake by 102 per cent, an increase equal to that of
the English sparrow.   This greater need of water by the white-throat
would seem to indicate that it is less capable of withstanding high
temperatures than the other two species.   This may be an important
factor explaining why white-throats, under starvation conditions at
37°, survived only seven hours, whereas the junco and the English
sparrow survived 12 and 15 hours, respectively (Kendeigh, 1945: 223).

DISCUSSION

Of the many factors that control the distribution and migration of
birds, the biological and physical aspects of the habitat (plants,
terrain) and such climatic factors as temperature have generally been
regarded as the major ones.   The results of these experiments confirm
the increasing evidence that photoperiod is also a major determinant.
The length of day controls the feeding time available and, thereby,
the amount of energy that the bird is able to obtain.   Whenever the
daylight period is so short that the food intake is insufficient to meet
the demands of the bird's activities and to carry the bird over the
night, the bird must respond by leaving the region before the environ-
ment becomes intolerable.   This is especially true at low air tempera-
tures when much energy must be expended to maintain body tempera-
ture and existence.   At high air temperatures the length of day is less
important, as the critical factor involved is keeping the body tempera-
ture from rising to a harmful degree.

It is, therefore, pertinent to determine whether the summer and
winter distributions of the slate-colored junco, white-throated sparrow,
English sparrow, blue jay, and field sparrow can be correlated with

their ability or inability for maintaining an adequate energy balance at different temperatures and photoperiods, and whether there are any distinguishable differences between migrants and non-migrants.

The data on the distribution of the first three species during the summer breeding season were collected from numerous published sources, including state lists, reports on collections, and the National Audubon Society's annual breeding-bird census. The winter distribution was determined primarily from the National Audubon Society's annual Christmas bird count. These counts are made within four days of December 25 and can, therefore, be considered as defining rather accurately the early wintering status of the species.
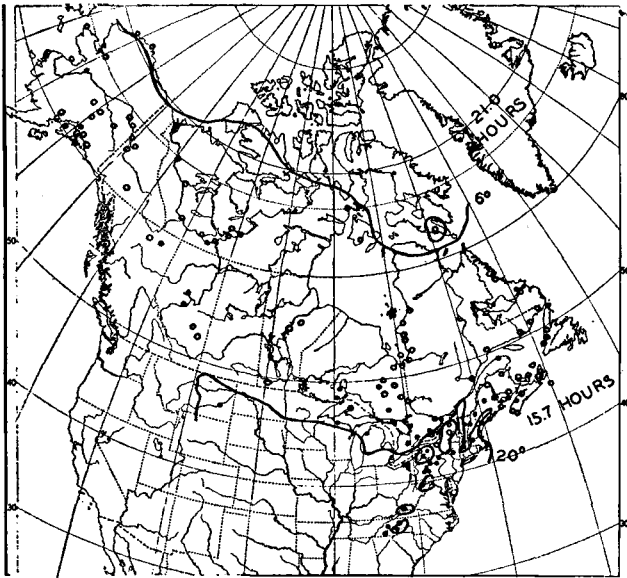
FIGURE 4.—Breeding range of junco, *Junco hyemalis*, in North America, with maximum photoperiods and mid-July isotherms at northern and southern limits. Summer records indicated by open circles, nesting records by solid dots.

Mid-July isotherms were drawn along the southern and northern boundaries of the breeding ranges and mid-January isotherms around the extremities of the wintering ranges. The normal ranges were determined by the preponderance of records; scattered records around the periphery were not included. The choice of the proper isotherm was made visually and may represent an error of a degree or two in either direction. Isotherms of the United States were taken from the

United States Department of Agriculture's Atlas of American Agriculture, Part II, Section B, 1928, and those of Canada from the Atlas of Canada, Department of Interior of Canada, 1915.   The approximate boundaries of the northern and southern distributions during the summer and winter, the total daylight hours at those boundaries in the same seasons, and the mid-July and mid-January isotherms at those boundaries are shown in Figures 4 to 8.

To determine how these birds might respond to the extreme conditions of temperature and photoperiod that occur in their breeding ranges during the winter, a curve for each species was temporarily inserted in Figure 3 at the corresponding photoperiod.   In placing this line it was assumed that the relationship existing between 10 and
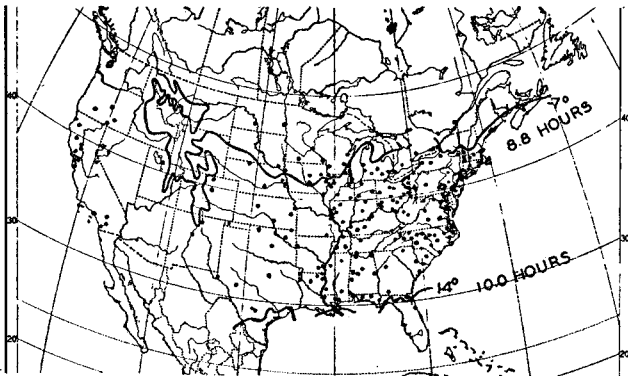

FIGURE 5.—Winter range of junco, *Junco hyemalis*, in North America, with minimum photoperiods and mid-January isotherms at northern and southern limits.

15-hour photoperiods would hold for intermediate or extreme periods. Thus, a 12.5–hour photoperiod would fall halfway between the two known curves, while one of 7.5 hours would fall the same distance below that of the 10.

The data in Table 3, derived by this method, give the number of calories metabolized per bird per hour, which is the rate at which the bird would have to absorb calories at the prevailing photoperiod. This rate can then be compared with the maximum hourly rate obtained from the experimental birds.

The maximum rate of energy absorption observed for the junco was 2.0 calories per bird per hour, but it may go somewhat higher at lower temperatures.   Within its normal winter range this observed maximum suffices, but it is not adequate to meet the rigorous winter conditions in its breeding range.   This is also true for the white-throated sparrow.   Within its wintering range the most extreme average con-

TABLE 3

CALCULATED WINTER ENERGY REQUIREMENTS OF THE JUNCO, WHITE-THROATED
SPARROW AND ENGLISH SPARROW AT THE EXTREMES OF THEIR
BREEDING AND WINTER RANGES

Species	Boundary of range	Minimum requirements in breeding range during winter (Cal./bird/hr.)	Minimum requirements in winter range during winter (Cal./bird/hr.)	Maximum rate of absorption observed in experiments (Cal./bird/hr.)
Junco	Northern	4.8	2.0	2.0
	Southern	2.2	1.5	
White-throat	Northern	3.3	1.9	1.9
	Southern	2.2	1.7	
English sparrow	Northern	3.1	3.1	3.3
	Southern	1.7	1.7	

dition that the white-throat must tolerate is a photoperiod of 9.3 hours at an average temperature of 0° C., requiring 1.9 calories per hour. This must represent the limit of tolerance for this species since it migrates from those parts of the breeding range where conditions of 9.2 hours at − 2° C., requiring 2.2 calories per hour, would be encountered. In both these species the average conditions existing at the northern edge of their respective winter ranges are severe enough to prevent the birds' obtaining any excess energy to meet emergencies. It is to be expected that during seasons of severe cold both of these species would be forced to move progressively farther south.
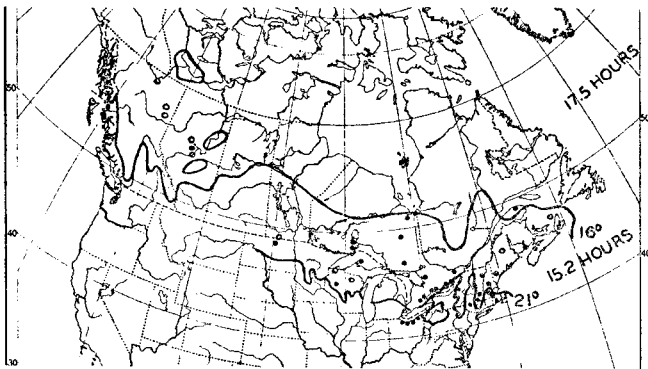

FIGURE 6.—Breeding range of white-throated sparrow, *Zonotrichia albicollis*, in North America, with maximum photoperiods and mid-July isotherms at northern and southern limits. Summer records indicated by open circles, nesting records by solid dots.

Summer conditions within the breeding ranges of these species are sufficiently favorable for them to exist without discomfort. Using energy absorption as a criterion, the white-throat can not adapt to extreme low temperatures as well as the junco (Fig. 3). It would be expected *a priori* that the former's range would not extend so far north as the latter's; this postulation is supported by the distributional data.

The English sparrow's maximum rate of 3.3 calories per hour at − 31° C., as calculated from data of Kendeigh (1949), is sufficiently fast to fulfill all its requirements within its range. Even in the far north during the winter, the average requirements are 3.1 calories per hour, and the bird would still have enough surplus for periods of stress.
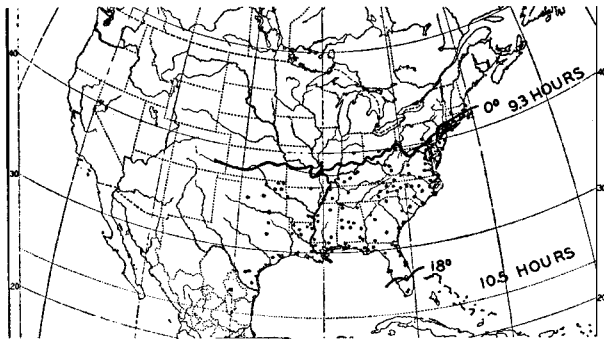

FIGURE 7.—Winter range of white-throated sparrow, *Zonotrichia albicollis*, in North America, with minimum photoperiods and mid-January isotherms at northern and southern limits.

During the winter, the short days at the cold temperatures, which caused the junco and the white-throat to migrate, do not affect the English sparrow because its rate of food consumption is stimulated to such a degree that energy intake at − 13° C. on a 10-hour day is equal to that on a 15-hour day (Fig. 3). Kendeigh (1945: 223) showed that when deprived of food the English sparrow survived only 19 hours at − 14° C. and that survival time was reduced to around four hours when the temperature fell below − 22° C. Therefore, 16 hours of darkness at − 12° C. is close to the limit beyond which it could not safely tolerate daily fluctuations that are likely to occur.

During the summer in the southern part of its range, the English sparrow is exposed to average maximum temperatures ranging up to 38° C. The migrant junco and white-throated sparrow would also be exposed to this high temperature, were they to remain in their winter ranges during the summer months. Kendeigh's data showed that the

survival period for the English sparrow at 38° C. was 15 hours; for the junco, 12 hours at 37°; and for the white-throat, 7 hours at 37°. The two-fold survival time of the first species, as compared to the white-throat, is related to the fact that the English sparrow has a more conservative water balance. Although a maximum temperature may exist for only a short period of the day, it would be of greater importance to the white-throat since it would produce a greater dehydration than in the junco and English sparrow. This fact is indicated by the extreme water requirements of this species at high temperatures (Table 2).
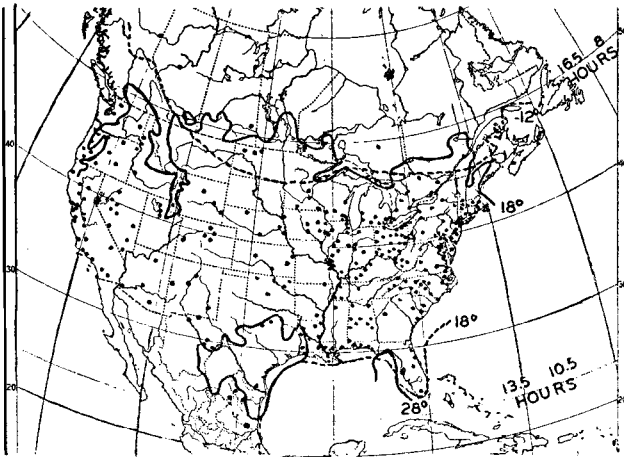

FIGURE 8.—Range of English sparrow, *Passer domesticus*, in North America, with maximum photoperiods and mid-July isotherms (solid lines) and minimum photoperiods and mid-January isotherms (dashed lines) at northern and southern limits.

If a more perfect water and heat regulating mechanism permits the English sparrow to remain in the south and its absence causes the white-throat to migrate north in the summer, it fails to explain the northward migration of the junco. Our data indicate that the junco has a favorable water metabolism at high temperatures, and Kendeigh's results showed this species capable of withstanding high temperatures almost as well as the English sparrow. Factors other than those discussed here must be important in regulating its behavior. Likewise, the restriction of the northward spread of the English sparrow during the breeding season must be effected by other factors than lack of energy resources.

Because of the paucity of data, any detailed discussion of the blue jay and the field sparrow would be unjustified. The blue jay is a

permanent resident species, occupying a range from 52° N. latitude south to the Gulf states and west to the 100th meridian. Its range approximates the eastern half of that of the English sparrow. At 22° C., this species was able to consume as much food on the 10-hour day as on the 15-hour day. The only other bird thus able to increase its hourly rate of food absorption to the extent needed was the English sparrow, also a permanent resident.

The field sparrow is a summer resident over only part of its range. Its breeding range extends from southern Maine, Ontario, and Manitoba to central Alabama, Mississippi, and Texas. Its breeding range is thus south of either the junco's or the white-throat's. During the winter its range is more southerly in the United States, occurring northward to about Maryland and Southern Illinois, approximately the wintering range of the white-throat. It may be that it does not occur in colder regions because its capacity for food absorption, considering its small size, has already reached its limit of maximum efficiency in the relatively warmer climate of the South.

In view of the foregoing data and discussion, certain characteristics are found to distinguish migrants and non-migrants. In the latter, English sparrow and blue jay, the hourly rate of food consumption per bird is increased and the total on the short day at low temperatures is the same as that on the long day, so that the effect of photoperiod as a limiting factor is minimized. Within certain limits, this allows a permanent resident to remain in a cold environment with short day lengths. Rising temperatures have less effect in decreasing food intake during long photoperiods for non-migrants than for migrants. This is essential if a bird is to remain where it is hot during the summer.

In contradistinction, a migrant species, such as the white-throated sparrow, is unable to stay in its breeding range because low temperatures do not stimulate a sufficiently fast hourly rate of food consumption to bring the daily total on a short photoperiod up to an amount adequate for existence. The change in photoperiod is, therefore, a primary factor causing southward migration in the fall. The field sparrow further demonstrates that some migrants have innately such a high requirement for food, even at moderate temperatures, that for physical and mechanical reasons they could not increase effectively their hourly rate of consumption to compensate for any significant drop in temperature. The more a species can increase its hourly food intake, the farther north it can be expected during the winter. Just why different species should vary in their ability to increase their hourly rate of food consumption still remains a problem. The psychological aspect of food ingestion, as indicated by Beck's (1930)

work with chickens, is apparently not to be dismissed lightly. However, it would seem more likely that a study of the comparative physiological capabilities of the digestive systems will provide the decisive answers.

As Kendeigh (1934: 396) and others have pointed out, long nights at low temperatures make it necessary for certain species of birds to migrate, and this investigation has borne out the fact that the combination of these environmental conditions has a pronounced effect on food consumption. The emphasis in this paper has been on extreme conditions. Variations within these extremes, especially a gradual change from one to the other, may have a regulatory effect on the time of migration. Variations beyond the extremes may cause the sudden disappearance or unexpected appearance of migrants outside their usual time and place or may have catastrophic effects on segments of a population.

SUMMARY

1. The food consumption of the slate-colored junco, white-throated sparrow, and English sparrow was measured at temperatures ranging from 34° to − 13° C. and at photoperiods of 10 and 15 hours. The food consumption of a field sparrow and a blue jay was measured at 22° C., on a 15- and 10-hour day for the latter and on a 15-hour day for the former.

2. The gross energy consumed per day by the junco, white-throat, and English sparrow increased at different rates with decreased temperatures.

3. The gross energy consumed per hour was greater on the 10-hour photoperiod than on the 15-, but this greater rate of food consumption was not sufficient in most instances to make the total energy consumed during the day equal to that consumed on the longer photoperiod. The blue jay at 22° and the English sparrow at − 13° C. were, however, able to consume as much during the short day as during the long day.

4. The energy lost per gram of dry feces was greatest at 34°–37° C. in the junco, white-throat, and English sparrow and least at 22°. The energy lost in the feces per day per bird decreased with a rise in temperature up to 22°, but above 22° it varied with the species and the photoperiod.

5. The metabolizable energy absorbed by the junco, white-throat, and English sparrow on a 10-hour day increased at the average rate of 8.2, 6.2, 10.6 calories per gram per day, or 23.8, 18.4, 31.3 calories per square meter per day per degree drop in temperature, respectively.

On a 15-hour day the corresponding rates were 13.0, 7.6, 6.7 calories per gram per day and 33.1, 22.8, 19.4 calories per square meter per day. The energy absorbed by a field sparrow at 22° C. was considerably more than by the other species, when compared in terms of unit weight or surface area.

6. Water consumption by the English sparrow, junco, and white-throat was measured at temperatures from 0° to 37° C. At all temperatures, the white-throat drank the most water and the junco the least.

7. These experimental results, when interpreted in terms of winter conditions in the breeding ranges of the junco and white-throat, indicate that migration south in the fall may be induced because decreasing photoperiods and colder temperatures combine to prevent the birds from absorbing sufficient food to maintain an energy balance over the 24-hour day.

8. The English sparrow and the blue jay are not forced to migrate south in the autumn because short photoperiods at low temperatures induce a rate of energy absorption sufficiently great to minimize the effect of the shortened day-length. High temperatures at long photoperiods do not reduce the energy absorption in the English sparrow to the same extent as in a migrant species.

9. The field sparrow may be limited in its northward migration and distribution by its innately high food requirements.

10. Northward migration in the spring in the white-throat may be influenced by a delicate water balance that is easily upset by high temperatures.

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