

THE BIOENERGETICS OF VERNAL PREMIGRATORY FAT DEPOSITION IN THE WHITE-CROWNED SPARROW

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In seeking to identify the external factors and internal mechanisms which initiate and characterize avian migration, it appears that one of the more profitable avenues of approach is through an analysis of the physiology of premigratory fat deposition. It has been emphasized by many investigators (Wolfson, 1942; de Bont, 1947; Farner, 1955; Helms and Drury, 1960) that this deposition is characteristic of many small migratory species, that it does not occur in sedentary species, and that it is one of the earliest and most prominent signs of the physiological preparation for migration. In an analysis of the component mechanisms of premigratory fat deposition there are several obvious preliminary questions which delimit the approaches to orderly field observation and meaningful experimental design: (1) What are the quantitative and temporal characteristics of fat deposition under natural conditions? (2) What are the sources of energy which underlie intensive fat deposition? (3) What are the environmental timers, if any, which initiate deposition and the dissipation of the surplus reserves? (4) What neuro-endocrine changes and alterations in intermediary metabolism are involved?

In an earlier paper concerning the first of these questions (King and Farner, 1959), we have quantitatively analyzed the phases of vernal premigratory fattening in wild White-crowned Sparrows of the race *Zonotrichia leucophrys gambelii* and compared the pattern with that of captive members of this same race. It was emphasized that quantitative differences between wild and captive birds were relatively minor and that temporal differences were not detectable. Because of this similarity, it was concluded that captive birds could legitimately be used in experimental analysis of the physiology of premigratory fattening. The investigations to be described below relate to question 2 and, in part, to question 3 as they apply to captive *Zonotrichia leucophrys gambelii*.

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MATERIALS AND METHODS

The birds employed in this investigation were obtained from overwintering populations in the Snake River Canyon of southeastern Washington. This population represents the northernmost limit of the regular winter range of *Z. l. gambelii*. This is a strongly migratory race of the White-crowned Sparrow which breeds in the boreal zones of northwestern North America and overwinters in a broad area of the West extending from southern Washington to Utah, Nevada, Oregon, California, and northern México. The northern limit of the major wintering range is separated from the southern limit of the breeding range by about 200 miles, although the majority of the population migrates much greater distances (up to 3300 miles; Blanchard and Erickson, 1949).

From mid-March to early June of 1955 and 1956, six male *Z. l. gambelii* were studied under outdoor conditions at Pullman, Washington. The birds used in 1955 had been captured between October, 1954, and February, 1955, and had been held in outdoor aviaries until 10 days before the beginning of the study, when they were placed in the metabolism-activity cages described beyond. The six males used in the spring of 1956

had been captured in January of that year and in October of 1955. They were also given a 10-day period of acclimation to the small cages.

The outdoor laboratory was a walled enclosure on a roof four floors above the street level. The metabolism-activity cages were placed on a shelf with an east exposure and protected from rain and snow by an overhanging roof. Except for this necessary protection of the apparatus from precipitation, and for a somewhat reduced wind velocity, the birds were subjected to normal variations in weather conditions and photoperiod. Climatic conditions at Pullman do not differ markedly from conditions on the nearby wintering grounds in the Snake River Canyon. Mean temperatures in January for these two areas are -2.6°C . and 0.8°C ., respectively.

Measurement of energy intake.—For the study of energy income, birds were confined individually to Hendryx breeding cages ($23 \times 36 \times 28$ cm.) from which the floors had been removed. Each cage was set in an aluminum pan 12.5 cm. in depth which prevented the loss of spilled food and excreta. Aluminum tubing was used for perches in order to facilitate the quantitative recovery of droppings, and an aluminum partition was inserted across the lower half of the cage beneath the central perch. The procedure for measuring energy intake was similar in principle to that of Kendeigh (1949), Seibert (1949), and Davis (1955). A quantity of food weighed to the nearest 0.05 gm. was supplied daily in a tared glass hopper. The food consisted of a chick-starter mash prepared by the Department of Poultry Science at the Washington State University. This is a nutritionally adequate ration consisting of 74.7 per cent carbohydrate, 20.7 per cent protein, 3.1 per cent fat, and 1.5 per cent ash, and it also includes mineral and vitamin additives. For use in these observations the mash was passed through a corn grinder to reduce the size of particulate components (mostly cracked corn). This eliminated the possibility of selective feeding and facilitated the preparation of a homogeneous mixture. The moisture content of the ration was determined each week by drying to constant weight at 98°C .

At prescribed intervals (4 to 7 days, as noted beyond), the metabolism pans were changed. All food and excreta adhering to the bird's feet, the cage and its accessories were collected and placed in the pan. The spilled food and excreta in the pan were then mechanically separated by multiple screenings and hand picking. The separated materials were dried to constant weight at 98°C . It was not possible by this procedure to separate completely the excreta and spilled food, but with sufficient care the mutual contamination was reduced to about 100 to 200 mg. in an average collection. Because the caloric values of food and excreta are not very different (*ca.* 4.5 kcal./gm. and *ca.* 3.5 kcal./gm., respectively) this contamination is largely cancelled. It is estimated that the maximum experimental error was about three per cent.

The energy content of the food and excreta was determined by routine oxygen-bomb calorimetry. The acceptable limit of error between duplicate samples was set at 0.4 per cent of the mean value. The energy content of three different batches of chick-starter used in this investigation was 4.439, 4.540, and 4.552 kcal./gm. dry weight. There was no detectable selective feeding by the birds. Residual food gave the same combustion values in several tests as the food supplied to the cages.

The computation of energy income was accomplished as follows: The dry weight of the food supplied was computed from the measured moisture content of the ration. The dry weight of the residual food was determined directly by drying to constant weight. The difference between the food supplied and the residual food was multiplied by the energy content as determined by bomb calorimetry, giving the gross energy income of the bird for the period. Subtracting from this the energy content of the excreta for the

same period (excretory energy), also determined by bomb calorimetry, yields the metabolizable energy, which is the energy actually available to the bird for maintenance, storage, and work (minus the indeterminate fraction lost in the specific dynamic effect of the ration and in fermentation, if any, in the gut). The utilization coefficient is obtained from the equation: metabolizable energy/gross energy \times 100. It denotes the percentage of the gross energy income which is actually assimilated by the bird.

In these investigations it was very desirable to obtain an estimate of the energy expended in maintenance functions and muscular work. In order to estimate this energy quantity, which will be called the catabolized energy, it is necessary to know the caloric equivalent of change in body weight during periods of fat deposition and depletion. In man, this factor is estimated to be between 6 kcal./gm. of weight change (Keys and Brozek, 1953) and 7.8 kcal./gm. (Wishnofsky, 1958). In the White-crowned Sparrow during the premigratory period the water content of the subcutaneous fat varies between means of 13 and 37 per cent (McGreal and Farner, 1956). The caloric equivalent of weight change in this species will therefore lie between about 6 kcal./gm. and 8 kcal./gm. For present purposes the median value, 7 kcal./gm., has been accepted. In estimating the catabolized energy for a given period, the metabolizable energy is increased or decreased by the caloric equivalent of the change in body weight for the same period.

The ratio of metabolizable energy to catabolized energy, that is, of input to output, provides a measurement of energy balance and will be called the balance coefficient. A value of 1.00 prevails when energy intake is equal to energy expenditure; values above 1.00 result from a positive energy balance with gain in body weight, and conversely. This coefficient should not be confused with the *Energiebilanz* of Rautenberg (1957), which denotes a different ratio.

In 1955, the metabolizable energy was measured continuously by successive 7-day periods. In 1956, it was considered desirable to follow variation in energy metabolism in greater detail and the period was reduced to 4 days. The birds were weighed at the beginning and end of each metabolism period and the state of molt was recorded. Weighings were uniformly made between 11:30 a.m. and 12:30 p.m. This routine time was selected as preferable to the pre-dawn weighings which many European investigators employ (see, for example, Rautenberg, 1957; Merkel, 1958). If variation in body weight is to be utilized as an index of premigratory fattening, as in these investigations, it seems inadvisable to weigh the birds at dawn, immediately following a night of *Zugunruhe* (see beyond) during which 15 to 20 per cent of the body weight may be dissipated to supply energy for muscular activity.

Measurement of standard metabolic rate.—The respiratory metabolism of birds in standard physiological conditions (28°C. ambient temperature, quiescent at night, after 3 to 4 hours of fasting; see King and Farner, 1961) was determined in a small modification of the volumetric device developed by Schwabe and Griffith (1938), who describe in detail its structure and operation. The maximum error in the estimation of oxygen consumption and carbon dioxide production was about three per cent. The coefficient of variation in 25 calibrations was 2.05, which included the error in the measurement of the graphic record. All gas volumes were reduced to standard conditions (760 mm. Hg, 0°C., dry). The standard metabolic rate determined in this manner approximates the minimum or "basal" energy expenditure of the birds in a thermoneutral environment.

Measurement of activity.—Concurrently with the measurements of energy intake and expenditure, the activity (movement) of each bird in its metabolism cage was continuously sampled. This was accomplished by a modification of the apparatus described by Farner and Mewaldt (1953). Movements of a central perch-microswitch assembly

in each cage were detected separately by an Esterline-Angus operations recorder and an impulse counter. A numerical total of perch movements was recorded for each hour of the day. A continuous graphic and numerical index of movement within each cage was thus available. These data clearly do not yield an absolute measurement of activity, but they do give an activity index as a fraction of total activity. For individual birds this is a relatively constant fraction. Shortly after confinement to small cages the birds de-

TABLE 1

MEAN DATA ON ENERGY METABOLISM OF SIX MALE *Zonotrichia leucophrys gambelii*
EXPOSED TO NATURAL TEMPERATURE AND PHOTOPERIOD

Interval	Body weight in grams		Metabolizable energy Kcal./bird/day		Catabolized energy Kcal./bird/day		Ambient temperature Mean °C.
	Mean	SD	Mean	SD	Mean	SD	
1955							
Mar. 8-20	26.3	1.4	25.73	1.11	25.5	1.8	-0.3
Mar. 21-31	26.4	1.3	25.52	2.40	25.1	1.9	-0.1
Apr. 1-10	26.2	0.4	24.22	3.27	24.4	4.4	5.7
Apr. 11-20	26.8	2.3	28.15	2.58	25.8	2.5	3.5
Apr. 21-30	32.4	2.9	30.79	2.66	27.3	3.2	4.9
May 1-10	33.3	1.4	22.45	1.19	24.1	1.6	8.6
May 11-20	31.6	2.0	22.53	1.24	24.0	2.2	9.4
May 21-30	30.9	1.4
June 1-10	28.0	2.3	20.48	5.50	22.6	2.2	12.0
1956							
Mar. 16-20	26.8	0.9
Mar. 21-25	26.7	1.0	23.69	1.11	23.4	1.2	8.9
Mar. 26-31	26.8	0.7	23.48	1.56	23.8	2.0	5.0
Apr. 1-5	27.1	3.3	23.21	0.82	23.3	1.2	4.7
Apr. 6-10	26.6	0.9	24.54	1.00	23.4	1.3	7.6
Apr. 11-15	28.3	1.9	26.36	2.80	22.5	1.3	12.1
Apr. 16-20	31.3	2.1	28.23	2.08	24.0	1.6	11.1
Apr. 21-25	33.6	1.2	25.17	2.16	23.1	1.8	12.6
Apr. 26-30	34.5	0.7	23.21	1.71	23.0	0.9	14.7
May 1-5	34.0	0.9	22.26	1.02	23.8	1.3	9.9
May 6-10	33.4	1.1
May 14-20	32.6	0.8	21.19	0.61	21.8	0.9	10.2

velop characteristic and almost invariable exercise patterns which include activation of the recording perch. It is true, however, that different birds exhibit different patterns of movement, and hence that different fractions of the total activity are recorded. For this reason, the data must be interpreted and compared on a relative basis as an activity pattern. This problem is discussed at length by Farner, Mewaldt, and King (1954).

In the present investigation the activity data were used chiefly to detect the onset and development of nocturnal migratory restlessness, or *Zugunruhe*. There no longer appears to be any significant doubt that this phenomenon (see reviews by Eyster, 1954; Farner, 1955; Weise, 1956; Lack, 1960) is the expression by caged birds of the urge to migrate. It is therefore an adequate index of the time at which migratory behavior is "released." The similarity between the onset of *Zugunruhe* in captive birds and the timing of northward migration in the wild populations has already been demonstrated in several forms of *Zonotrichia* (Farner, King, and Wilson, 1957). The most conspicuous change in the diurnal activity pattern as *Zugunruhe* develops in spring is a burst of activity which begins at twilight and continues at a high level through midnight (Farner, Mewaldt, and King, *op. cit.*). Accordingly, the activity during this period has

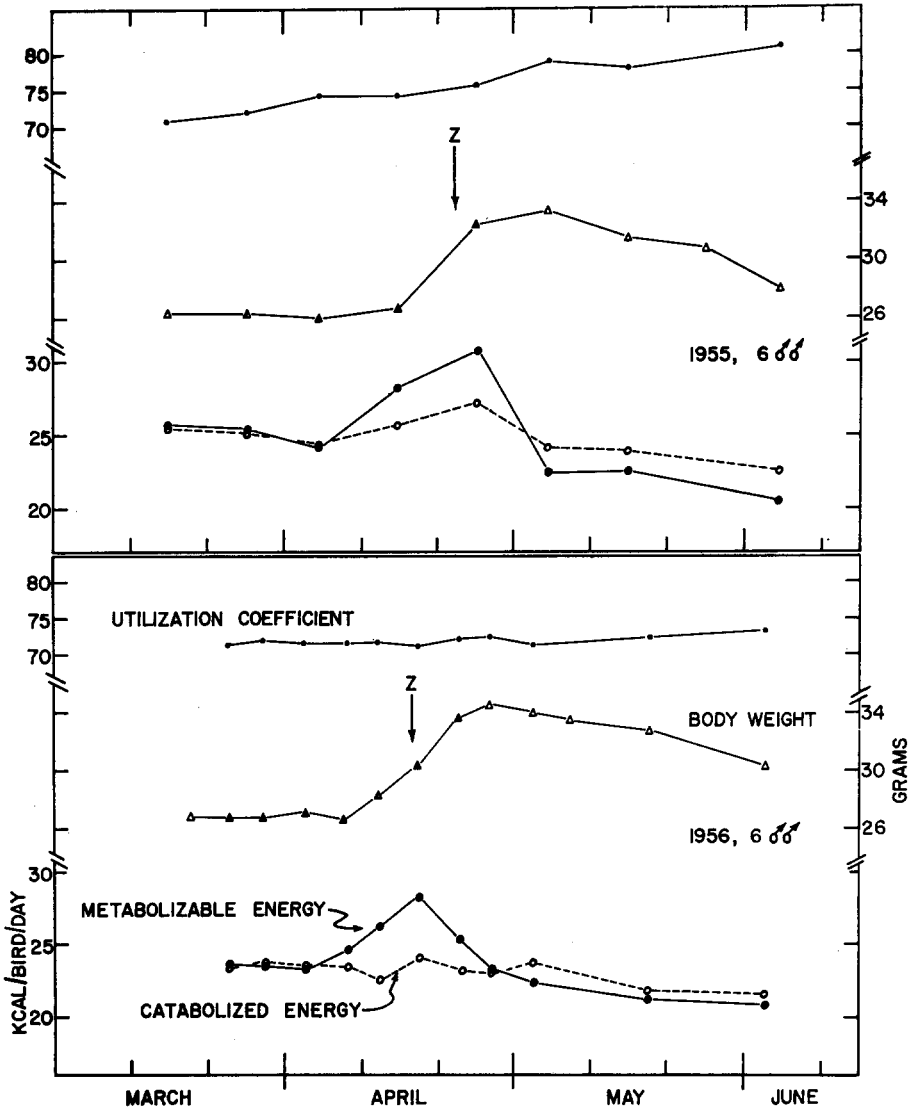


Fig. 1. Averaged data for White-crowned Sparrows confined out of doors. The curves and units labeled in the lower panel have the same significance in the upper panel. The Z-arrow indicates the beginning of *Zugunruhe*. The intensity of molt is shown by the triangles of the body weight curve as heavy molt (solid), medium or light molt (half-filled), or no molt (open).

been taken as a *Zugunruhe* index, expressed as the mean "recorded hops per hour" for the 4-hour period between 8 p.m. and midnight.

RESULTS

The averaged data for all six birds are compiled in tables 1, 2, 3 and in figures 1, 2, and 3. In these summaries, the data for 1955 and 1956, except for the standard metabolic rates, have been averaged by 10-day and 5-day intervals, respectively. In this proce-

dure, those "median dates" (in 1955 the initial date of the metabolism period plus 3 days; in 1956, initial date plus 2 days) which fell within the interval indicated were included in the average value for that interval. This statistical procedure leads to a slight reduction of maximum average values because the attainment of maxima was not precisely coincident in all of the birds. However, the pattern of variation was so similar quantitatively and qualitatively in all the individuals in the two years that it is not justifiable to use the space necessary to display complete data for each individual. The averaged data represent faithfully the changes characteristic of the premigratory period.

TABLE 2

MEAN BALANCE COEFFICIENT AND UTILIZATION COEFFICIENT IN SIX MALE *Zonotrichia leucophrys gambelii* EXPOSED TO NATURAL TEMPERATURE AND PHOTOPERIOD

Interval	Balance	Utilization	SD
	coefficient	coefficient	
	Mean	Mean	
1955			
Mar. 8-20	1.01	70.7	2.1
Mar. 21-31	1.02	72.1	2.2
Apr. 1-10	0.99	74.5	2.1
Apr. 11-20	1.09	74.4	1.7
Apr. 21-30	1.13	75.9	2.2
May 1-10	0.93	78.9	2.2
May 11-20	0.94	78.0	3.2
May 21-30
June 1-10	0.91	80.8	1.6
1956			
Mar. 21-25	1.01	71.2	1.0
Mar. 26-31	0.99	71.7	1.4
Apr. 1-5	1.00	71.5	1.9
Apr. 6-10	1.05	71.4	1.4
Apr. 11-15	1.17	71.6	1.9
Apr. 16-20	1.18	71.1	1.4
Apr. 21-25	1.09	72.0	2.2
Apr. 26-30	1.01	72.2	2.3
May 1-5	0.94	71.2	2.0
May 6-10
May 14-20	0.97	72.3	2.1

Body weight.—All six of the birds in 1955 and 1956 exhibited typical premigratory fat deposition. There was a precipitant increase in body weight which began in mid-April and reached a peak about the first of May. In 1955, the median date for the onset of fat deposit was April 17 ± 4 days; in 1956, it was April 13 ± 3 days. The percentage weight increase, as computed from the mean values in table 1, was 27 in 1955 and 30 in 1956.

After reaching its peak in early May, the body weight began immediately to decline toward a midsummer low which was reached in June and early July at about the time of the start of postnuptial molt. The period of maximum and declining body reserves thus corresponds approximately with the spring migration and early breeding season of the wild population.

Energy intake and utilization.—The principle change in the energy economy associated with the development of the premigratory fat reserves was a sudden increase in metabolizable energy income. This resulted almost entirely from a large increase in gross energy intake, that is, from an increase in appetite. The median date at which increase in gross energy intake became apparent in 1955 was April 9 ± 2 days; in 1956

the initial date was also April 9 ± 3 days. The daily energy expenditure (catabolized energy) of the birds in general increased during the active phase of fat deposition, although in one individual in each year an initial decline in this energy fraction contributed part of the surplus energy deposited as fat. The mean balance coefficients are summarized in table 2. The development of premigratory fat deposits in different individuals is associated with a maximum energy income some 16 to 35 per cent in excess of energy expenditure. The mean maxima shown in table 2 are somewhat lower because of slight temporal differences in attaining peak values.

The variation in the utilization coefficient was small but showed some definite differences in the two years of the investigation. In 1955, it increased from an initial value of about 71 to a level of about 81 in early June, with a maximum rate of increase coinciding roughly with the period of maximum gain in weight. In 1956, there was no important increase in the utilization coefficient.

The standard metabolic rates were determined only in 1956, with results shown in table 3. The averages in each case represent the data from the group of six birds as studied individually over a period of 6 to 8 days. Because of the desirability of making the metabolism determinations at strictly comparable times of the night (11:30 p.m. to 12:30 a.m.), it was possible to make only one determination per night. The date which accompanies each average in table 3 is the median date for the period. It appears from these data that the absolute metabolic rate, expressed on a "per bird" basis was essentially unaltered during the premigratory period. Because of the large dispersion of the individual values there are no statistically significant differences among the means. The 13 per cent increase in the means between April 10 and April 21 thus may or may not be a physiological reality. It is worthy of note, however, that it corresponds in part with the prenuptial molt, which has often been associated with an increase in metabolic rate (Schildmacher, 1952; Wallgren, 1954).

TABLE 3
STANDARD METABOLIC RATE AT 28°C. OF SIX MALE *Zonotrichia leucophrys gambelii*
DURING THE VERNAL PREMIGRATORY PERIOD, 1956

Date	Ml. O ₂ /bird/hr.		Mean R. Q.	Kcal./bird/day	Body weight
	Mean	SD		Mean	Mean
March 24	126.7	20.2	0.79	14.56	26.0 gm.
April 2	129.2	23.2	0.78	14.82	25.6
April 10	120.3	27.5	0.79	13.83	26.0
April 21	136.1	16.9	0.80	15.68	30.7
April 30	132.4	20.7	0.79	15.22	32.9
May 10	130.0	17.5	0.78	14.91	33.8

It should be noted also that the standard metabolic rate of these birds is considerably higher than the minimum standard rate for birds of similar size. The minimum mean rate in 4 weight-matched male *Z. l. gambelii* in November and December was about 8.6 kcal./bird/day (King and Farner, 1961). The higher rate in the present investigations was undoubtedly due to the decreased depth of sleep (Bergman, 1950) and overt nocturnal restlessness associated with the approach and development of *Zugunruhe*. Merkel (1958) discusses this problem in relation to other species. It is not possible to establish, short of anesthetizing the birds, just how much of such an increase is a result of real alteration of maintenance metabolism, if any, and how much is due simply to wakefulness and increased muscular tonus.

Pre-nuptial molt.—No quantitative measurements of the intensity of molt were undertaken. Molt was arbitrarily classed as light, medium, or heavy. In general, birds in light molt had about a dozen feathers in sheaths in the spinal, ventral, or capital tracts. Birds in heavy molt had the pinfeathered appearance characteristic of intensive plumage growth. Although this method of classification is clearly subjective, it provides satisfactory comparative data when applied consistently by a single investigator.

It is evident from inspection of the molt symbols on the weight curves in figure 1

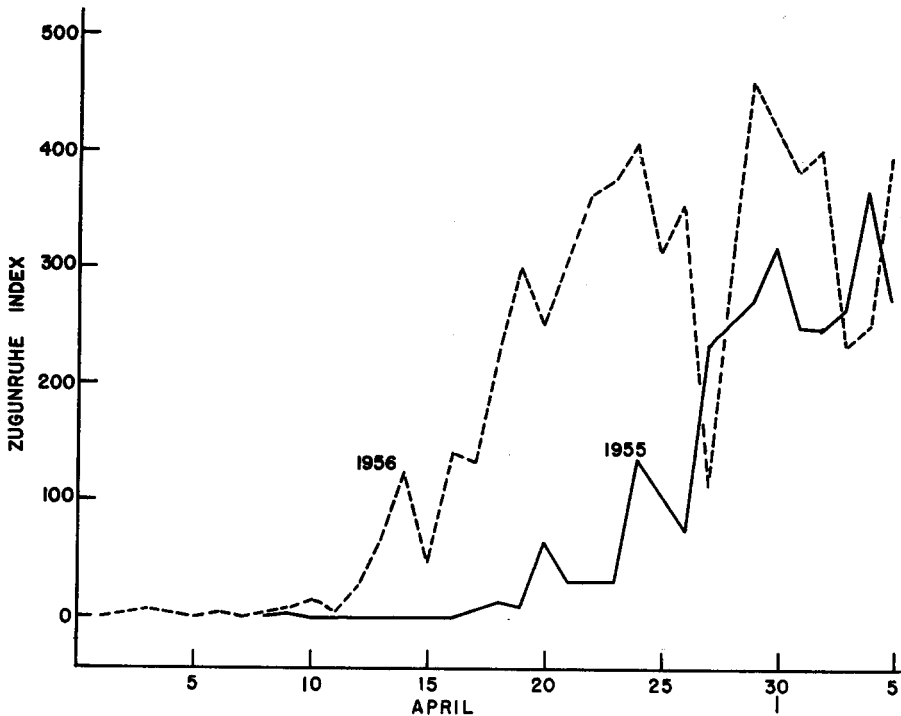


Fig. 2. Average *Zugunruhe* index for six male White-crowned Sparrows.

that the intensity of molt was declining at the onset of vernal fat deposition. By the time the maximum weight was attained, most of the birds had finished the pre-nuptial molt or were showing only very light molt. This appears to agree very well with the sequence observed in wild populations (King and Farner, 1959).

Zugunruhe.—The development of migratory restlessness is shown as the *Zugunruhe* index in figure 2. Although the onset of *Zugunruhe* in several of the birds was quite abrupt, especially in 1955, when environmental temperature was lower, the change in the activity pattern of other individuals was comparatively gradual. In these cases it is difficult to state a definite date for the beginning of *Zugunruhe*. Hence, in order to establish comparative data, *Zugunruhe* is considered to begin in these individuals on the date when the *Zugunruhe* index exceeded a mean value of 100 hops per hour.

It is evident from figure 2 that nocturnal activity began to develop on about April 17 in 1955 and was well established by April 24. The median date for the start of *Zugunruhe*, as determined from the data for individual birds, was April 24 \pm 4 days. In 1956, nocturnal activity began to diverge from premigratory levels on April 12 and more or

less steadily increased after April 15. The median arbitrary date for the onset of *Zugunruhe* was April 17 \pm 4 days. In general, it appears that the development of *Zugunruhe* coincides with an increasing or maximal positive energy balance and with the active phase of vernal fattening. It is clear, however, that the maintenance of *Zugunruhe* is not dependent upon the continuation of a positive energy balance *per se*. The duration of *Zugunruhe* is correlated better with the period of excess reserves of fat. The records for the summer months show that nocturnal activity declines and ceases as the body weight diminishes to its base level in the first half of July.

Ambient temperature.—The mean ambient temperature of the outdoor laboratory is summarized in table 1 for each of the metabolism periods. The mean values were obtained by averaging the daily minimum and maximum temperatures for the period. It can be seen that the premigratory period in 1956 was considerably warmer than in the preceding year. This has caused a general downward displacement of the metabolizable energy curve as a consequence of decreased thermoregulatory expenditure. During the periods associated with the start of fat deposition, the mean temperature was considerably different in the two years of the investigation. In 1955, comparing the periods of April 1 to 10 and April 11 to 20, it is evident that fat deposition started after a large increase in temperature (from -0.1°C . to 5.7°C . during April 1 to 10), but it was concurrent with a period of moderate temperature decline. In 1956, fat deposition was preceded and accompanied by a period of rapidly increasing temperature. It should be noted that the mean catabolized energy, which includes the thermoregulatory expenditure, was relatively stable during these periods.

DISCUSSION

Several hypotheses concerning the energy sources for migratory fat deposition require examination in relation to the present data for the White-crowned Sparrow. It has been recognized generally that a positive energy balance is a prerequisite for any accumulation of fat. Obviously, input must exceed output. The hypotheses which have been advanced to explain all or part of this positive balance appear to fall into one or the other of the following classes: (1) The positive balance results from a premigratory alteration in the partitioning of a more or less constant energy income, that is, a decline in maintenance fractions with a consequent increase in "surplus" energy which may be stored as fat. This may be called the "energy-sparing" hypothesis. (2) The positive balance results from an adaptively increased energy income which periodically exceeds energy output as the birds establish and replenish their fat reserves. There is no reason to regard these concepts as mutually exclusive, although it seems that they previously have been regarded as alternative points of view.

With regard to the first type, Groebbels (1928, 1930, 1932) originated the idea that a premigratory decline in standard ("basal") metabolism spares energy which can be used in fat deposition. However, there is no acceptable experimental evidence that the maintenance metabolism declines during the premigratory period. In the present investigation, the standard metabolic rate was essentially constant during March and April. It is clear also from the data on catabolized energy that there was no amelioration in energy expenditure which could spare calories for fat deposition. In addition, there are good data from other migratory passerines which show that the standard metabolism is not significantly diminished during the premigratory periods (Koch and de Bont, 1952; Wallgren, 1954; Rautenberg, 1957 [cf. King, 1958]; Merkel, 1958).

Another energy-sparing hypothesis is that of Wachs (1926), who proposed that the efficiency of energy utilization increases during the migratory periods. Any such increase,

as measured by the utilization coefficient in the present investigation, will reduce the relative energy cost of food procurement, but the efficiency factor becomes limiting, as is the case with any energy-sparing mechanism, only when some relative limit is placed upon energy intake or the stimulus for energy intake. This may occur during periods of food scarcity or under extreme metabolic stress when the organism has attained the maximum rate of absorption from the gut. The White-crowned Sparrow, even at the northern boundary of its winter range, only rarely encounters the first situation and probably never faces the latter (see Kendeigh, 1949; Seibert, 1949; and West, MS, for data on the limits of energy absorption in small birds). However, in the interests of exploration, the potential contribution of increased efficiency of utilization with constant gross energy intake (28.6 kcal./bird/day) and constant catabolized energy output (20.0 kcal./bird/day) has been assessed. It is assumed that the utilization coefficient increased by 0.33 units/day (equal to the maximum rate of increase in 1955). In this sample, an energy surplus equivalent to about 3.2 gms. of adipose tissue will accumulate during a period of 24 days. The body weight thus hypothetically increases by about 0.13 gms./day. The change in the efficiency function may potentially contribute a small but appreciable fraction of the vernal weight increment and may have done so in the birds studied in 1955. In 1956, however, the utilization coefficient was essentially constant during the premigratory period, indicating that increase in efficiency is not a necessary concomitant of vernal fattening in the White-crowned Sparrow. Other migratory species have not as yet been studied in this regard.

The most prominent of the energy-sparing hypotheses is that first suggested in rudimentary form by Groebbels (1932), fully developed by Kendeigh (1934, 1949), and advocated by several subsequent investigators (Seibert, 1949; Davis, 1955; West, 1960). According to this viewpoint, the surplus energy for storage as fat originates at least in part with (a) the energy-sparing effect of declining thermoregulatory demands as the ambient temperature increases in spring, (b) the energy-sparing effect of the cessation of molt, if any, and (c) the increasing time available for feeding as the daily photoperiod increases in spring. This hypothesis necessarily assumes that there is a significant inertia or "physiological lag" (Davis, 1955) in the regulatory systems which correlate energy intake and energy expenditure. As the intensity of energy-demanding functions declines in spring, it is supposed that energy intake continues temporarily at its former high level because of inertia in the regulatory system.

We submit that the present data for the White-crowned Sparrow cannot be rationalized on the basis of energy-sparing mechanisms or a repartitioning of the energy expenditure during the premigratory period. The major source of energy deposited in fat derives from a marked increase in energy income with constant or slightly elevated energy expenditure (catabolized energy) during the premigratory period. The birds have exhibited a definite hyperphagia (King and Farner, 1956), or increase in appetite, and there has to be an upward shift in the regulated level of body reserves. This is in agreement with data from investigations of the White-throated Sparrow, *Zonotrichia albicollis* (Odum and Major, 1956; Weise, 1956), Slate-colored Junco, *Junco hyemalis*, and Tree Sparrow, *Spizella arborea* (Weise, 1956), Chaffinch, *Fringilla coelebs* (Koch and de Bont, 1952), and the Whitethroat, *Sylvia communis*, and European Robin, *Erithacus rubecula* (Merkel, 1958).

With regard to the importance of increased feeding time with increasing daily photoperiod in spring, it would appear from data presented in figure 3 that this has no marked significance. Energy intake per hour declines in a regular manner, except for the superimposed period of over-eating, and shows no evidence of "physiological lag." Exclusive

of the period of increased intake, the rate of energy intake declines seasonally faster than the photoperiod increases. It is difficult to see how the slow, regular increments in daily photoperiod have any permissive relation to this increase in appetite. It is equally difficult to rationalize the increase in the hourly rate of energy intake on the basis of a "physiological lag" mechanism. Support for this viewpoint comes also from the investiga-

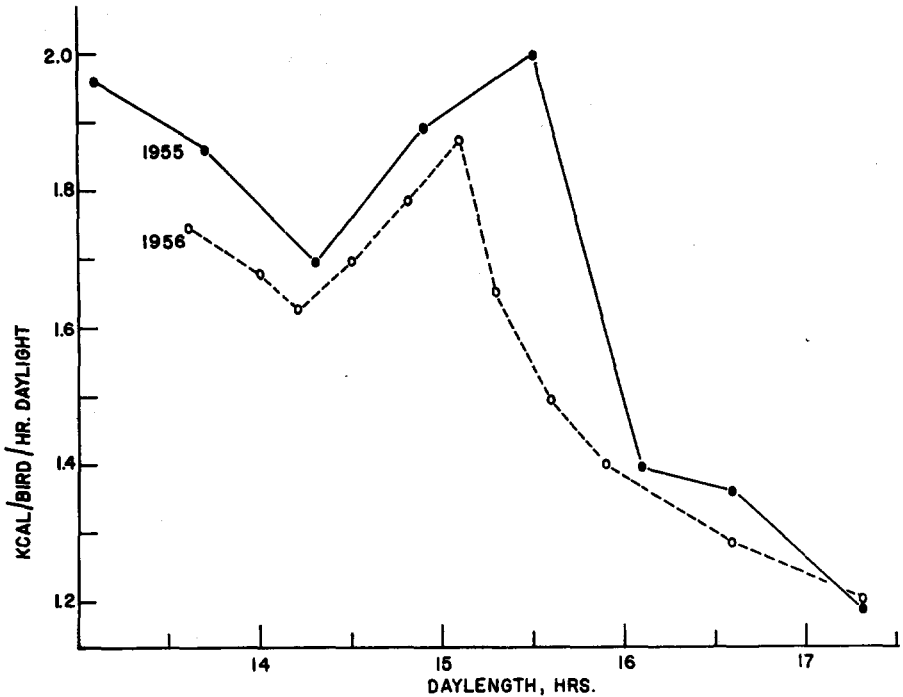


Fig. 3. Average metabolizable energy as a function of daylength (including civil twilight) from March to June in six male White-crowned Sparrows.

tions by Koch and de Bont (1952) of migratory and sedentary races of *Fringilla coelebs* subjected at 10°C. to a photoperiod which was gradually increased from 8 to 16 hours per day. Food consumption by the member of the sedentary race fluctuated around a gradually increasing mean as the duration of the photoperiod increased. This bird did not become fat. In the member of the migratory race there was a definite increase in energy intake which lasted for about 7 days and a corresponding increase in body weight from about 20 gms. to about 28 gms. Although the evidence would be more gratifying if more than one individual of each race had been studied, the data nonetheless show that increased time for feeding is not alone sufficient to induce fat deposition. There must also be the hereditary capacity, which evidently exists in certain migratory species but not in the sedentary ones, for the metabolic response to light stimulation.

It thus appears from the data assembled here that the major source of energy for the establishment of premigratory fat reserves in several species of passerines does not derive from passive sparing mechanisms, but from a strong stimulation of appetite which leads to simple over-eating. The role of energy-sparing mechanisms in other species, particularly those which overwinter in marginal environments, may of course assume

greater importance than is evident in the White-crowned Sparrow. It is widely agreed that migratory fat deposition is an important adaptation in small birds, but different species very possibly emphasize different sources of energy.

Adaptive hyperphagia cannot be demonstrated in the wild population by direct methods. However, we have previously emphasized the striking similarity between wild and captive birds in the events of the premigratory period, including the timing and rate of fat deposition (King and Farner, 1959). There does not appear to be any reason to believe that the metabolic changes which accompany this fat deposition are basically different in wild and captive populations. As a working hypothesis, we therefore assume that adaptive increase in appetite occurs also in the wild population from which we have obtained our experimental birds.

Consideration of the differences in nocturnal work by wild and captive birds, however, leads to the conclusion that the pattern of hyperphagia must be somewhat different in the wild birds and that it must persist throughout the migratory season. The energy expenditure and weight loss of a night of migratory flight must be considerably greater than during a night of *Zugunruhe* in a small cage. In the captives, hyperphagia is detected only during the initial deposition of fat in the premigratory period. After this new level of reserves is established it can of course be maintained without increased intake if the total energy expenditure does not increase. The data on catabolized energy indicate that the total daily energy expenditure is not greatly changed in the caged birds during the period of *Zugunruhe*, and they imply that there is merely a shift between daytime and nighttime expenditure. This situation is very similar to the energetics of "active" and "static" obesity in laboratory mammals (Mayer, 1955).

It should perhaps be emphasized that the negative balance coefficients observed during May and June reflect only the long-term regulation of body reserves around a slowly decreasing mean. Because the metabolism determinations occupied 4- to 7-day periods in the present investigation, the balance coefficient does not provide information about the short-term, day-to-day regulation of energy intake. For this reason we have not directly demonstrated the persistence of hyperphagia in these investigations.

In view of this deficiency, a pilot experiment was undertaken during the period of autumn *Zugunruhe* in 1956. Three male *Z. l. gambelii* which had established migratory fat reserves and which were exhibiting nocturnal activity were periodically starved to a nonmigratory level of body weight (24-25 gms.). It was reasoned that in the absence of some special stimulus to appetite the fat reserves would not be restored. The results of this experiment are shown in figure 4. It is evident that the body reserves were rapidly restored to what appeared to be an increasing maximum as the season progressed, indicating that there was an active regulation of the magnitude of body reserves. The rapidity with which these reserves were restored following depletion can be explained only by the same mechanism of hyperphagia through which they were originally established. This experimental procedure provides a method for detecting the existence of potential hyperphagia and for identifying the regulated level of body reserves. It is desirable that it be applied to the vernal migratory period, together with measurements of energy intake, in order to confirm the inferences made previously.

The pattern of weight variation shown in figure 4 probably conforms qualitatively with what happens in wild birds during migration. Zimmerman (quoted by Wolfson, 1954) stated that *Zonotrichia albicollis* appears to move northward in jumps of at least 300 miles at intervals of 7 to 10 days. Analysis of trapping and retrapping data for this species, however, indicates that the stop-over time is somewhat less, averaging 3 to 5 days (Stack and Harned, 1944; Borror, 1948; Blake, 1950). It may be assumed that the

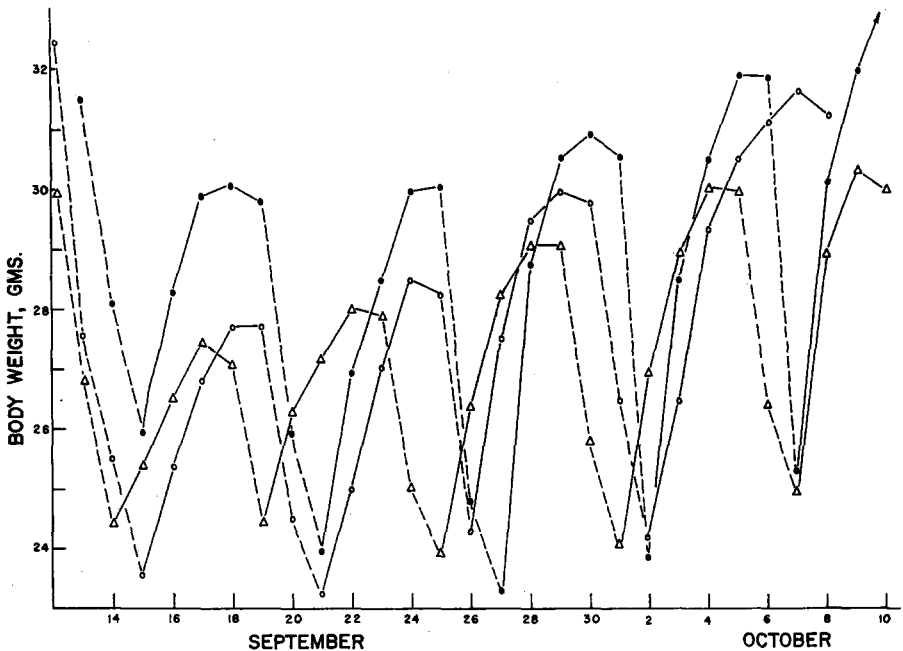


Fig. 4. Variation in body weight of three male White-crowned Sparrows as produced by intermittent fasting (broken line) and re-feeding *ad libitum* (solid line).

birds arrive at the stop-over point in a state of depleted or at least decreased fat reserves. The persistence of adaptive hyperphagia assures that the body reserves will be rapidly restored. Wolfson (1954) has shown that the time required by *Zonotrichia albicollis* to increase its fat deposits from "none" to "heavy" when supplied with ample food is 4 to 6 days, or about the same as the apparent stop-over time. It can be seen from figure 4 that *Z. l. gambelii* can increase its body weight to a maximum in about 3 to 5 days.

SUMMARY AND CONCLUSIONS

Energy intake, energy expenditure, body weight, and nocturnal activity (*Zugunruhe*) were studied in captive males of the White-crowned Sparrow of the race *Zonotrichia leucophrys gambelii* during March to June of two successive years. The birds were exposed out of doors to essentially normal weather conditions and photoperiod.

During the second week of April in both years all of the birds exhibited an abrupt increase in gross energy intake (hyperphagia) and a simultaneous deposition of migratory fat. Total energy expenditure in most birds was practically unchanged during this period, indicating that the only significant source of surplus calories was from the increased intake. Nocturnal activity began several days after the beginning of fat deposition and the termination of the prenuptial molt.

It is emphasized that energy intake and the variation in the level of body reserves are regulated functions. During the premigratory and migratory periods it is evident that the characteristics of the regulatory systems are adaptively altered to provide a much increased level of reserves of fat. One of the obvious elements of this adaptation is a strong stimulus to appetite which probably persists throughout the migratory period and assures that fat reserves will be replenished rapidly during stop-over periods in the migratory itinerary.

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