WEIGHT AND FAT DEPOSITION IN RELATION TO SPRING MIGRATION IN TRANSIENT WHITE-THROATED SPARROWS

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INTRODUCTION

THE results of a series of observations and experiments on the regulative factors for migration in the Oregon Junco (*Junco oreganus*) led to the conclusion that spring migration was induced by a marked change in physiological state (Wolfson, 1940, 1942, 1945). The manifestations of this change included the recrudescence of the gonads, an increase in the secretory activity of the anterior pituitary, the deposition of large amounts of subcutaneous and intraperitoneal fat, and an increase in weight to a maximum. Of these manifestations, the most readily discernible and diagnostic of a readiness to migrate were the heavy deposition of fat and the concomitant increase in weight. Their significance was attested by the fact that individuals of a resident race showed neither marked variation in body weight nor heavy deposition of fat.

To ascertain whether this was true for other resident and migratory species a critical study of the weight data in the literature was made (Wolfson, 1945). The comparable data for six resident species, when interpreted in the light of the studies of the Oregon Junco, corroborated the fact that resident individuals do not show a marked increase in weight in the spring. Comparable data for four migratory species also proved to be substantiating. However the data for three of the migratory species were collected at Berkeley, California, where the initial study of the Oregon Junco was made and where winter temperatures are relatively mild. Inasmuch as the extensive data of Nice (1937, 1938) and Baldwin and Kendeigh (1938) revealed maximum weights in several species of the interior and eastern United States during the winter, but not immediately preceding spring migration, the question was raised whether eastern species, which are subjected to low temperatures in winter, differ from western species in their annual weight cycles. The only comparable data in the literature for an eastern migratory species which I interpreted as corroborative were for the Tree Sparrow (*Spizella arborea*) at Ithaca, New York (Heydweiller, 1935; Baumgartner, 1938). Data from other eastern migratory species although suggestive of confirmation were not conclusive.

To determine whether fat deposition occurs in other eastern passerine migrants, studies of weight and fat deposition in relation to migration were undertaken at Evanston, Illinois, beginning in the spring of 1945. Of particular interest also were the weight and fat deposition of transient individuals. The weight data obtained in the original studies of migrant races of the Oregon Junco were taken primarily from winter residents. Similarly, the comparable weight data in the literature were from winter residents. There were no data to indicate the fate of the large fat deposits during the spring migratory period. This present report is confined to data for the White-throated Sparrow (*Zonotrichia albicollis*) for the three years from 1945 to 1947.

The White-throated Sparrow is a common transient at Evanston. Little is known about its route of migration (Fischer and Gill, 1946). The origin and destination of the individuals which pass through Evanston are not known, but it is not unreasonable to assume for the present that the route of migration is similar to that of other passerines in the Middle West, namely through the Mississippi Valley.

To obtain data for winter resident individuals the coöperation of Dr. Eugene Odum of Athens, Georgia, who is well situated in the wintering range of the species, was invited. The results of his studies have already been published (Odum, 1949, and Odum and Perkinson, 1951). Mrs. Louise de Kiriline Lawrence, who lives in Rutherglen, Ontario, became interested in the problem and volunteered to obtain data from the time of arrival on the breeding grounds until the time of departure in the fall. Her study is still in progress. I am indebted to Dr. Robert A. McCabe of Madison, Wisconsin, who generously turned over to me his data on body weights of White-throats captured at Madison. Miss Vera Fisher helped with the statistical analyses. It is a pleasure to acknowledge her assistance.

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METHODS

The methods employed in capturing the birds, weighing them, and determining their fat class were essentially similar to those in the earlier studies. In 1945 only two sparrow traps were available. The trapping station was set up early in April about one-hundred yards west of Lake Michigan on the campus of Northwestern University. Additional traps were available in 1946 and 1947, making a total of 3 sparrow traps and 22 Potter-style traps. The increase in the number of traps in the last two years, however, seemed to have little effect on the number of White-throats captured. The traps were operated daily with few exceptions from early April until the end of the migratory period, about the first week of June. The daily procedure involved emptying the traps three or four times, once in the morning, once at noon, and twice in the afternoon when the birds were numerous. From the traps the birds were taken to the laboratory, and as soon as possible thereafter they were weighed and other pertinent data were obtained. The interval between the time of capture and weighing varied from one to three hours depending on the time of day. When circumstances prevented weighing them within this interval, the birds were placed in large cages with food and water until they could be examined. Careful records of the time of capture, the time of weighing, and feeding in captivity were kept for all individuals to avoid possible errors of interpretation.

All weights were taken with a Cenco balance with a sensitivity of one-tenth of a gram. After weighing, each bird was banded and the following observations were made: the amount and distribution of fat, the length of the wing, the appearance and size of the cloacal area, and the plumage of the crown, lore, throat, and breast.

To observe the fat deposits, the feathers were blown gently to expose the following regions which were examined in order: area surrounded by the wishbone (furculum), the axilla (under the shoulder joint), the lower back (synsacrum), and the abdomen. The four fat classes which were designated in the studies of the Oregon Junco (Wolfson, 1945: 109) were found to be applicable. These were "none," "little," "medium," and "heavy." In the "none class," fat is not readily visible in the regions mentioned. The best criterion of this condition is the concavity between the clavicles (furculum). When this area is deeply concave, the other regions are usually also devoid of fat. In the "little class," fat can be seen in the furculum, but usually fails to fill it completely. If it is filled completely, the clavicles are still visible. The fat is identified by its yellow color, which contrasts well with the dark or light red color of muscle. In the axilla, lower back, and abdomen small amounts of fat can also be identified. In the "medium class," the furculum is full with some covering of the clavicles; the other regions show an increased amount with some protuberance of the skin in the axilla and lower back. In the "heavy class," the region of the furculum is swollen with fat so that the clavicles and lower neck vertebrae are completely covered. The fat literally seems to have overflowed the original hollow of the furculum. In the axilla and lower back the fat deposits protrude markedly, but by far the greatest change occurs in the abdomen. Whereas before small amounts of fat were visible and the region was normal in appearance, now it appears swollen with fat, which forms a continuous yellow layer throughout.

One of the unusual characteristics of the process of fat deposition is that the fat appears to be laid down in a definite sequence and perhaps at different rates in the regions studied. Moreover, the sequence for deposit is apparently the reverse of the sequence for utilization. The abdominal fat, which is intraperitoneal, is the first to be utilized, but the last to be deposited; that in the hollow of the furculum seems to be retained to the last, but is deposited first. The rapidity with which the products of the intraperitoneal fat could be brought to the hepatic portal circulation might conceivably be a factor in this sequence of utilization.

Since differences in sex and age are known to be correlated with body weight it was important that these be known. Nice (1932) reported that wing length proved to be a valid criterion of sex in the White-throated Sparrow. Measurements were taken in the present investigation, but were of little value for the first two years since the wings were not always measured on the day of capture. Wear in captivity made the measurements unreliable. In the third year, the sex of all birds was determined either by examination of the gonads or by the character of the cloacal area. The cloaca is an unquestionable criterion when the birds are in breeding condition, and this was reached in captivity usually within 3 weeks after capture (Wolfson, 1952). Plumage was of no value in distinguishing the sexes. In the tables the sex has been stated only for the birds captured in 1947.

Although one gains the impression from descriptions of White-throat plumages that there is an adult type, it was soon apparent from examining the plumages of spring and breeding birds and the few data in the literature, that we do not know exactly what characterizes the plumage of an "adult" White-throat. Nor do we know the sequence of plumages. On the assumption that the type of plumage of the head and breast may be correlated with age differences, the plumage of these regions was recorded. Fundamental differences were found in the crown, lore, throat, and breast. In many instances the variations occurred in specific combinations, thereby establishing definite patterns which could be easily recognized. In other cases, the mixture of characteristics defied classification. A complete analysis and discussion of the problem will be presented at a later date. For the purposes of the present paper three classes have been designated: "adult," "intermediate," and "immature." The significance of these classes is not known, but the differences in plumage were too marked to be overlooked in the analysis of the data. In the present state of our knowledge it seems likely that age differences would account for some of them, but it is also possible that sexual and racial factors are involved.

Birds classified as "adult" showed the following characteristics: crown with black lateral and white central stripes; yellow portion of superciliary stripe bright in color and extending as far back as the middle of the eye; chin, upper throat, and malar region white; lower throat and upper breast uniformly dark gray, sharply delimiting the white of the upper throat. For the "immature class" the following characteristics pertain: crown with brown lateral stripes and buffy central stripe; yellow of superciliary stripe absent, or just a tinge restricted to the region at the base of the bill; throat region light gray, separated from malar region by a prominent dusky streak; malar region flecked or barred with dusky; lower throat and breast dull buffy gray, not sharply demarcated from upper throat, often mottled or streaked with dusky. The birds classified as "intermediate" showed numerous gradations between these two extremes. The lateral stripes of the crown, for example, were a mixture of brown and black with some tending to be predominantly black, others predominantly brown. The central crown stripe was either a buffy white or light gray with flecks of dusky. The yellow of the superciliary line was dull and restricted in extent. In many instances one could readily determine whether an intermediate bird possessed plumage more like that of the adult or immature, but in others there were no such tendencies. Birds were also placed in the intermediate group when a mixture of characteristics occurred that was not necessarily gradational. For example, the crown stripes and yellow area may have been of the adult type, but the throat and breast showed immature characteristics. This meant that the intermediate group was the most heterogeneous of the three, but at least by placing these birds together, the other two groups would in effect be more homogeneous and consequently more reliable for comparison. In the text and tables the terms adult, intermediate, and immature are listed for convenience under the heading of "age" and refer to the classes just presented.

The data were studied in two basic ways. First, variations in body weight were analyzed in relation to the date of capture. The determination of mean body weight in relation to a particular season, month, or phase in the annual cycle has been the usual approach in other studies. This method, therefore, will permit comparisons with these other studies. Second, body weight was analyzed in relation to the classes of fat deposition, sex, age (plumage types), and date of capture. This method revealed how uninformative, and occasionally misleading, a knowledge of variation in body weight alone could be.

In order to improve our understanding of the weight variations in premigratory and transient birds, it was deemed worth-while to follow the changes in body weight and fat deposition in captive birds during the winter and spring at Evanston. Accordingly, ten birds were captured during the fall migration of 1946 and were housed in small cages in an unheated room until June of 1947. A maximum and minimum thermometer was used to determine the daily range in temperature. The birds were fed unmixed canary seed, millet seed, dried insects, and dog food. Food, water, cuttlebone, and gravel were available at all times. The data for these birds have been analyzed in two ways, by actual change in weight and by percentage change.

RESULTS

Variations in Weight during the Period of Migration.—The variations in mean weight at Evanston are recorded for intervals of three days for the three years in table 1. The mean weights for the three years are remarkably similar and range from 27.1 gms. to 27.6 gms. The variation in mean weight for the individuals captured during three-day periods are minor for the most part and irregular. The percentage differences between these means and the mean for each year are small in most cases. In some instances the differences are larger and suggest that a difference in mean weight can be expected in birds arriving at different times during the migratory period, but there does not seem to be an obvious correlation between high and low body weights and the time of migration. When fairly good numbers were trapped in a given three-day period, the mean body weight for that period tended to approach the average for the entire period of migration.

TABLE 1

MEAN WEIGHT DURING PERIOD OF MIGRATION IN WHITE-THROATED SPARROWS

	Evanston, Illinois				*Madison, Wisconsin*		
	1945	*1946*	*1947*		*1943*		*1946*
Date	*Weight*	*Weight*	*Weight*	*Date*	*Weight*	*Date*	*Weight*
Apr. 25–27	26.8 (3)	—	—	—	—	Apr. 23	27.9 (18)
Apr. 28–30	27.5 (1)	—	28.1 (3)	—	—	Apr. 24	28.4 (12)
May 1–3	—	—	22.6 (3)	—	—	Apr. 25	29.5 (9)
May 4–6	—	25.9 (3)	—	May 4	28.6 (11)	Apr. 26	28.7 (9)
May 7–9	25.7 (11)	26.4 (6)	29.8 (5)	May 5	30.4 (12)	Apr. 30	28.6 (8)
May 10–12	29.6 (5)	27.9 (10)	29.1 (5)	May 6	28.9 (29)	May 1–6	29.0 (5)
May 13–15	27.3 (12)	27.7 (6)	22.7 (2)	May 7	29.4 (11)	May 7	27.9 (16)
May 16–18	30.9 (5)	26.3 (5)	31.2 (2)	May 8	26.3 (8)	—	—
May 19–21	—	—	24.0 (3)	May 9	26.6 (7)	—	—
May 22–24	—	—	27.2 (14)	May 10	29.3 (16)	—	—
May 25–27	—	—	—	May 12–14	28.9 (8)	May 13	29.5 (4)
May 28–30	—	—	24.8 (2)	May 17–19	27.7 (7)	—	—
All dates	27.6 (37)	27.1 (30)	27.1 (39)		28.7 (109)		28.5 (81)
	(Mean weight 1945–7: 27.3 (106)						

Numbers in parentheses indicate numbers of individuals.

Also in table 1 similar data are presented for birds captured at Madison, Wisconsin, in 1943 and 1946. These data also show a remarkable similarity in mean weight for the two years. The means for each day again show small variations from the overall mean.

Taking all the data into account, it seems clear that the mean weight for the entire migratory period tends to be the same each year in a given locality. The mean weight for each day, or a period of a few days, will vary, but when a good number of birds is trapped each day, the differences are small.

Variations in Weight in Relation to Fat Class, Sex, and Age.—The mean weight at the time of capture for each of the fat classes was calculated according to plumage types for 1945 and 1946 and for plumage types and sex for 1947. The numbers of individual were small in almost all categories, and for some categories no data were available. Because of this the data for the three years have been com-

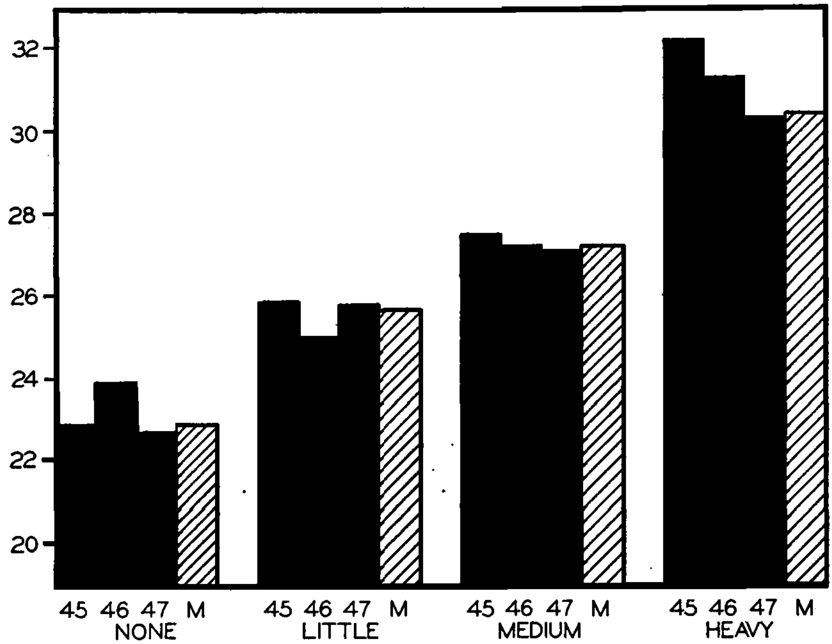

FIGURE 1. Mean weights of transients for each of the fat classes for each year and for the three-year period of study. Weights are in grams; M indicates the mean for the three-year period.

bined and are presented in tables 2 and 3 and in figure 1. In table 2 mean weight for each of the fat classes is presented. A statistical test of the difference between the means (t test) shows that the difference between all the means is significant at the 1 per cent level except the difference between the "medium" and "little" fat classes. The difference between these classes is significant at about the 5 per cent level. In actual practice these two classes are the most difficult to separate. In table 3 the weight is analyzed in relation to age for each fat class. The data show that the mean weights of all the adults and intermediates are similar in each fat class. The differences between the totals for each of these two groups and for the immatures are significantly different (1 per cent level) throughout. In the "heavy" and "medium" fat classes the differences between the same groups (adults and intermediates versus immatures) are also significant (1 per cent level). In the "little" fat class the means are similar. In the "none" fat class the numbers are too small for comparison.

Fat Classes and Plumage Types in Relation to Date of Capture.—Birds with "no," "little," "medium," or "heavy" deposits of fat can arrive at any time during the migratory period. In 1947, when the sexes were known, the data show an earlier arrival of the males in all fat classes.

TABLE 2

MEANS AND EXTREMES OF WEIGHT OF FAT CLASSES AT TIME OF CAPTURE, 1945–1947

Year		*Fat Class* *Heavy*	*Medium*	*Little*	*None*
1945	Mean	32.14 (11)	27.43 (6)	25.93 (15)	22.88 (5)
	Extremes	28.8–36.6	24.9–28.7	24.6–27.5	21.8–23.7
1946	Mean	31.24 (5)	27.15 (16)	25.04 (7)	23.90 (2)
	Extremes	30.0–32.2	23.3–31.1	23.1–26.9	22.0–25.8
1947	Mean	29.24 (22)	27.10 (4)	25.80 (5)	22.65 (8)
	Extremes	25.5–34.8	25.5–30.4	23.7–28.0	18.8–26.4
1945–47	Mean	30.34 (38)	27.20 (26)	25.67 (27)	22.89 (15)
	Extremes	25.5–36.6	23.3–31.1	23.1–28.0	18.8–26.4
Standard deviation		2.66	1.64	1.32	1.98
Standard error of mean		0.457	0.331	0.258	0.529
Percentage increase from None class—all records		32.5	18.8	12.1	—
Percentage increase from lower preceding class		11.5	6.0	12.1	—
Percentage difference from mean wt. (27.33) of all records		+11.0	−0.5	−6.1	−16.3

Numbers in parentheses indicate numbers of individuals

TABLE 3

MEAN BODY WEIGHT IN RELATION TO FAT CLASS AND AGE, 1945–1947

	Heavy *Ad.*	*Inter.*	*Imm.*	*Medium* *Ad.*	*Inter.*	*Imm.*	*Little* *Ad.*	*Inter.*	*Imm.*	*None* *Ad.*	*Inter.*	*Imm.*	*Totals* *Ad.*	*Inter.*	*Imm.*
No.	15	14	9	11	10	5	8	11	8	7	5	3	41	40	25
Mean	30.9	31.4	27.9	27.9	27.1	25.9	25.8	26.1	25.0	22.8	24.3	20.8	27.7	27.9	25.7
S.D.	2.26	1.13	1.57	1.37	2.13	1.07	1.25	1.38	0.9	1.49	1.58	1.49	3.55	3.07	2.51
S.E.	0.60	0.31	0.55	0.43	1.46	0.54	0.47	0.44	0.37	0.61	0.79	—	0.56	0.49	0.51

The data for plumage types are presented in table 4. They show clearly a tendency for adult types to arrive first, followed by the "intermediates," with the "immatures" arriving last. There is considerable overlap, because of a sex difference to some extent, but it remains for future work to establish the sequence of migration for each sex of each plumage type.

Changes in Weight of Captive Birds.—In figure 2 the changes in weight are shown. The dates of weighing are indicated by the vertical lines, and the points on each date line represent the mean weights of the individuals in each group. There were 3 adult males, 3 immature males, and 4 immature females. The adult male group included 2 birds that were intermediate in plumage.

The data show a gradual increase in weight in the adult males from the beginning of the experiment, and on January 27 they were about

TABLE 4

FREQUENCY OF AGE TYPES DURING THE PERIOD OF MIGRATION, AT EVANSTON, 1945–1947

	Age								
	Adult			*Intermediate*			*Immature*		
Date	*1945*	*1946*	*1947*	*1945*	*1946*	*1947*	*1945*	*1946*	*1947*
Apr. 25	1	—	—	1	—	—	—	—	—
Apr. 26	—	—	—	1	—	—	—	—	—
Apr. 28	1	—	—	—	—	—	—	—	—
Apr. 29	—	—	—	—	—	1 (♂)	—	—	—
Apr. 30	—	—	2 (♂♂)	—	—	—	—	—	—
May 1	—	—	3 (♂♂)	—	—	—	—	—	—
May 6	—	—	—	—	2	—	—	1	—
May 7	—	1	—	—	—	4 (♂♂)	—	—	—
May 8	—	—	—	—	2	1 (♂)	—	—	—
May 9	5	1	—	3	2	—	3	—	—
May 10	1	—	3 (♂♂)	1	1	1 (♂)	—	—	—
May 11	—	4	—	1	1	—	—	3	—
May 12	1	1	1 (♀)	1	—	—	—	—	—
May 13	2	—	—	7	—	—	3	—	—
May 14	—	2	—	—	1	—	—	1	1 (♀)
May 15	—	—	—	—	1	1 (♂)	—	1	—
May 16	1	1	—	2	2	1 (♀)	1	—	—
May 17	—	1	1 (♀)	—	1	—	—	—	—
May 18	—	—	—	1	—	—	—	—	—
May 21	—	—	3 (♀♀)	—	—	—	—	—	2 (♀♀)
May 23	—	—	1 (♀)	—	—	—	—	—	5 (♀♀)
May 24	—	—	4 (♀♀)	—	—	—	—	—	2 (♀♀)
May 30	—	—	—	—	—	1 (♀)	—	—	1 (♀)
Totals	12	11	18 (8♂♂–10♀♀)	18	13	10 (8♂♂–2♀♀)	7	6	11 (♀♀)

6 gms. heavier than at the start. The immatures of both sexes varied slightly during this same period, and on January 27 their weights were about the same as their initial weights; from January 27 or 29 to February 8 there was a sharp increase in the weight of the males and a smaller one in that of the females. On the latter date, the males reached their maximum mean weight for the entire period of captivity —34.9 gms. for the adults, and 30.9 gms. for the immatures. The mean weight of the females reached a peak of 28.2 gms. on February 8, but this was exceeded by the premigratory peak of 29.5 gms. After February 26 the weights of all groups began to decrease gradually, and the immatures continued to lose weight until by April 30 their weights were markedly lower than the peak of February 8. From April 30 to May 16 the most marked change occurred in the immature females, which showed an average increase in weight of 6.4 gms. The immature males showed a slight increase (+ 1.7 gms.), and the adult males a slight decrease (− 2.7 gms.) From May 16 to June 10 previous weights were in general maintained. It is interesting to note that the initial mean weights of the three groups were similar and ranged from 25.7 to 26.5 gms.; the final weights were also similar and

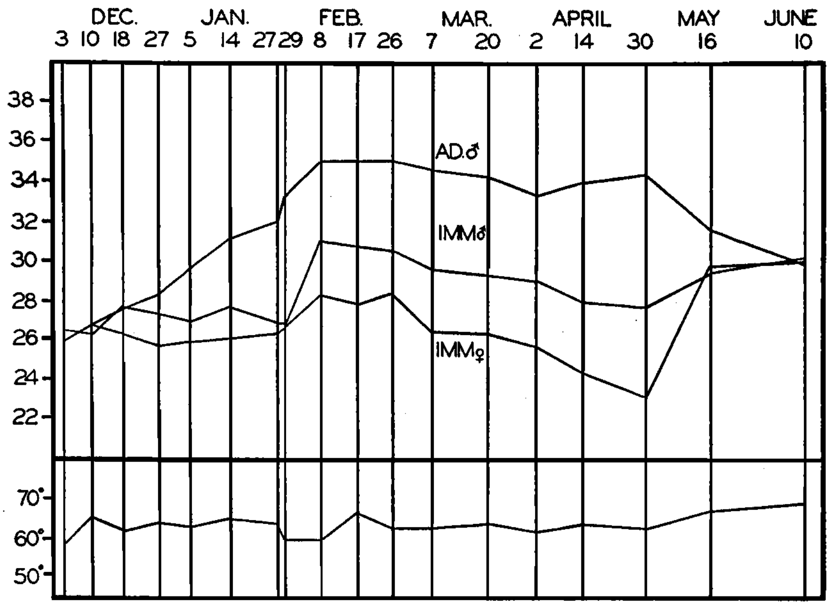

FIGURE 2. Changes in weight of captive birds, December to June. Weights are given in grams. Temperatures are in Fahrenheit and represent the average of the mean daily temperatures for the period preceding the date of weighing.

ranged from 29.9 to 30.0 gms. It was exactly the same at 29.9 gms. for the two groups of males.

When one considers the percentage change from the initial weight of December 3, it is seen that there was an increase of about 35 per cent in the adult males by February 8. An increase in the weight of a bird of about one-third of its original weight is, biologically speaking, a marked change. In this case, the increase in weight is clearly associated with a marked deposition of fat. In the immatures the changes in weight from December 3 to January 27 varied within 5 per cent of the initial weight. Judging from the many birds that we have handled in the laboratory, differences of this magnitude are well within the normal range of daily variation in captive birds, and they are not regarded as significant variations. The change from January 27 or 29 to February 8 was about 17 per cent in the immature males and 10 per cent in the immature females and is significant. The increase in the immature females from April 30 to May 16 of about 28 per cent was also significant.

In view of the fact that "mean" figures obscure the extent of response in individuals, especially in a group where variations in time of response occur, the following summary is presented. The adult males showed the most marked increase in weight in winter: 25.9, 34.0, and 47.1 per cent. The increase in the immature males was moderate: 12.0, 18.6, and 19.1 per cent. In the immature females it was marked in one bird, 34.2 per cent, and moderate in the others, 7.1 and 19.1 per cent. Where the data permit comparisons between winter and spring increases (four birds), they show that the spring increases are higher, with one exception. The average of the per cent increases in spring for these four birds was 33.75 (range: 28.0–40.0); in the winter it was 19.87 (range: 7.1–34.2).

The observations on fat deposition in these captive birds indicate that in most cases marked changes in weight were correlated with changes in fat deposition. The major exception to this was the birds which showed excessive amounts of fat. They had so much fat that they could lose weight and fat and still remain in the "heavy" fat class.

DISCUSSION

Mean Weight before and during Migration.—The mean weight of all the White-throats captured at Evanston during the period of spring migration was 27.3 gms. For each of the three years the means were, respectively, 27.6 gms., 27.1 gms., and 27.1 gms. The means for two years at Madison, Wisconsin, were 28.7 and 28.5 gms. These data agree closely with some of the results of other investigators. Baldwin and Kendeigh (1938) report a mean of 28.7 gms. for 16 individuals in April and a mean of 29.4 gms. for 90 individuals in May. Nice (1938) reported a mean of 28.6 gms. for 35 birds captured during the spring migration. When sexes were differentiated by the size of the wing, the mean for the males was 29.4 gms. (17 birds) and for the females 26.4 gms. (18 birds). Becker and Stack (1944) found a mean weight of 27.2 ± 0.1 for 375 birds. In all of these cases the birds were transients.

Odum (1949) studied winter residents. The mean weight for the entire period of winter residency is not given, but it is given for each month and half-month for each sex. The data show that there are sex differences in weight and that there are two peaks in weight, one in midwinter and one in the spring just prior to migration. This is also shown in the record of the 10 captives herein reported. Odum's weights for each month for the males range from a low of 26.0 gms. in October to 29.8 gms. in April. The weights in grams for the months between are in order, 27.0, 27.0, 28.9, 28.7, and 28.1. The difference between March and April means is 1.7 grams. The mean weights for each month and half-month obscure the marked increase in weight which occurs in individuals just prior to migration. The greater quantitative response in our captive birds is to be expected since we were following the same individuals. Odum was using the mean weight of a varying "population." The conditions of captivity may also be a contributing factor.

When we compare our figures for mean weight (of captive birds) with Odum's, we find that our maximum winter increase was 22.4 per cent (5.8 gms.) for all birds as compared with 11.2 per cent for his males and 10.2 per cent for his females. In Georgia, the weights began to decrease during the latter half of February, reached a minimum in the first part of March, and remained about the same through early April. In the latter half of April only the males showed a marked increase in weight, but the increase in mean weight over the first half of April was only 2.3 gms. In the males at Athens, the difference between the spring maximum and the lowest weights of October and November was 4.0 gms., or about 15 per cent. In our birds the comparable figures for all birds (using mean body weights) would be 4.1 gms. and 15.8 per cent. However, it is evident from the earlier discussion of the responses of individual captive birds, that these figures, despite their remarkable agreement, are far from an accurate measure of premigratory increase in weight. The failure to find a marked increase in weight in the females at Athens can be accounted for by the failure to retrap the birds at the proper time, or as Odum and Perkinson (1951) have suggested, by the arrival of lean, immature transients from farther south which depressed the mean weight. Our data show quite clearly that immature females are *capable* of depositing large amounts of fat in the premigratory period. It is likely that they do so in nature before migrating, but whether they do still remains to be determined on the wintering grounds. If birds are collected, however, it is obviously impossible to say whether they deposited fat before migrating.

Odum showed in his study that the winter increase in weight was correlated with changes in temperature, and he concluded ". . . that temperature is a factor, perhaps the chief one, in bringing about the winter increase." In our study the adult males began their increase in weight when the mean temperature was above 60° F. In the immatures the marked increase in weight began after a slight drop in temperature. There is certainly good reason to suspect that the winter increase in weight is stimulated by low temperatures. On the other hand, there is reason to doubt that it is the only factor involved. The birds in captivity showed remarkable increases in weight and yet the temperatures were certainly moderate. I think that the short photoperiod of winter may also be a factor.

It was found by experimentation (Kendeigh, 1934) that heavier birds had a greater resistance to low air temperature, whereas lighter birds tolerated high air temperature for a longer time. From this observation it was argued that heavier individuals of a species should arrive earlier in the spring, while in the fall the reverse should be true. Furthermore, upon analysis a relation between weight and time of migration was found for the White-throated Sparrow and the White-crowned Sparrow (*Zonotrichia leucophrys*) in the spring and in the fall at Gates Mills, Ohio. The average weight for the first half of the spring migration period was found to be greater than in the last half. In the fall the reverse was true. Although some of the differences are small and of questionable significance, there is no doubt about their existence. What is open to question, however, is the interpretation of the differences. On the basis of our studies and Odum's data it seems more likely that the higher mean weight in the first half of spring migration is due to the preponderance of males. The females, and especially the immature females, which come later, weigh less. In the fall the sequence is reversed, with the immatures migrating first. Kendeigh states (1934: 364) that no distinction was made between age and sex in analyzing the data, because it was shown that temperature resistance is not influenced by these factors. I do not mean to imply that there is no relation between body weight and temperature, but wish only to emphasize that interpretations of data on mean weight are open to question when other variables such as sex, age, fat deposition, and previous migratory behavior and expenditure of energy are not known. Similarly, when mean weights for a particular season are compared in different years to determine the effect of temperature, one must know the composition and properties of the population for each year. If one captured more adults, or more males, or more individuals that were fattening up before departure, or more lean individuals that had just arrived, the mean weight in one spring might be significantly different and correlated with differences in mean temperature. The slight differences in mean weight which have been reported by various authors could be explained by variations in treatment of birds before weighing, or by differences in the composition and properties of the population as described above.

Another weakness of calculating the mean weight for a given period of time is that it may mask or distort important information. For example, if one studied variations in weight in a winter resident population in a species in which transients also passed through the area of study and then determined the mean weight for each month, the data might show a decrease in mean weight before the species left the area. But if the winter residents could be analyzed separately for each week, they might show an increase in mean weight before departure. The decrease shown in the analysis by months could well be due to an influx of transients and the concomitant use of too large a time unit. For example, see the discussion of Baumgartner's data on the Tree Sparrow (Wolfson, 1945: 113–115). In a similar vein, Odum missed the premigration increase in weight in the White-throat in his preliminary study because not enough individuals were obtained during the critical period of late April. Also, by averaging the weights for each month and half-month the marked increase in weight which occurs in late April was obscured.

In summary, the mean weight of a group of White-throated Sparrows (and other species) is of little dynamic value. Interpretations based on it are open to question unless other variables are known. The variables which seem to be important so far are age, sex, fat deposition, and previous migratory behavior. When calculating the mean body weight for a period of time, the best procedure is to use the smallest time unit possible. The month and half-month are usually not adequate. Analysis by days or weeks is best when the data are available.

Weight in Relation to Fat Deposition.—The ease with which transients can be segregated into fat classes, the significant differences in the mean weights of these classes, and Odum's data show clearly that fat deposition occurs in the White-throated Sparrow in relation to spring migration. Other studies (Wolfson, 1947) indicate that this fat deposition can be induced experimentally in December and January by subjecting the birds to increases in day length. The White-throated Sparrow, therefore, seems to be similar to the Oregon Junco and other species (Wolfson, 1945) with respect to fat deposition and increase in weight prior to spring migration.

The percentage differences between the various fat classes and the "none" class for all of the White-throats captured at Evanston were as follows: +12.1 for the "little" class, +18.8 for the "medium" class, and +32.5 for the "heavy" class. In the Oregon Junco and in the race *pugetensis* of the White-crowned Sparrow (Wolfson, 1945) the comparable figures (for males only) are, respectively, +5.3 and +4.5 (little class), +10.7 and +8.6 (medium class), and +18.7 and +15.3 (heavy class). The figures for the White-throat are not comparable with those for the other species since they are based on transient individuals of both sexes. The others are based on winter resident males primarily. Moreover since the lowest weights are found in transients in the "none" class and the percentage increases are based on this figure, the increases in the White-throat are much greater than they would be if winter residents were used. The mean weight of White-throats in the "none" class which are not recent transients is about 26.0 grams. When this figure is used instead of the figure for recent arrivals, the percentage increase for the "heavy" fat class in the White-throat would be 16.5.

Blanchard (1941) determined the mean weight of various fat classes in adult male White-crowned Sparrows of the race *pugetensis*, as follows: 26.8 gms. (none), 28.0 gms. (little), 29.1 gms. (moderate), 29.3 gms. (fat), and 32.6 gms. (very fat). The difference between the "very fat" and the "none" class is +21.6 per cent. In the race *gambelii* (Blanchard and Erickson, 1949) the means of the "none" and "very fat" classes (adult males) at Davis, California, were respectively, 24.6 gms. and 27.8 gms. The percentage difference is +13.0. At Santa Barbara, California, the comparable figures are 25.7 gms., 30.1 gms., and +17.1 per cent for the same race; the increase is exaggerated by the fact that only 4 individuals were in the "very fat" class.

Odum and Perkinson (1951) did not classify their White-throated Sparrows according to fat deposits, but they determined the actual amount of fat present. The average premigration amount of fat was 16.5 per cent of the total weight, whereas in October and November, and March and early April, when there is the least amount of fat, the amount extracted was about 6 per cent of the total weight. The premigration increase, therefore, was about 10 per cent. It was higher in the males (about 12 per cent) than in the females (about 8 per cent). This percentage difference seems low when compared with the differences in weight, but the calculations are different and are not strictly comparable. If one considers only the amount of fat in the premigratory males, which was about 18.8 per cent of the total weight, and compares this with the increase in mean weight in the "heavy" class for male Oregon Juncos (+18.7) and White-crowned Sparrows (+15.3), the percentage increases are quite similar.

In summary, the amount of fat in some passerine birds can be estimated and the birds classified accordingly. By comparing them one gains a clearer picture of the changes in weight prior to and during migration than when one considers mean weight without reference to fat deposition. One can extract the fat and determine the actual amount, although I would judge from Odum and Perkinson's data and my data that observations on subcutaneous and intraperitoneal fat in relation to body weight are reliable and can be used in studies of living birds. Sex differences have been clearly established by Odum and Odum and Perkinson. My data are confirmatory and suggest also that there are age differences.

Weight and Fat Deposition in Relation to Migration.—The real value of the data on the variations in weight and fat deposition lies in their contribution to the understanding of the regulation and conduct of migration. What happens to the heavy, premigratory fat deposits and to weight during the period of migration? On the wintering grounds at Athens, Georgia, the weights in October and November and in March and early April, when the birds show the least amount of fat, are 27.2 and 26.6 grams, respectively. These birds are probably comparable to those at Evanston which are classified as having little fat and whose mean body weight is 25.6 grams. Birds arriving at Evanston without fat have a mean weight of 22.9 gms. The difference between this mean and the mean weight before migration (31.5 grams) at Athens, Georgia, is 8.6 gms. The difference between the means of the "none" and "heavy" fat classes at Evanston is 7.4 gms. My interpretation of these data is that a White-throated Sparrow has about 8 grams of "body tissue" which can be used to provide energy for long migratory flights. If all this tissue were fat, the maximum amount of energy available would be about 72 calories. Of course, some energy would be used for maintaining normal body functions, but in a flight during one night this amount would be small compared to the amount utilized for flying. In Odum and Perkinson's determinations (1951) the average amount of fat extracted in the premigratory period was 5.2 gms. for both sexes. In the males it was 6.4 gms.; in the females it was 3.9 gms. The largest amount extracted was 7.7 gms. in a male. Taking into account the variables in the methods of extraction and determining body weights, there is remarkably good agreement in the amount of fat extracted and the maximum loss in weight observed in transients at Evanston.

If we assume that 50–70 calories are available for one flight, how far could a White-throat fly? Many factors enter into such a calculation. I have sent some specimens and data to Dr. Charles Blake who will undertake to make the calculations. However, some observations permit speculations at the present time. Siebert (1949) found that the metabolizable energy in captive White-throats in the fall was about 18 calories per bird per day, at a temperature of 22° C. and for a 15-hour photoperiod. If we assume that this represents approximately the rate for birds in the spring and that a White-throat consumes 6 to 8 grams (54–72 calories) of stored fat during a night flight of approximately 12 hours, the energy consumption would be about 6 to 8 times the normal daily requirements. Considering that not all birds arrive without fat and at the minimum weight, and other variables, I would judge this figure to be a maximum. If the arrival weight of the birds in the "little" fat class is used (25.6 grams) the energy consumed would be about 45 calories. This would be about 5 times the normal daily requirement.

Using an energy expenditure of 1.0 calories per hour at rest, and assuming a rate 6 times greater during a migratory flight at a speed of about 30 miles per hour, a White-throat would be able to fly non-stop about 9 hours on 6 grams of fat, or a distance of about 270 miles. With 8 grams of fat, a bird would be able to fly almost 12 hours or a distance of about 360 miles. These calculations are based obviously on many assumptions and do not take into account the presence of strong tail or head winds, which can modify greatly the distance traveled.

It is interesting to compare these calculations with some observations of Pearson (1950). He found that in the Allen Hummingbird (*Selasphorus sasin*) the rate of metabolism of hovering birds was about 6 times the resting rate. In the Anna Hummingbird (*Calypte anna*), it was about 5½ times the resting rate.

It is evident from our data that only a small proportion of the birds which arrive in Evanston have reached the minimum weight. During the three years the numbers of birds trapped in each fat class were: none, 15; little, 27; medium, 26; and heavy, 38. On many days a number of birds in each fat class was caught. More data at various points along the migratory route are needed, but for the present the following assumptions may be made. The birds which arrive in Evanston after a long flight during the previous night are low in weight and show little or no fat. These birds feed in the area for a day or two, or longer, depending on how long it takes to deposit a medium amount of fat or restore their weight. During this period some birds move out of the area of arrival as they forage, but they do not undertake a long flight at night. After achieving a heavy fat deposition, the birds are ready for a long flight, which takes place when the weather or other conditions provide the necessary stimulus.

In our study, the transient birds were not released after capture but were held captive to follow their weight response (Wolfson, 1954). The data from them show clearly that the birds with no fat or little fat at the time of capture gained weight rapidly, while those with medium or heavy fat deposits lost weight. The maximum gain in weight for the "none" class was about 15 per cent; the maximum loss in weight for the "heavy" class was about 25 per cent. It is also important to note that after the birds in the "none" class had reached their maximum weight in the first week in captivity, they began to lose weight. They lost eventually about 22 per cent of their maximum weight, which agrees closely with the 25 per cent loss in the "heavy" class and with the 24.4 per cent difference in weight between the birds arriving with "heavy" fat and "no" fat. Whether birds in nature will show similar responses remains to be determined. One of the great weaknesses in studying the weight and fat deposition in transient "repeats," however, is that the birds may be in the area and not be retrapped. If they are not retrapped, one would not know whether they are foraging nearby or whether they have undertaken a major flight. The weight before "departure," therefore, would be difficult to ascertain. These weaknesses can be overcome by the accumulation of many data of the type reported here and their correlation with data on time of occurrence in different localities.

Borror (1948) has analyzed the repeat records of White-throated Sparrows at Columbus, Ohio. His data suggest that non-repeating birds probably stayed more than a day. The repeating birds in the spring stayed an average of 5.3 $\pm$0.3 days. Stack and Harned (1944) report an average stop-over period of 4.5 $\pm$1.56 days at East Lansing, Michigan. In Borror's study the average per cent repeating in several spring seasons was 48.5. In Stack and Harned's study the average was 24.0. Is there any relation between stop-over time and the rate at which White-throats deposit fat? In our laboratory studies we have determined that a bird can put on as much as one gram of weight per day and advance from the "none" class to the "heavy" fat class in 4 to 6 days. When birds (White-crowned Sparrows) with heavy fat deposits were starved until their minimum weights were reached and then given food again, they restored their weights at a rate of about 2 grams per day. In three days some birds had returned to the heavy fat class. In experiments in which spring fat deposition was induced by manipulating the day length, the records for some individuals indicate that a maximum fat deposition can be achieved in four days. In one experiment the average for seven birds was 7 days $\pm$3 (Wolfson, 1953). Under natural conditions, it is difficult to determine the amount of time it takes to achieve a heavy fat deposition since the same individuals are not always captured at the right time. It is clear though from Odum's study that fat deposition occurs rapidly. He states that it "may occur within 7 to 10 days, or perhaps less," but the data presented indicate only that it occurs within the last two weeks in April and primarily between April 15 and 25 for the male population. In the White-crowned Sparrow under natural conditions Blanchard and Erickson (1949) reported that most of the increase in fat occurs quickly within 12 days before departure.

These data on stop-over time and the amount of time required to deposit large amounts of fat are still too meagre for definitive conclusions, but when considered along with the weight data and observations on fat deposits in transients, we can begin to formulate a more precise picture of the process of migration. For example, in the White-throat, the stop-over times reported so far would be long enough to permit birds of minimum weight to restore a large part of their fat deposits. Weather conditions and available food supply would of course be important factors in regulating the rate of response. Those birds that do not repeat are perhaps those whose weights are not at a minimum on arrival. It would be interesting to see an analysis of "repeats" in terms of initial weight and fat deposition. Studies of captive White-throats (spring transients) suggest that "repeats" might be primarily birds that have no fat on arrival and are near their minimum weight.

Movements of a species during spring migration can also be correlated with data on weight and fat deposition and may yield valuable information. For example, in a coöperative study of the movements of White-throated Sparrows by the Wisconsin Society for Ornithology in 1951, Zimmerman reports (1952) that the birds seemed to move "north in a series of major impulses, 7–10 days apart, and . . . appeared to make jumps of at least 300 miles at a time." The observations on the major impulses correlate well with our observations on the time it takes to replenish fat deposits and the time it takes to deposit fat before migration.

We have no data on the ultimate fate of the fat deposits of transients in the White-throated Sparrow, but it seems likely from the data Mrs. Lawrence has obtained thus far in Ontario and from the few observations in the literature that the fat deposits are eventually lost. They are not found in breeding birds. The condition of White-throats on arrival on the breeding grounds would be interesting to know. Such information would give us a clue as to whether the breeding grounds were reached by a long final flight or by a gradual advance. Blanchard's studies of the White-crowned Sparrow (1941) indicate that the weight of recent arrivals on the breeding grounds is considerably lower than the maximum at which they started. On the wintering grounds at Berkeley the average weight of male White-crowned Sparrows which are ready to migrate, and hence have a heavy deposition of fat, is 32.6 grams. None of five males which were collected on the day of the main influx into Friday Harbor, Washington, had any fat, and they averaged 27.1 grams in weight. Of three males collected at Vancouver, British Columbia, two had little fat and one was moderately fat, and their weights averaged 26.6 grams. The average weight of adult male winter residents at Berkeley which have no fat is 26.8 grams. The "arrival weight," therefore, seems to be equivalent to the weight of winter residents before the occurrence of fat deposition. For the Tree Sparrow, Baumgartner (1938) presents no data for birds arriving on the breeding grounds at Churchill, but she remarks that "fat tracts were still well developed in the specimens of the first week of June before breeding activities had begun." McCabe (1943) comments on the large amount of easily detachable fat on newly arriving Savannah Sparrows (*Passerculus sandwichensis*) and shrikes in the north. These observations of condition on arrival would be more meaningful if we knew whether the birds that were weighed bred in the area of arrival. The most valuable data will be obtained from birds that are banded on arrival and which are retrapped during the breeding season.

Summary

White-throated Sparrows, which are transients at Evanston, Illinois, were captured during spring migration in the years from 1945 to 1947. Observations were made on weight and fat deposition, and the data were considered in relation to the process of migration.

The mean weights for each of the three years were 27.6, 27.1, and 27.1 grams, respectively. The mean weight for all records (106) was 27.3 grams. The variations in mean weight for three-day periods for the duration of migration were minor for the most part and irregular.

The mean weights of White-throated Sparrows captured at Madison, Wisconsin, in 1943 and 1946 were 28.7 and 28.5 grams, respectively. The variations from day to day, or for periods of several days, were small.

The mean weights of the fat classes into which the birds were segregated were: none, 22.9; little, 25.7; medium, 27.2; heavy, 30.3 grams. The differences between the means are significant at the 1 per cent level, except that between the "little" and "medium" classes where it is significant at about the 5 per cent level.

Birds were classified as "adults," "intermediates," and "immatures" by means of the plumage of the head and throat, but the relation between these "plumage types" and age is not definitely known. The "adults" and "intermediates" are similar in weight in each fat class, but they are significantly different from the "immatures." When the sexes were definitely known (1947), the males exceeded the

females in mean weight in all fat classes, but the numbers of individuals were too small to test the significance of the differences.

Birds with "no," "little," "medium," or "heavy" deposits of fat arrived irregularly during the migratory period. A day's catch frequently included birds from different fat classes. "Adults" tended to arrive first followed by the "intermediates," with the "immatures" arriving last, but there was considerable overlap. When the sexes were known definitely (1947), the males preceded the females.

The value of the determination of mean weight is discussed. Without consideration of variables such as sex, age, fat deposition, and previous migratory behavior, interpretations based on mean weight are shown to be open to question. It is demonstrated also that mean weight determinations can mask or distort important information. The variations in weight which are accounted for by changes in fat deposition are summarized for several species and compared.

Data for 10 captive White-throated Sparrows demonstrate an increase in weight and in fat deposition in winter which reached a maximum in the period from February 8 to 26 and a second, premigratory peak which was reached in late May and early June; sex and age differences occurred in these increases.

The relation of the data on weight and fat deposition to migration is discussed. On the basis of several speculations and assumptions the extent of a single migratory flight of the White-throated Sparrow is estimated roughly to be between 270 and 360 miles. Data on weight and fat deposition are considered in relation to stop-over time, arrival on the breeding grounds, and other observations in the field.

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