WEIGHT VARIATIONS IN WINTERING WHITE-THROATED SPARROWS IN RELATION TO TEMPERATURE AND MIGRATION

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MANY wild birds in temperate regions undergo seasonal weight variations which presumedly are the result of changes in endocrine balances. Since internal changes may be related to environmental changes or perhaps be the result of an inherent rhythm, knowledge of the seasonal "weight picture" is of both physiological and ecological interest. A regular seasonal rhythm, with an increase in weight in winter and a decrease in weight in summer, has been demonstrated for many species of birds (Nice, 1938; Baldwin and Kendeigh, 1938). It has been suggested that this seasonal cycle is correlated, roughly at least, with temperature, since individual birds usually gain weight during cold weather (provided adequate food is obtained) and lose weight during warm weather (Baldwin and Kendeigh, 1938). It is advantageous to a warm-blooded animal to be heavy at low temperatures (heat loss is decreased) and lighter at high temperatures (heat loss is increased), but of course this does not mean that all birds will necessarily show such an adaptation; changes in feather covering and rate of metabolism, for example, could adapt a bird to seasonal temperature changes without a change in basic weight.

In addition to (or superimposed upon) the winter-summer weight rhythm it would seem logical to suppose that migratory species would show marked weight variations directly related to migration. Despite the fact that collectors have long known that many species become fat (and hence presumedly increase in weight) prior to and during migration, actual weight data demonstrating a migration increase is meager. Since Wolfson (1942, 1945) has recently summarized the literature on the subject, only a brief resume need be given here. Linsdale and Sumner (1934a, 1934b) found that the Golden-crowned Sparrow (*Zonotrichia coronata*) on its California wintering grounds not only gained weight in winter (up to 31 grams in January) but reached an even greater peak just before spring migration (35 gm. in May). Baumgartner (1938) who weighed Tree Sparrows (*Spizella arborea*) both on wintering and breeding grounds found that the highest weights occurred in late February and early March, prior to and during spring migration. Weights were also higher during fall migration than in late summer or early winter. Wolfson (1945) has reported that migratory races of Oregon Junco (several races of *Junco oreganus*) and White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*) are heaviest just prior to spring migration. He also presented preliminary evidence to indicate that fat deposition was largely responsible for the spring peak in the Junco. In the case of the Tree Sparrow, White-crowned Sparrow, and Junco, which migrate early, the premigration peak follows directly after the winter increase resulting in only one major peak in weight. In the Golden-crowned and Fox Sparrows (*Passerella iliaca* data of Linsdale and Sumner, 1934b), which migrate later, the weight decreases in late winter and early spring before the pre-migration increase occurs resulting in two major weight peaks. Wolfson (1945) further presents a table of winter and spring weights of 7 species of permanent residents which shows that these nonmigratory species decrease in weight in the spring without undergoing fat deposition. The data on non-migratory subspecies of the Oregon Junco (*J. o. pinosus*) and White-crowned Sparrow (*Z. l. nuttalli*) are especially significant since the resident forms, in contrast to migratory forms of same species, do not show a spring weight increase.

In analyzing thousands of weights at all seasons taken over a period of several years at the Baldwin Bird Laboratory at Cleveland, Ohio, Baldwin and Kendeigh (1938) failed to note significant weight variations that might be related to migration. However, it should be noted (as has been pointed out by Wolfson, 1945) that most of the weights discussed in this paper were obtained from permanent resident species or individuals of migratory species during or after migration; few weights were obtained *prior* to migration. Also, as will be discussed later, monthly averages may obscure significant variations if they happen to occur in a short period or come partly during one month and partly during another.

There can be no doubt that fat deposition and weight increase before or during migration is advantageous to a migratory bird since extra energy would be provided for the strenuous journey. However, as in case of a winter-induced weight increase, demonstration of advantage does not prove that all migratory species, subspecies or even both sexes of same species necessarily show the adaptation. Species of various seasonal status living in various climatic regions must be studied to determine the actual situation.

Because the White-throated Sparrow (*Zonotrichia albicollis*) is a late migrant and may be easily trapped and collected on its wintering grounds in southeastern United States, it has proved a favorable species for the study of the relative effects of winter and spring on the weight of a migratory bird. A study of the White-throated Sparrow has been undertaken as a part of a joint project with Albert Wolfson, who is continuing his experimental work on the physiology of migration at Northwestern University. The present paper is concerned with the analysis of data on total body weight. A study of weights of body parts and the exact determination of the amount and distribution of body lipids in collected birds is now being made as a joint research with Jesse D. Perkinson, biochemist at the University of Georgia, with the aid of a grant administered jointly by the University and the Carnegie Foundation.

Materials and Methods

For two successive seasons, 1946–47 and 1947–48, weights of White-throated Sparrows were obtained during the seven-months wintering period (mid-October to mid-May) of the species at Athens, Georgia. Of the total of 247 weights (142 males, 105 females) available for analysis, 116 were obtained from collected specimens shot in the late afternoon and weighed within an average of an hour after death. The remaining weights were obtained from 85 individual birds captured and banded on the University campus. Three funnel traps were used which were set near the Biology Building where they could be closely watched and birds removed soon after capture. Weights of repeat and return birds were treated as individual weights provided at least three days had elapsed since the last capture. In order to minimize the daily rhythm factor which is so prominent in small birds (*see* Baldwin and Kendeigh, 1938) and to make weights of banded birds comparable with those of collected birds (which were always taken in afternoon) weights of birds taken in traps before 10:00 A.M. were eliminated from the final data. Our experience has been that at about midday birds recover weight lost during the preceding night. Therefore, weights analyzed in this paper may be considered close to the daily maximum weights. A little over half (133) of the total weights were obtained during the first season (1946–1947). All birds, both collected and trapped, were weighed on the same Ohaus double-beam balance accurate to 0.1 gram. Live birds were placed in a small aluminum box counterbalanced on the scale before each weighing.

The sex of collected specimens was determined positively by internal dissection. For banded birds wing measurements proved to be the most reliable, although by no means infallible, basis for sexing. Wing measurements (the chord measurement without flattening normal curvature) of 116 birds of definitely known sex (collected specimens) were distributed as shown in Table 1. On the basis of these data, banded birds with wings of 74 mm. and over were recorded as males, those with wings of 69 mm. or less, females. Birds of intermediate size were recorded as either males or females according to wing measurement and plumage characters, females having a more brownish cast to nape, head and back. By the second season of work our experience was such that we very rarely were wrong when we predicted the sex of a collected bird before dissection. Undoubtedly, however, errors were made in sexing banded birds, especially intermediate-sized birds, but I do not believe that such errors affect the validity of the trends in weight being analyzed.

We are not sure that we have discovered reliable criteria for age determination and have not attempted to break down the total data into adults and immatures (first-winter birds), although some of the collected birds could be aged with certainty. The possible significance of age is discussed later.

Grateful acknowledgement is made to David W. Johnston, who was largely

responsible for operating banding traps and collecting birds in 1946–47 and to James C. Major who performed the same duties in 1947–48. Robert A. Norris also aided in collection of specimens, especially in the important month of April. Without the diligence of these students in the field it would have been impossible to fit this type of research into a busy academic schedule.

Results

The total data (247 weights) for the two seasons are averaged by months and half-months in Table 2, and plotted by half-months in Figure 1. In effect, the histogram in Figure 1 gives, at a glance, the average "weight picture" of the White-throated Sparrow on its north-Georgia wintering grounds. In

TABLE 1
Wing Measurements of White-throated Sparrows of Known Sex

WING MEASUREMENT IN MM.	NUMBER MALES	NUMBER FEMALES
65	0	2
66	0	1
67	0	9
68	1	12
69	1	18
70	1	8
71	3	4
72	5	4
73	9	4
74	10	1
75	10	1
76	9	0
77	1	0
78	1	0
79	1	0
Total	52	64

Figure 2, data for the first season only (1946–47) are plotted for short intervals together with the average daily air temperatures for the same periods. In Figure 3, 97 weights (for both years) in the critical spring period are plotted individually to give a picture of changes occurring just before northward migration.

Two distinct cycles are evident from the data, a peak in weight being reached in midwinter and another, greater peak in males, being reached in late April just prior to northward migration. Average weights were lowest in October and November shortly after the end of fall migration. The averages for these months (males 26.8; females 25.4) are very close to averages given by Nice (1938) and Baldwin and Kendeigh (1938) for birds trapped during the fall migration in Ohio. From the low point in the autumn, weight gradually increased with a winter peak being reached in early February, males 29.8, females

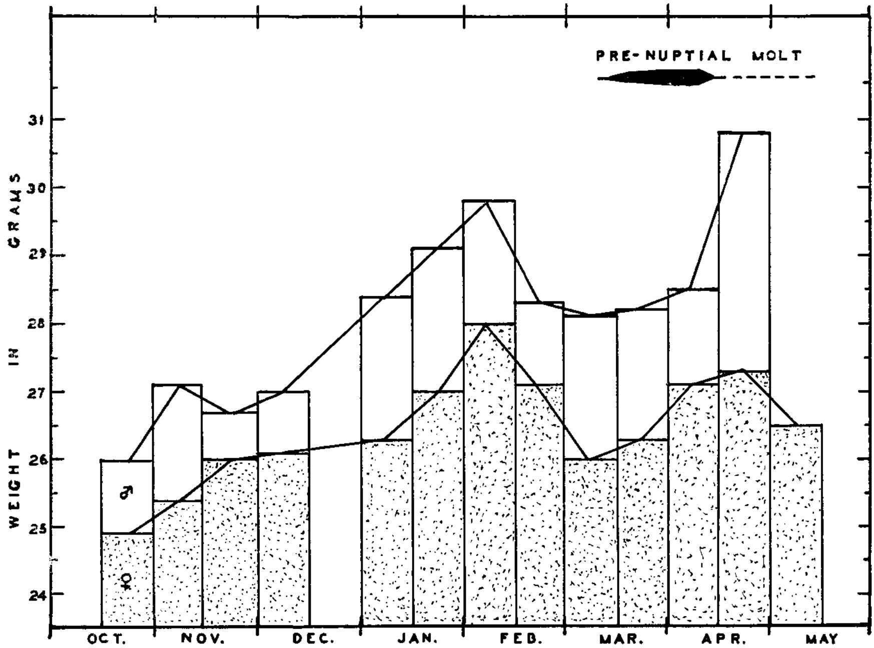

FIG. 1. Histogram of "weight picture" of White-throated Sparrow on its wintering grounds at Athens, Georgia. A summary of two seasons' data (247 weights, see Table 2) with averages plotted for half-month intervals; upper curve male, lower, female.

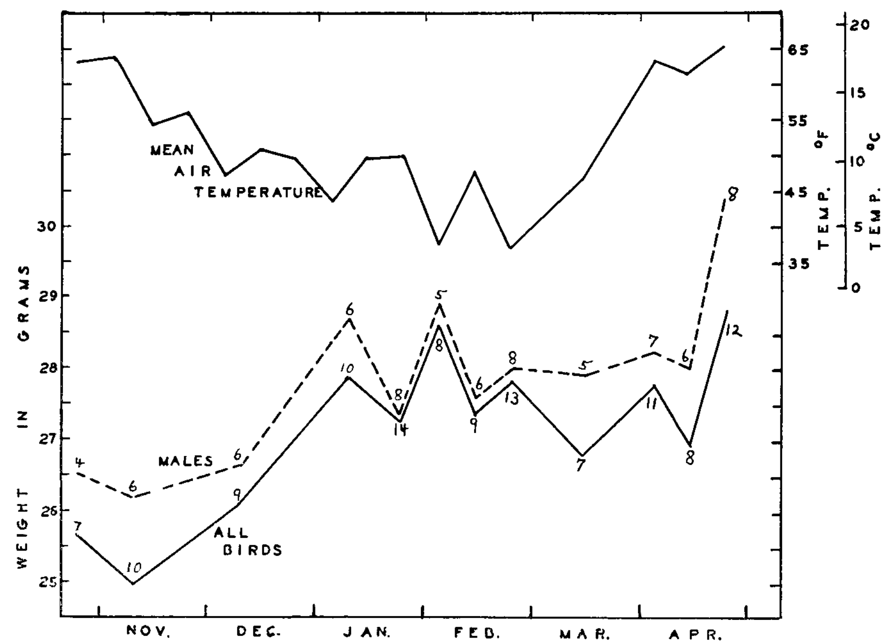

FIG. 2. Average weights of White-throated Sparrows for the 1946-47 season only with means of air temperature recorded for same period by the US Weather Station at Athens, Ga. Figures on the weight curves represent number of individuals on which averages are based.

28.0. As shown in Figure 2, variations in winter weight in 1946–47 are inversely correlated with temperature. Thus, the coldest periods during that year were the first 10 days in January, the first 10 and last 10 days in February; each cold period, especially the first two, coincides with a peak in weight. The same relation to temperature is indicated by 1947–48 data although the weights for this winter are not sufficiently distributed to permit plotting a complete curve. The coldest period in the 1947–48 winter was the last half of

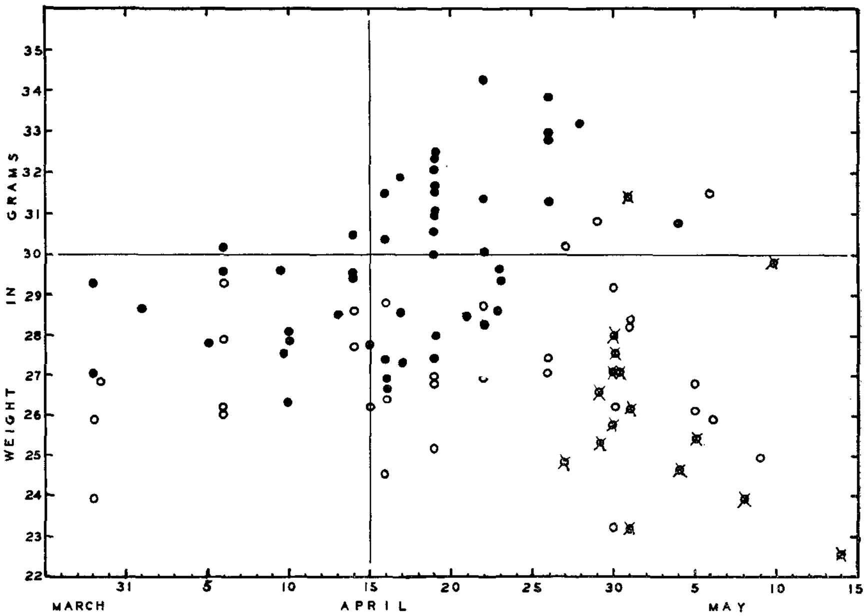

FIG. 3. Distribution of 97 weights from both seasons during the critical late-spring period. Each symbol represents an individual weight record, largely an individual bird since over half the records are from collected birds. Solid circles are males, open circles, femalees. Dull-plumaged, late-molting females, believed to be first-year birds are indicated by ⊠. Note that after April 15 males increase in weight rapidly and leave the region, while response in females is later and much more variable.

January and first part of February and both average peak weights and peak weights for individuals were recorded during this period.

The stimulating effect of low temperatures in winter is further indicated by the fact that males averaged heavier during the cold period January 1 to February 15, 1948, than during the same but warmer period of 1947 as shown in Table 3. The difference, 1.6 grams, is reasonably significant since it is 2.5 times the standard error of difference (0.62) as determined by use of formula for small samples (Fisher, 1936).

Another difference between the two years seems related to temperature. Early November, 1947, was colder than the same period in 1946; likewise November 1947 birds were heavier. This produced the "hump" in the curve of males (see Figure 1) since a large proportion of November weights were obtained in 1947.

TABLE 2
Average Weight of White-throats at Athens, Georgia; two season's data combined

PERIOD OF OBSERVATION		MALE		FEMALE	
		No.	Wt. in grams	No.	Wt. in grams
October	Last half	4	26.0	7	24.9
November	First half	8	27.1	5	25.4
	Last half	10	26.7	6	26.0
	Total	18	27.0	11	25.8
December	First half	10	27.0	5	26.1
January	First half	7	28.4	3	26.3
	Last half	16	29.1	8	27.0
	Total	23	28.9	11	26.8
February	First half	13	29.8	10	28.0
	Last half	11	28.3	8	27.1
	Total	24	28.7	18	27.7
March	First half	4	28.1	6	26.0
	Last half	8	28.2	6	26.3
	Total	13	28.1	12	26.2
April	First half	20	28.5	11	27.1
	Last half	26	30.8	19	27.3
	Total	46	29.8	30	27.2
May	First half	*		15	26.5

* Virtually all males migrated north by May 1. One exception (May 4) is included in late April weights.

TABLE 3
Comparison of Winter Weights of Male White-throated Sparrows for Two Seasons

YEAR	AVERAGE TEMP. JAN. 1–FEB. 15	NUMBER MALES	AVERAGE WEIGHT, GRAMS	PER CENT INDIVIDUALS OVER 30 GRAMS
1947	45.2° F	21	28.6 ± 1.36	19
1948	40.6° F	15	30.2 ± 2.02	53
Difference			1.6 0.62	

During the early spring, weights dropped below the winter peak. The prenuptial molt, a partial molt in this species involving feathers of head and body tracts, began the middle of March and continued into April, every individual examined the first half of April being in molt. By April 15 molting was virtually complete in males, which then began a rapid, almost spectacular increase in weight as shown in all three figures. In Figure 3, for example, it will be noted that during the first half of April only two males out of 17 weighed over 30 grams and none reached 31 grams. Between April 15 and 30, however, 20 out of 31 weights topped 30 grams, and 16 of the 20 exceeded 31 grams. The late April average for males was over 2 grams greater than peak weight for winter of 1946–47 and 1 gram greater than the higher 1947–48 winter peak (see Table 2). By May 1 almost all males had departed from the vicinity of Athens. In 1947, one male was obtained on May 4, while in 1948 no males were collected or trapped after April 25 despite intensive search for them.

Weights of four individual banded males which repeated over long periods are given in grams in Table 4. It will be seen that these individual variations parallel average trends as shown in Figure 1. The first 3 individuals clearly show an increase from fall to winter. Individuals No. 2 and No. 4 demonstrate

TABLE 4

Afternoon Weights (in gms.) of 4 Male White-throated Sparrows (1946–47)

NO. 1		NO. 2		NO. 3		NO. 4	
Date	Wt.	Date	Wt.	Date	Wt.	Date	Wt.
Nov. 6	26.4	Nov. 15	27.9	Nov. 8	25.4	Jan. 18	30.0
Jan. 28	27.4	Jan. 23	27.4	Feb. 12	29.2	Feb. 27	29.4
Feb. 4	30.1	Feb. 4	30.9	Feb. 28	26.3	Apr. 9	29.6
Feb. 11	28.5	Feb. 8	27.6	Apr. 10	27.9	Apr. 28	33.2
Mar. 4	26.3	Feb. 11	28.5	Apr. 17	27.3		
Apr. 1	28.7	Feb. 18	27.0				
		Feb. 27	29.3				
		Apr. 19	31.6				

the premigration peak; the other 2 birds did not repeat late enough in April for this increase to be evident.

The situation in regard to females was not so clear cut. In late April, females increased in weight, but not nearly to the extent of males. Several females exceeded 30 grams but many others remained low in weight (see Figure 3). Females remaining into May were, with two exceptions, low in weight. Seven out of 15 May females were in very dull plumage and still molting; these were evidently immature birds and were very light in weight as shown in Figure 3. The other 8 females were in bright plumage, evidently having completed molting, but most showed little evident fat deposition or weight increase. Thus, even if dull-plumaged immatures were separated from bright-plumaged birds (adults), the weight curve for May would still show a downward trend.

As summarized in Table 5 the sex differential in weight is significantly greater in the spring than in midwinter, the difference, 2.1 gms, being 3 times the standard error (determined by taking the square root of sum of standard deviations squared divided by number of all 4 means). The age factor is probably involved, since there seems to be a tendency for immature females to linger longest on the wintering grounds or perhaps winter further south and move into the area in May. However, even if the May birds believed to be immatures (see figure 3) are not included, raising the spring female average to 27.6, the difference is still of considerable statistical significance. In this connection it might be noted that female White-throats weighed by Nice (1938) during the spring migration in Ohio averaged only 26.4 grams as compared with 29.4 grams for males, a much greater sex difference than found by the same author during the fall migration.

TABLE 5

Comparison of Sex Difference in Weight During Mid-winter and Spring

	JAN. 1–FEB. 15		APRIL 15–MAY 15	
	No.	Average wt.	No.	Average wt.
Male	36	29.2 ± 1.93 gms.	26	30.8 ± 1.77 gms.
Female	21	27.5 ± 1.66 gms.	34	27.0 ± 2.10 gms.
Difference in sexes		1.7 gms.		3.8 gms.
Seasonal difference in sex difference		2.1 ± 0.697 gms.		

Discussion

It is important to note that while the winter increase in weight was a relatively gradual one, the premigration increase in males occurred within an amazingly short time. From the study so far made on collected birds it appears that fat deposition is largely responsible for both weight increases, but especially the spring one. Apparently, more than 2 grams (about 10% of body weight) of fat may be added in about a 7–10 days, the fat being largely deposited subcutaneously and underneath the ventral abdominal wall. In 1947, for example, 10 males taken between April 1 and April 17 showed no evidence of a major increase in weight, all weighing less than 30 grams. On April 19, 2 out of 5 birds exceeded 31 grams while all of a series of 5 males taken April 27–28 exceeded 31 grams, 1 individual reaching 33.9 for highest weight recorded for that year (in 1948 one February bird weighed 35 grams and one April 22 bird, 34.3 grams). In previous years when some weights were obtained at Athens, this premigration peak was largely missed because not enough individuals were obtained during the critical period of late April. Averaging weights by months or other long periods could easily obscure such a weight peak. For example, the average weight for the month of April as a whole might not be greatly different from that of winter months. Yet it is obvious that, when weights are plotted individually as in Figure 3, the weight picture for April 1 is quite different from that of any other month.

Comparison with published data for other migratory species reveals that the White-throat weight curve for winter and spring is very similar to the "two-peaked" curve of Golden-crowned Sparrows on the west coast previously mentioned (Linsdale and Sumner 1934a). Migratory races of Oregon Junco and White-crowned Sparrow have a similar weight picture (Wolfson 1945) but migrate north much earlier in the spring; hence the winter increase and spring increase are not so well separated as in late migrant White-throat.

As has already been indicated, the general winter increase in weight as well as fluctuations during the colder months are definitely related to temperature. Males and females appear to respond equally to stimulating effect of decreasing temperature so that weight curves for both sexes are roughly parallel. In the cold period of midwinter, females come nearest to equalling males in weight. The spring increase is different and appears to be related to length of day, since Wolfson has been able to induce fat deposition experimentally in juncos (Wolfson 1942) and in White-throats (MS) by artificial lighting. In nature, temperature or other climatic factors apparently may influence the light response as is indicated by the fact that males "fattened up" and disappeared from the Athens area about 5 days earlier in the spring of 1948 when compared with 1947. In Figure 3, all records of males after April 25 are from 1947 despite the fact great effort was made in 1948 to obtain males after this time. Spring, especially March, temperatures were higher in 1948.

The unequal response of the sexes in the spring is puzzling, although it is well known that female birds in general respond more irregularly than males to experimental length-of-day increases, at least in regard to gonad recrudescence. One thing our study has definitely shown is that females remain on the wintering ground at least 2 weeks longer than males. We also discovered that these lingering females may sing, as one was shot in the act. While males responded uniformly and departed abruptly, the females showed all degrees of variation, some birds becoming fat, others not (*see* Figure 3 and note large standard deviation of spring females, Table 5). In general, late April females showed a fair degree of weight increase, while May birds did not. To the casual observer, the White-throated Sparrow disappears from the Athens vicinity about May 1, almost no birds being found on the uplands or on the University campus (only 2 birds were caught in banding traps in May). However, in the bottomland thickets small bands of females may still be found for two weeks or longer, May 18 being the latest sight record for this vicinity. These lingering females are quiet, elusive, and difficult to collect. Many of the 15 birds collected in May were dull plumaged, often still molting and were judged to be immatures; they may represent migrants from further south. In any event, most of these birds disappear from this area without "fattening up." The last bird collected (on May 14) was also the smallest on record, weighing only 22.6 grams.

Since it has been known for many years that males of many species migrate ahead of females, it is logical to assume that females would remain on the wintering grounds longer, although this has not often been actually demonstrated. Likewise, it has been suggested that immature birds may migrate north later than adults. Since males push north when the weather may be unfavorable for the species and since males must expend a great deal of energy setting up territory, it is easy to see that a premigration deposition of fat would be of survival value. Perhaps the less extensive weight buildup (or lack of it in late migrants) in females is related to the less rigorous conditions encountered in later migration, or perhaps fat deposition does not occur until the birds are enroute. This is a question that can not be answered as yet.

Summary

During 1946–47 and 1947–48, 247 weights of White-throated Sparrows (131 from banded birds, 116 from collected birds) were obtained over the 7-month wintering period of the species at Athens, Georgia. Two distinct cycles are evident from the data, a peak in weight being reached in mid-winter and another, greater peak in males, being reached just prior to northward migration. On arrival in October, birds were lightest, males averaging 26.0, females 24.9 grams. A gradual increase occurred with winter peak being reached (in both years) in early February, males 29.8, females 28.0 grams. The winter increase seems well correlated with temperature since the coldest periods coincided with peak weights; also, birds averaged heavier in the cold 1947–48 winter as compared with warmer 1946–47 one. During late March and early April, birds underwent prenuptial molt, and weight dropped below the winter level. During the last half of April all males increased greatly in weight, averaging 30.8 grams, with a number of individuals weighing up to 33 and 34 grams. A heavy deposition of fat appears largely responsible for this increase which may occur within 7 to 10 days, or perhaps less. Virtually all males had departed by May 1. Females averaged heavier in April (27.3 gms) but the increase was much less evident than in males and the response was irregular, some females becoming quite fat, others showing little change. Females lingering into May were generally light (average 26.6), many still molting, and some, at least, being first-year birds. Apparently many females leave the Athens region before or without evident fat deposition or weight increase. For the entire spring period, April 15 to May 15, males averaged 3.8 grams heavier than females as compared with a 1.7 gram sex difference during midwinter period, Jan. 1 to Feb. 15. The difference between these differences is statistically significant, 2.1 ± 0.69 gms.

By way of general conclusion, it appears from observational and experimental data so far available that temperature is a factor, perhaps the chief one, in bringing about the winter increase. Light, that is, length of day, is apparently the chief factor in bringing about the spring increase, temperature

being only a modifying factor. In species of birds which migrate early the significance of this difference is lost since the 2 weight peaks may coincide or be superimposed upon one another. A late migrant species, such as the White-throated Sparrow, is a more favorable subject for study since the 2 peaks are distinct and, therefore, may be studied separately. It is hoped that detailed study of collected specimens now in progress may further clarify the physiology of the temperature-correlated (winter) and light-correlated (spring) weight increases.

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