

VARIATION IN MAJOR BODY COMPONENTS OF THE
TREE SPARROW (*SPIZELLA ARBOREA*) SAMPLED
WITHIN THE WINTER RANGE

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ODUM et al. (1961) divided migratory populations of small birds into three groups based upon patterns of fat deposition and migration: "1) short-range migrants that become moderately obese but begin migration before peak deposition, 2) short-range migrants that attain moderate obesity but begin migration after peak deposition levels have been reached, 3) long-range migrants that become extremely obese just prior to long flights" (Odum loc. cit., p. 516). We have been interested in the seasonal bioenergetics, particularly during migration, of populations assigned to the first of these categories because their initial depot fat reserves are unspectacular, yet, must provide energy for at least the first migratory flight.

This paper 1) extends the earlier work of Helms and Drury (1960) on the Tree Sparrow (*Spizella arborea*) a cold-temperate to sub-arctic migrant with no detectible premigratory obesity in free-living representatives of the species, and 2) leads to reformulation of the migrant categories given above.

METHODS

Collection.—During the winter of 1962–1963, 60 Tree Sparrows were collected in the vicinity of Lewisburg, Pennsylvania (see Table 1).

Individuals were weighed after collection (± 0.1 g); fat class was determined (Helms and Drury, 1960); wing length was measured to the tip of the longest primary with the wing flattened and straightened; sex was estimated by cloacal examination; and birds were killed by cardiac pressure if collected by net or trap and sealed in an individual plastic bag. Within two hours, each specimen was weighed (± 0.2 mg), re-sealed in a plastic bag, and frozen at -29°C . Birds were held at this temperature two to six months before extraction.

Extraction.—Specimens were thawed within their plastic bags to prevent moisture condensation and weighed (± 0.2 mg) to determine weight loss during storage (less than 0.1 g in all cases and usually less than 0.02 g).

a. "Short" Method.—Half of the sample was extracted using the following method adapted from Odum (1960).

Thawed birds were aged and sexed by dissection and refrozen. They were sliced in a freezer and transferred to a weighed (± 0.2 mg) pan. After thawing in a closed desiccator (without desiccant), the pan and bird were weighed to determine grinding loss (under 1 g in all cases). The pan and bird were placed in a vacuum oven at 40°C for 72 hours, cooled in a desiccator for 20 minutes, and weighed. Tissues were quantitatively transferred to a pint jar using a 5:1 petroleum ether-chloroform mixture and covered with solvent. The jar was sealed, placed on a shaker for 24–48 hours, opened, and the solvent mixture heated to boiling for 5–10 minutes. Solvent was decanted from the specimen into a filter flask under vacuum through a Büchner funnel containing a dry weighed disc of number 1 filter paper. The specimen was covered with the original

TABLE I
TREE SPARROW SAMPLES, LEWISBURG, PENNSYLVANIA

Period:	Dates:	Sample Sizes:				Immatures	How Collected:		When Collected:		How Extracted:	
		Total	♂♂	♀♀	Adults		Net	Trap	Morning	Afternoon	Short Method	Soxhlet Method
Fall Migration	13-30 November 1962	12	5	7	2	10	12	0	0	12	6	6
Early Winter	8-12 December 1962	12	8	4	7	5	0	12	4	8	6	6
Mid-Winter	1-7 February 1963	12	4	8	12	0	0	12	2	10	6	6
Late Winter	4-7 March 1963	9	3	6	9	0	0	9	3	6	6	3
Spring Migration	17-27 March 1963	15	8	7	15	0	15	0	6	9	6	9
Total Period:	13 November 1962 — 27 March 1963	60	28	32	45	15	27	33	15	45	30	30

amount of solvent and boiled for 10-20 minutes. This solvent and the extracted tissues were decanted onto the filter paper used previously and the jar and tissues rinsed with petroleum ether. The filter paper and extracted tissues were dried under vacuum for 6 hours at room temperature and weighed.

Suggested modifications of the procedure include 1) razor blade slicing of thawed carcasses, 2) a change of solvent after 12-24 hours, and 3) use of a top-loading pan balance (± 0.02 g). The first modification would eliminate condensation upon cold tissues during handling. The second would be particularly desirable for very fat birds. The third would involve no loss in precision due to the large errors inherent in handling exposed hygroscopic tissues and might improve reliability by speeding all steps of the process.

b. *Soxhlet Method for Sectional Extraction.*—The second half of the sample was extracted by the following method adapted from Odum and Perkinson (1951).

Thawed specimens were rapidly dissected, noting age and sex, into the following body regions: a) skin and feathers with subcutaneous fat, b) ventral abdominal wall (abdomen) with peritoneal fat, c) viscera (proventriculus through large intestine) with

visceral fat, d) liver with hepatic fat, e) posterior (back), f) thorax and heart, and g) head and neck (see Odum and Perkinson, 1951—sections were identical except that the heart and thorax were not extracted separately). Except for perforation of the skull and four incisions through the pectoralis masses, sections were not further macerated.

These body sections were placed in separate weighed (± 0.2 mg) glass extraction thimbles of appropriate size, and weighed. Tissues were dried as above, transferred to a desiccator for 20 minutes, and weighed. Each section was extracted for a minimum of 18 hours in a Soxhlet extractor using a 5:1 mixture of reagent grade petroleum ether (30–60°C) and reagent grade chloroform. Tissues were dried under vacuum at room temperature for six hours and weighed. Solvent and fat were transferred quantitatively to weighed beakers with petroleum ether, and dried with heat to tackiness and under vacuum to constant weight.

c. *Methodological Differences.*—The birds used in the short and Soxhlet methods did not differ significantly in weight weight ($\bar{d} = 0.17 \pm 0.33$ g, $P > 0.5$) although they may have been heterogeneous with respect to this variable ($F = 1.86$, $df = 29, 29$, $P \cong 0.05$). They did not differ significantly in wing length ($\bar{d} = -0.1 \pm 0.4$ mm, $P > 0.5$) nor were wing lengths heterogeneous ($F = 1.03$, $df = 29, 29$, $P > 0.1$). Total water ($\bar{d} = 0.14 \pm 0.18$ g, $0.5 > P > 0.4$) and total fat ($\bar{d} = -0.04 \pm 0.16$ g, $P > 0.5$) did not differ significantly but dry fat-free weight did ($\bar{d} = -0.28 \pm 0.13$ g, $0.5 > P > 0.2$). However, this difference was not highly significant and was less than 5 per cent of the mean dry fat-free weight. Moreover, variances were not significantly heterogeneous ($F = 1.19$, $df = 29, 29$, $P > 0.1$). We concluded that differences due to extraction method were negligible and pooled all birds in subsequent analyses.

Calculations.—Weight at capture was designated Wet Weight. The difference between weights before and after grinding or dissecting was used to calculate a correction factor for losses which were assumed to be evenly distributed among all body components. These losses were under 5 per cent of wet weight in all cases and were under 1 per cent in most. [(Weight before drying minus weight after drying) multiplied by (the correction factor)] plus (the difference between wet weight and weight before grinding or dissection) equalled Total Water. (Weight before extraction minus weight after extraction) multiplied by the correction factor equalled Total Fat. Wet weight minus total fat equalled Wet Fat-free Weight and this value minus total water equalled Dry Fat-free Weight which was equal to the tissue weight after extraction and drying times the correction factor. Water and fat as percentages of wet weight and Water and Fat Indices (Total Water/Dry Fat-free Weight and Total Fat/Dry Fat-free Weight, respectively) were also calculated. Total Lipid equalled the net weight of ether: chloroform soluble material from all sections extracted by refluxing multiplied by the correction factor. This value did not differ significantly from calculated total fat for these birds and will not be reported because it was not determined from the total sample. Results from the individual sections extracted by the Soxhlet method will be reported separately.

Statistical Notations.—Various symbols are used throughout this paper. For the sake of brevity, they will be listed here (see Steel and Torrie, 1960).

a. *Averages.* Sample mean = \bar{x} ; sample median = \hat{x} ; sample standard deviation = s ; and sample standard error = $s_{\bar{x}}$.

b. *Differences.* Difference between sample means = \bar{d} ; standard error of the difference = $s_{\bar{d}}$; $t = \bar{d}/s_{\bar{d}}$; variance ratio = F ; degrees of freedom = df ; probability = P ; * = $0.05 > P > 0.01$; and ** = $0.01 > P$. The term "significant" is reserved for tested observations attributable to chance no oftener than once in twenty occurrences, i.e., $0.05 > P$.

RESULTS

Age and Sex.—Adults were significantly heavier (wet weight and fat-free weights) and larger (wing length) than immatures, but within the fall and early winter periods (the only subsamples containing known immatures), adults differed significantly from immatures only in wet weight ($\bar{d} = 1.24 \pm 0.60$ g, $P \cong 0.05$). The only significant heterogeneity between adults and immatures within the fall and early winter periods was also in wet weight ($F = 4.31$, $df = 3, 14$, $0.025 > P > 0.01$). In spite of these differences, the data will be pooled with respect to age in the subsequent sections of this paper because birds of the year could not be separated from older birds in the February and later subsamples. See Heydweiller (1935).

Males were heavier (wet weight $\bar{d} = 0.88 \pm 0.44$ g, $P \cong 0.05$; total water $\bar{d} = 0.55 \pm 0.17$ g, $0.005 > P > 0.001$; dry fat-free weight $\bar{d} = 0.25 \pm 0.12$ g, $P \cong 0.05$) and larger (wing length $\bar{d} = 2.6 \pm 0.5$ mm, $0.001 > P$) than females, but did not differ significantly from them in any fat variables or in water index or per cent. These differences appear to be compatible with the wet weight difference between sexes of 0.85 g (adults only) reported by Heydweiller (1935).

In the Tree Sparrow, the differences between sexes in variables that could be determined in intact individuals were not large enough to be reliable aids in determining sex. Using the shape of the cloacal protuberance (rounded abdominal junction and conical structure in females; angular abdominal junction and cylindrical structure in males), 67 per cent of the birds taken in this study were correctly sexed in the field. This is close to the reliability obtained by Heydweiller (1936) who sexed this species using plumage characteristics. It is doubtful that more reliable sexing is possible without laparotomy or autopsy.

The only significant heterogeneity between sexes was in dry fat-free weight ($F = 2.53$, $df = 31, 27$, $0.025 > P > 0.01$). Data were separated by sex in the subsequent treatments in this paper but no major differences appeared and results will be reported from the pooled sample for the sake of simplicity even though this entails a certain loss of efficiency in statistical testing.

Time of Day.—More birds were collected in the afternoon than in the morning during this study. However, morning collections were made in all subsample periods except the first (see Table 1) and there was no significant diel heterogeneity so that temporal bias does not seem to be a major concern. The most conspicuous trend during the day was an expected increase in body fat (total fat $\bar{d} = 0.50 \pm 0.21$ g, $0.05 > P > 0.025$). Helms and Drury (1960) discuss diel variations in wet weight and visible fat in this species. Due to the small number of morning collections, their distribu-

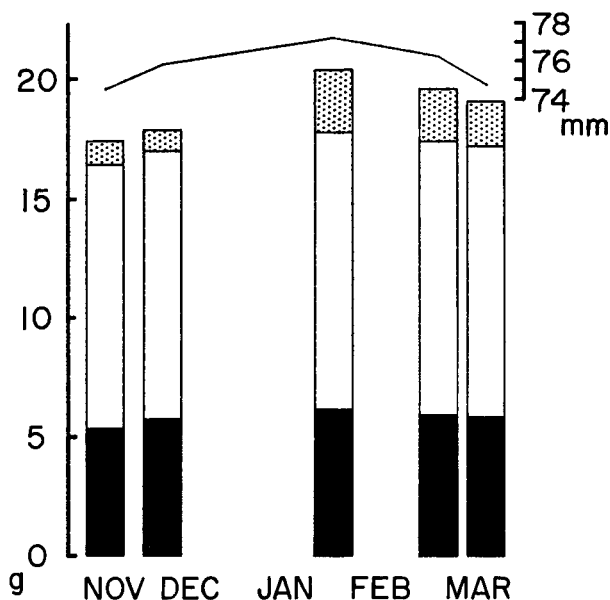


FIG. 1. Seasonal Changes in Body Composition and Wing Length. Black rectangles represent dry fat-free weight, white rectangles represent total water and the two together represent wet fat-free weight. Stippled rectangles represent total fat. All components in each sample equal wet weight. Wing length is indicated by the upper line. Fat-free weights (dry and wet), water, and wing length did not differ significantly between samples. Wet weight and total fat were significantly higher in early February than in early December. They were also higher in spring than in fall. (See Tables 2 and 3).

tion throughout the subsamples, and the general lack of significant differences between morning and afternoon collections, diel differences will be neglected in the remainder of this study.

Season.—Data from each subsample are given in Tables 2 and 4. Sample differences are given in Tables 3 and 4. Some of these data are plotted in Figures 1 and 2.

Seasonal trends are apparent and agree closely with those found by Helms and Drury (1960). Weight and fat were highest in mid-winter and lower in spring and fall. Fall to winter comparisons reveal significant differences in wet weight and fat, but not in fat-free weights or total water (when only adults are compared). However, winter to spring comparisons indicate no significant differences in any of the components analyzed. There was no period of vernal premigratory or migratory fattening in the Tree Sparrow sampled on its wintering ground.

The data in Table 2 and Figure 1 suggest that size (wing length) and mass

TABLE 2
MEAN FIELD AND EXTRACTION DATA¹

Period:	Wing Length (mm)	Visible Fat (fc)	Wet Weight (g)	Wet Fat-Free Weight (g)	Total Water (g)	Total Fat (g)	Dry Fat-Free Weight (g)
A. Fall Migration	74.5 ± 0.7	2.9	17.44 ± 0.26	16.37 ± 0.24	11.06 ± 0.16	1.07 ± 0.05	5.31 ± 0.10
B. Early Winter	76.2 ± 0.8	2.7	17.94 ± 0.48	16.98 ± 0.38	11.28 ± 0.31	0.97 ± 0.12	5.70 ± 0.15
C. Mid-Winter	77.3 ± 0.7	2.9	20.40 ± 0.43	17.81 ± 0.22	11.75 ± 0.14	2.59 ± 0.26	6.06 ± 0.12
D. Late Winter	76.3 ± 0.6	3.2	19.55 ± 0.48	17.45 ± 0.41	11.52 ± 0.25	2.10 ± 0.16	5.93 ± 0.18
E. Spring Migration	75.6 ± 0.5	2.8	19.15 ± 0.46	17.17 ± 0.29	11.39 ± 0.19	1.98 ± 0.21	5.78 ± 0.11
All Data	76.0 ± 0.3,	2.9	18.88 ± 0.23,	17.14 ± 0.15,	11.39 ± 0.09,	1.74 ± 0.11,	5.75 ± 0.07,

¹ Values reported as $\bar{x} \pm S_x$ except Visible Fat where x is tabulated.

TABLE 3
FIELD AND EXTRACTION DATA, DIFFERENCES.¹

Period:	\bar{d} Wing Length (mm)	Visible Fat (fc)	\bar{d} Wet Weight (g)	\bar{d} Wet Fat-Free Weight (g)	\bar{d} Total Water (g)	\bar{d} Total Fat (g)	\bar{d} Dry Fat-Free Weight (g)
A—B							
Fall— Winter	+1.7 ± 1.0	-0.2	+0.51 ± 0.55	+0.61 ± 0.45	+0.22 ± 0.35	-0.10 ± 0.13	+0.39 ± 0.18* ²
B—C							
Winter— Winter	+1.2 ± 1.0	+0.2	+2.45 ± 0.65**	+0.83 ± 0.44	+0.47 ± 0.34	+1.62 ± 0.28**	+0.36 ± 0.20
C—D							
Winter— Winter	-1.0 ± 1.0	+0.3	-0.85 ± 0.65	-0.35 ± 0.47	-0.22 ± 0.28	-0.50 ± 0.30	-0.13 ± 0.22
D—E							
Winter— Spring	-0.7 ± 0.8	-0.4	-0.40 ± 0.67	-0.29 ± 0.50	-0.13 ± 0.32	-0.11 ± 0.27	-0.16 ± 0.21
E—A							
Spring— Fall	-1.1 ± 0.9	+0.1	-1.71 ± 0.53** ²	-1.02 ± 0.37* ²	-0.46 ± 0.25	-0.91 ± 0.22** ³	-0.46 ± 0.15** ²

¹ Values reported as $\bar{d} \pm s_{\bar{d}}$ except for Visible Fat where $\hat{x}_2 - \hat{x}_1$ is given.

² Adults only, difference not significant ($P > 0.05$).

³ Adults only, difference significant ($0.05 > P$).

TABLE 4
WATER AND LIPID PERCENTAGES AND INDICES, MEANS AND DIFFERENCES.¹

Period:	Means:			Differences:			\bar{d} Fat Index (g/g)
	Water % Wet Weight	Fat % Wet Weight	Water Index (g/g)	\bar{d} Water % Wet Weight	\bar{d} Fat % Wet Weight	\bar{d} Water Index (g/g)	
A. Fall							
Migration	63.4 ± 0.4	6.1 ± 0.3	2.08 ± 0.03				0.202 ± 0.009
B. Early							
Winter	62.9 ± 0.4	5.3 ± 0.6	1.98 ± 0.03	-0.5 ± 0.6	-0.9 ± 0.6	-0.10 ± 0.04* ²	-0.034 ± 0.021
C. Mid-							
Winter	57.7 ± 0.8	12.5 ± 1.00	1.95 ± 0.04	-5.2 ± 0.9**	+7.2 ± 1.1**	-0.03 ± 0.04	+0.257 ± 0.043**
D. Late							
Winter	59.0 ± 0.5	10.7 ± 0.7	1.95 ± 0.04	+1.2 ± 1.0	-1.8 ± 1.2	0.00 ± 0.06	-0.050 ± 0.054
E. Spring							
Migration	59.7 ± 0.7	10.1 ± 0.9	1.98 ± 0.023	+0.7 ± 0.8	-0.6 ± 1.1	+0.03 ± 0.05	-0.037 ± 0.050
All							
Data	60.6 ± 0.4	8.9 ± 0.5	1.99 ± 0.01	+3.8 ± 0.8** ³	-3.9 ± 0.9** ³	+0.10 ± 0.04* ²	-0.136 ± 0.034** ³

¹ Means tabulated as $\bar{x} \pm s_x$; differences tabulated as $\bar{d} \pm s_d$.

² Adults only, difference not significant ($P > 0.05$).

³ Adults only, difference significant ($0.05 > P$).

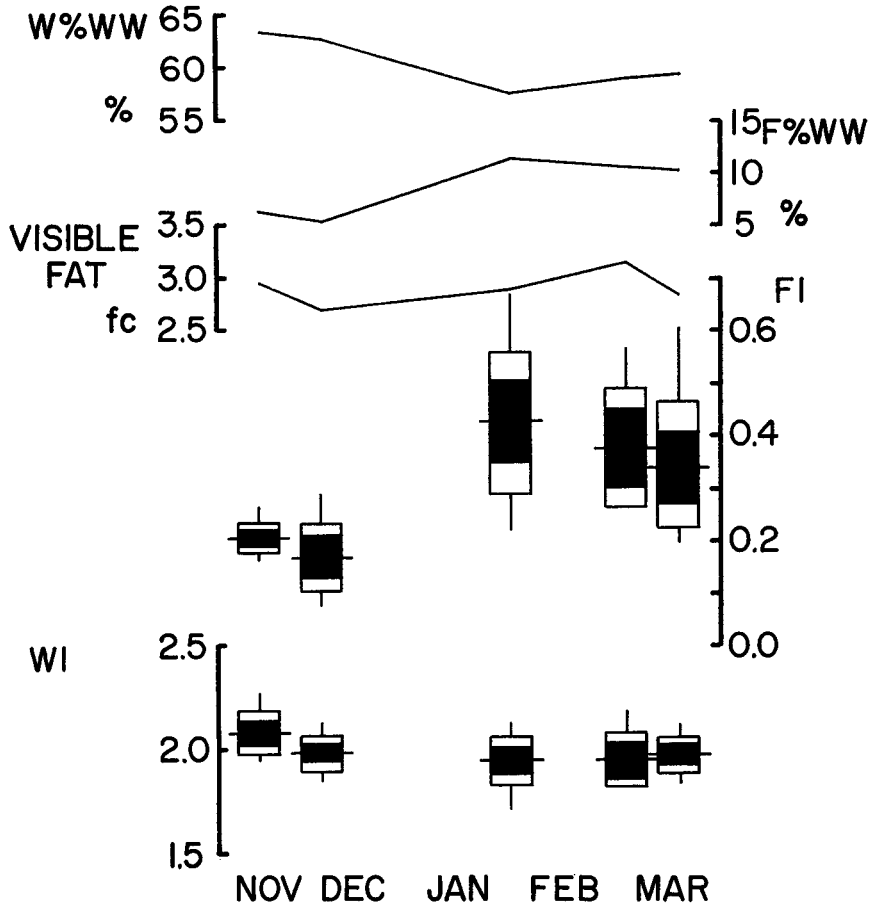


FIG. 2. Seasonal Changes in Relative Body Composition. Water as a per cent of wet weight (W%WW), fat as a per cent of wet weight (F%WW), visible fat, fat index (FI), and water index (WI) are plotted. For fat and water indices, range is given as a vertical line, mean as a horizontal line, two standard errors above and below the mean as a solid rectangle, and one standard deviation above and below the mean as an open rectangle. Non-overlap of black rectangles indicates that means probably differ significantly. (See Tables 2 and 4).

(fat-free weights) may tend to increase in mid-winter. Although these tendencies are insignificant, they are regular and parallel. If verified with larger samples, the latter trend might reflect the maturation of birds of the year (Heydweiller, 1936; Baumgartner, 1938), but further growth of primaries would not be expected during this period. While Helms and Drury (1960) emphasized the constancy of individuals within the winter population

and the fidelity (*Ortstreue*) of returning adults, many Tree Sparrows were banded at all seasons and not seen again. It is possible that the winter population of this species undergoes a flux of individuals in a given area, particularly in the juvenile component (see Heydweiller, 1935). Whether this flux represents movement of individuals or mortality of smaller birds is uncertain. From the work of Helms and Drury (1960), it is evident that quasi-migratory or migratory movements may alter the population by late February. These possibilities need investigation.

DISCUSSION

Fat and Migration. In two independent field studies (Helms and Drury, 1960; this paper), the Tree Sparrow has been found not to increase in weight on its wintering grounds prior to migration. According to the migrant patterns proposed by Odum et al. (1961), the Tree Sparrow could be assigned only to the first category as a bird that does become moderately obese but attains this condition only after the initiation of migration.

Tree Sparrows collected in Pennsylvania (this study) had an average fat below 2.0 g and a fat index below 0.4 at the onset of migration (total fat ranged between 1.0 and 3.6 g, fat index between 0.2 and 0.4). In Massachusetts samples, there was no indication that heavy individuals were more likely to undertake flight than light ones (Helms and Drury, 1960). As the migratory season progressed, birds taken within the winter area tended to be both lighter and leaner (both studies). A sample of three Tree Sparrows collected by F. N. Cowell at Agava Bay, Ontario, between 23 and 26 April 1965, averaged 17.3 g. Thus, none of the available field data suggest that this species increases in weight as migration proceeds. Moreover, upon arrival at the breeding grounds, members of other species tend to be consistently lean (Oakeson, 1954; King et al., 1965).

The only data suggesting weight increases in Tree Sparrows during migration come from caged birds. Individuals kept by Weise (1956) and West (1960) in Illinois increased in weight between late March and the end of April; birds in our own laboratory behaved similarly, reaching a peak weight between 19 and 20 g by early May. These weights, however, only approximated normal field weights at the onset of migration. Winter Tree Sparrows held in cages appear to be in an unfavorable energy balance and their weights seem to be quite anomalous when compared with those of free-living birds in winter. We suggest that captive individuals of this species which are 1) exposed to low ambient temperatures with relatively high rates of air movement leading to wind-chill, 2) prevented from seeking protected habitat day and night, 3) excluded from direct solar radiation, or 4) fed an atypical diet (Martin, 1965) are in bioenergetic difficulty reflected in weight loss

and, in very cold periods, by winter mortality. Therefore, patterns of weight variation seen in caged birds of this species cannot be valid reflections of normal processes in wild individuals and populations. Until evidence appears to the contrary, it is logical to assume that the Tree Sparrow does not increase its lipid reserve during the course of vernal migration. Moreover, increased reserves seem to be unnecessary. Total fat during the first half of March averaged 1.98 ± 0.21 g. Assuming that 0.22 g of this reserve was unavailable structural lipids (based upon unpublished regressions of sectional and total fat in this species), 1.76 g of fat would have been available for energetic utilization (16.7 kcal of reserve). Using the power consumption estimate of Nisbet et al. (1963) of 0.076 kcal/g body weight·hr for migratory flight, an average Tree Sparrow, weighing 19.15 g, could have flown for over 11 hours on fat alone. At an average ground speed of 25 miles per hour (Drury and Keith, 1962), this would have taken an average individual about 290 miles. Assuming full replenishment of reserves between flights, fewer than eight flights of this distance would take a Tree Sparrow to the vicinity of Coppermine, N. W. T., Canada, in the most distant portion of the breeding range of the eastern population, while fewer than five flights would take him to Churchill, Manitoba, Canada. Upper James Bay (Lake River area), Ontario, Canada, could similarly have been reached in three flights. Assuming abundant food and a suitable thermal environment, flight losses could be replaced in a week or less (based upon data from caged birds), so that a migrant beginning flight in mid-March could reach the most distant part of the breeding range by early or mid-May and nearer areas by early April. Actual arrival is not before late May (Baumgartner, 1937; Snyder, 1957). Therefore, due to the early start on migration and the leisurely movements necessitated by the climatic situations encountered en route and in the breeding areas, there is no need to postulate an increased weight for this species as movement progresses. With the relatively long spring migratory period of this species, weights and fat reserves could decrease during the period of migration and, as suggested by the small Agava Bay sample, may actually do so.

The Tree Sparrow, therefore, does not fit the categorization of Odum et al. (1961) with respect to patterns of fat-deposition—it is also doubtful that potential migratory distances in excess of 2,000 miles are “short-range.” The distance from central Pennsylvania to Coppermine is roughly equivalent to that from the former location to northern South America, although, with its limited energetic reserves, the Tree Sparrow would not be able to cross the Gulf of Mexico. In contrast, the trans-Gulf migrants studied by Caldwell, Odum, and Marshall (1964) and trans-oceanic migrants studied by Nisbet et al. (1964) add appreciable fat before making the required water crossing.

It is interesting to note that in this group of migrants, weight and fat reserves are not high during periods of intracontinental movement but become elevated when needed, prior to sustained over-water flight. *Extra* fuel exacts an energetic price and would be selected against in all cases. It appears, therefore, that the categorization of Odum et al. (1961) should be simplified to two categories as follows: 1) intracontinental migrants, and 2) intercontinental migrants. In the former category there would be a complete spectrum of migratory populations from those with low initial reserves performing a leisurely migration with essentially short flights in sequence to those with high initial reserves performing a more rapid migration with fewer but longer flights. In the latter category, intracontinental patterns of fat deposition would be expected until individuals approached the region of departure for extensive single over-water (or desert) flights at which point massive reserves, adapted to the distance to be flown, might be added. Although more data are needed, these patterns seem to be clear. Increasing attention should now be directed to functional differences in the patterns revealed and to the ecological and evolutionary implications of such differences.

SUMMARY

1. Sixty Tree Sparrows (*Spizella arborea*) were collected during the winter of 1962-1963 in central Pennsylvania. Birds were measured, weighed, and frozen. Subsequently, specimens were thawed, weighed, dried, and extracted (petroleum ether: chloroform, 5:1) to determine wet weight, total fat, total water, fat-free weights, and fat and water indices. Age and sex were noted.

2. Adults were heavier (wet and fat-free weights) and larger (wing length) than immatures, but age classes could not be separated throughout the study. Age groups were, therefore, pooled. Males were heavier (wet and fat-free weights) and larger (wing length) than females, but the sexes did not differ significantly in fat. The most conspicuous diurnal change in major body components was in fat.

3. Subsamples collected from mid-winter through spring migration contained birds that were significantly fatter than fall and early winter birds. Wet weight and fat did not increase prior to vernal migration. There were no significant seasonal changes in water, fat-free weights, or wing length.

4. There is no field evidence for vernal premigratory fattening or for increased reserves as migration proceeds in this species, nor do additional reserves appear to be necessary since the Tree Sparrow should have adequate lipid levels to reach any portion of the breeding range in the time at its disposal. Therefore, we suggest a modification of the migrant categories proposed by Odum et al. (1961) to a) intracontinental migrants showing varying but moderate migratory reserves adapted to the species flight patterns (frequency of flights, distance of flights, time available for migration), and b) intercontinental migrants with varying but more massive maximal migratory reserves adapted to the barriers that must be crossed in a single flight but whose reserves are usually deposited only prior to such single flights.

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