ADIPOSE TISSUE COMPOSITION AND CELL SIZE IN FALL MIGRATORY THRUSHES (TURDIDAE)

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Fat deposition is one of the most important and constant physiological events associated with migration in birds (see reviews by King and Farner, 1956 and 1965; Farner, 1960; and Odum, 1960a, 1960b, and 1965). Odum, Rogers, and Hicks (1964) have advanced the hypothesis that before and during migration periods lipid deposition and depletion in adipose tissues occur without appreciable changes in the weight of water and other nonfat components in the body as a whole, in possible contrast to man, where changes in nonfat components may accompany obesity.

In spite of the intensity of recent investigation of this subject, the morphology and histology of the storage adipose tissue have not been adequately described. In this study the gross morphology, composition, and histology of the easily dissectible fat bodies were investigated in samples of thrushes obtained during autumn migration. The special purpose of this effort was to determine if the changes of histology and composition of the adipose tissue are consistent with the hypothesis of the homeostasis of the nonfat components in migrating birds. As an index of possible concurrent changes in fatty acid composition, iodine numbers were also determined.

METHODS AND MATERIALS

Three species of migrant thrushes, Wood Thrush (*Hylocichla mustelina*), Veery (*H. fuscescens*), and Swainson's Thrush (*H. ustulata*), were used in this study. All specimens were fall migrants killed between 14 September and 19 October 1963 in nocturnal collisions with a television tower near Tallahassee, Leon County, Florida. Personnel of the Tall Timbers Research Station collected the fallen birds daily at dawn and identified, weighed, and froze them sealed in plastic bags. This collection of migrant thrushes was assumed to be a random sample, since it represented the total kill for these three species during fall migration at this location.

Wing length was measured to the nearest 0.5 mm from the proximal end of the carpometacarpus to the end of the longest primary with the primaries flattened on the measuring scale. Wet weights were taken at the time of dissection, but showed only insignificant variations from wet weights taken at the time of collection.

Specimens were dissected while partially frozen so that their fat, which tends to melt at room temperatures, would remain solid for easier dissection. Feathers and skin were removed, leaving all subcutaneous adipose tissues attached to the carcass. These were then carefully lifted and teased away from the underlying structures. The smallest lobules were trimmed away with scissors until all visible lobular fat had been dissected. The abdominal cavity was then opened and the visceral fat masses carefully removed. Sex was determined by observation of the gonads. All the dissected lobular fat was then frozen for later analysis.

After removal of the easily dissectible adipose tissue, carcasses were dried to constant weights in vacuum ovens at 40° C and 30 mm Hg. Most specimens reached constant weight after 72 hours of drying, some after 96 hours, and after 108 hours all had reached constant weight. The carcasses were then minced in a Waring blendor, and the remaining fat was extracted with ethanol and petroleum ether (Rogers and Odum, 1964). The weight of the extracted residue was designated the nonfat dry weight.

Iodine numbers (Hanus method) were determined from pooled samples of dissected fat from the five thinnest and the five fattest specimens in each species following the methods described in Official Methods of Analysis of the Association of Official Agricultural Chemists (Horowitz, 1960). The iodine number is an index of the extent of unsaturation of glycerides or fatty acids in a mixture of lipids, *i.e.*, the grams of I_2 consumed in the halogenation of 100 g of fat. These values were used as a potential index of functional change in the adipose tissue. In the thinnest birds,

TABLE 1

WHOLE-BODY MEASUREMENTS OF SOME MIGRATORY THRUSHES BY SEX AND SPECIES

	Wood Thrush 7 females 9 males		Veery 15 females 25 males		Swainson's 13 females 18 males	
	Mean	CV[a]	Mean	CV[a]	Mean	CV[a]
Wing length, mm						
Females	105.8	2.77	96.8	2.80	97.2	1.60
Males	107.2	1.88	100.8	3.35	100.9	2.73
Wet weight, g						
Females	54.6	12.25	36.1	16.46	36.6	12.80
Males	59.9	13.04	38.7	15.21	41.3	12.27
Fat-free weight, g						
Females	41.3	6.46	25.6	7.07	25.5	7.21
Males	43.1	7.81	27.7	6.17	26.2	5.04
Nonfat dry weight, g						
Females	12.2	4.65	7.5	6.63	7.3	5.61
Males	12.7	6.12	8.2	4.40	7.7	5.29
Total body fat, g						
Females	13.3	46.49	10.5	56.29	11.1	49.14
Males	16.8	51.01	11.0	58.45	15.2	32.32
Total body water, g						
Females	29.1	7.39	18.0	7.42	18.1	8.65
Males	30.4	8.65	19.5	7.22	18.4	5.43

[a] Coefficient of variation, %.

four replications for the Wood Thrush, one for the Veery, and two for the Swainson's Thrush used all available fat. Quantities of fat from the fattest specimens were plentiful; therefore 10 replications each for the Wood Thrush and Veery and 13 for Swainson's Thrush were run. Pooled samples represented contributions from both subcutaneous and visceral regions, since insufficient amounts of fat were available to test possible differences in saturated-unsaturated fatty acid ratios of lipids deposited in different anatomical sites.

Blocks of adipose tissue weighing 0.5 to 2.0 g and representing 20 to 90 per cent of the total dissectible fat were taken from both subcutaneous and visceral regions of all specimens. Each block was divided into two equal parts. One part was used for histological examination, and the other part for analysis of the percentage composition of water, extractable fat, and nonextractable residue. Histological parameters and composition analyses could then be compared, since both were derived from the same original block of adipose tissue.

Most samples of adipose tissue reached constant weight after vacuum drying for 36 hours at 40° C and 30 mm Hg. Some samples required 48 hours, but even the largest sample reached constant weight after 60 hours. Dried samples were then ground with chloroform in a tube-and-pestle tissue homogenizer, 16 by 150 mm. The resulting slurry was vacuum filtered in a Buchner funnel on tared filter paper, 9 cm diameter, Whatman No. 40. Large volumes of chloroform were washed over the residue until no fat remained on the filter paper, which was then dried at 90° C for 12 hours and weighed. The net weight of the nonfilterable particulate matter was designated the nonextractable residue. Refiltration of the filtrate showed consistently less than 1 per cent loss of residue through the filter paper.

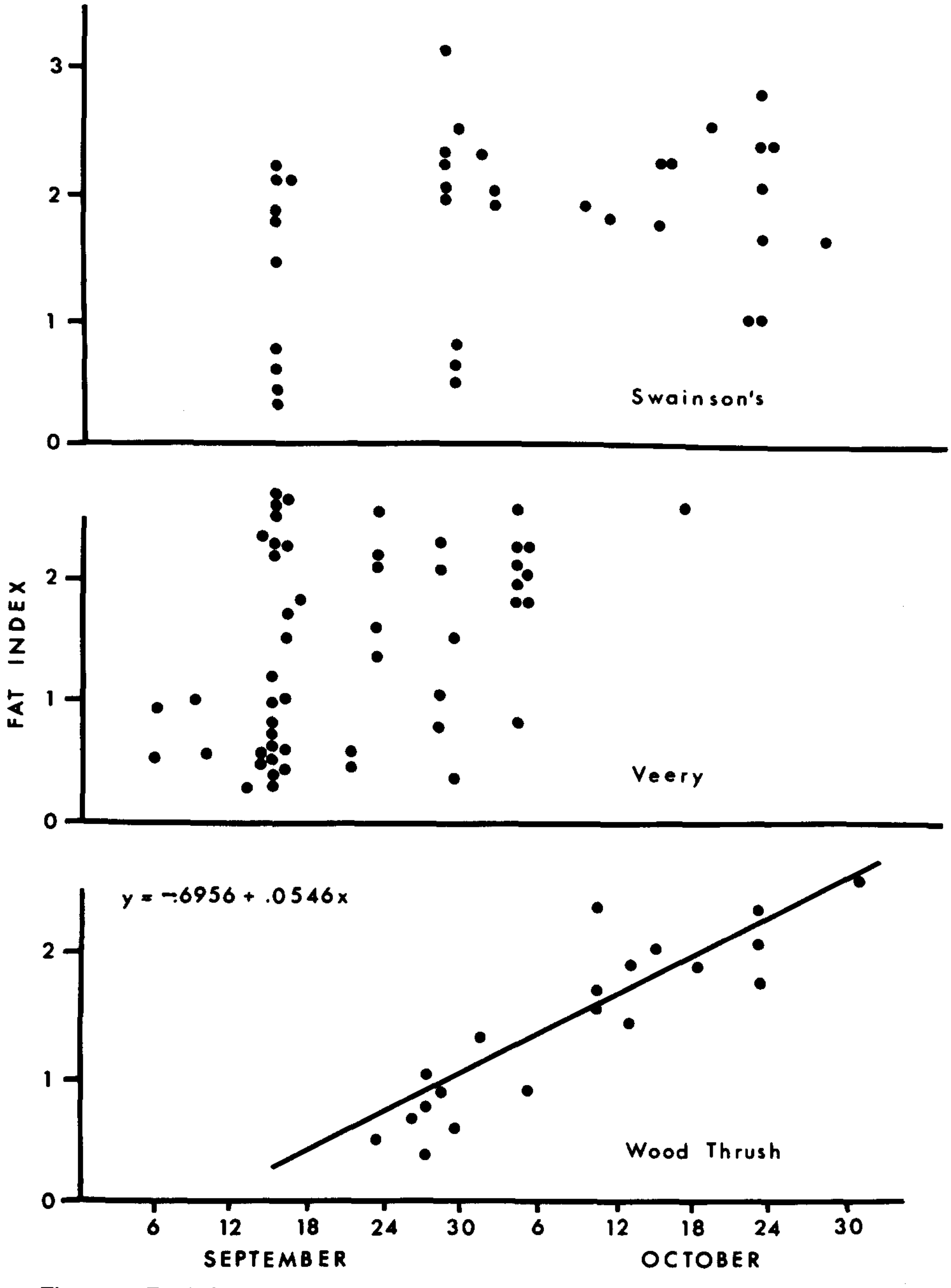

Figure 1. Fat indexes (g fat/g nonfat dry weight) of thrushes killed by collision with a television tower during autumn migration.

TABLE 2

FAT AND WATER INDEXES BY SEX, SPECIES, AND FAT LEVEL

	Wood Thrush 7 females 9 males		Veery 15 females 25 males		Swainson's 13 females 18 males	
	Mean	CV[a]	Mean	CV[a]	Mean	CV[a]
Fat index (g fat/ g nonfat dry weight)						
Females	1.08	45.37	1.39	55.39	1.54	51.29
Males	1.33	52.47	1.35	59.25	1.96	32.65
Fat index (g fat/ g nonfat dry weight)						
Fat index less than 1.7	0.96	44.79	0.85	52.94	0.69	49.27
Fat index more than 1.7	2.02	11.38	2.23	10.31	2.17	14.28
Water index (g water/ g nonfat dry weight)						
Females	2.37	3.46	2.39	2.92	2.48	5.64
Males	2.39	3.64	2.38	4.62	2.38	3.95
Water index (g water/ g nonfat dry weight)						
Fat index less than 1.7	2.40	3.54	2.42	3.60	2.54	6.29
Fat index more than 1.7	2.33	2.49	2.33	3.43	2.38	2.94

[a] Coefficient of variation, %.

Weight of the water in the sample was calculated as wet weight minus dry weight. Dry weight minus residue weight gave extractable fat weight. The latter agreed within 2 per cent with the actual weight of fat recovered from the filtrate by evaporation of the solvent.

Although the dissectible fat was processed separately from the remainder of the carcass, the calculated weights for water, extractable fat, and nonextractable residue were added to the appropriate weights of the corresponding carcass fractions. Values for total water, total fat, and nonfat dry weight were thus obtained for the whole bird and for the dissectible adipose tissue.

Adipose tissue from specimens of different degrees of fatness in each species was selected for histological examination. After fixation in 10 per cent formalin, samples from both subcutaneous and visceral regions were embedded in paraffin, cut at 10 microns, and stained in hematoxylin and eosin (Gray, 1954:94–141, 287, 320). Photomicrographs were taken with a Zeiss Photomicroscope and processed as positive prints. Cell numbers and diameters (mean least diameter of the 20 to 80 cells in a typical high-power field) were measured directly from the positive prints. Approximate cell volumes were estimated assuming the adipocytes were essentially spherical in shape (for purposes of comparison, see fig. 3).

RESULTS

The major anterior subcutaneous fat deposits are located in the furcular and axillary regions. In the most obese specimens, fat fills the furcular notch and spreads over most of the pectoral muscle mass, while in the leanest specimens, only small tags of adipose tissue are visible. The axillary portions of these deposits connect ventrally at the inferior margin of the pectoral muscles. In addition, a spur of fat runs upward into the cervical and occipital regions dorsally, and upward along the trachea ventrally.

The major posterior subcutaneous fat deposits are dispersed over the abdominal wall ventrally and cover the synsacral area dorsally. Extensions of these deposits

TABLE 3

VARIATION IN DISSECTIBLE ADIPOSE TISSUE BY SPECIES, SITE, AND FAT LEVEL

	Wood Thrush (16)		Veery (40)		Swainson's (31)	
	Mean and CV[a]	% Mean TBF[b]	Mean and CV[a]	% Mean TBF[b]	Mean and CV[a]	% Mean TBF[b]
Subcutaneous deposits, g						
Fat index less than 1.7	3.63	30.3	2.12	31.9	1.52	29.6
	43.53		65.09		84.21	
Fat index more than 1.7	8.60	34.4	7.83	44.1	6.86	41.9
	29.19		19.54		20.41	
Visceral deposits, g						
Fat index less than 1.7	1.54	12.8	0.78	11.7	0.62	12.1
	62.99		85.90		109.68	
Fat index more than 1.7	3.42	13.7	3.00	16.9	2.99	18.3
	26.02		26.33		31.10	
Total deposits, g						
Fat index less than 1.7	5.17	43.1	2.91	43.8	2.14	41.7
	47.58		79.38		91.12	
Fat index more than 1.7	12.02	48.1	10.44	61.0	9.85	60.2
	27.37		32.47		21.83	

[a] Coefficient of variation, %.
[b] Percentage mean total body fat.

run down the medial and dorsal aspects of the thighs. Subcutaneous deposits reach a maximum thickness of 10 to 12 mm around the pygostyle. The visceral fat deposits were largely contained in the omentum and mesenteries, with additional lobules attached to the kidneys, gizzard, and cloaca. Stomachs were examined, and all were found empty.

Table 1 summarizes various whole-body measurements of the migratory thrushes by sex and species. Wing length, fat-free weight, nonfat dry weight, and total body water all show a high degree of uniformity within a species, as indicated by the low

TABLE 4

PERCENTAGE COMPOSITION OF DISSECTIBLE ADIPOSE TISSUE

	Wood Thrush (16)		Veery (40)		Swainson's (31)	
	Mean	CV[a]	Mean	CV[a]	Mean	CV[a]
Water						
Subcutaneous	8.33	60.86	9.47	77.29	7.89	94.55
Visceral	7.63	55.04	11.03	77.78	8.26	92.61
Nonextractable residue						
Subcutaneous	2.45	57.55	2.78	80.93	2.28	95.17
Visceral	1.95	48.20	2.68	84.70	2.34	90.17
Extractable fat						
Subcutaneous	89.14	7.08	87.47	10.96	89.90	10.70
Visceral	90.41	5.50	86.24	12.43	89.37	10.88

[a] Coefficient of variation, %.

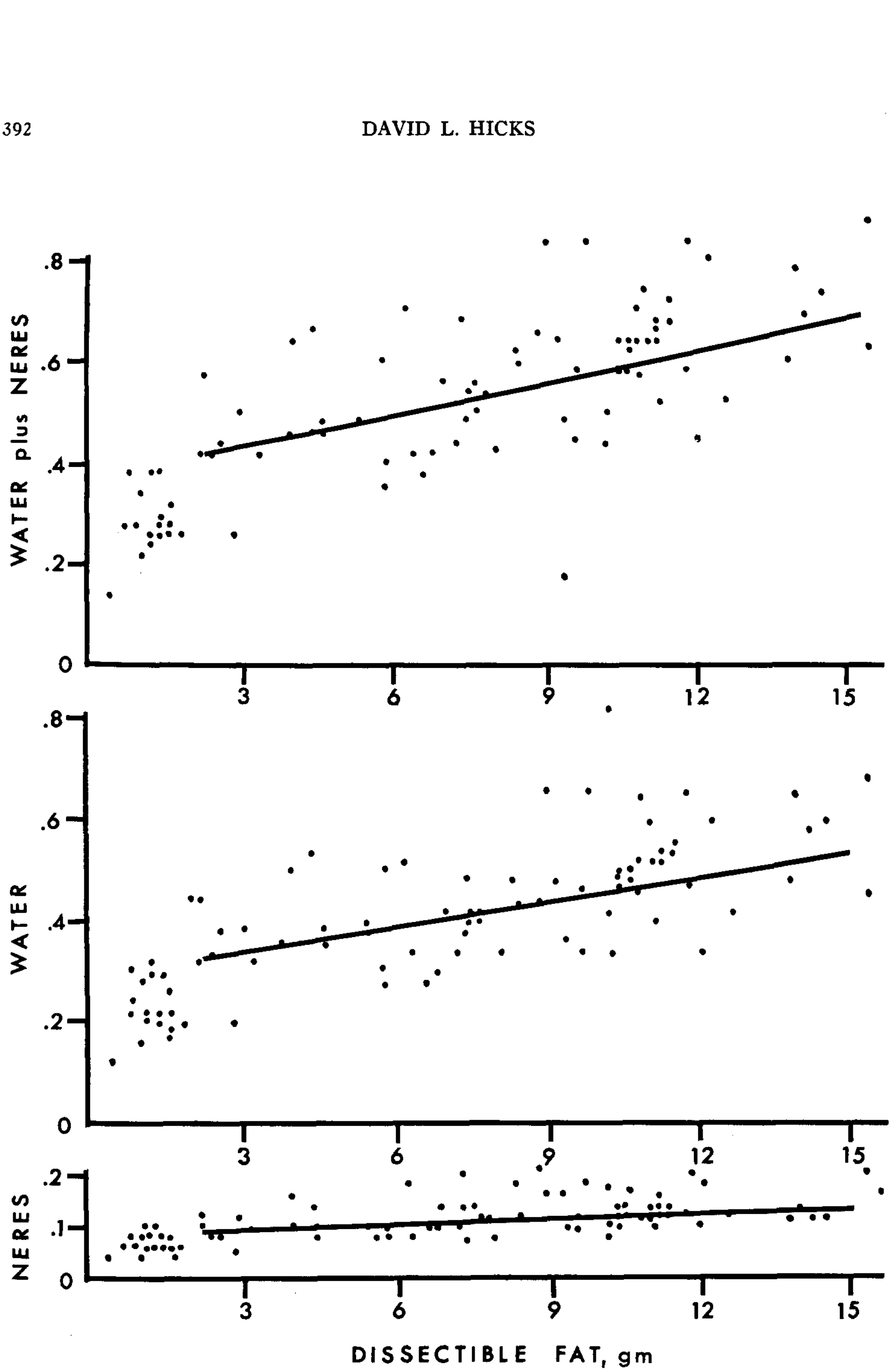

Figure 2. Relation of weights (g) of water and nonextractable residue (NERES) to total weight of dissectible adipose tissue. Lines fitted by inspection.

TABLE 5

t TEST ANALYSIS OF THE NONFAT COMPOSITION OF ADIPOSE TISSUE

Species[a]	Fat class[b]	MNW[c]	CV[d]	Species[a]	Fat class[b]	MNW[c]	CV[d]	d.f.[e]
1 + 2 + 3	A	0.43	34.88	1 + 2 + 3	B	0.63	20.63	85**
1	A	0.58	24.14	2	A	0.36	30.56	35**
2	A	0.36	30.56	3	A	0.43	23.26	31
3	A	0.43	23.26	1	A	0.58	24.14	18*
1	B	0.65	15.38	2	B	0.66	16.67	17
2	B	0.66	16.67	3	B	0.60	25.00	36
3	B	0.60	25.00	1	B	0.65	15.38	25

[a] Species 1 = Wood Thrush, 2 = Veery, 3 = Swainson's Thrush.
[b] A = Fat index less than 1.7, B = Fat index more than 1.7.
[c] MNW = Mean nonfat weight = g water + g nonextractable residue.
[d] CV = Coefficient of variation, %.
[e] d.f. = degrees of freedom; significance of difference between samples in row: $P \leq 0.02$ (*), or $P \leq 0.01$ (**).

coefficients of variation. Wet weight and total fat show much variation in all species, as expected from the wide range of fatness encountered in the specimens.

Figure 1 shows tower-kill dates and level of fatness of migrating thrushes. The wet weights of eight Wood Thrushes collected 23 September through 1 October 1963 averaged 10 g lighter than eight Wood Thrushes collected 5 to 18 October 1963. The weight difference is significant at the 1% level of probability by Student's *t*-test (Steel and Torrie, 1960). The regression line and equation shown in figure 1 account for 81 per cent of the variability in the data, and thus some biological predictive value can be assigned to them. No regression lines are shown for the other two species; lines of best fit accounted for only 14 per cent (Veery) and 4 per cent (Swainson's Thrush) of the variability in the data. In the latter two species, fat and thin birds were well mixed throughout the period of migration.

Table 2 shows variations in fat and water indexes, in relation to sex, species, and fat level. No sex or species differences can be shown. A group of thin birds with fat indexes less than 1.7 was compared with a group of fat birds with fat indexes greater than 1.7. This arbitrary division separates the specimens into two approximately equal groups. While the mean fat indexes for fat and thin birds differ significantly in all species, as would be expected (with a higher variation in the thin group), the mean water indexes did not differ significantly in the fat and thin groups.

Table 3 shows the relations of dissectible adipose tissues to total body fat and level of fatness. In thin birds the subcutaneous, visceral, and total deposits form similar percentages of the total body fat in all three species, while in the fat birds, the subcutaneous, visceral, and total deposits form a smaller percentage of the total body fat in the Wood Thrush than in the other two species. Thus the smaller migrating Veery and Swainson's Thrushes have a relatively greater amount of dissectible adipose tissue than do the larger Wood Thrushes.

The composition of dissectible adipose tissue is shown in table 4. No significant differences can be shown in the composition of subcutaneous and visceral adipose tissue. No interspecific differences can be found for any of these components.

Water and nonextractable residues (nonfat components of adipose tissue) are plotted against weights of dissectible adipose tissue in figure 2. When nonfat components weights of birds with fat indexes less than 1.7 were compared with nonfat components weights of birds with fat indexes greater than 1.7, a highly significant

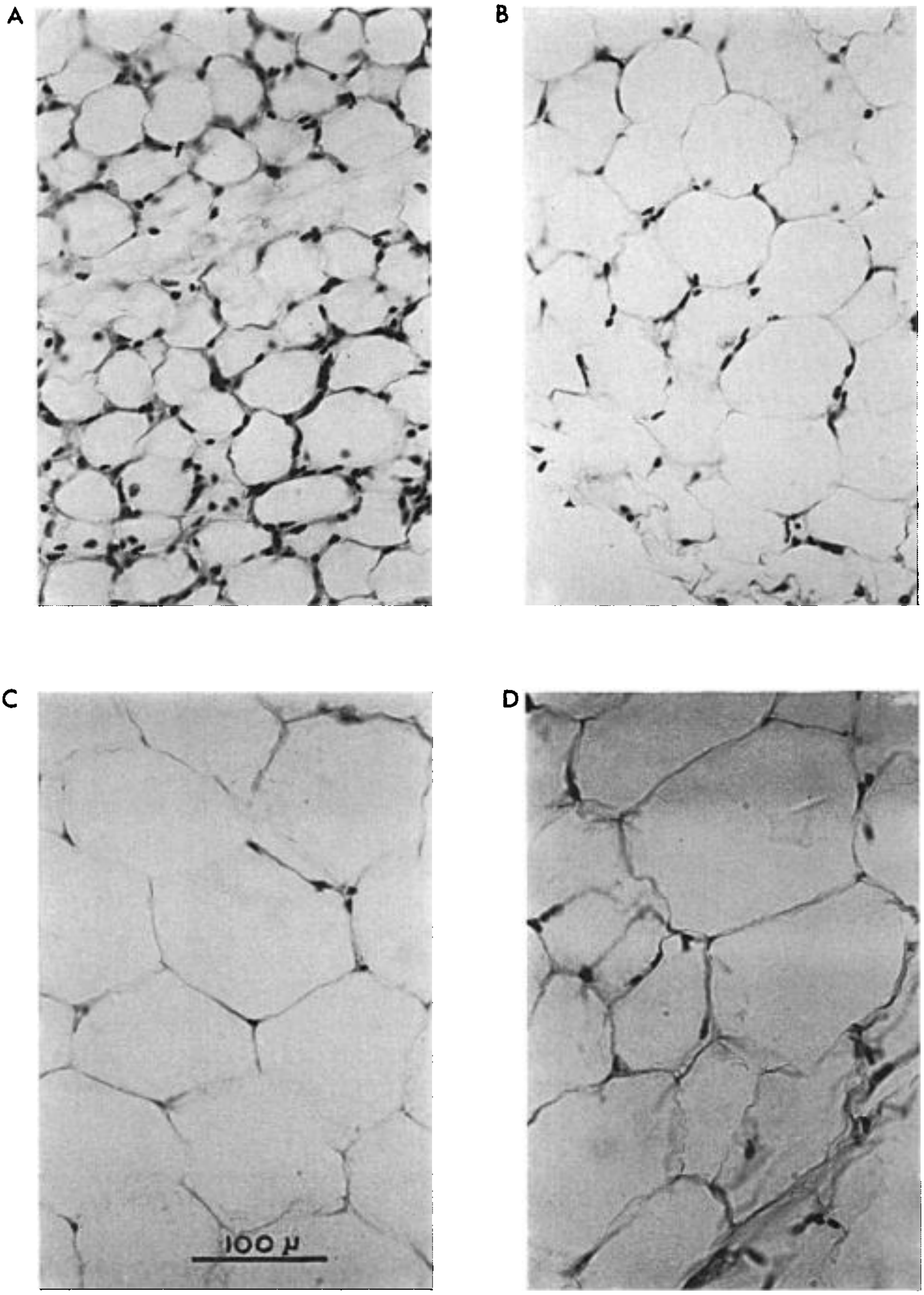

Figure 3. Photomicrographs of adipose tissue from thrushes of different degrees of fatness. Fat indexes and mean cell volumes, respectively, are as follows: A. 0.31, 12,500 μ^3; B. 0.49, 23,600 μ^3; C. 1.68, 98,000 μ^3; D. 2.48, 149,000 μ^3. Mean cell volume was calculated from the least diameters of 20 to 80 cells in a typical high-power field, assuming that the cells were spherical.

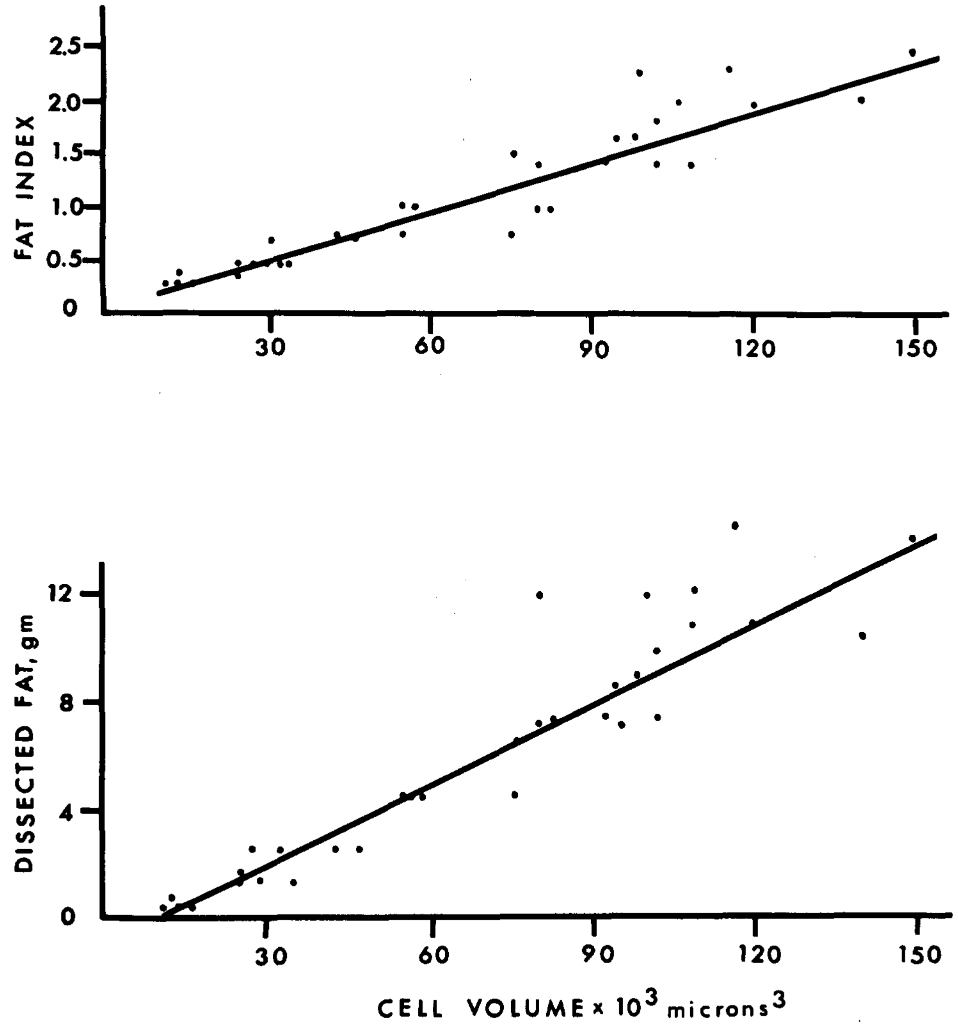

Figure 4. Relation of cell volume (0 to 150,000 μ^3) to fat index and weight of total dissectible fat. Lines fitted by inspection.

difference was noted as indicated in table 5. The 45 thin birds included 12 Wood Thrushes, 25 Veeries, and 8 Swainson's Thrushes. The 42 fat birds included 4 Wood Thrushes, 15 Veeries, and 23 Swainson's Thrushes. Species comparisons using only thin birds showed significant differences between the Wood Thrush and Veery ($P < 0.01$), the Wood Thrush and Swainson's Thrush ($P < 0.02$), but not between the Veery and Swainson's Thrush. Species comparisons using only fat birds showed no significant differences between any pair of species.

Table 5 shows that there is an average gain of 0.20 g (range 0.07 to 0.30 g) in the nonfat components from the thin group (0.43 g) to the fat group (0.63 g). A similar gain may be interpolated from the upper graph in figure 2.

Photomicrographs in figure 3 show adipocytes at four different stages of fat

TABLE 6

ANALYSIS OF VARIANCE OF IODINE NUMBERS FROM POOLED SAMPLES OF DISSECTED ADIPOSE TISSUE[a]

Source	df	Mean squares	Signif.
Species	2	419.1415	0.01
Fat level	1	57.4879	0.01
Species × fat	2	520.4899	0.01
Error	34	2.9333	
Total	39		

Species	Adj. means	Species	Adj. means	Signif.
Wood Thrush	87.8067	Veery	87.3864	ns
Veery	87.3864	Swainson's	74.4219	0.01
Swainson's	74.4219	Wood Thrush	87.8067	0.01
Fat level				
Thinnest	85.0041	Fattest	81.4059	0.01
Species × fat				
Thin W. Thrush	91.9124	Thin Veery	97.2999	0.01
Thin Veery	97.2999	Thin Swainson's	65.8000	0.01
Thin Swainson's	65.8000	Thin W. Thrush	91.9124	0.01
Fat W. Thrush	83.7010	Fat Veery	77.4729	0.01
Fat Veery	77.4729	Fat Swainson's	83.0438	0.01
Fat Swainson's	83.0438	Fat W. Thrush	83.7010	ns

[a] Duncan's multiple range test (Steel and Torrie, 1960).

deposition. Cell volumes increase markedly while cell membranes appear to become thinner as the fat index increases. The adipose tissue is quite vascular as shown by the number of blood cells visible among the adipocytes.

Mean estimated cell volumes are plotted against fat indexes and weight of dissectible fat in figure 4. A fivefold increase in the volume of fat as measured by either scale is linearly related to approximately a fivefold increase in cell volume, again indicating that little but lipid is added to or removed from the tissues of the bird during the southward migration.

Data on iodine numbers are summarized in table 6. Data shown in each category are highly consistent as indicated by the level of statistical significance. Comparisons of species means for thin and fat groups show no consistent trend. Duncan's multiple-range test was used for analysis of variance of iodine numbers from pooled samples of dissected adipose tissue. In species interactions Swainson's Thrush differed significantly ($P < 0.01$) from both the Wood Thrush and Veery. Species means for thin and fat groups show that the Swainson's Thrush increases the proportion of unsaturated fatty acids with increasing fat deposition, while both the Wood Thrush and Veery show the opposite trend, *i.e.*, a decrease in the proportion of unsaturated fatty acids with increasing fat deposition. All thin specimens differ from all fat specimens in mean iodine number at the 1% level of probability. In the species × fat interactions, all species differ from one another in a highly significant manner ($P < 0.01$), while in the fat group, only Swainson's Thrush and Wood Thrush show no significant difference. Other species × fat interactions in the fat group are highly significant ($P < 0.01$).

DISCUSSION

The nonfat components of adipose tissue remain nearly constant in weight during migratory fat deposition, as indicated by the negligible slope of the lines in figure 2. The mean weight of the nonfat components and the mean total body fat of all birds with fat indexes less than 1.7 are 0.43 and 7.58 g, respectively. The mean weight of the nonfat components and the mean total body fat of all birds with fat indexes greater than 1.7 are 0.63 and 17.67 g, respectively. Thus the addition of 10 g of fat to the adipose tissue is accompanied by an increase of only 0.20 g water and nonextractable residue. These values are also easily interpolated from figure 2.

The Wood Thrush differs significantly from both the Veery and Swainson's Thrush in weight of the nonfat components of birds with fat indexes less than 1.7. Since mean nonfat dry weight shows the Veery and Swainson's Thrush to be only 60 per cent as large as the Wood Thrush, differences in the weight of nonfat components may be attributed to body-size differences. Similar differences do not appear, however, in birds with fat indexes greater than 1.7. A possible explanation is that 27 per cent of the thin birds are Wood Thrushes. Thus the small proportion of Wood Thrushes in the fat group does not affect the mean significantly.

McGreal and Farner (1956) described 15 discrete fat bodies in the Gambel White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Attempts were made in this study to delimit these various fat bodies, but due to the extreme obesity of many specimens, these fat bodies coalesced into larger masses.

This study confirms the evidence of McGreal and Farner (1956) who found that increases in the size of the fat bodies in the Gambel White-crowned Sparrow result predominantly from addition of lipid, and only slightly from addition of water and other nonlipid materials. Similar findings with rats are reported by Liebelt (1959) and by Pandazi, Herrington, and Schlueter (1960).

Zingg, Angel, and Steinberg (1962) found that increases in perirenal fat deposits in the rat are linearly related to both cell size and cell number, and concluded that neither cell size nor cell number was fixed in the adipose tissue of the rat. Diagrams in Maximow and Bloom (1948) show subcutaneous fat cells in the rat with an average diameter of 50 microns. In a moderately thin (fat index of 1.00) migrating thrush, average cell diameter is also approximately 50 microns, while in the fatter specimens, cell diameters of 120 to 150 microns are not uncommon. In the migrant thrushes cell-size increase is very evident in histological preparations (fig. 3), indicating a strongly developed hypertrophic mechanism in fat deposition. Direct evidence for increase in cell number is not available from this study, but the very small increase in weight of the nonfat components shown in figure 2 may be taken as indirect evidence of only a slight increase in cell numbers, if any.

This modest increase in nonfat components along with the evidence of a very large increase in cell size supports the hypothesis that premigratory fat deposition is principally a process of hypertrophy with only minimal hyperplasia.

The range of iodine numbers in passerine birds is wide, extending from 38 in the Red-cheeked Starling (*Sturnia violacea*) to 146 in the Kamtschatken Wagtail (*Motacilla alba lugens*), according to McGreal and Farner (1956). MacDonald (1961) shows that iodine number is dependent on ambient temperature, diet, species, and temperature of a fat deposit within the body. Deposits deep within the viscera show more saturation (a higher proportion of saturated fatty acids in triglycerides) than subcutaneous deposits, and MacDonald (1961) considers this to be a temperature-gradient phenomenon. In the Gambel White-crowned Sparrow, McGreal and Farner (1956) found no significant difference ($P > 0.05$) in iodine numbers among premolt, molt, and premigratory fat deposits in spring birds. The means for these categories ranged from 84.1 to 86.8. Subcutaneous and carcass lipids were not significantly different during these periods.

Nakamura (1962) found a mean iodine number of 69 (range 58 to 76) in fat deposits of the Eastern Great Reedwarbler (*Acrocephalus arundinaceus orientalis*) captured on the wintering grounds prior to spring migration. A downward trend in the proportion of unsaturated fatty acids was evident during vernal premigratory fattening, presumably owing to dietary changes in the premigratory period.

In wintering and migrating Slate-colored Juncos (*Junco hyemalis*), Bower and Helms (1967) found that the proportion of linoleic acid (C-18:2) decreased in the lipid reserves from November through April as the diet of the bird changed from seeds (high in linoleic acid) to insects (low in linoleic acid).

The observed lack of a consistent pattern of changes in iodine numbers with increasing fat deposition in three species of *Hylocichla* may be attributed to basic species differences. However, as suggested by Walker (1964), it is likely that the nature of the food ingested during premigratory fattening has some effect on the composition of the fat deposited. Changes in the fatty acid composition of the diets of migrating thrushes are highly probable, since thrushes begin their migratory flights before maximum fatness is achieved, and stop to feed en route and fatten during a series of progressively longer flights until they reach the Gulf of Mexico at peak fatness prepared for the trans-Gulf crossing to Central America (Stevenson, 1957; Odum, 1960b).

CONCLUSIONS

The nonfat components of adipose tissue in fall migrant thrushes are essentially stable, despite large changes in total body fat.

Photomicrographs showing increases in cell size with increasing fat deposition together with data showing only a small accompanying increase in nonfat tissue components constitute direct evidence for hypertrophy of fat cells as a major mechanism in premigratory fattening.

Observed significant differences in iodine numbers between species are attributed to basic species differences. Since no consistent pattern was evident, differences in iodine numbers between stages of fatness within a species are attributed to differences in food available to individuals that may have originated their migratory flights from a wide geographical area to the north.

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