A STUDY OF NONFAT WEIGHTS IN MIGRATING SWAINSON'S THRUSHES (*HYLOCICHLA USTULATA*)

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Odum et al. (1964) suggest that the nonfat components of migrating birds are essentially homeostatic despite the extensive deposition and utilization of fat that results in large variations in total body weight. Their hypothesis that "fat is added to and used from preexisting tissue spaces without appreciable change in the water content or the nonfat dry weight of the body as a whole" is based largely on the studies of Connell et al. (1960) on Savannah Sparrows (*Passerculus sandwichensis*), Rogers and Odum (1964) on wood warblers (*Parulidae*), and Hicks (1967) on thrushes. In general these studies present results from circumscribed localities and seasons. King et al. (1965) show that the fat-free weight of the Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) does vary seasonally although not neccessarily associated with migration. Furthermore, Zimmerman (1965) reports that various environmental stresses may reduce the fat-free weight in moderately fat Dickcissels (*Spiza americana*).

To test the idea of the constancy of the nonfat weight during migration, measurements were made on the fat, water, and nonfat weights of Swainson's Thrushes (*Hylocichla ustulata*) collected at seven points along their migration route between northern North America and northern South America (Figure 1).

Methods

Sites, methods of collection, collection dates, and sample sizes were as follows:

I. WWTV television tower, Cadillac, Wexford County, Michigan. Collected after nocturnal collision with the tower by Larry D. Caldwell between 26 August and 11 October 1962 (N = 23).

II. WJBF television tower, Jackson, Aiken County, South Carolina. Collected after nocturnal collision with the tower by Jay Schnell on 30 September 1960 (N = 21).

III. WCTV television tower, Tall Timbers Research Station, just north of Tallahassee, Leon County, Florida. Collected after nocturnal collision with the tower by Herbert L. Stoddard, Sr. and associates in September and October during several fall migration seasons between 1957 and 1965 (N = 110).

IV. Almirante, Bocas del Toro, Panama. Casualties of a nocturnal rainstorm during fall migration collected by David T. Rogers, Jr. on 13 October 1963 (Rogers, 1965) (N = 12).

V. San Francisco, Veraguas, Panama. Netted by the author during northward spring migration between 18 and 22 April 1965 (N = 21).

VI. Brant Bayou, 1 mile north of Pilottown, Louisiana. Netted by Rexford D. Lord, Jr. and associates between 22 April and 9 May 1966 (N = 39).

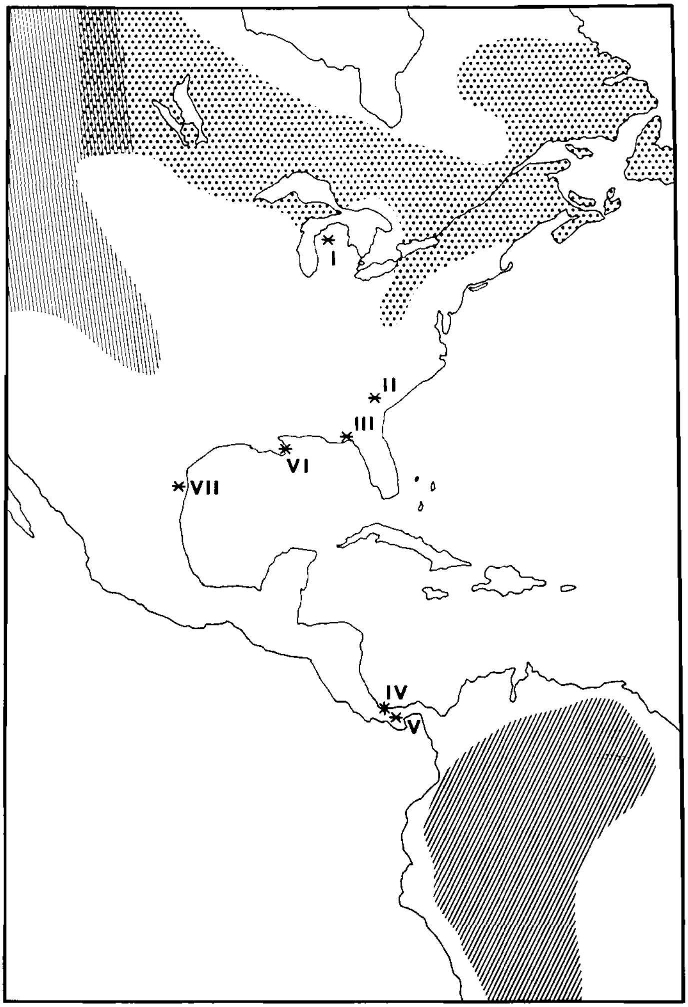

Figure 1. Collection sites within the migratory pathways of Swainson's Thrushes are shown by Roman numerals I–VII. See text for listing of sites. Breeding ranges of eastern and western subspecies are indicated (Bond, 1963) as is the winter range in South America (A.O.U., 1957).

VII. Ingleside by the Bay, Texas. Netted by James Richardson and associates between 15 April and 7 May 1966 (N = 53).

All netted specimens were weighed to the nearest 0.01 g on a triple-beam balance in the field within 1½ hours after netting. They were then killed and frozen in individual plastic bags as soon as possible, except for specimens from site V, which were preserved in 95 per cent ethanol in individual glass vials. Specimens were reweighed in the laboratory and, if differences were appreciable, the laboratory weights were accepted as the more accurate. Examination of the stomachs showed that the handling process usually afforded enough time to clear the digestive tract. Nocturnal migrants killed at television towers were collected early every morning, frozen, and later weighed in the laboratory. Stomachs of nocturnal migrants were generally empty.

At the Louisiana and Texas locations (sites VI and VII) an average of 0.05 cc of blood was removed from each bird. As blood is approximately 85-87 per cent water (Spector, 1956), the blood removed was considered as water in subsequent calculations.

Wing lengths were measured, as chords, to the nearest 0.5 mm from the proximal end of the carpometacarpus to the tip of the longest primary while the wing was flattened (not straightened) on a rule. The majority of wing lengths were remeasured in the laboratory by the author.

Sex was determined by dissection. In the fall adults and immatures were separated by skull ossification. All spring birds were considered adults.

Laboratory procedures for removing water and fat from specimens were as follows:

Water content was determined by vacuum drying at 40°C for a minimum of 5 days, and then desiccating in the presence of calcium chloride until the weight remained constant.

The carcass was then macerated in a blendor with 95 per cent ethanol, and one of two fat extraction methods was used:

(1) The macerated carcass was repeatedly boiled in petroleum ether and carefully drained through a fine strainer to separate solvent and fat, or (2) the macerated carcass was funneled into the bottom of a tared acetate rayon bag (volume approximately 200 ml). The sealed bag was submerged in boiling petroleum ether. At 45-minute intervals the bags were transferred to clean ether until no fat was visible in the solvent.

The extracted residue was dried at least 12 hours at 80°C, allowed to cool in a desiccator, and weighed.

Each extraction method had small inherent errors (mean, 0.01 g) resulting from a loss of nonfat residue, but prior to the final weighing, a gain of moisture ensued that was sufficient to cancel out the errors of extraction.

Duncan's new multiple range test (Duncan, 1955) was used for mean separation and Student's "t" test was utilized when appropriate for determining significant differences between any two means. Statistical significance was accepted at the 0.01 level of probability unless otherwise noted.

Terms used throughout this paper are defined as follows: (1) Wet weight = entire weight. (2) Fat-free weight = wet weight minus weight of ether-extracted fat. (3) Nonfat dry weight = wet weight minus water and weights of ether-extracted fat, or, alternately, fat-free weight minus weight of water. (4) Fat index = grams of fat/grams nonfat dry weight. (5) Water index = grams of water/grams of nonfat dry weight. (6) Pretrans-Gulf migrants = thrushes southbound in the fall collected at sites II and III. (7) Posttrans-Gulf migrants = thrushes northbound in the spring collected at sites VI and VII.

Results

A frequency distribution by wing length and sex of 257 Swainson's Thrushes is plotted in Figure 2. The sex ratio was approximately 1:1 for the entire collection. For purposes of statistical analysis of the body com-

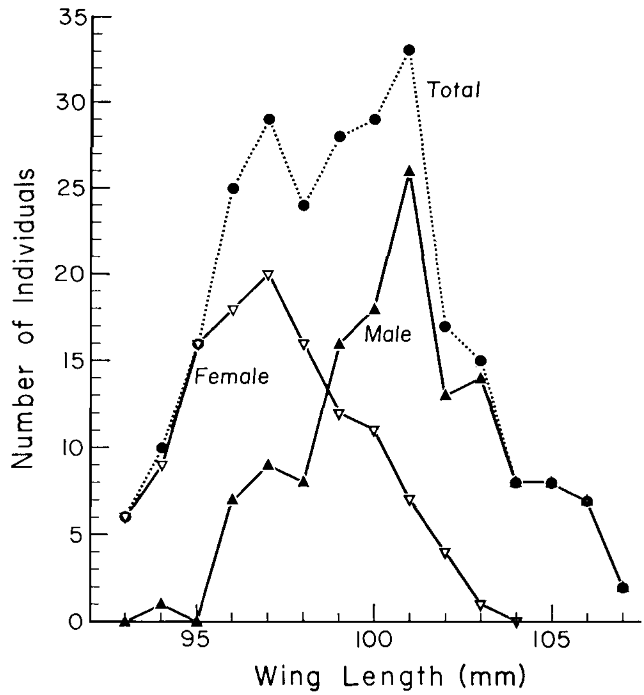

Figure 2. Frequency distribution by sex and wing length of 257 migrating Swainson's Thrushes.

ponents, two size categories were selected, namely: size category (1) wing lengths 93–99 mm, and size category (2) wing lengths 100–107 mm. Such a division separates the collections into two approximately equal groups, divides equally the range of wing lengths, and also results in a 75 per cent sex separation.

To test for homogeneity of body size among the sample populations, the wing length data (as an indicator of body size) by sex for the sample populations were subjected to an analysis of variance and the sample populations were found to be similar. In reference to subsequent analysis of fat-free weights, it is important to note that the birds from the seven sites did not differ in body size (as indicated by wing length). The variations in mean wing lengths were not clearly ascribable to subspecific differences.

Wing lengths of migrants collected at sites II, III, VI and VII are compared as to sex, age and season in Table 1. Adults had significantly longer wings than immatures in the fall, but fall and spring birds as a whole

TABLE 1

MEAN WING LENGTHS OF MIGRANT SWAINSON'S THRUSHES BY SEX, AGE, AND SEASON[1]

Age	Sex	Season	Mean wing length mm	No.
Adults	Males	Fall	102.00	27
Immatures	Males	Fall	100.64[2]	33
Adults	Females	Fall	97.88	17
Immatures	Females	Fall	96.44[2]	41
All ages	Males	Fall	101.10	49
All ages	Males	Spring	100.29	51
All ages	Females	Fall	96.86	58
All ages	Females	Spring	96.93	41

[1] Fall specimens are from Tallahassee, Florida, and Jackson, South Carolina. Spring specimens are from Pilottown, Louisiana, and Ingleside by the Bay, Texas.

[2] Larger mean significantly greater than the smaller mean at $P \leqslant 0.01$. Males are significantly larger than females in all categories.

did not differ. As would be expected, males had significantly longer wings than females.

Comparison of fall pretrans-Gulf migrants of the same wing length showed no difference in the fat-free weights due to sex, age, and fatness (Table 2), though males averaged 0.98 g heavier than females, a difference significant at the 0.025 level.

The fat-free weights of both fall and spring migrant Swainson's Thrushes tended to increase with increasing wing length as would be expected, but the scatter around a linear regression was wide. Among the posttrans-Gulf migrants the coefficient of correlation ($r = 0.164$) was not significant, but it was significant for the pretrans-Gulf migrants ($r = 0.395$).

Nonfat components.—Tables 3 and 4 summarize means of six variables

TABLE 2

EFFECT OF SEX, AGE, AND DEGREE OF FATNESS ON FAT-FREE WEIGHTS OF FALL MIGRANT SWAINSON'S THRUSHES[1]

Comparison	No.	Mean fat-free weight (g)
All males	24	25.87
All females	19	24.79[2]
Adult males	9	25.86
Immature males	15	25.87
Adult females	7	24.97
Immature females	12	24.69
Thin birds (fat index < 1.00) adults and immatures	18	25.05
Fat birds (fat index > 2.00) adults and immatures	7	24.89

[1] With wing lengths between 98 and 101 mm. All birds were killed at a Florida or South Carolina television tower during nocturnal migratory flights in late September and early October.

[2] Larger mean significantly greater than smaller mean at $P \leqslant 0.025$.

TABLE 3

A COMPARISON OF MEANS[1] OF SIX VARIABLES OF MIGRATING SWAINSON'S THRUSHES[2] FROM SEVEN SITES[3] ALONG THE MIGRATION ROUTE

Site	No.	Wet weight (g)[4]	Fat-free weight (g)	Nonfat dry weight (g)	Fat (g)	Water index	Water % fat-free weight
I	6	30.03 b,c	26.05 a	7.74 a	3.98 b,c	2.37 a,b	70.29 a,b
II	7	38.07 a	25.24 a,b	7.56 a	12.83 a	2.34 a,b,c	70.04 a,b,c
III	67	37.27 a	24.95 b	7.54 a	12.37 a	2.31 a,b,c	69.54 a,b,c
IV	3	32.93 a,b	25.05 a,b	7.34 a,b	7.75 a,b	2.36 a,b,c	69.09 a,b,c
V	10	27.41 b,c,d	23.84 b	7.00 b,c	3.58 b,c	2.41 a	70.61 a
VI	25	26.84 c,d	22.28 b,c	7.03 b,c	4.57 a,b,c	2.17 c	68.39 c
VII	32	25.82 d	22.21 c	6.92 c	3.61 c	2.22 b,c	68.99 b,c

[1] Duncan's new multiple range test.

[2] Wing length category 93–99 mm.

[3] Sites I through IV were southbound fall migrants; V through VII were northbound spring migrants.

[4] Within a column any two means with the same letter are homogeneous at $P \leqslant 0.01$.

at each of the seven sites. Means at each site and for each of the two wing length categories were compared according to the new Duncan's multiple range test with means arranged in sequence I through VII. These same means with corresponding standard errors and coefficients of variation are given elsewhere (Child, 1966, appendix Tables 1–7).

The means of fat-free weights along the migration route differed by as much as 3.8 g, while nonfat dry weight means differed by less than a gram (Tables 3 and 4). The highest means occurred in Michigan (site I) at the beginning of southward migration and the lowest were recorded for spring arrivals on the Gulf coast (sites VI and VII). Thus a decrease in the nonfat weights roughly paralleled the migration sequence. As shown by

TABLE 4

A COMPARISON OF MEANS OF SIX VARIABLES OF MIGRATING SWAINSON'S THRUSHES[1] FROM SEVEN SITES ALONG THE MIGRATION ROUTE[2]

Site	No.	Wet weight (g)	Fat-free weight (g)	Nonfat dry weight (g)	Fat (g)	Water index	Water % fat-free weight
I	17	31.86 b	27.20 a	8.18 a	4.66 b,c	2.33 a	69.91 a,b
II	14	42.65 a	26.77 a,b	8.28 a	15.88 a	2.23 a	69.05 b,c
III	43	41.31 a	25.95 b	8.01 a	15.36 a	2.26 a	69.09 c
IV	9	33.71 b	26.56 a,b	7.86 a,b	7.15 b	2.35 a	69.75 a,b,c
V	11	25.11 b,c	25.11 b	7.48 b,c	4.86 b,c	2.37 a	70.53 a
VI	14	27.67 c	23.44 c	7.43 b,c	4.20 b,c	2.15 a	68.42 c
VII	21	27.26 c	23.38 c	7.25 c	3.88 c	2.22 a	68.85 c

[1] Wing length category 100–107 mm.

[2] See Table 3 for explanation of sites and symbols.

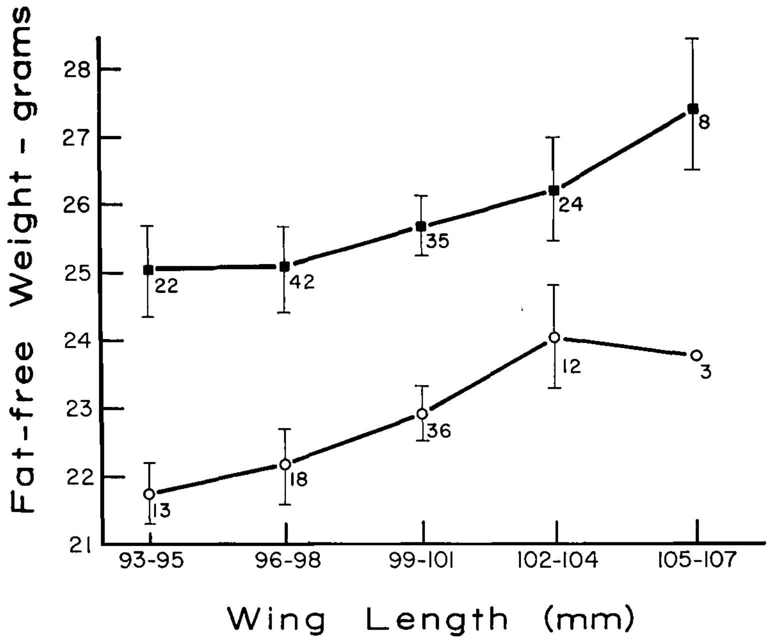

Figure 3. A comparison of the relationships between wing length and fat-free weight in fall pretrans-Gulf (■) and spring posttrans-Gulf (○) migrant Swainson's Thrushes. All fall birds were collected following their nocturnal collision with a television tower at Tallahassee, Florida, and Jackson, South Carolina. All spring birds netted at Ingleside by the Bay, Texas, and Pilottown, Louisiana. Horizontal lines are 95 per cent confidence intervals for the means.

Duncan's test in Tables 3 and 4, the nonfat components of spring migrants (sites VI and VII) differed significantly from fall migrants (sites I–IV). This difference is illustrated graphically in Figure 3. Also, fall birds near the northern and southern termini of the migration differed in their nonfat weights, but the loss of nonfat dry weight was so small and gradual that means for adjacent localities and seasons did not differ significantly. In a similar species, the Gray-cheeked Thrush (*Hylocichla minima*), the fat-free weights in spring and fall on the Gulf coast also differed significantly (Table 5).

Water expressed as a percentage of fat-free weight and the ratio to nonfat dry weight (water index) were the least variable of the nonfat variables. No geographical or seasonal trend in the water ratios was evident. With but two exceptions, all water index means were homogeneous (Tables 3 and 4). The posttrans-Gulf migrants had the lowest values, suggesting the possibility of a slight dehydration during flights northward

TABLE 5

FALL AND SPRING COMPARISONS OF MEAN FAT-FREE AND NONFAT DRY WEIGHTS OF MIGRATORY SWAINSON'S AND GRAY-CHEEKED THRUSHES[1]

Swainson's Thrush						Gray-cheeked Thrush					
Site	Season	Wing length category (mm)	No.	Fat-free weight (g)	Nonfat dry weight (g)	Site	Season	Wing length category (mm)	No.	Fat-free weight (g)	Nonfat dry weight (g)
III	Fall	93–99	67	24.95 (0.21)[2]	7.54 (0.05)	III	Fall	93–100	11	25.86 (0.54)	8.03 (0.10)
VII	Spring	93–99	25	22.28 (0.24)	7.03[3] (0.07)	III	Spring	93–100	58	23.41[3] (0.20)	7.47[3] (0.06)
III	Fall	100–107	43	25.95 (0.28)	8.01 (0.09)	III	Fall	101–108	16	26.09 (0.49)	8.23 (0.12)
VII	Spring	100–107	14	23.44[3] (0.24)	7.43[3] (0.09)	III	Spring	101–108	29	24.80[4] (0.27)	7.91[4] (0.08)

[1] Collected along the coast of the Gulf of Mexico; site III Tallahassee, Florida, and site VII Pilottown, Louisiana.

[2] Parentheses enclose 1 SE of the mean.

[3] Means different at $P \leqslant 0.01$.

[4] Means different at $P \leqslant 0.05$.

from the tropics. In each site collection, the two water indices were slightly greater in the smaller than in the larger birds, but the difference was significant only in the large sample at site III.

Fat.—Clearly fat was the most variable of the body components studied. As shown in Tables 3 and 4, the fat reserves in the pretrans-Gulf migrants at sites II and III were significantly greater than in any of the other populations except for the small sample of migrants killed during a nocturnal rainstorm in Panama (site IV). For all practical purposes the very fat birds killed at the two southeastern U. S. TV towers in the fall were in marked contrast to the moderately fat to thin birds collected at the other five sites; furthermore, the means of these five sites were statistically homogeneous.

Larger birds tended to have relatively greater quantities of fat per gram of nonfat dry weight (i.e. higher fat index) than the smaller ones (Child, 1966), but only at site III was a difference significant.

The relative contributions of fat, water, and nonfat dry weight to total weights are shown in Figures 4 and 5 for the seven sites arranged in the migration sequence. These figures show graphically what has been demonstrated statistically, namely: (1) southbound migrants have slightly higher nonfat weights than northbound migrants. (2) Birds are fattest as they approach the northern Gulf coast in the fall. (3) There is an overall trend of decreasing fat-free weight from north to south and north again to the U. S. Gulf coast. As mean wing lengths of spring samples

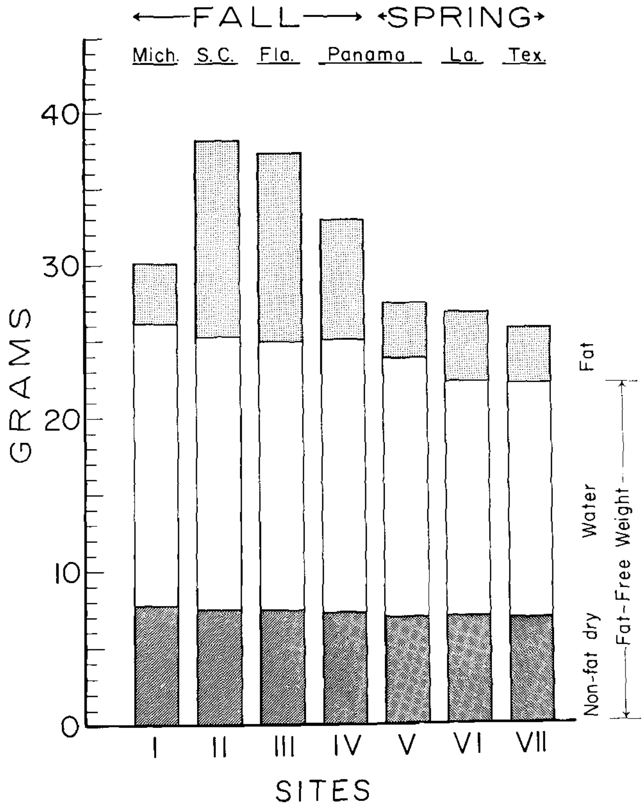

Figure 4. Mean body composition of Swainson's Thrushes (wing lengths between 93 and 99 mm) in sequence of migration (see text for description of sites).

did not differ significantly from fall samples, it is reasonably certain that the low fat-free weights of Louisiana and Texas spring birds were not due to significant body size differences. If wing lengths had been significantly different between the spring and fall samples one might suspect the difference in fat-free weights to be attributable to two distinct populations.

The slight decline in nonfat weight from Michigan to Panama was not an entirely unexpected result, because birds would be expected to catabolize some nonfat materials during long flights even though fat is the chief flight fuel (Odum et al., 1964). In mammals a gain and loss of lean body mass occurs with fat accumulation and depletion, respectively (Dole, 1962; Behnke, 1962). Recently Helms et al. (1967) showed that changes in the total fat and nonfat weights were positively related in the Slate-colored Junco. What was unexpected was that nonfat losses were apparently not

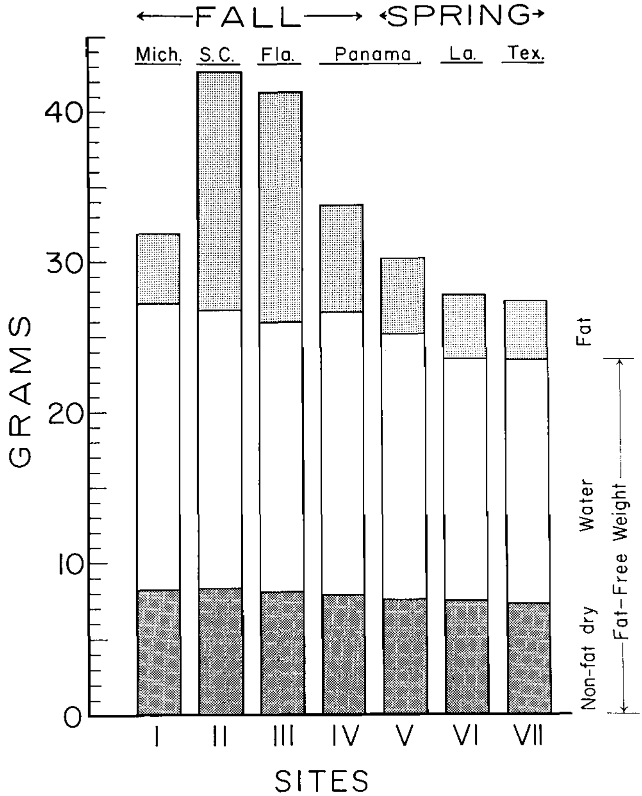

Figure 5. Mean body composition of Swainson's Thrushes (wing lengths between 100 and 107 mm) in sequence of migration (see text for description of sites).

recouped either during or after the fall migration. Thus birds migrating north in Panama in spring had significantly lower fat-free weights than birds starting south in Michigan in the fall. One explanation might be that remaining light in body weight has survival value for birds while migrating or wintering in tropical and subtropical climates. Spring and summer specimens from northern United States are obviously needed to determine when fat-free weight increases again in the north.

Another point of interest is that no really fat birds (fat index $\geqslant 2.0$) of this or any other species have been found during the northward migration in Central America. Spring collections of North American breeders have been obtained in Costa Rica and Honduras as well as in Panama. Either birds do not get as fat in spring as in fall, or collections have not yet been made in the right place at the right time.

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Summary

Collections totaling 279 Swainson's Thrushes were made during the fall and spring migrations at seven locations along the migration route between Michigan and Panama to test the idea of the constancy in nonfat weights.

A gradual and comparatively small decrease in fat-free and nonfat dry weight roughly paralleled the migration sequence, so that mean values were significantly lower in spring arrivals on the U. S. Gulf coast than in Michigan fall birds. Differences between fall birds within the United States or between spring and fall birds in Panama were not significant. The slight losses occurring during southward migration were apparently not recouped during the winter. As wing lengths of the seven populations were homogeneous, the differences in fat-free weights were probably not due to size differences resulting from different racial composition of populations.

Ratios of water to nonfat weights were remarkably similar at all localities and indicated a proportionate change in water and nonfat dry components. Only in the posttrans-Gulf migrants was a slight but nonsignificant dehydration noted.

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