A REVIEW OF THE VERNAL FAT DEPOSITION PICTURE IN OVERLAND MIGRANT BIRDS

By David W. Johnston

Part I: The White-throated Sparrow at the Southern Edge of its Wintering Range.

A favorite of the bird-bander is the White-throated Sparrow (*Zonotrichia albicollis*), hundreds of which have been trapped and banded in the eastern United States and Canada. Capitalizing upon the ease and frequency with which the species may be obtained, a number of workers have amassed valuable weight, mensural, and other data from banding these birds. In recent years Eugene P. Odum and his coworkers have described weight and fat variations of the White-throats wintering in northern Georgia (Athens) and northwestern Florida near Tallahassee (Odum, 1949, 1958; Odum and Connell, 1956; Odum and Perkinson, 1951). Both of these sites are within the wintering range of the species, not at the southernmost edge. Several significant conclusions emerged from their investigations: (1) White-throats arriving in north Georgia, and also those killed at the Tallahassee TV tower in autumn, are both light in weight and lean; (2) there is a mid-winter peak in weight and fatness; (3) during the prenuptial molt the birds weigh less than at any other time during their sojourn in the South; and (4) the birds reach a reported premigratory peak in weight and obesity in late April and early May. It is the purpose of this paper to examine weight and fat data for the White-throat population wintering at Gainesville, Florida, a locality representative of the southern edge of this species' wintering range.

White-throats are fairly common winter residents around Gainesville (Chapman, 1888), but farther south in Florida the species is noticeably rarer (Sprunt, 1954). In the autumn White-throats generally arrive at Gainesville about the first week or ten days of November. The arrival time at Gainesville is about two weeks after the birds first arrive at Athens, Georgia, 300 miles to the north, and about one week after they arrive in the Tallahassee, Florida region, 150 miles west-northwest. Twelve birds caught in November, 1963 at Gainesville in mist nets were subjectively judged to be lean, and their body weights (Table 1) were considerably less (by about 2-3 g) than the autumnal postmigratory birds at Athens (Odum and Perkinson, 1951) but only about 1 g less than autumnal arrivals near Tallahassee. In fact, Odum (1958: 106) suggested that "the White-throats striking the tower at Tallahassee had used up all or most all of their fat, which is not unexpected since the Gulf coast is near the 'end of the line' for fall migration . . . ." By comparison, the data in Table 1 show, in addition to the distributional information cited above, that the Gainesville White-throats were at the "end of the line."

TABLE 1. AVERAGE WEIGHTS OF WHITE-THROATED SPARROWS AT GAINESVILLE, FLORIDA

	Males		Females	
	Number	Weight in Grams	Number	Weight in Grams
November, 1963				
First half	2	25.6	5	23.3
Second half	2	26.1	3	21.4
March, 1964				
First half	–	——	4	25.2
Second half	4	28.3	7	25.4
April, 1964				
First half	–	——	4	25.9

Most White-throats have migrated northward from the Gainesville area by the first week in April. (There are rare records as late as April 27, reported by Chapman in 1888, and April 30, reported by Sprunt in 1954.) During March and April, 1964, I undertook a systematic collecting of premigratory White-throats around Gainesville. At this time of year the birds nearly always occurred in scattered small flocks of three to seven individuals, but the last bird found (April 10) was alone.

Each of the 19 birds collected was subjected to complete fat extaction by a technique previously described (Johnston, 1962). The results of the fat extractions are shown in Table 2. These vernal premigrants were both relatively light in weight and lean, the mean fat per cent of body weight being only 4.7 after mid-March. Table 2 also shows that the premigratory sample at Gainesville did not have a dramatic increase in weight or fat in spring as Odum and Perkinson (1951) demonstrated in their studies of White-throats at Athens.

Insofar as prenuptial molt is concerned, the Gainesville White-throats resembled those studied in northern Georgia by Odum, at least in a temporal sense. At Athens White-throats underwent their heaviest prenuptial molt in late March and early April with this molt being completed in most birds by mid-April. Prenuptial molt was undetected in the Gainesville birds until March 22; after that time the molt became more extensive and intensive by the end of the month but tapered off by April 4. In most individuals of both sexes molt involved head, neck, and body feathers, but on several females, judged to be subadults, crown feathers were not being molted. It was during this prenuptial molt that the Gainesville birds were light in weight and lean.

The data presented here on vernal features of White-throats at Gainesville provide supporting evidence for two suggestions of Odum (1958). First, Odum proposed that the White-throats occurring at Athens in the bottomlands in May ". . . were probably migrants from further south which had used up one load of fat and had stopped to accumulate another deposit" (p. 108). As shown in Table 2, White-throats leaving Gainesville in the latter

TABLE 2. BODY AND FAT WEIGHTS OF WHITE-THROATED SPARROWS IN THE SPRING OF 1964 AT GAINESVILLE, FLORIDA

Date		Sex	Body Weight	Fat Weight	Fat as per cent of body weight
March	6	♀	24.5g	1.4g	5.7
	6	♀	25.1	1.2	4.8
	13	♀	26.3	2.0	7.6
	13	♀	24.9	0.8	3.2
March	19	♀	23.1	0.8	3.5
	19	♀	25.4	1.0	3.9
March	22	♂	28.5	0.9	3.2
	22	♂	27.3	0.7	2.6
March	27	♀	24.3	1.5	6.2
	27	♀	23.9	1.0	4.2
	27	♂	28.0	1.1	3.9
	27	♀	26.4	1.4	5.3
March	29	♂	29.3	1.6	5.5
	29	♀	26.6	1.8	6.8
March	31	♀	27.8	1.4	5.0
April	3	♀	25.4	1.1	4.4
	3	♀	25.2	1.4	5.6
April	4	♀	28.0	1.2	4.3
	10	♀	25.2	1.7	6.8
Averages	4	♂♂	28.3	1.1	3.8
	15	♀♀	25.5	1.3	5.2

half of March or first part of April have a mean fat content of only 1.2 g (4.7 per cent of the body weight). These figures are markedly less than the average fat weight (16.7) and percentage of body weight (extremes = 9.7-24.8 per cent) found in "premigratory" White-throats in late April in Georgia. Probably the "bottom-land" White-throats of north Georgia included individuals migrating from Florida or south Georgia, especially as regards the weight and fat differences.

The second suggestion made by Odum was ". . . that immature or first-year females probably tend to winter further south than adults in general and males in particular" (p. 108). Accordingly, in the autumnal series of 45 White-throats examined by Odum from the Tallahassee TV tower were 35 females, and all 45 birds were first-year birds. Although the adult condition could not be determined accurately in our vernal sample of 19 birds taken at Gainesville, only four of these proved to be males (by dissection). Furthermore in the bird collections at the University of Florida there are 30 White-throats taken between November and April in northern Florida. In this group, there are 3 adult males, 9 immature males, 3 adult females, and 15 immature females. Thus, 60 per cent of the White-throat specimens in this collection are females and 83 per cent of the females are immatures. This set of figures certainly tends to substantiate Odum's earlier proposal on differential migratory distances of the sex and age groups in this species.

Since White-throats leave the Gainesville area in such a lean condition, it seems likely that in the spring they move northward both slowly and for short distances at first. I believe this suggestion to be strengthened by the fact that Stoddard gets very few vernal White-throats at the Tallahassee TV tower as compared with autumnal kills. Stoddard (1962: 92) reported only six spring records as opposed to 186 in the fall. This marked contrast suggests a difference in migratory flights of the species at these two seasons, a feature suggested earlier by Borror (1948). He found in Ohio that the number of White-throats migrating through in the spring was less than the number in the fall, and that migration in the fall spanned a longer period of time than in the spring. It is also true that migrating White-throats stopover longer in the fall than in the spring. Borror (1948) calculated the length of stopover time in the fall at 8.7 days and in the spring at 5.2 days. (Blake (1950) recalculated the fall stopover time at 4.4 days.) And in Pennsylvania Middleton (1939) determined the average length of stay in the fall to be 6.3 days and in the spring 3.8 days.

These data support the hypothesis that in the spring White-throats initiate migration in the south with short flights and frequent stopovers. The farther northward they move, the longer the flights and less frequent the stopovers. In the autumn, however, White-throats evidently make longer flights with fewer stopovers toward the southern terminus of their journey.

Estimated Flight Ranges. In recent years various methods and formulae have been advocated to calculate estimates of flight ranges of migrating birds. One of the earliest estimates for White-throats was that of Wolfson (1954) who calculated that an individual with 6 g fat could fly 270 miles, with 8 g. fat, about 360 miles. On the basis of his assumptions, the White-throats leaving Gainesville with an average fat content of 1.2 g could fly only about 40 miles nonstop.

Assuming flight energy expenditure to be 3 times the existence rate and an average flight speed of 30 mph, Odum (1960) estimated a flight range of about 100 miles for White-throats of fat content similar to the premigratory Gainesville birds. Based primarily upon weight-loss during migration Nisbet et al. (1963: 144) postulated that the "average rate of weight-loss corresponds to an average power consumption of about 0.076 Kcal./gm. total weight/hr." Applying this figure to a 26 g White-throat, assuming a fat load of 1.2 g and a flight speed of 20 mph, the bird could fly about 115 miles.

More recent quantitative data suggest the use of basal and flight rates of metabolism to calculate flight range. Both LeFebvre (1964) and Lasiewski (1963) report that the rate of energy expenditure in flight is seven or eight times the basal rate. For determination of basal rate of metabolism in small birds, King and Farner (1961) give the formula

$$\log M = \log 80.1 + 0.659 \log W \pm 0.076$$

or

$$M_b \text{ (kcal/day)} = 80.1 W^{0.66}$$

From the vernal premigratory sample of White-throats at Gainesville, the following average fat-free weights were obtained: 15 ♀ ♀ = 24.1 g; 4 ♂ ♂ = 27.2 g. Using an average fat-free weight of 25 g (for the sexes combined), the basal rate of metabolism for the White-throat is 0.29 kcal/hr. If we now assume Mflight = 8Mbasal, then Mf = 2.32 kcal/hr. The flight speed of a White-throat has apparently never been measured directly, but it appears to be in the order of 20 mph (Cooke, 1937; Pearson, 1961). With all of these data one can now obtain an estimate of flight ranges for White-throats containing given quantities of fat utilized in flight:

body fat	*kcal available**	*flight range*
0.5 g	4.75	41 miles
1.0	9.50	82
1.5	14.25	123

Furthermore, because White-throats departing Gainesville in early spring contain on the average 1.2 g fat, those birds could normally fly about 90 miles nonstop. This distance approximates that which was calculated from the weight-loss method mentioned above.

Regardless of which of these methods one uses in calculating estimated flight ranges, clearly the premigratory vernal White-throats at Gainesville are incapable of long sustained flights even if they metabolize all their stored fat during flight.

Part II: Vernal Weight and Fat Characteristics of Other Migrant Passerines.

The literature on North American migrants is liberally sprinkled with allusions to premigratory vernal weight (and in some cases, fat) increase. Though it cannot be denied that vernal weight increases may occur in a given overland migratory species, a closer examination of the timing of this increase, migratory habits, and quantitative fat studies suggests a different interpretation than has previously been made. In speaking about the temporal aspects of fat deposition, it is becoming increasingly important to make a distinction between premigrant and intramigrant (transient), that is, an individual that has not yet begun to migrate and one already in the course of its migratory movement. A true premigrant is, therefore, an incipient migrant. An intramigrant is a bird already migrating, even though it might have flown for only a short distance and has stopped briefly to refuel, reorient, or rest. Thus, many of the papers published about vernal migrants and alluding to "premigrants" were likely discussing intramigrants solely or in combination with true premigrants. In the absence of a marked population at a location *within* the winter range of a species but not at the southernmost boundary, it would be difficult, if not impossible, to distinguish accurately between individuals over-winter-

*Using a caloric value of 9.5 kcal/g fat (King and Farner, 1961) ing at that location and individuals migrating through. Thus, late in the spring, for example in May in Virginia, a given White-throat could be a premigrant or an intramigrant; or, to put it another way, one that has arrived at the site from some point farther south.

Farner (1955) has reviewed premigratory fat deposition in spring migrants, his comments pertaining especially to non-quantitative aspects. He observed (p. 212) that ". . . in a variety of species . . . an increase in weight involving fat deposition is characteristic of the premigratory period . . ." but (p. 214) ". . . premigratory deposition of fat does not necessarily occur in some species." The species listed in Table 3 are North American fringillids for which a

Table 3. Species In Which a Vernal Weight or Fat Increase Has Been Observed

Species	Location	Reference
Oregon Junco (*Junco oreganus*)	California	Wolfson, 1942
Slate-colored Junco (*J. hyemalis*)	Illinois	Weise, 1963
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	California	Linsdale and Sumner, 1934
White-throated Sparrow (*Z. albicollis*)	Georgia	Odum, 1949
White-crowned Sparrow (*Z. leucophrys*)	California	Blanchard, 1941
Fox Sparrow (*Passerella iliaca*)	California	Linsdale and Sumner, 1934

vernal premigratory weight or fat increase (subjective evaluation) or both have been reported. (For a more complete list of additional species showing fat increases, see Dolnik and Blumenthal, 1964). With only one possible exception among these species, the reported weight gain and concomitant fat increase occurred *late* in the spring —late April or May. Furthermore, in all of these species the alleged "premigratory" sample very likely included some intramigrants from farther south. The one possible exception is that of the Oregon Junco studied by Wolfson (1945: 110): "heavy [fat] class occurs only in March the month of departure for migrant juncos which have wintered in Berkeley." It seems possible, though, that his small March sample of ten males included some intramigrants.

Wolfson (1945), interpreting Blanchard's (1941) data for *Z. leucophrys pugetensis*, reported an increase in body weight from a December "low" of 27.0 g to 28.8 g (March) and 31.2 g (April). Since only a very small sample was taken in April, as opposed to March, it appears that most of the local population had already migrated in March at which time the birds had not reached a peak in weight, and that the April sample likely included birds that had arrived from farther south (intramigrants).

On the other hand, a number of species evidently do not show a vernal increase in weight or fat (qualitatively judged). Among these are: Purple Finch (*Carpodacus purpureus*; Bartleson and Jensen, 1955), Tree Sparrow (*Spizella arborea;* Helms and Drury, 1960;

TABLE 4. FAT CHARACTERISTICS OF SOME VERNAL OVERLAND PREMIGRANTS

Species	Location	Time of Departure	Mean Body Weight	Mean Fat Weight	Fat as Per Cent of Body Weight	Reference
White-throated Sparrow	Florida	late March and early April	26.6g	1.2g	4.9	This paper
Slate-colored Junco	North Carolina	late March	19-20g	1.4g	6.8	Johnston, 1962
Rosy Finches	Utah	late March	26-30g	....	9-16*	King and Wales, 1965
Myrtle Warbler	coastal North Carolina	April	12.4g	0.8g	5.8	Yarbrough and Johnston, 1965
Savannah Sparrow	South Carolina	late April	18.3g	2.1g	11.2	C. E. Connell
White-crowned Sparrow	Washington	May	32g	....	20.2*	King and Farner, 1959
Yellow Wagtail	Nigeria	March and early April	22.1g	3.8g	17.3	Ward, 1963
Common Wheatear	Nigeria	early March	24.7g	4.3g	17.5	Ward, 1963

*Lipid index (percentage of *lean* body weight)

Baumgartner, 1938), and Song Sparrow (*Melospiza melodia*; Nice, 1946). Significantly, all these species are *early* spring migrants that leave their wintering grounds (where studied) in March or early April.

Quantitative data on vernal fat increases are now available for several other passerines (Table 4). Again, with few exceptions, it can be seen that the early premigrants are not markedly obese.

The species in Table 4 that appear to have a "premigratory" fat increase merit closer examination. In the cases of the White-crowned Sparrow (McGreal and Farner, 1956; King and Farner, 1959), Yellow Wagtail, and Common Wheatear (Ward, 1963), again I suspect that intramigrants were included in the sample. Ward (1963: 109) even suggested for the Common Wheatear that "all the birds shot must have been preparing for fairly imminent departure, *or were already migrating* . . ." (italics mine). Furthermore Curry-Lindahl (1963: 966) wrote that "males and females of *M.* [*otacilla*] *flava* do not exhibit an abrupt and extensive deposition of body fat just prior to the spring migration . . . ." His figure on page 964 shows, rather, a gradual increase in mean body weight in March and April, at which time the mean body weight in the Congo was only about 19 g. Farther north in Nigeria where Ward's studies were made in late March and early April, the reported mean body weight was about 22 g. Incidentally, fat deposition in Yellow Wagtails migrating overland resembles that of overseas migrants (see Odum, Connell, and Stoddard, 1961) in that the wagtails migrate partly over the inhospitable Sahara Desert.

Another interesting case of vernal weight increase is that of the Rosy Pastor (*Sturnus roseus*) in India. Naik (1963) reported (p. 45) "a sharp increase of fat in the liver with increase in body weight up to the time of migration." The collecting site was evidently at Baroda in northern India, but the species is known to occur in winter much farther south, even to Ceylon. In late April, when the greatest weight and fat values were obtained, the sample could have included not only premigrants but also intramigrants from farther south.

An instance of moderate premigratory fattening early in the spring has been reported by King and Wales (1965). Working with several taxa of Rosy Finches (*Leucosticte*), they noted (p. 66) that "although we did not detect a distinct increase in mean body weight or mean lipid index in the feral population before vernal migration, there was a definite increase in maximum values." It is important to point out that, of the three forms studied, the Gray-crowned Rosy Finch evidently migrates farther than the other two and has the highest maximum lipid index in March.

Two factors, then, are important in assessing vernal fat deposition associated with overland migration; place and time. If a species is studied at or near the southernmost limit of its winter range (for example, Myrtle Warbler, Slate-colored Junco, White-throated Sparrow), it may not show marked premigratory vernal fat deposition. On the other hand, if a species is studied north of the southernmost wintering points, the observer must take care that intramigrants are not included in the sample, for the premigrants may be lean whereas the intramigrants are fat. Time is of the essence too, for early premigrants are usually lean though late spring premigrants generally do amass much fat. These ideas are not necessarily original here, for they have been variously expressed by several other authors. Wolfson (1954), for example, noted that birds migrating early and slowly do not necessarily have marked, premigratory fat deposits. Although Odum, Connell, and Stoddard (1961) believed that the White-throat does not begin its migration in a lean condition, they suggested that ". . . a gradual increase in fat reserves during migration is characteristic of land migrants that breed in the far north." And Mascher (1966) noted for Dunlins (*Calidris alpina*): ". . . it cannot be stated that a certain amount of fat is a necessary prerequisite for departing."

It now appears from the reports of Nisbet et al. (1963), Johnston (1964), and Caldwell et al. (1963) that some autumnal overland migrants in North America also initiate migration in a lean state. As I pointed out (1964) these autumnal species include both short- and long-range migrants which, according to the classification of Odum et al. (1961), ". . . become moderately obese, but begin migration before [any] peak [fat] deposition." Extensive fat deposition, then, is not necessarily characteristic of the premigratory period at least early in the season in many overland migrant species. Recently Zimmerman (1965) reported Dickcissels (*Spiza americana*) beginning to migrate northward from the Canal Zone before significant fat deposition occurred.

If early premigrants are relatively lean and become progressively obese in time and distance traveled, some interesting questions are raised concerning the mechanisms underlying both fat deposition and migration. King and Farner (1963) have demonstrated experimentally that fat deposition and *zugunruhe* are under independent control mechanisms and that vernal fat deposition generally precedes *zugunruhe*, at least in some *Zonotrichia* sparrows. Other experimental evidence shows that some caged birds (especially Bramblings, *Fringilla montifringilla*) can undergo *zugunruhe* in the absence of fat deposition (Lofts, Marshall, and Wolfson, 1963). The caged *Zonotrichia* King and Farner used showed a slight but noticeable increase in *zugunruhe* although the birds were not gaining weight on restricted food intake. Apparently early vernal overland premigrants, however, differ from the caged birds in that they initiate migration in a lean condition.

Is it possible that different thresholds of day length underlie the differences in timing of fat deposition and migration? For example when the lean White-throats are departing Gainesville about April 1, the day length is about 12 hours. In early May White-throats (whether the same birds or different individuals) are fat and (many) already migrating in north Georgia. At this time the day length is in excess of 13 hours. Thus, perhaps something like 13 hours of light is threshold for massive fat deposition. Possibly environmental temperature exercises a modifying effect because King and Farner (1963) observed *zugunruhe* activity in White-crowned Sparrows earliest in the warmest spring and latest in the coldest spring.

SUMMARY

The White-throated Sparrow leaves northcentral Florida at least by early April, at which time individuals are both light in weight and lean. On the average the premigratory bird contains only about 1.2 g of fat, enough fuel to sustain a continuous flight of about 90 miles. Evidently these lean premigrants initiate their northward movements with short flights, making frequent stopovers en route. As they migrate northward and as the season progresses evidently they become more and more obese. Certainly the evidence in this species indicates that only the late premigrants or intramigrants are markedly fat.

Vernal increases in weight and fat deposition for other overland migrant passerines are discussed. Two factors, time and place, are important in assessing fat deposition. The data on fat deposition, both qualitative and quantitative, amassed so far indicate that the early premigrants generally do not show a sharp increase in weight involving fat deposition whereas the late premigrants, as well as intramigrants, generally do. Especially is vernal fat deposition characteristic of late migrants at locations north of the southernmost edge of the wintering grounds.

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ECOLOGY OF ARBOVIRUS INFECTION IN NEW JERSEY
Review of a 5-Year Mist-netting Program

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Introduction

Bird banding activities have been pursued intermittently by the New Jersey State Department of Health since 1953. An intensive study of bird populations was initiated in 1960 as part of a more extensive study of the ecology of Eastern and Western encephalitis. The purpose of this report is to present an introductory review of the ornithologic aspects of this study and to present information on the size, structure, and stability of the avian populations, such as might relate to the ecology of arboviruses.

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