# LIPID DEPOSITION IN WINTERING AND PREMIGRATORY MYRTLE WARBLERS

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FOR some time it has been known that many birds have characteristic lipid deposits associated with the time of migration (Wolfson, 1945, 1952; Odum, 1949; McGreal and Farner, 1956; King, Barker, and Farner, 1963), the lipid evidently supplying the energy required for a sustained flight. Odum and Perkinson (1951) considered lipid deposition to be a premigratory prerequisite, but, in spite of the fact that overseas migrants might have as much as 50 per cent of the body weight in lipids (Odum and Connell, 1956; Odum, Connell, and Stoddard, 1961), it is becoming increasingly evident that intracontinental migrants might be lean at the onset of migration (Hanson, 1962; Johnston, 1962; Nisbet, Drury, and Baird, 1963; Caldwell, Odum, and Marshall, 1963). The precise timing of premigratory lipid deposition is, therefore, being clarified at present, especially at it relates to Zugunruhe (King and Farner, 1963), hyperphagia (Odum and Major, 1956), and migratory pattern (Odum, Connell, and Stoddard, 1961). In the many investigations of lipid deposits in North American species (Odum, 1958; 1960b; Connell, Odum, and Kale, 1960; Farner, 1955; Wolfson, 1945; Helms and Drury, 1960), little attention has been given to either the correlation between natural food habits of the species and lipid deposition or to the qualitative nature of the lipids deposited (see recent work of Walker, 1964).

The present investigation is a report on the relationships among diet, lipids (quantitatively and qualitatively), and migratory patterns in the Myrtle Warbler (*Dendroica coronata*), especially on its wintering grounds in North Carolina. Its preferred diet of wax myrtle berries (*Myrica cerifera*) has been known for many years (Brewer, 1840), and in winter on the Coastal Plain of North Carolina this warbler reaches its peak of abundance in wax myrtle thickets (Pearson, Brimley, and Brimley, 1959). On the Piedmont Plateau of North Carolina Myrtle Warblers are frequently found associated with red cedars (*Juniperus virginiana*). Chamberlain (1961) noted that these birds are more plentiful along the coast in winter and that they disappear early in the spring from coastal localities. He suggested that the increase in Myrtle Warblers on the Piedmont in the spring is due to the arrival of birds from the Coastal Plain of the Carolinas, from farther south (Georgia and Florida), or both.

# MATERIALS AND METHODS

Eighty-three Myrtle Warblers were collected in the winters of 1961-62 and 1962-63 from two localities in North Carolina: at Bladenboro (typical of

		T.	ABLE	1					
NUMBERS OF SPECI	IMENS OF M	YRTLE	WARBL	ers Co	LLECTE	d in N	ORTH	Carol	INA
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Мау	Totals
Coastal Plain	3	4	8	6	4	2	6		33
Piedmont Plateau	4	4	4	4	4	4	6	20	50
			—			—			
	7	8	12	10	8	6	12	20	83

the Coastal Plain) and Winston-Salem (typical of the Piedmont Plateau). Table 1 shows the numbers of birds taken in each month for the two localities. In addition, 81 Myrtle Warblers killed at a Gulf Coast TV tower (Leon County, Florida) in 1960-61 were sent to us by H. L. Stoddard, Sr. and E. P. Odum.

Before lipids were extracted, each specimen was weighed, measured (wing chord, tail, bill), checked for molt, the sex and age determined, and the stomach contents removed. The lack of complete skull ossification was used to identify immature birds from October through December after which time ossification was generally complete in all birds. In this paper data for adults and known immatures are combined. Sex was determined by plumage differences, wing length (Tables 2 and 3), and examination of the gonads. Wing length alone proved to be reliable in distinguishing the sexes except in birds whose wings were 70 or 71 mm.

Stomach contents were stored in 70 per cent alcohol for subsequent examination. Food in the stomach did not greatly affect body weight, as might be true of some larger birds whose stomach capacities are considerably greater than those of this small bird. The empty stomach was put back into the body cavity to be extracted along with the rest of the bird. This technique has not previously been employed by others in extracting lipids. Stomach contents were placed in a watch glass and examined under a dissecting microscope. Plant materials (seeds or fruits) were identified to genus and species, animal materials (arthropods) only to order, due to their macerated condition. The per cent of plant and animal matter in each stomach was estimated on the basis of mass. These stomach contents were then dried in an oven (70 C) and weighed.

In the lipid extraction process, the technique employed by Odum (1958), and modified by Johnston (1962), was used. Briefly, the process involved dehydration of the opened, whole bird, grinding the bird in a blendor, lipid extraction with alcohol and ether solvents, and drying and weighing the lipidfree, dehydrated mass of bones, feathers, etc. Thus, for each bird we obtained three values: water weight, lipid-free dry weight, and, by subtraction, lipid weight.

		McGregor*			Museum of Vertebrate Zoology			
	No.	Wing	Tail	No.	Wing	Tail		
Males								
California								
(hooveri)	7	76.7**	58.4	8	72.6	54.0		
		(75.7–78.0)	(56.4-60.5)		(69.6 - 75.1)	(50.3-56.8)		
Eastern								
(coronata)	8	72.9	54.9	8	72.6	52.3		
		(71.1–74.4)	(52.8–57.4)		(69.7-77.0)	(48.3–55.0)		
Females								
California								
(hooveri)	10	72.9	56.4	7	71.1	53.5		
		(70.4 - 75.2)	(54.1–57.9)		(70.0-73.6)	(50.9–56.3)		
Eastern								
(coronata)	10	68.6	53.3	7	68.7	50.7		
. ,	-	(67.6-76.7)	(51.3 - 55.4)		(65.5 - 71.4)	(48.5–53.3)		

TABLE 2

\* Data computed from McGregor, 1899:33.

\*\* Average and extremes in millimeters.

The total lipid fraction of three representative birds were each subjected to an assay to determine the weight of sterols, glycerides, and phospholipids per bird. This was an exploratory study carried out to give some indication of the relationships of these three lipid fractions in wintering and premigratory birds. Two "premigratory" birds were selected from groups taken just prior to migration, one from the Coastal Plain (21 April 1962) and one from the Piedmont Plateau (14 May 1962). The analytical methods utilized here followed the procedures for (1) sterols outlined by Zak (1957), (2) glycerides by Lambert and Neish (1950), Van Handel and Zilversmit (1957), Van Handel (1961), and (3) phospholipids by Stewart and Hendry (1935) and Fiske and Subbarow (1925).

# SUBSPECIES OF THE MYRTLE WARBLER

Currently the A.O.U. Check-list (1957) recognizes two subspecies of *Dendroica coronata*—an eastern form, *D. c. coronata* (Linnaeus) and a western one, *D. c. hooveri* McGregor. Since *hooveri* has been reported rarely from Georgia (Burleigh, 1958) and South Carolina (Sprunt and Chamberlain, 1949), we thought it advisable to look for this subspecies among our North Carolina and Florida birds.

McGregor (1899) described *hooveri* as differing from *coronata* on the basis of a longer wing and tail in the former, with no mention being made of

				TABLE 3	3		_		
I	Measu	JREMENTS OF M	YRTLE	WARBLERS FRO	м No	orth Carolina	and F	LORIDA	
	Wing No. Mean ± SD			Tail Mean ± SD	No.	Bill (culmen) Mean ± SD	Bill (nostril) No. Mean ± S		
Males	90	$73.6 \pm 2.6 \\ (68.2 - 80.9)$	90	$\begin{array}{r} 53.9 \pm \ 0.8 \\ (48.3 - 61.1) \end{array}$	88	$9.41 \pm 0.69 \\ (8.2 - 12.0)$	87	$7.01 \pm 0.92 \\ (6.4 - 7.8)$	
Females	74	$\begin{array}{r} 69.2 \pm 1.6 \\ (66.0 - 73.3) \end{array}$	73	$\begin{array}{rrr} 50.7 \pm & 0.8 \\ (46.8 - 56.9) \end{array}$	71	$\begin{array}{r} 9.22 \pm \ 0.42 \\ (8.3 \ - \ 10.8) \end{array}$	72	$\begin{array}{c} 6.84 \pm 0.36 \\ (6.4 \ - \ 7.4) \end{array}$	

color differences. If his data are averaged, the measurements of *hooveri* and coronata appear as in Table 2. Subsequently, small series of both subspecies were borrowed from the Museum of Vertebrate Zoology and were likewise measured. These measurements also appear in Table 2 and do not show, as did McGregor's, a significant difference between the two subspecies in either wing or tail length, except possibly in females. Color comparisons of these two subspecies likewise failed to reveal reliable differences, even though Sprunt and Chamberlain (1949:455) have stated that hooveri is "decidedly larger, the male with black of breast more extensive and often of a more solid color" when compared with coronata. Hooveri was not originally described on any color differences, and the color differences reported by Sprunt and Chamberlain could be attributed to seasonal differences between the sexes and/or progression of the prenuptial molt. In the present study no reliable color differences ascribable to subspecific variation were detected. Therefore, since this study was not intended to be a detailed taxonomic one and since these preliminary examinations of specimens failed to indicate reliable differences in the two subspecies, no attempt was made to identify subspecifically the specimens utilized for lipid extractions.

Measurements from the 164 North Carolina and Florida birds (Table 3) correspond more closely to McGregor's concept of D. c. coronata than they do to hooveri, although there are 34 individuals that have wing lengths above the minimum established for hooveri by McGregor.

## STOMACH CONTENTS

Identifications of fruits and seeds in stomachs were facilitated by use of comparative illustrations in Martin and Barkley (1961). Most of this vegetable matter was entire. On the other hand, the macerated and fragmentary animal contents were identifiable, usually, only to order by using Borror and DeLong (1960) and Jaques (1947). Weight comparisons of the stomach contents are included, but obviously the amount of food in the stomach varies with the time of day when the bird was taken, the availability of food, and

	-		-			
FOMACE	CONTENTS OF	MYRTLE W	ARBL	ERS		
	0			Premigratory birds		
No.	Mean $\pm$ SD	Range	No.	Mean $\pm$ SD	Range	
25	$0.08\pm0.05$	0.01 - 0.18	8	0.04	0.01-0.13	
25	$78.0 \hspace{0.2cm} \pm \hspace{0.2cm} 2.4 \hspace{0.2cm}$	20-100	8	0		
25	$22.0 \pm 2.4$	0-80	8	100		
28	$0.07\pm0.03$	0.02 - 0.13	21	$0.04\pm0.02$	0.01 - 0.12	
28	$51.1 \pm 2.6$	0–95	21	0		
				-		
28	48.9 + 2.6	5-100	21	100		
	No. 25 25 25 25 28	Wintering bird           No.         Wintering bird           25 $0.08 \pm 0.05$ 25 $78.0 \pm 2.4$ 25 $22.0 \pm 2.4$ 28 $0.07 \pm 0.03$ 28 $51.1 \pm 2.6$	Wintering birds Mean $\pm$ SD         Range           25 $0.08 \pm 0.05$ $0.01-0.18$ 25 $78.0 \pm 2.4$ $20-100$ 25 $22.0 \pm 2.4$ $0-80$ 28 $0.07 \pm 0.03$ $0.02-0.13$ 28 $51.1 \pm 2.6$ $0-95$	Wintering birds Mean $\pm$ SD         Range         No.           25 $0.08 \pm 0.05$ $0.01-0.18$ 8           25 $78.0 \pm 2.4$ $20-100$ 8           25 $22.0 \pm 2.4$ $0-80$ 8           28 $0.07 \pm 0.03$ $0.02-0.13$ $21$ 28 $51.1 \pm 2.6$ $0-95$ $21$	Wintering birds Mean $\pm$ SD         Premigratory Range           25 $0.08 \pm 0.05$ $0.01-0.18$ 8 $0.04$ 25 $78.0 \pm 2.4$ $20-100$ 8         0           25 $22.0 \pm 2.4$ $0-80$ 8 $100$ 28 $0.07 \pm 0.03$ $0.02-0.13$ $21$ $0.04 \pm 0.02$ $28$ $51.1 \pm 2.6$ $0-95$ $21$ $0$	

TABLE 4

\* Wintering = Oct.-Feb.; premigratory = Mar.-Apr.

\*\* Wintering = Oct.-Apr.; premigratory = late Apr.-May.

other factors. Another interesting point is that the stomaches of all 81 of the Florida Gulf Coast birds were completely empty. These Florida birds were killed during night flights, at which time it is probable that digestive processes are at a minimum; whatever food might have been in their stomachs prior to the flight had already been rapidly digested. In their more extensive studies of migrating birds at this Florida site, Odum and his co-workers have found that most migrants have empty stomachs.

In general, the results of these stomach analyses (Table 4) agree with information on food habits of the species given by Bent (1953), but differ significantly from the report of Martin, Zim, and Nelson (1961). Bent gives qualitative information regarding the wax myrtle and red cedar in the diet. According to Martin, Zim, and Nelson 17 per cent of the food in winter was plant material, but our data show plant material to be more abundant at this season.

In stomachs from wintering birds on the Coastal Plain, an average of 78.0 per cent was vegetable matter, this being almost entirely wax myrtle berries. In fact, out of the 25 stomachs examined, 22 contained only these berries. The other three stomachs contained only berries of red cedar and poison ivy (Rhus radicans). These wintering birds' stomachs contained, on the average, 22.0 per cent animal matter with the orders Hymenoptera, Coleoptera, Dip-

	No.	Coastal Plain	No.	Piedmont Plateau
1 Mar14 Mar.	2	None	3	None
15 Mar.–31 Mar.	2	Medium	3	None
1 Apr.–15 Apr.	3	Heavy	5	Medium
16 Apr.– 1 May	3	1 None; 2 Medium	6	Medium
2 May– 9 May	-		8	Heavy
10 May-17 May	_		7	4 None; 3 Ligh

 TABLE 5

 PROGRESS OF PRENUPTIAL MOLT IN MYRTLE WARBLER

tera, Hemiptera, and Lepidoptera (larvae) being the most common types. There were some arachnids and Homoptera, although these were not common. The average dry weight of the stomach contents in winter was 0.08 gram. This was the heaviest weight at any season, and is likely correlated with the greater per cent of vegetable matter in the stomachs.

In the winter birds from the Piedmont, plant matter comprised, on the average, only 51.1 per cent. The only type of seed or fruit found in the stomachs of these birds was that of the red cedar. Animal matter averaged 48.9 per cent of the stomach contents (principally Hymenoptera, Coleoptera, Diptera, Hemiptera, and larval Lepidoptera). Concomitant with the decrease in plant matter was a decrease in the average weight of the stomach contents to 0.07 gram. Thus the birds in the Piedmont have a diet that includes a much higher percentage of arthropods than birds from the Coastal Plain, during the winter months.

The higher percentage of plant matter eaten by the Coastal Plain birds in the winter may be due to the preference for wax myrtle berries, these being absent from the Piedmont.

The stomach contents of birds in the spring from both the Piedmont and Coastal Plain were composed entirely of animal matter. In addition to the above-mentioned orders of insects commonly found in the stomachs of wintering Piedmont birds, spring birds from the Piedmont also ate considerable numbers of Homoptera (chiefly aphids) and a few Neuroptera.

## MOLT AND GONADS

*Molt.*—Table 5 indicates the extent and intensity of the prenuptial molt. Of the areas of the body involved, molt on the breast and back seemed to be completed faster than molt on the head, neck, rump, and flanks. Molt occurred commonly among the secondary wing coverts and occasionally in the primary coverts.

Gonads.—All seven males taken on the Piedmont during May showed testicular recrudescence. The maximum testis size was 4 mm, with an average

Piedmont males312.7212.0112.8212.0214.1312.631Coastal females111.2413.1112.031Piedmont females111.5211.7311.7212.0214.6112.031Florida males111.5212.4712.2212.32611.921Florida females110.9113.3312.7111.93111.221Mean % H2O358.657.9461.4262.366Piedmont461.9461.9462.9465.0457.1462.866Florida261.2359.21058.0358.65759.646Mean % fat-free dry wtCoastal (N.C.)328.3430.7828.4627.0432.4228.362Florida228.6326.61024.9326.05728.342Mean % lipid1024.9326.05728.342Mean % lipid1024.9326.0 <t< th=""><th></th><th>No.</th><th>Oct.</th><th>No.</th><th>Nov.</th><th>No.</th><th>Dec.</th><th>No.</th><th>Jan.</th><th>No.</th><th>Feb.</th><th>No.</th><th>Mar.</th><th>No.</th><th>Apr.</th></t<>		No.	Oct.	No.	Nov.	No.	Dec.	No.	Jan.	No.	Feb.	No.	Mar.	No.	Apr.
Piedmont males312.7212.0112.8212.0214.1312.631Coastal females111.2413.1112.0214.1312.631Piedmont females111.2413.1112.031Florida males111.5212.4712.2212.32611.921Florida females110.9113.3312.7111.93111.221Mean % H_2O358.657.9461.4262.366Piedmont461.9461.9462.9465.0457.1462.866Florida261.2359.21058.0358.65759.646Mean % fat-free dry wtCoastal (N.C.)328.3430.7828.4627.0432.4228.362Florida228.6326.61024.9326.05728.342Mean % lipid1024.9326.05728.34228.342Mean % lipid102	Mean orig. wet wt														
Coastal females111.2413.1112.031Piedmont females113.1211.7311.7212.0214.6112.031Florida males111.5212.4712.2212.32611.921Florida females110.9113.3312.7111.93111.221Mean % H2O361.5463.7861.2657.9461.4262.366Piedmont461.9461.9462.9465.0457.1462.866Florida261.2359.21058.0358.65759.646Mean % fat-free dry wt1058.0358.65728.362Piedmont426.3427.3427.3428.0430.3427.762Florida228.6326.61024.9326.05728.342Mean % lipid10.1615.146.329.56 <t< td=""><td>Coastal males</td><td>2</td><td>14.4</td><td>4</td><td>12.4</td><td>4</td><td>13.2</td><td>6</td><td>14.3</td><td>3</td><td>12.0</td><td>2</td><td>12.2</td><td>3</td><td>12.5</td></t<>	Coastal males	2	14.4	4	12.4	4	13.2	6	14.3	3	12.0	2	12.2	3	12.5
Piedmont females113.1211.7311.7212.0214.6112.031Florida males111.5212.4712.2212.32611.921Florida females110.9113.3312.7111.93111.221Mean % H2O312.7111.93111.221Coastal (N.C.)361.5463.7861.2657.9461.4262.366Piedmont461.9461.9462.9465.0457.1462.866Florida261.2359.21058.0358.65759.646Mean % fat-free dry wt1058.0358.65759.646Mean % fat-free dry wt1024.9326.05728.342Florida228.6326.61024.9326.05728.342Mean % lipid1024.9326.05728.3422Mean % lipid1024.9326.05728.342Mea	Piedmont males	3	12.7	2	12.0	1	12.8	2	12.0	2	14.1	3	12.6	3	12.8
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Coastal females	1	11.2			4	13.1		_	1	12.0		—	3	11.8
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Piedmont female	s l	13.1	2	11.7	3	11.7	2	12.0	2	14.6	1	12.0	3	11.4
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Florida males	1	11.5	2	12.4			7	12.2	2	12.3	26	11.9	2	11.8
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Florida females	1	10.9	1	13.3		—	3	12.7	1	11.9	31	11.2	2	10.9
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Mean % H₂O														
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Coastal (N.C.)	3	61.5	4	63.7	8	61.2	6	57.9	4	61.4	2	62.3	6	66.1
Mean % fat-free dry wt       Coastal (N.C.)       3       28.3       4       30.7       8       28.4       6       27.0       4       32.4       2       28.3       6       2         Piedmont       4       26.3       4       27.3       4       28.0       4       30.3       4       27.7       6       2         Florida       2       28.6       3       26.6        10       24.9       3       26.0       57       28.3       4       2         Mean % lipid       Coastal (N.C.)       3       10.2       4       5.6       8       10.1       6       15.1       4       6.3       2       9.5       6         Piedmont       4       11.7       4       9.3       4       7.7       4       12.6       4       9.4       6	Piedmont	4	61.9	4	61.9	4	62.9	4	65.0	4	57.1	4	62.8	6	63.9
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Florida	2	61.2	3	59.2		_	10	58.0	3	58.6	57	59.6	4	60.6
Piedmont       4       26.3       4       27.3       4       28.0       4       30.3       4       27.7       6       2         Florida       2       28.6       3       26.6        10       24.9       3       26.0       57       28.3       4       2         Mean % lipid       Coastal (N.C.)       3       10.2       4       5.6       8       10.1       6       15.1       4       6.3       2       9.5       6         Piedmont       4       11.7       4       9.3       4       9.3       4       7.7       4       12.6       4       9.4       6	Mean % fat-free d	ry w	rt												
Florida       2       28.6       3       26.6        10       24.9       3       26.0       57       28.3       4       2         Mean % lipid       Coastal (N.C.)       3       10.2       4       5.6       8       10.1       6       15.1       4       6.3       2       9.5       6         Piedmont       4       11.7       4       9.3       4       9.3       4       7.7       4       12.6       4       9.4       6	Coastal (N.C.)	3	28.3	4	30.7	8	28.4	6	27.0	4	32.4	2	28.3	6	28.1
Mean % lipid         Coastal (N.C.)         3         10.2         4         5.6         8         10.1         6         15.1         4         6.3         2         9.5         6           Piedmont         4         11.7         4         9.3         4         7.7         4         12.6         4         9.4         6	Piedmont	4	26.3	4	27.3	4	27.3	4	28.0	4	30.3	4	27.7	6	27.1
Coastal (N.C.)         3         10.2         4         5.6         8         10.1         6         15.1         4         6.3         2         9.5         6           Piedmont         4         11.7         4         9.3         4         9.3         4         7.7         4         12.6         4         9.4         6	Florida	2	28.6	3	26.6			10	24.9	3	26.0	57	28.3	4	29.4
Piedmont 4 11.7 4 9.3 4 9.3 4 7.7 4 12.6 4 9.4 6	Mean % lipid														
	Coastal (N.C.)	3	10.2	4	5.6	8	10.1	6	15.1	4	6.3	2	9.5	6	5.8
Florida 2 10.3 3 14.2 — 10 17.0 3 15.4 57 12.3 4 1	Piedmont	4	11.7	4	9.3	4	9.3	4	7.7	4	12.6	4	9.4	6	8.9
	Florida	2	10.3	3	14.2			10	17.0	3	15.4	57	12.3	4	10.0

Table 6

of 3.1 mm, compared to a size in wintering birds of 1 mm or less. Even though no males taken prior to 1 May had enlarged testes and no follicular enlargement was found in females at any time, it is quite possible that sex hormones were becoming active. There is evidence to indicate that some birds have active gonads before leaving their wintering grounds, even though there is no noticeable increase in gonad size (Marshall, 1961:328–329).

## LIPIDS

Results of the lipid extractions appear in Tables 6 and 7. The three body fractions (water, nonfat dry weight, lipids) are given in per cent of the wet weight of the body minus the stomach contents (see Table 4). The weight of water was rather constant per gram of body weight, as was the amount of nonfat dry material. This observation agrees with the findings of McGreal and Farner (1956), who noted that variation in size of the lateral thoracic fat bodies in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) was due to an increase in lipid content, the water and nonfat dry weights remaining nearly constant. The mean water content (per cent) of the Myrtle Warbler was very close to that given by Turček (1960) for the Old World Warblers (Family Sylviidae). The mean (Oct.-May) water content for

<u>.                                    </u>	No.	1 May	No.	8 May	No.	14 May	No.	16 May	No.	May Avg
Mean original										
wet weight	5	12.4	8	12.6	4	14.1	3	13.4	20	13.0
% water	5	63.5	8	61.7	4	55.6	3	55.2	20	59.8
% fat-free										
dry weight	5	27.0	8	26.1	4	24.8	3	24.4	20	25.8
% lipid	5	9.7	8	12.3	4	19.6	3	20.4	20	14.3

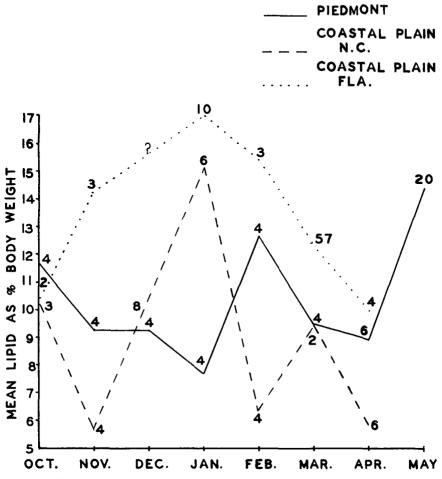
 TABLE 7

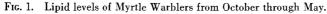
 Body Weights and Results of Lipid Extractions (Piedmont Birds in May)

Myrtle Warblers was 61.3 per cent, and the per cent of fat-free dry matter (at least protein and carbohydrate) was 28.1. These percentages varied only slightly from bird to bird, the variations in wet weight being due to the fluctuations in lipid levels. The average lipid per cent was 10.5 for all 162 specimens, but individuals were extremely variable seasonally, the means ranging (Table 6) from 5.6 per cent in November birds (coastal North Carolina) to a mean of 20.4 per cent (Piedmont birds in late May) (Table 7).

It is unlikely that the changeover to a completely insectivorous diet facilitated lipid deposition prior to migration. Odum and Major (1956) have shown that White-throated Sparrows deposit considerable amounts of premigratory fat whether they are fed on a low fat or a high fat diet. This is probably also true of the Myrtle Warbler, in that the higher animals are generally capable of breaking down a variety of organic compounds in foodstuffs and depositing these as specific lipid molecules in their bodies (Hawk, Oser, and Summerson, 1954). The fact that extensive lipid deposits are not restricted to birds on diets principally of insects is seen in Figure 1 and Table 6, because birds with midwinter lipid peaks were largely herbivorous.

Seasonal lipid deposition in Piedmont birds was bimodal with the higher peak occurring from middle to late May. A somewhat lower peak was noted in February. This midwinter peak in Piedmont birds occurs about one month later than the winter peak in Coastal Plain birds of North Carolina and Florida. A similar midwinter peak of lipid deposition was observed in the White-throated Sparrow by Odum (1949). He postulated that the midwinter peak in the White-throated Sparrow is "well-correlated with temperature since the coldest period coincided with peak weights." A similar correlation between temperature and lipid peak is apparently not true of the Myrtle Warbler, since the birds in the colder Piedmont had considerably lower lipid peaks in midwinter than those in the warmer Coastal Plain of North Carolina and Florida. Also, this explanation would not suffice for the Piedmont and Coastal Plain birds whose midwinter lipid peaks were not coincidental (Fig.





1). Possibly the midwinter lipid peak in the Myrtle Warbler is a vestige of an adaptation that was once of survival value, but present environmental conditions may be somewhat different, and adaptive significance is not now so evident.

Coastal Plain birds from North Carolina and from Florida follow basically the same pattern with regard to lipid level, in that both groups show only one prominent peak (in January). Both groups also show a decline in lipid content until their disappearance from the Coastal Plain. At this time in late April, the lipid levels in both groups of Coastal Plain birds were the lowest at any time while the birds were on the wintering grounds. Since these birds depart from the Coastal Plain with a low lipid reserve, it would seem that they could not migrate very far without stopping to replenish this reserve. Thus, they probably move in short hops at first, either moving northward along the Coastal Plain or northwestward into the Piedmont Plateau or both. This hypothesis is compatible with that of Chamberlain (1961) mentioned previously.

In Piedmont North Carolina birds (Fig. 1), there is also a midwinter lipid peak, which occurs in February and is followed by a decline in lipid level until late April. The periods of decline in lipid level partially correspond to the onset of the prenuptial molt, but Piedmont birds in early May were undergoing both prenuptial molt and moderate lipid deposition (cf. Tables 5 and 7). This picture is roughly similar to the one in the White-throated Sparrow (Odum and Perkinson, 1951:224), wherein premigratory "males became uniformly lean while molting, then uniformly fat." In the Myrtle Warbler, apparently most lipid deposition occurs after migration has begun. Odum and Perkinson (1951) also found a sex difference in White-throated Sparrows —the males, which migrate first, show earlier lipid deposition.

Odum, Connell, and Stoddard (1961) classified migratory birds into three basic types, depending upon lipid deposition and migratory patterns. The Myrtle Warbler, by their classification, would be considered a short-range migrant which becomes moderately fat, but begins migration before peak deposition has occurred. This is especially noticeable in Coastal Plain birds, as they begin migration at one of the lowest lipid levels of the season in late April. The same is probably true of the Piedmont birds as well, because the photoperiodic stimulus is practically the same in both Coastal and Piedmont areas. The Piedmont Plateau seems to be the main avenue of vernal migration in this species; thus there would be a continuous replacement of the numbers in the Piedmont until the last birds had passed this latitude on their way north in late May. The later birds arriving at this latitude in the Piedmont would probably be migrating at a faster rate (more miles per day), a feature reflected in the increasing lipid reserves during May (Fig. 2). In various other migratory species Cooke (1915) and Lincoln (1950) suggested that as the season progresses birds fly in longer hops.

The data presented here for vernal premigratory Myrtle Warblers clearly support the hypothesis of Caldwell, Odum, and Marshall (1963) on migrating birds elsewhere in the United States. Their contention was (pp. 433-434): "... long-range northern migrants begin southward migration with low to moderate fat reserves and with consequent short flights, then increase their reserves with each stop until the maximum level is reached at or near points ... where long nonstop flights are undertaken." Our data do not necessarily show a maximum fat level for the Myrtle Warbler nor is there concrete eviYarbrough and

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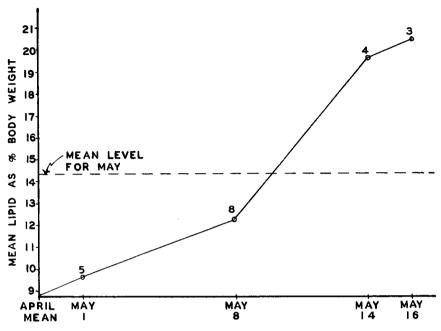


FIG. 2. Lipid levels of Myrtle Warblers taken in May on the Piedmont.

dence that this overland migrant undertakes long nonstop flights, but certainly this species does begin migration with a low body lipid level.

Some possible flight ranges based on lipid content were calculated for premigratory birds from both the Coastal Plain and the Piedmont Plateau. These estimates are based on certain assumptions (flight speed and flight energy requirements) employed by Odum, Connell, and Stoddard (1961). Values have been computed for individuals representing the extremes in fatness of each group (birds in a migratory condition from the Coastal Plain and Piedmont Plateau). The maximum flight range for the leanest Coastal Plain premigratory birds was only 77 miles and for the most obese ones, 209 miles. Of the Piedmont premigratory birds the leanest could fly 168 miles and the most obese ones, 500 miles. These maximum flight ranges are probably too high for at least two reasons. First, the gross lipid extract from the warblers was found by further refinements to contain small quantities of nonlipid impurities, presumably nonlipid portions of conjugated proteins and/or some sugars. To what extent nonlipids can be and are metabolized for flight energy has not been determined. Second, we have not considered any lipid quantity that might be necessary to sustain existence (as opposed to that providing

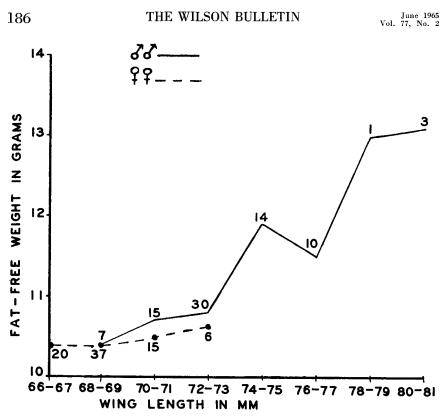


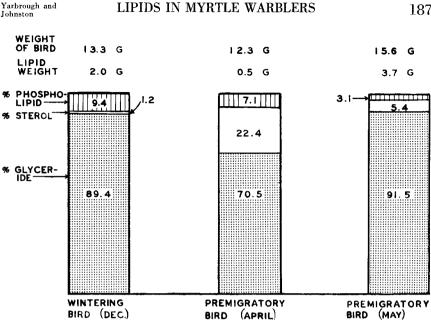
FIG. 3. Correlation between wing length and fat-free weight of Myrtle Warblers.

flight energy). For a bird the size of a Myrtle Warbler this quantity of lipid should be about 0.5 g according to Odum (1960a).

According to Connell, Odum, and Kale (1960), fat-free weight (total weight minus lipids) of a given species is reflected in its wing length. Thus, in the Savannah Sparrow (*Passerculus sandwichensis*), they have shown that wing length increases proportionally as the fat-free weight. In general, this is also true of the Myrtle Warbler (Fig. 3).

## QUALITATIVE ASPECTS OF LIPID DEPOSITS

Three Myrtle Warblers were selected for qualitative lipid analyses. An exploratory investigation was made of the composition of the gross lipid extracts of these birds. The principal purpose of this aspect of the study was to ascertain the quantitative relationships among the three basic lipid fractions (glycerides, sterols, and phospholipids) of birds in wintering and premigratory conditions and with varying amounts of lipid deposits. The first was a wintering bird from the Coastal Plain that had a relatively high lipid level,



F1G. 4. Qualitative aspects of lipids from three Myrtle Warblers.

COASTAL PLAIN

COASTAL PLAIN

as it was building up to the midwinter peak in late December when collected. Another Coastal Plain bird in the premigratory condition (late April) was

utilized. The third bird was an obese premigratory specimen from the Piedmont (mid-May). The relative amounts of the three lipid fractions from each of the three birds are shown in Figure 4.

As might be expected, there were insignificant amounts of free fatty acids found in the lipids from the entire bird. Preliminary studies, though inconclusive, indicate that the per cent of phospholipid decreases as the time for migration approaches, and that the per cent of sterols increases. The actual amounts of sterols present in the entire bird show almost a fivefold increase in April and an eightfold increase in May over the December level. Ratios of sterol/glyceride, phospholipid/glyceride, and sterol/phospholipid varied considerably from bird to bird. Musacchia (1953) has given similar ratios (for liver and kidney lipids in some arctic migratory birds) which are comparable to December-May averages in this study.

Although there is considerable fluctuation in the ratio of sterols/phospholipids, the sum of these two fractions varies inversely as the total weight of lipid per bird. Another way of expressing this relationship which is more meaningful is that the per cent of glycerides in each sample varies directly as the amount of total lipid. Based upon these few birds in the midwinter and

PIEDMONT

premigratory conditions, these data indicate that lipid deposition is due to increases in glycerides. It is also of interest to note that peaks in lipid deposition and glyceride percentages were independent of diet (vegetable vs. animal matter; cf. Table 4 and Fig. 1).

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## SUMMARY

From 1961-63, 84 wintering and premigratory Myrtle Warblers were taken from localities in the Coastal Plain and Piedmont Plateau of North Carolina. In addition, 81 birds were obtained from northern Florida (1960-61). These birds were weighed, measured, and sexed; ages were determined where possible; stomach contents were removed; and the birds were checked for molt. After dehydration, the lipids were extracted from each bird. The lipids of three selected specimens were assayed for the amounts of glycerides, sterols, and phospholipids present.

Subspecific identifications of the Myrtle Warblers used in this study were not attempted, and some of the difficulties involved in trying to separate D. c. coronata from D. c. hooveri are discussed.

Plant and animal matter in the stomachs were identified. Premigratory birds from both the Coastal Plain and the Piedmont Plateau changed their diets from chiefly plant material in winter to 100 per cent animal matter in spring.

Lipid deposition is not necessarily correlated with the change to an insectivorous diet, but probably to altered intermediary metabolism of the birds prior to or during migration. Support for this statement comes from the fact that the midwinter lipid peak occurs when the diet is largely herbivorous. The sharp increases in lipid level, whether midwinter or migratory, appear to be due to increases in the amounts of glycerides present.

Data on lipid levels were correlated with the relative abundance of the species in the Coastal Plain and Piedmont Plateau at different periods during the spring to explain the migratory movements of various segments of the species population. Myrtle Warblers evidently begin migrating from both localities in April with a low lipid level, these early migrants moving only a few miles a day at first. By late April, the birds had disappeared from the Coastal Plain of North Carolina. The same could be true of the Piedmont also, except that east of the Appalachians the Piedmont appears to be the main avenue of spring migration for this species and birds moving north from the Piedmont are replaced by those from farther south. The birds passing through the Piedmont later in the spring are probably migrating at a faster rate, and the longer flights can be correlated with increasing lipid levels during May. By the middle of May, Myrtle Warblers are noticeably more obese, some individuals having as much as 20 per cent of the body weight in lipid.

The prenuptial molt was almost completed by the time the birds migrated from Piedmont North Carolina. After 1 May all males taken while moving northward through this area had somewhat enlarged testes.

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