A STUDY OF THE LIPIDS IN ARCTIC MIGRATORY BIRDS

By X. J. MUSACCHIA

In a wide variety of animals, studies of the lipids from "key organs," such as liver, kidney and blood, have been found to reflect levels of fat metabolism. As a consequence, relationships have been shown to exist between the physiological state of an animal, at a given time, and the tissue lipids (Bloor, 1943; Wilber and Musacchia, 1950; Musacchia, MS). Wilber and Musacchia (1950) have shown that the lipid composition of the liver, kidney and blood from the arctic ground squirrel, *Citellus parryi barrowensis*, can be correlated with seasonal activity and hibernation. Lorenz, Chaikoff and Entenman (1938) and Chaikoff and Entenman (1946) showed that there are tissue lipid changes during egg laying in chickens and in turtles. There are seasonal variations in tissue lipids in the arctic cod, *Boreogadus saidi* (Musacchia, MS).

There is some evidence of seasonal or periodic variation in fat metabolism in migratory birds. Wolfson (1945 and 1952), as a result of extensive experimentation with the Oregon Junco (*Junco oreganus*), showed that prior to spring migratory flight there is a prodigious deposition of subcutaneous and intraperitoneal fat. Wolfson suggests that these newly formed fat stores and "the concomitant increase in the body weight, reaches a state that will enable the bird to meet the energy requirements of migration." Odum and Perkinson (1951) found seasonal variations in the body and tissue lipids of the White-throated Sparrow (*Zonotrichia albicollis*).

On the basis of these widespread findings, it seems reasonable to assume that there may be some significant lipid pattern in the tissues of migratory birds.

In the present work four species of arctic migratory birds were selected with the following objectives in mind: (1) to study the lipids in tissues of arctic migratory birds in late summer during molting and pre-migratory periods, and (2) to correlate these results with the physiological state of the animals when collected.

The author expresses his sincere gratitude to Dr. Charles G. Wilber for his guidance during the period of this investigation. Acknowledgment is also made for the use of the facilities of the Office of Naval Research at the Arctic Research Laboratory, Point Barrow, Alaska.

MATERIAL AND METHODS

The four species selected were the Oldsquaw Duck (*Clangula hyemalis*), the Golden Plover (*Pluvialis dominica*), the Red Phalarope (*Phalaropus fulicarius*), and the Redbacked Sandpiper (*Erolia alpina*). These birds are summer residents in arctic Alaska (Bailey, 1948), and in 1948, in the Point Barrow region, where these studies were conducted, all four were common. Male specimens were taken whenever possible. This was done in order to minimize differences due to sexual variations.

Natural history.—The Oldsquaw breeds along the entire northern Alaskan coast and winters chiefly on the Atlantic and Pacific shores of the United States and Canada. Flocks of Oldsquaw were found along the ocean shore and on coastal lakes. Bent's (1925) records show that molting occurs predominantly in August and September, and Bailey (1948) found that during the summer "These ducks were in every conceivable stage of feather." Both investigators agree that southward migrations occur primarily during September. Only adult male Oldsquaws were taken for study. These specimens were collected on July 20 and 21.

Stomach contents of a few specimens were examined. They had been feeding predominantly on plant matter. Concerning feeding habits of the Oldsquaw, Bent (1925) says, "On their breeding grounds the food consists largely of roots, leaves, buds and seeds of various aquatic plants; the young live largely on insects, larvae and soft animal food which abounds in the tundra pools."

Specimens of the Golden Plover were collected in and around the marshy tundra pools within a few miles of Point Barrow. Nine males and one female (specimen 106) were taken for study. Specimens 105, 107 and 110 were identified as immature males and therefore young of the year. All other specimens were adults. Collections were made from July 31 through August 13. This period falls within the recorded time of molting (Bent, 1929). The Golden Plover starts molting in August and continues through September while migrating. There is general agreement between Bent (1929) and Bailey (1948) that migrations occur predominantly during August and early September.

Some examinations of stomach contents were made and the material was found to be chiefly insect and crustacean matter. These findings are in accord with previous records. Bent (1929) says of the Golden Plover, "Its food consists almost entirely of insects."

The Red Phalarope was readily collected in and around small lakes and pools and along the banks of streams. All collected were immature males. Six specimens were taken on July 23, and six on August 13.

According to Bent (1929) the postjuvenal molt begins during August, and molting is not completed until late in October. Migration occurs chiefly throughout the latter part of summer and early fall (Bent, 1929). In 1921 Bailey found that the majority left the Barrow area before the end of September.

The Red Phalarope, like many other shore birds, feeds upon worms, crustacea, and insects. Examination of a few stomachs showed that the birds had been feeding on animal matter. This is in agreement with the records of Bent (1927).

The Red-backed Sandpiper was generally found in the vicinity of the seashore, especially around sandbars and coastal tundra pools. These birds were common and breeding almost everywhere in the Point Barrow region, as Bailey (1948) reports. Four males and six females were taken from July 23 through September 1. Bailey's (1948) records show that these birds were common at Point Barrow. The time of collection falls within the recorded period for early phases of molt and the period prior to migration (Bent, 1927).

The Red-backs collected had been feeding on insects and other animal matter. Regarding feeding habits, Bent (1927) says, "Their food consists of small mollusks, sand fleas and other small crustaceans, amphipods, flies and other insects and their larvae, diving and other aquatic beetles, marine worms, and occasionally a few seeds of aquatic plants."

Field operations.—Field work was conducted in July, August and September. All birds used for the study of lipids were from the immediate vicinity of Point Barrow. Short daily trips in the Point Barrow area were facilitated by use of a weasel (a tracked vehicle) and a canoe. Specimens were hunted with shotguns. A felled bird was killed by draining blood from the heart with a syringe. Approximately a gram of tissue was cut from the distal margin of the right or left liver lobe in the large birds. In the smaller birds, a whole lobe was utilized. Kidney pieces, of approximately one gram, were cut from the right or left anterior and/or median lobes in the large specimens, and in the smaller birds whole kidneys were removed.

The Oldsquaw Ducks were weighed by means of an ordinary cylindrical, metric spring balance. Golden Plovers, Red Phalaropes, and Red-backed Sandpipers were weighed on a triple-beam balance.

Chemical methods.—The piece of fresh tissue to be analyzed was weighed accurately on an analytical torsion balance. The tissue was minced by means of a fine scissors and put into an alcohol-ether mixture (3 parts ethanol to 1 part petroleum ether) and ground with silica or sand. Extraction of the lipids was done according to Bloor's (1929) method. Detailed description of extraction processes may be found in AF Technical Report No. 6463 (Wilber and Musacchia, 1951). This technique yielded a quantity of extract which was more than sufficient for the estimations of total fatty acids, lipid phosphorus, cholesterol and cholesterol esters.

Total fatty acids were estimated using the method of Bloor as modified by Snell and Snell (1937). Cholesterol estimations of the tissue were made using a modified Bloor (1916) method. Cholesterol ester estimations were made according to the technique developed by Bloor and Knudson (1916). Free cholesterol values were derived by subtracting cholesterol esters from total cholesterol. The lipid phosphorus was estimated by using a modified Youngburg and Youngburg (1930) technique. Values for phospholipid were obtained by the calculation, lipid phosphorus $\times 25$ = phospholipid as lecithin (Bloor, 1943). Total lipid values were derived by adding total cholesterol and total fatty acids.

A Klett Duboscq colorimeter was used to measure color intensity and turbidity in the various analyses.

OBSERVATIONS AND RESULTS

The results of tissue lipid estimations are listed as follows: Oldsquaw Duck, table 1; Golden Plover, table 2; Red Phalarope, table 3; Red-backed Sandpiper, table 4. In these tables all determinations are given as per cent of fresh tissue. The tabulated results show that there is some variation in the tissue lipid components among individuals of a given species. Furthermore, there is sometimes a wide variation in the mean values of the various lipid constituents of the liver and kidney among the different species. An outstanding similarity exists in the liver and kidney lipid phosphorus of the Golden Plover and the Red-backed Sandpiper (tables 2 and 4). An overall view indicates that the Oldsquaw has less lipid phosphorus in its tissues than the other three species.

The amount of total lipid (fatty acid plus total cholesterol) is greatest in the liver from the Red Phalarope. The total lipid content of the liver and kidney tissue of the Oldsquaw and the Golden Plover is similar.

There is no correlation between the body weights and the tissue lipid components

Specimen number	Sex	Body weight	Date taken	Chole	esterol	r lipids Lipid p hos-	Total f atty		Kidn esterol	ey lipids Lipid phos-	Total fatty
		(grams)		Esters	Total	phorus	acids	Esters	Total	phorus	acids
101	м	600	July 20	0.29	0.39	0.10	2.0	0.11	0.30	0.15	3.2
102	\mathbf{M}	525	20	0.12	0.33	0.12	3.1	0.10	0.25	0.13	2.8
103	\mathbf{M}	800	21	0.26	0.33	0.12	2.1	0.10	0.23	0.11	2.0
104	\mathbf{M}	725	21	0.30	0.40	0.18	3.0	0.10	0.26	0.13	2.6
105	М	750	21	0.46	0.55	0.23	1.8	0.10	0.24	0.12	2.7
106	Μ	750	21	0.28	0.41	0.10	3.3	0.13	0.23	0.11	2.5
107	М	900	21	0.11	0.30	0.22	2.7	0.14	0.32	0.14	3.0
108	Μ	810	21	0.18	0.37	0.11	2.9	0.15	0.33	0.10	2.1
109	Μ	850	21	0.20	0.42	0.14	4.3	0.14	0.34	0.11	2.4
110	М	995	21	0.33	0.53	0.13	3.3	0.11	0.32	0.14	2.6
111	М	825	21	0.30	0.44	0.13	3.8	0.11	0.34	0.13	4.2
112	М	910	21	0.30	0.46	0.15	3.8	0.11	0.33	0.12	3.8
Mean				0.26	0.41	0.14	3.0	0.12	0.29	0.13	2.8
Minimu	ım			0.11	0.30	0.10	1.8	0.10	0.23	0.10	2.0
Maxim	um			0.46	0.55	0.23	4.3	0.15	0.34	0.15	4.2

Table 1

Amounts of Lipids in Tissues from 12 Oldsquaws

Specimen		Body			Live	r lipids Lipid	Total	1	Kidne	y lipids Lipid	Total
number	Sex	weight (grams)	Date taken	Chole Esters	sterol Total	phos- phorus	fatty acids	Chole Esters	sterol Total	phos- phorus	fatty acids
101	М	175	July 31	0.19	0.31	0.17	3.1	0.13	0.45	0.15	2.1
102	М	177	Aug. 6	0.10	0.26	0.19	3.7	0.11	0.42	0.16	1.7
103	М	173	6	0.12	0.27	0.19	3.2	0.11	0.37	0.18	1.7
104	Μ	153	6	0.16	0.35	0.19	3.3	0.10	0.38	0.15	2.0
105	М	128	13	0.12	0.30	0.16	3.9	0.10	0.39	0.19	2.2
106	F	150	13	0.16	0.28	0.15	2.8	0.10	0.37	0.16	2.0
107	Μ	136	13	0.17	0.31	0.14	2.3	0.11	0.37	0.14	2.1
108	Μ	148	13	0.18	0.38	0.15	2.3	0.11	0.36	0.16	2.5
109	М	184	13	0.16	0.28	0.16	3.3	0.11	0.34	0.15	2.6
110	М	138	13	0.17	0.29	0.14	3.3	0.11	0.40	0.16	2.7
Mean				0.15	0.30	0.16	3.1	0.11	0.39	0.16	2.2
Minimu	ım			0.10	0.26	0.14	2.3	0.10	0.34	0.14	1.7
Maxim	um			0.19	0.38	0.19	3.9	0.13	0.45	0.19	2.7

Table 2							
Amounts	of Lipids in	Tissues	from	10 Golden	Plovers		

in the birds studied. Nor can any correlation be made between sex and the amounts of lipids in the tissues of the Red-backed Sandpiper.

In many of the specimens, especially the Oldsquaw, there was much visible subcutaneous fat. During dissections and handling of internal organs, the Golden Plover was found to be very oily, that is, the peritoneal body fluids contained considerable oily matter.

DISCUSSION

It is evident from the data that mean values of total lipids are consistently greater for the liver than for the kidney in all four species studied. Furthermore, the livers contain appreciably more fatty acid than do the kidneys, with the exception of the Oldsquaw, in which the mean values for liver and kidney are almost equal (3.0 and 2.8, respectively). In both the liver and the kidney of all four species of arctic migratory birds,

. .		.			Live	r lipids	m (1	I	Kidne	y lipids	m . 1
Specimen number	Sex	Body weight (grams)	Date taken	Chole Esters	sterol Total	Lipid phos- phorus	Total fatty acids	Chole Esters	sterol Total	Lipid phos- phorus	Total fatty acids
103	м	44.0	July 23	0.15	0.27	0.25	3.6	0.17	0.29	0.14	2.7
104	М	46.0	23	0.15	0.27	0.21	6.6	0.18	0.34	0.17	2.7
105	м	46.5	23	0.13	0.27	0.18	4.8	0.19	0.40	0.20	3.2
106	М	46.0	23	0.10	0.42	0.18	5.8	0.11	0.37	0.12	2.5
107	М	42.0	23	0.10	0.24	0.19	4.5	0.10	0.25	0.12	2.0
108	м	45.0	23	0.12	0.24	0.19	4.3	0.13	0.31	0.17	1.4
109	м	43.7	Aug. 13	0.14	0.43	0.23	3.7	0.11	0.32	0.15	1.9
110	м	56.8	13	0.20	0.44	0.23	4.4	0.13	0.26	0.11	2.4
111	М	43.3	13	0.18	0.46	0.25	5.0	0.22	0.36	0.17	2.1
112*	м	48.5	13	0.14	0.40	0.22	3.6				
113	Μ	49.2	13	0.18	0.35	0.25	4.6	0.12	0.35	0.20	2.0
114	м	44.0	13	0.10	0.40	0.21	5.0	0.12	0.43	0.15	2.6
Mean				0.14	0.35	0.22	4.7	0.14	0.32	0.15	2.3
Minim	um			0.10	0.24	0.18	3.6	0.10	0.25	0.11	1.4
Maxim	um			0.20	0.46	0.25	6.6	0.22	0.43	0.20	3.2

Table 3 Amounts of Lipids in Tissues from 12 Red Phalaropes

* Kidney sample lost in transportation.

phospholipids are by far the most prominent. This is in accord with Bloor (1943) who says of the liver, "The lipid present in largest amount is phospholipid; neutral fat is generally present in smaller amounts."

Peters and Van Slyke (1946) point out that the liver performs "a major part in the intermediary metabolism of fat." It is known, also, that the kidneys of many animals

- ·			-		Live	r lipids	T-4-1		Kidne	ey lipids Lipid	Total
Specimen number	Sex	Body weight (grams)	Date taken	Chole Esters	sterol Total	Lipid phos- phorus	Total fatty acids	Chole Esters	sterol Total	phos- phorus	fatty acids
101	F	59.0	July 23	0.15	0.29	0.17	3.9	0.06	0.33	0.14	1.2
102	F	48.0	31	0.16	0.29	0.18	3.7	0.08	0.38	0.17	2.4
103	F	59.0	31	0.12	0.29	0.17	4.8	0.08	0.34	0.16	1.8
104	\mathbf{F}	52.5	Aug. 3	0.14	0.29	0.21	2.7	0.09	0.35	0.16	2.3
105	Μ	51.5	6	0.18	0.29	0.14	3.8	0.07	0.39	0.17	2.2
106	Μ	48.5	6	0.10	0.25	0.13	2.1	0.06	0.35	0.17	1.2
107	F	61.5	13	0.13	0.24	0.15	3.3	0.06	0.36	0.13	1.2
108	М	46.0	13	0.15	0.33	0.14	4.4	0.08	0.36	0.19	1.7
109	Μ	56.8	13	0.19	0.36	0.16	4.6	0.08	0.32	0.16	1.2
110	F	58.0	Sept. 1	0.12	0.29	0.16	2.5	0.07	0.39	0.17	1.4
Mean				0.14	0.29	0.16	3.6	0.07	0.35	0.14	1.7
Minimu	ım			0.10	0.24	0.13	2.1	0.06	0.32	0.13	1.2
Maxim	um			0.19	0.36	0.21	4.8	0.09	0.39	0.19	2.4

 Table 4

 Amounts of Lipids in Tissues from 10 Red-backed Sandpipers

behave toward lipids in a manner resembling the responses of the liver. Bloor (1943) and Bull (1937) maintain that the amounts of phospholipid in tissue such as the liver are indicative of the level of fat metabolism in an organism. The four species of birds studied have consistently high phospholipid mean values (calculated from lipid phosphorus) for liver, 3.5 to 5.5 per cent wet weight and for kidney 3.3 to 4.0 per cent wet weight. These amounts of phospholipid indicate an elevated level of lipid metabolism in the four species. Data for comparison may be taken from the work of Javillier, Crémieu and Hinglais (1928), who found the liver lipid phosphorus values from a number of widely different animals to be: rat, 114; guinea pig, 115; pigeon, 116; frog, 125 (values are given as mg/100 gm fresh tissue). These values recalculated as phospholipid range from 2.9 to 3.1 per cent wet weight.

It has been stated by Peters and Van Slyke (1946) that "the sterol which predominates in animals is cholesterol." Cholesterol is outstanding, particularly in its capacity to combine with fatty acids to form cholesterol fatty esters. It is evident, therefore, that cholesterol and cholesterol esters deserve a good deal of attention in any studies concerning fat metabolism.

Peters and Van Slyke (op. cit.) indicate that in the liver of healthy mammals there is almost invariably an excess of cholesterol esters. Lorenz, Chaikoff and Entenman (1938), on the other hand, found in white leghorn chickens that the free cholesterol fraction is generally in excess. Similarly, Datta (1934) reports values of the order of 0.363 to 0.380 per cent for total cholesterol and 0.272 to 0.359 per cent for free cholesterol in the liver of the pigeon. A portion of the present results is in accord with Peters and Van Slyke: in the Oldsquaw liver 63.4 per cent of the cholesterol is in the esterified state; the Golden Plover and the Red-backed Sandpiper have approximately equal fractions of free and esterified cholesterol; whereas in the Red Phalarope, the value for free cholesterol in the liver was 60 per cent. In addition, among the four species studied, the mean values show that the Oldsquaw has almost twice as much liver cholesterol ester as do the other three species.

These facts suggest that there are considerable differences in liver cholesterol, free and esterified, in various members of the class Aves.

There is marked variation in the amount of cholesterol ester in the kidneys of the four species studied. The lowest percentage of cholesterol ester in the kidneys is found in the Red-backed Sandpiper.

Mayer and Schaeffer (1913 and 1914) have shown that the ratios of one lipid to another are fundamentally significant. The ratio cholesterol/fatty acid ("coefficient lipocytique") was found by them to be relatively constant in tissues from a number of animals of diverse species. The lipocytic coefficients for the arctic species of birds studied are listed below:

	Liver	Kidney
Oldsquaw	0.14	0.10
Golden Plover	0.09	0.18
Red Phalarope	0.07	0.14
Red-backed Sandpiper	0.08	0.20

From these figures it can be seen that liver cholesterol is highest, relative to fatty acids, in the Oldsquaw. In the Oldsquaw kidney there is less cholesterol, in relation to fatty acids, than in any other kidney. There is a constancy in the lipocytic coefficient in the tissues from the Golden Plover, the Red Phalarope and the Red-backed Sandpiper.

The relation cholesterol/lipid phosphorus is considered to be a measure of the ability of a tissue to hold water (Mayer and Schaeffer, 1913). The values for cholesterol/lipid phosphorus in the liver and kidney of the four arctic birds are listed below:

	Liver	Kidney
Oldsquaw	2.9	2.2
Golden Plover	1.9	2.4
Red Phalarope	1.6	2.1
Red-backed Sandpiper	1.8	2.2

If the above contention is universally true, it is apparent that the Oldsquaw liver has the greatest water-holding capacity of all the tissues studied, and the liver of the Red Phalarope has the least. The kidneys of all the birds have approximately the same cholesterol/lipid phosphorus ratio, which may be a reflection of functional similarity.

Further speculation on these facts is not warranted until direct measurements of water content in the different tissues can be made.

From the results as a whole, one is struck by differences between the representative of the order Anseriformes (*Clangula hyemalis*) and those of the order Charadriiformes (*Pluvialis dominica, Phalaropus fulicarius*, and *Erolia alpina*). These differences are in accord with the viewpoint expressed by Hilditch (1947), who maintains that major groups of animals show characteristic lipid patterns. It must be recalled, however, that: "The sea-birds... form an exception to the broad rule that fat types can be correlated with phylogenetic relationships. Lovern suggests two possible explanations for this: (a) that they have no specific requirements and any type of depot fat will serve equally well, or (b) that in the course of evolution their specific requirements have been produced or modified to suit the normal diet" (Hilditch, 1947). It is well to note at this time the fact that among the four species studied the Oldsquaw was consuming predominantly vegetable foods whereas the Golden Plover, the Red Phalarope and the Redbacked Sandpiper were feeding on animal organisms. The differences in lipid pattern may be in part due to the feeding habits. Nov., 1953

Lipid products which are accumulated in the subcutaneous and intraperitoneal fat depots are generally considered to be stored. These stored fats are utilized by an organism during time of need. Description of the lipid storage phenomenon in the Mallard (*Anas platyrhynchos*) is found in the work of Shen (1934).

The present results indicate a relatively high level of fat turnover in bird livers and a similar pattern in the kidneys. It is known that the four species studied were collected in early stages of molt and prior to their southward migration. It is generally accepted that molt and premigratory phases in birds are accompanied by changes in metabolism.

The present work is therefore offered as evidence that during stages of molt and prior to migration, intermediary metabolism of fat was going on at a pronounced level in four species of arctic migratory birds. The suggestion is made that the ultimate purpose of a high level of lipid turnover may well be related to the phenomenon of fat storage associated with migration.

SUMMARY

1. Values for fatty acids, lipid phosphorus, cholesterol and cholesterol esters in liver and kidney of four arctic migratory birds (*Clangula hyemalis, Pluvialis dominica, Phalaropus fulicarius* and *Erolia alpina*) are presented. These are based on specimens collected near Point Barrow, Alaska.

2. The lipid studies indicate that at the time of collection, in late summer, there was a high level of fat turnover in all four species.

3. Some pronounced differences were found to exist in the lipid pattern between the representatives of the order Anseriformes (*Clangula hyemalis*) and those of the order Charadriiformes (*Pluvialis dominica*, *Phalaropus fulicarius* and *Erolia alpina*).

4. The suggestion is made that a high level of lipid metabolism is related to the increased storage of fat associated with periods of migration.

LITERATURE CITED

Bailey, A. M.

1948. Birds of arctic Alaska (Denver, Colorado Museum of Natural History). Bent, A. C.

1925. Life Histories of North American Wild Fowl. United States Nat. Mus. Bull. 130.

- 1927. Life Histories of North American Shore Birds, Order Limicolae (Part 1). United States Nat. Mus. Bull. 142.
- 1929. Life Histories of North American Shore Birds, Order Limicolae (Part 2). United States Nat. Mus. Bull. 146.

Bloor, W. R.

- 1916. The determination of cholesterol in the blood. Jour. Biol. Chem., 24:227-231.
- 1929. The oxidative determination of phospholipid (lecithin and cephalin) in blood and tissue. Jour. Biol. Chem., 82:273-286.

1943. Biochemistry of the fatty acids and their compounds, the lipids (New York, Reinhold).

Bloor, W. R., and Knudson, A.

1916. The separate determination of cholesterol and cholesterol esters in small amounts of blood. Jour. Biol. Chem., 27:107-112.

Bull, H. B.

1937. The biochemistry of the lipids (New York, Wiley).

Chaikoff, I. L., and Entenman, C.

1946. The lipids of blood, liver and egg yolk of the turtle. Jour. Biol. Chem., 166:683-689. Datta, N. C.

1934. Studies in lipoid metabolism. I. Variation in cholesterol content of blood and of different organs in pigeons consequent on administration of chloroform. Indian Jour. Medical Research, 22:353-364. Hilditch, T. P.

1947. The chemical constitution of natural fats (New York, Wiley).

Javillier, M., Crémieu, A., and Hinglais, H.

1928. Comparaison entre diverses espèces de vertébrés au point de vue des indices de phosphore nucléique et des bilans phosphorés de leurs organes. Bull. Soc. Chimie Biol., 10:327-337. Lorenz, F. W., Chaikoff, I. L., and Entenman, C.

1938. Liver lipids of the laying and non-laying bird. Jour. Biol. Chem., 123:577-585.

Mayer, A., and Schaeffer, G.

- 1913. Recherches sur la teneur des tissue en lipoides, existence possible d'une constance lipocytique. Jour. de Physiologie et de Pathologie Générale, 15:534-548.
- 1914. Recherches sur les constantes cellulaires teneur des cellules en eau. II. Rapport entre la teneur des cellules en lipoides et leur teneur en eau. Jour. de Physiologie et de Pathologie Générale, 16:23-38.

Odum, E.P., and Perkinson, J.D., Jr.

1951. Relation of lipid metabolism to migration in birds; seasonal variation in body lipids of the migratory white-throated sparrow. Physiol. Zool., 24:216-230.

Peters, J. P., and Van Slyke, D. D.

1946. Quantitative and clinical chemistry (Baltimore, Williams and Wilkins).

Shen, T. C.

1934. Studies on the metabolism of ducks (Anas platyrhyncha L.). I. Adiposity or gain of body weight through force- and voluntary-feeding. Chinese Jour. Physiol., 8(1):65-76.

Snell, F. D., and Snell, C. T.

1937. Colorimetric method of analysis (New York, Van Nostrand and Co.).

Wilber, C. G., and Musacchia, X. J.

1950. Fat metabolism in the arctic ground squirrel. Jour. Mamm., 31:304-309.

1951. A survey of lipids in arctic animals. AF Technical Report No. 6463. USAF, Wright-Patterson Air Force Base, Dayton, Ohio.

Wolfson, A.

1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, 47:95-127.

1952. Day length, migration, and breeding cycles in birds. Sci. Mon., 74:191-200. Youngburg, G. E., and Youngburg, M. V.

1930. A system of blood phosphorus analysis. Jour. Lab. and Clin. Med., 16:158-166.

St. Louis University, St. Louis, Missouri, January 30, 1953.