

SUMMER LIPID LEVELS OF SOME SUBARCTIC BIRDS

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THE considerable number of recent studies on lipid deposition have been concerned largely with birds that breed in the northern coniferous forest biome. As a result, data are usually obtained from birds that are wintering in the United States and/or are in the process of migrating to and from the more northerly breeding grounds. Little work has been done on their lipid levels during the summer season in North America, though such data are available for White-crowned Sparrows (*Zonotrichia leucophrys*) in central Alaska (King et al., 1965). A series of papers on Eurasian species has been published by Dolnik and Blyumental in the Soviet Union.

Little is known about summer lipid levels in tundra breeders, of which sandpipers (Scolopacidae) are a prominent segment. Johnston (1964) gives data on fat levels in some postbreeding arctic birds. Some subjective impressions of fat levels in a number of species of arctic birds have been provided by Irving (1960). Holmes (1966) has body weights for Dunlins (*Erolia alpina*) in Alaska, and Mascher (1966) body weights for this species during autumnal migration in Sweden. Information of this sort is important because lipid levels may provide an index to the nutritional state and the extent of physiologic and environmental demands. Such data can be of particular value when viewed relative to the annual cycle of the species concerned.

The major objectives of this study were to provide information on lipid deposition (as a measure of energy balance) in a few species of tundra and conifer breeders, and to relate these data to various energy-demanding aspects of the summer cycle. Churchill, Manitoba (58°45' N) made a convenient site for such a study, because it is on the same isotherm as Barrow, Alaska, and the timberline, passing just 4 miles south of Churchill, provides spruce forests of various heights and densities. The commonest breeding warbler in these forests is the Blackpoll Warbler (*Dendroica striata*), and this species was utilized for this study. The tundra region north of the tree line is fairly extensive here and a number of species of sandpipers are rather common breeders. Dunlins and Least Sandpipers (*Erolia minutilla*) were selected as representatives from the tundra.

COLLECTIONS AND METHODS

In the Churchill vicinity I collected series of 45 Dunlins, 58 Least Sandpipers, and 42 Blackpoll Warblers between 28 May and 2 August 1964. Specimens were sealed in airtight plastic bags immediately after being shot. These containers were then wrapped tightly in foil and placed in a freezer locker shortly thereafter to prevent

dehydration and deterioration. The birds were kept solidly frozen in dry ice during transport and until the time when they were weighed, examined for molt, and sexed. Stomach contents were removed and the lipids were then extracted by the method described by Johnston (1962). Three values were obtained for each bird: water weight, lipid-free dry weight, and by subtraction, lipid weight.

NATURAL HISTORY

Dunlin.—The birds of this species breeding at Churchill are ascribable to the subspecies *E. a. pacifica*, the largest of the races (A.O.U., 1957). The first group of Dunlins arrived 29 May and by 1 June about 75 individuals were feeding on the river tundra and tidal flats. At this time the low tundra adjoining the tidal flats was relatively free of snow and ice, whereas the higher tundra (grasses and *Cladonia*) inland was still snow-covered. The population size remained approximately the same on the river tundra until 19 June when the birds dispersed inland to nest on the higher tundra. I saw only two individuals away from the river prior to this movement, and these had a nest with two eggs on 16 June. Most birds had been paired since about 9 June and some were making nesting scrapes at the river just before leaving for the higher tundra. I found nests only in grass and sedge tundra inland from the river and bay. Hatching dates indicated that egg-laying began about 19 June.

Collecting was resumed in mid-July when the young were usually accompanied by both adults. By 20 July many young were flying and were generally accompanied by only the male parent. Many of the adults, presumably females, were beginning to show migratory behavior such as flocking and moving onto the bay shore to feed. The morning of 28 July saw a significant reduction in numbers of adults, and all birds collected after this date were adult males or young of the year.

Least Sandpiper.—This species nests commonly at Churchill on low, dry ridges covered with lichens and other low vegetation. These ridges are almost always adjacent to mud flats, and are ecologically quite different from the grass and sedge marshes where the Dunlin nests.

The first arrivals were a pair of courting birds seen on 3 June. The next day Least Sandpipers were abundant. They performed elaborate aerial displays and flight songs immediately after arrival and were soon paired.

I kept several nests under observation, and by color-marking the birds found that the male incubates during the "daylight" hours, the female during the "night" (approximately 21:00 to 08:00), and relieves the male for short periods during the day for feeding. General impressions (Bent, 1927) that the male performs most of the incubation probably arose from the fact that birds on the nest during normal collecting hours are usually males.

The earliest observed hatching date was 5 July, and flying young were first seen 15 July. The last day adult females were collected was 20 July, and the last adults were seen 23 July.

Blackpoll Warbler.—At Churchill the Blackpoll is by far the most plentiful breeding warbler. Here its distribution coincides with that of the black spruce (*Picea mariana*). In 1964 the species arrived as much as a week later than in some previous years (Taverner and Sutton, 1934; Bent, 1953), possibly because of the rather cold weather and snow during early June, but their arrival times coincided with those Harper (1953) reports for Blackpolls at Nuelin Lake, some 350 miles to the northwest. I saw two males 11 June, but none on 12 June following a snowstorm and cold weather. I saw the species again on 13 June, and from then on it was common among the

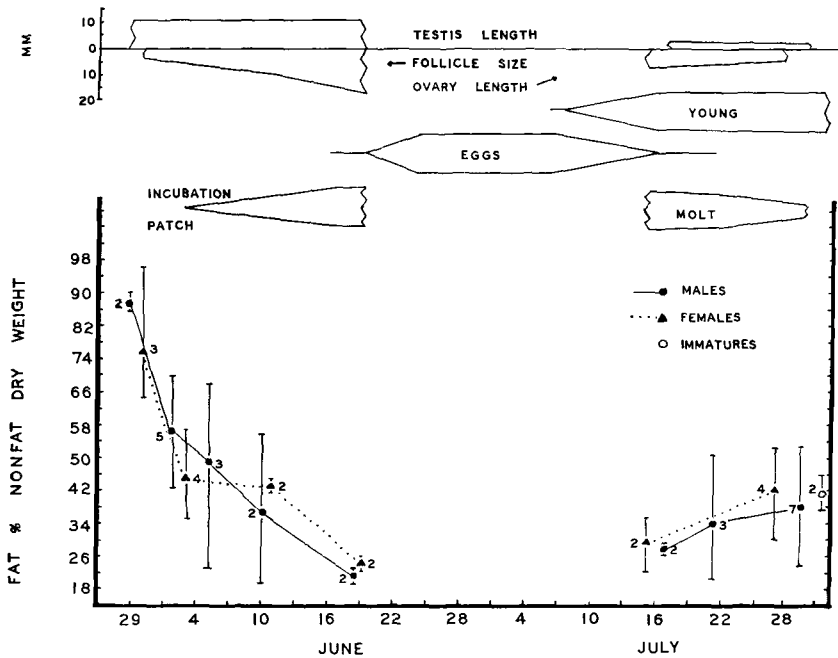


Figure 1. The relation of lipid levels of Dunlins to various aspects of the summering cycle (late May-July). Positions of the symbols represent the mean value for that date and the vertical bar represents the extremes.

spruces. Females I saw only rarely; they are very quiet and wary during the breeding season.

A female taken on 20 June had a complete incubation patch and an egg with shell in the oviduct. I found the first nest with eggs on 23 June. I saw the first flying young 19 July, and thereafter they were common.

For about 10 days after their arrival the birds fed almost exclusively among the spruce foliage. The appearance of numbers of flying insects the last of June greatly increased the incidence of fly-catching activity.

RESULTS AND DISCUSSION

Figures 1, 2, and 3 summarize the intensity and timing of molt and the progress of gonadal cycles in the three species.

Molt.—It is of interest that other than incubation patches, I noted no molt in adult Least Sandpipers before they migrated. Young birds of all species had acquired complete juvenal plumages by the end of July.

When collection of Dunlins was resumed on 16 July, the adults were undergoing a heavy postnuptial molt. Primary flight feathers were being replaced, new wing coverts were in evidence, and refeathering of incubation patches was in progress. By 30 July new breast feathers were re-

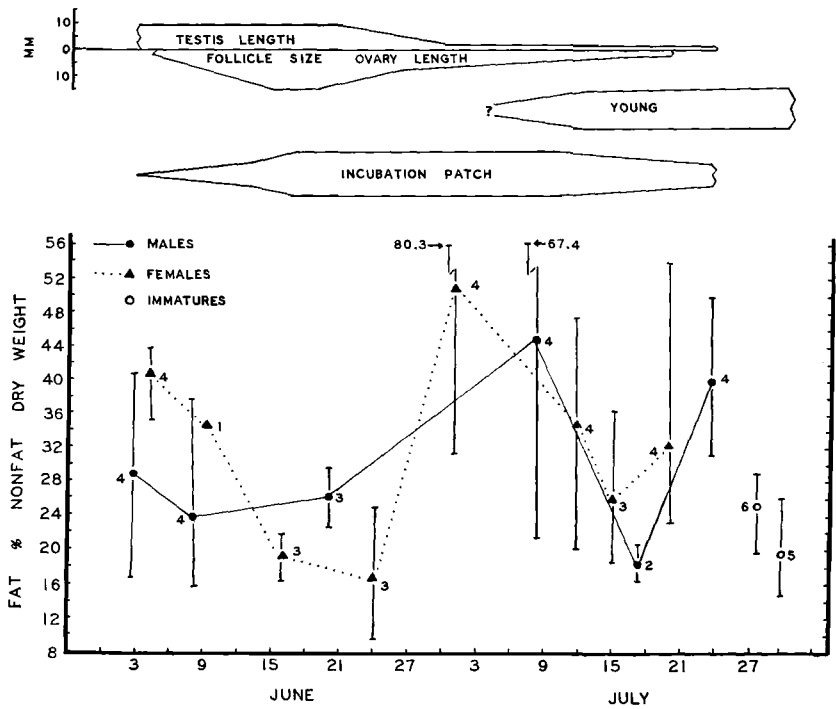


Figure 2. Lipid levels of Least Sandpipers during various phases of the summer cycle (June-July). Mean values are shown by the symbols, and the vertical bars represent the extremes.

placing the feathers that compose the black bellypatch of the breeding plumage. The postjuvinal molt of the young had not yet begun.

In Blackpoll Warblers the postnuptial molt began just after mid-July, and some adults collected on 23 July had partially sheathed primaries, secondary wing coverts, and yellowish breast feathers. By 30 July molt included the rectrices, and the dull fall plumage was evident. Three young birds collected 30 July had assumed the fall (first winter) plumage except for the head and sides of the belly where juvenal feathers still persisted. The young also had black legs, whereas adults had yellow legs.

The above observations on molt are in general agreement with those of Bent (1927, 1953).

Gonads.—When the birds arrived the gonads of the males of each species were of maximum size, but the females had small ova (Dunlins 3 mm, Least Sandpipers 2 mm, Blackpoll Warblers < 2 mm), and the major part of follicular enlargement occurred afterward. Eggs ready for laying were found in the oviducts of a Dunlin collected on 18 June, of

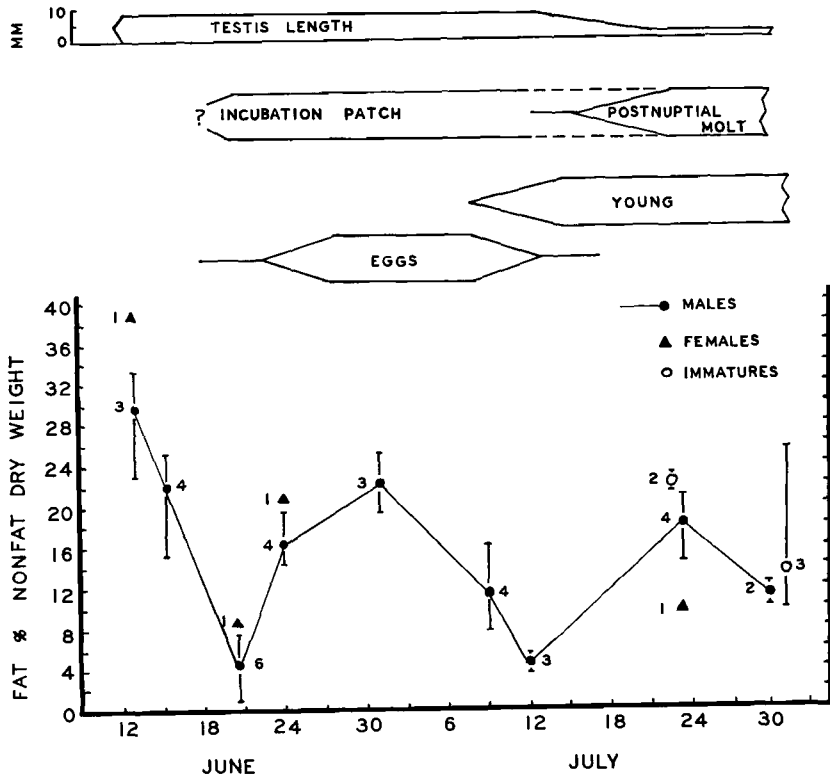


Figure 3. The relation between lipid levels of Blackpoll Warblers and various events of the summering cycle (June-July). Symbols represent mean values, and the extremes are shown by vertical bars.

a Least Sandpiper on 16 June, and of a Blackpoll Warbler on 20 June.

The gonads of the two species of sandpiper had essentially completed the regression phase before the birds migrated. Blackpoll males had gonads showing complete regression well before the end of July. Data on females are incomplete.

The above data for Dunlins agree generally with those of Holmes (1966) for birds near Barrow, Alaska, but the timing of egg-laying seem to differ in the two populations. Holmes found completed clutches from 6 June to 6 July with the peak in the interval 12 to 18 June. Near Churchill, except for a single nest with two eggs on 16 June, no nests with eggs were found until 20 June, and the peak of egg-laying was about 20-26 June, which is verified by hatching dates and ages of young. The latest hatching date was 23 July. The findings of Taverner and Sutton (1934) at Churchill also point to a considerably later nesting time than that Holmes

TABLE 1
BODY WEIGHTS AND RESULTS OF LIPID EXTRACTIONS (*EROLIA ALPINA*)

| Dates | N | Wet wt | Water wt | Nonfat dry wt | Lipid wt | Lipid % dry wt \pm SE |
|-----------|----|---|---------------------|---------------------|--------------------|---------------------------------|
| Adults | | | | | | |
| 5, 28-29 | 5 | 65.5 ¹ (57.6-71.4) ² | 37.3 (33.6-40.4) | 15.6 (12.9-17.3) | 12.5 (9.2-15.7) | 80.24 \pm 6.65 (64.4-96.5) |
| 6, 2-11 | 15 | 55.2 (49.3-60.1) | 34.4 (28.7-40.8) | 14.0 (12.2-15.6) | 7.0 (2.6-10.1) | 48.63 \pm 4.14 (16.5-69.7) |
| 6, 17 | 4 | 55.9 (50.2-59.9) | 36.7 (32.8-39.7) | 15.9 (14.7-16.9) | 3.3 (2.7-3.9) | 20.93 \pm 0.99 (18.4-23.2) |
| 7, 15-31 | 18 | 52.3 (46.0-57.9) | 35.1 (30.3-40.0) | 12.9 (10.3-15.6) | 4.4 (2.6-5.9) | 35.08 \pm 2.60 (18.1-53.7) |
| Immatures | | | | | | |
| 7, 25 | 2 | 47.2 | 32.9 | 9.6 | 4.7 | 49.30 |

¹ Mean (g).

² Range of values (g).

reports in Alaska. No reproductive data for arctic or subarctic populations of Least Sandpipers and Blackpoll Warblers were available for comparison with data from this study.

Lipid levels.—The results of the lipid extractions are shown in Figures 1-3 and in Tables 1-3.

TABLE 2
BODY WEIGHTS AND RESULTS OF LIPID EXTRACTIONS (*EROLIA MINUTILLA*)

| Dates | Sex | N | Wet wt | Water wt | Nonfat dry wt | Lipid wt | Lipid % dry wt \pm SE |
|-----------|-----|----|---|---------------------|------------------|------------------|----------------------------------|
| Adults | | | | | | | |
| 6, 3-9 | M | 8 | 21.0 ¹ (19.4-22.9) ² | 13.3 (12.6-14.7) | 6.2 (5.8-7.0) | 1.6 (0.8-2.4) | 25.45 \pm 3.72 (13.8-40.8) |
| | F | 5 | 26.3 (23.7-29.9) | 16.0 (14.0-18.1) | 7.4 (6.4-8.8) | 2.8 (2.5-3.3) | 38.14 \pm 1.84 (33.2-43.1) |
| 6, 15-24 | M | 3 | 22.7 (21.3-24.1) | 14.3 (13.1-15.3) | 6.8 (6.6-6.9) | 1.7 (1.5-2.0) | 24.73 \pm 2.06 (21.4-28.5) |
| | F | 6 | 24.1 (21.5-26.6) | 15.5 (13.7-17.0) | 7.3 (6.6-8.0) | 1.3 (0.7-1.9) | 17.68 \pm 2.28 (9.3-25.4) |
| 7, 1 | F | 4 | 25.7 (23.5-28.9) | 15.5 (13.6-17.5) | 6.8 (6.0-7.6) | 3.4 (1.9-4.8) | 50.78 \pm 10.78 (29.0-80.3) |
| 7, 8 | M | 4 | 24.8 (22.0-27.1) | 14.8 (14.0-16.1) | 6.9 (6.6-7.1) | 3.1 (1.4-4.8) | 44.83 \pm 11.66 (21.0-67.4) |
| 7, 17 | M | 2 | 20.4 (19.8-21.0) | 13.1 (12.7-13.6) | 6.2 (6.0-6.3) | 1.1 (1.0-1.2) | 17.40 (16.5-18.3) |
| 7, 12-21 | F | 11 | 22.3 (19.1-24.9) | 14.2 (11.9-16.2) | 6.2 (5.8-6.6) | 2.0 (1.3-3.5) | 31.65 \pm 3.63 (19.1-54.5) |
| 7, 23 | M | 4 | 22.6 (21.2-25.3) | 13.8 (12.7-14.9) | 6.3 (5.9-6.9) | 2.5 (2.0-3.5) | 39.65 \pm 4.23 (31.6-50.2) |
| Immatures | | | | | | | |
| 7, 28-30 | | 11 | 21.4 (19.3-23.3) | 14.3 (11.6-15.7) | 5.8 (5.0-6.6) | 1.3 (0.9-1.7) | 21.76 \pm 1.58 (14.9-28.4) |

¹ Mean (g).

² Range of values (g).

TABLE 3
BODY WEIGHTS AND RESULTS OF LIPID EXTRACTIONS (*DENDROICA STRIATA*)

| Dates | N | Wet wt | Water wt | Nonfat dry wt | Lipid wt | Lipid % dry wt \pm SE |
|------------|---|---|------------------|------------------|---------------------|---------------------------------|
| Adults | | | | | | |
| 6, 13-15 | 8 | 13.3 ¹ (12.6-14.6) ² | 8.2 (8.0-9.1) | 4.0 (3.6-4.4) | 1.1 (0.6-1.4) | 26.44 \pm 2.72 (14.7-38.0) |
| 6, 19-20 | 7 | 12.4 (11.3-14.8) | 8.0 (7.6-9.6) | 4.2 (3.9-4.8) | 0.16 (0.03-0.39) | 3.81 \pm 1.06 (0.7-8.1) |
| 6, 23-7, 1 | 8 | 13.3 (12.2-15.1) | 8.7 (8.0-9.9) | 3.9 (3.5-4.2) | 0.76 (0.52-0.99) | 19.18 \pm 1.24 (13.9-25.2) |
| 7, 9-12 | 7 | 13.2 (12.7-13.8) | 8.7 (8.4-9.2) | 4.2 (3.7-4.5) | 0.35 (0.16-0.58) | 8.51 \pm 1.68 (3.7-15.5) |
| 7, 23-30 | 7 | 12.8 (11.3-14.2) | 8.3 (7.3-9.3) | 3.9 (3.6-4.3) | 0.59 (0.35-0.84) | 14.96 \pm 1.77 (9.7-21.0) |
| Immatures | | | | | | |
| 7, 23-30 | 5 | 13.2 (12.3-14.0) | 8.7 (8.0-8.9) | 3.9 (3.6-4.1) | 0.68 (0.38-1.03) | 17.76 \pm 3.36 (9.3-25.1) |

¹ Mean (g).

² Range of values (g).

At present, no information is available in the literature on fat content of Dunlins except for some references in Mascher's study of body weights. There are a few references to total body weights of the species (Mascher, 1966; Holmes, 1966). Although total weight data are useful, this study shows that they do not always reflect fat content accurately, as King et al. (1965) also note for the White-crowned Sparrow in central Alaska. The variability of water content, the condition of the reproductive organs, and the progress of molts are the major factors contributing to the difficulty of extrapolating from total weight to weight of fat. It is true that a considerable degree of accuracy may be attained when the bird has large stores of fat, as in migration, because the fat then represents a much greater percentage of body weight.

Mascher (1966) gives weights for autumnal migrants in Sweden, but his data are for the small subspecies *alpina* and comparisons would probably be invalid. Mascher also gives information for a small series of wintering *pacifica* sent him from Coastal Georgia (which he misassigns to *sakhalina*), whose fat-free weights exceed total weights of some of his *alpina* specimens.

Holmes (1966) gives body weights for large numbers of Dunlins from Alaska. He found that birds just arriving at Barrow have very low body weights. At Churchill, newly arrived Dunlins are fairly heavy and are still carrying considerable amounts of migratory fat (Figures 1 and 4). These fat deposits are rapidly depleted during the 3 weeks following migration. In Holmes's paper, as in the present study, females showed rather large weight increases from increased follicle size at the time of

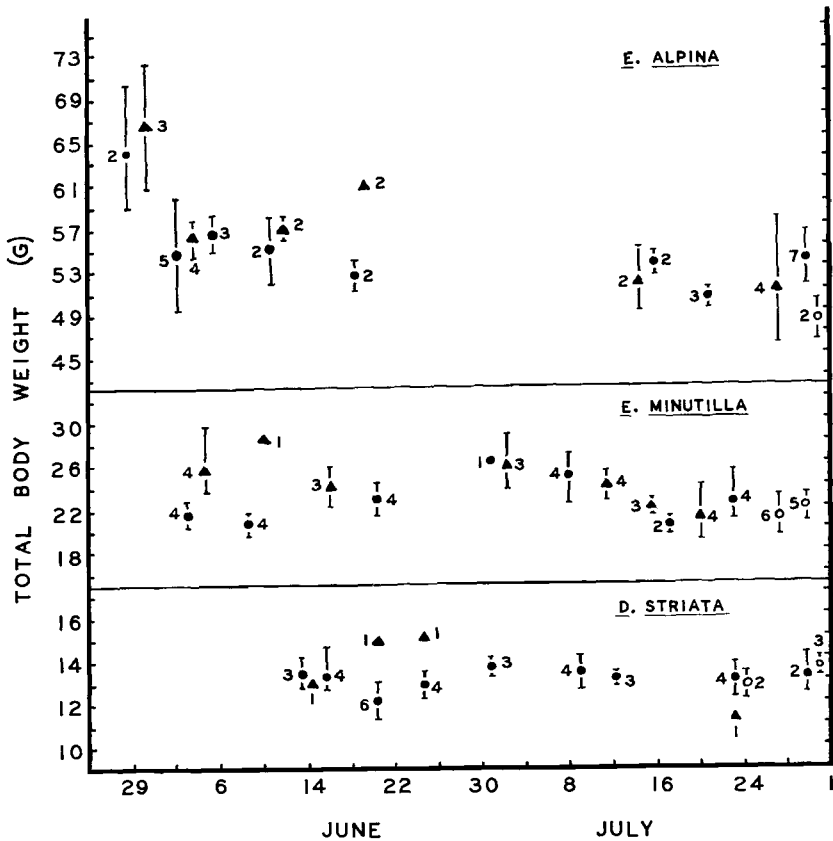


Figure 4. The total body weights of Dunlins, Least Sandpipers, and Blackpoll Warblers during the summer cycle. Triangles, adult females; solid circles, adult males; open circles, immature birds.

egg-laying. The lipid levels in my small sample of females for the period 10-18 June are slightly higher than those of males and probably reflect, in part, the lipid content of developing ova.

Published data on lipids of Least Sandpipers are nonexistent except for subjective impressions of Irving (1960). His data indicate that at Anaktuvuk, Alaska migrating male Least Sandpipers may range from "fat" to "very little fat" with body weight of 23-33 g. Although it is difficult to translate these impressions of fatness into quantitative terms, comparison of Irving's data on body weights with those in Figure 4 suggests that the May migrants in Alaska are carrying more fat than those arriving at Churchill in early June. At Churchill, Least Sandpipers arrived later than Dunlins and did not have the Dunlins' high fat levels.

A decline in lipid level also occurred during the first half of June in the Least Sandpiper (Figure 2). As with Dunlins, the percentage of fat was slightly higher in females than in males until eggs were laid; then this pattern was reversed. Figures 2 and 4 demonstrate that lipid levels are not necessarily reflected by the body weight.

Blackpoll Warblers arrived at Churchill with a greater percentage of fat than they showed at any time during the breeding season. Even so, the fat index (g fat/g nonfat dry weight) on arrival was only 0.3–0.4—very low compared to the maximum fat index value of 3.42 Odum (1965) gives for this species in transit. Odum also states that the usual fat index for birds not involved in migration ranges from 0.2–0.4. In spite of these initially low lipid levels upon arrival, they continued to decline until 20 June.

An interesting aspect of Figure 3 is the Blackpoll Warblers' extremely low values for lipid content. On 20 June the mean fat index for six males approximated 0.04. In mid-July the index dipped again to 0.05. These values are considerably lower than the fat index of 0.2 Rogers and Odum (1964) consider the level in wood warblers below which nonfat body tissues are also metabolized.

At any given time from arrival until the end of July, the lipid levels in Blackpoll Warblers were much lower than in the two species of *Erolia* (Figure 3). Still, similar patterns of utilization or deposition of lipids may be seen at various times during the summer. These patterns appear to correlate with energy-demanding aspects of climate and breeding. Cold snowy weather, during which thermoregulation is expensive and feeding efficiency low, persisted until the last week of June. Reproductive behavior such as displaying and flight singing was most intense during this period also.

An abrupt improvement in weather conditions around 20 June vastly increased the amount of available food. Higher temperatures reduced thermoregulatory energy expenditure. In Least Sandpipers (probably Dunlins and female Blackpoll Warblers also) the period of lipid increase was also characterized by gonadal regression. After the onset of egg-laying and incubation, the time spent in display and flight singing diminished sharply. Birds appeared to feed almost continuously when not actually on the nest.

The two species that were collected during this period showed an increase in lipid content (Figures 2 and 3). It should be kept in mind that even though these lipid increases may be three- or fourfold, the actual increase in lipid weight is about 3–4 g in Least Sandpipers and 0.7–0.9 g in Blackpoll Warblers. These are considerable increments when compared to summer minima, but are only relatively small fractions of the amounts

of fat stored during maximal migratory deposition. The magnitude of this summer fat deposition is reflected in total weight gains over this period.

The declines in lipid levels during the latter stages of incubation and the first few days following hatching (until mid-July) are not easily explained. The Least Sandpipers (particularly the males) spend increasing amounts of time incubating as hatching time approaches and, until the young learn to feed themselves efficiently, seem to devote significant amounts of time to caring for them. In Blackpoll Warblers, as hatching approaches the male feeds the female extensively. After the eggs hatch the time of both adults is largely occupied in feeding the young—to just what extent, however, is as yet unknown.

The second decrease in lipid levels halted in mid-July as the young became more self-sufficient and capable of flight. Fat stores were increasing at the time of departure, particularly in male Least Sandpipers (Figures 1 and 2). Many male Dunlins were still present when collecting was discontinued, and specimens collected at this time showed some increase in lipid content. Lipid gains are reflected in total body weight of males of both species.

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SUMMARY

Series of 45 Dunlins, 58 Least Sandpipers, and 42 Blackpoll Warblers were collected for lipid extraction during the summer of 1964 near Churchill, Manitoba. Relevant aspects of the natural history of the species are given, and data on molt and gonadal changes are presented. Lipid levels and their relationships to various aspects of the postmigratory and breeding phases of the life cycles are discussed.

Lipid content of all three species declined from the time of arrival until about the time of egg-laying. This decline occurred in all three species and coincided with energetically unfavorable climatic conditions and intensive reproductive behavior.

The advent of warmer weather, greater food availability, and decrease in sexual activity initiated a period of lipid increase. The decline in lipid levels following the midsummer peaks is difficult to explain and is discussed briefly.

Slight lipid increases were detected prior to migration in both species

of sandpipers. These increments were small and indicate the beginning of migratory fat deposition, most of which must occur later during migration. In the Dunlins, the small premigratory lipid gains were made in spite of a heavy postnuptial molt.

In general it can be seen that the overall patterns established by lipid levels are similar in all three species. (No data were obtained on the autumnal premigratory phase of Blackpoll Warblers.)

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