

BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. 43, No. 2

APRIL 1972

PAGES 85-160

FAT DEPOSITION DURING AUTUMN MIGRATION IN THE SEMIPALMATED SANDPIPER

By G. PAGE and A. L. A. MIDDLETON

It is generally recognized that fat is the primary energy source for migratory flight in birds, especially long-distance migrants (King and Farner, 1963; Odum, 1965; Johnston, 1966). At certain times of the year fat may account for more than 50 per cent of the body weight in some migratory species (Odum, 1960). It is assumed that fat reserves are replenished during migratory pauses, but such evidence is limited to a few species (Nisbet, Drury, and Baird, 1963; Mascher, 1966; Mueller and Berger, 1966). Since there is limited information on fat deposition during migratory pauses, particularly for shorebirds (Charadriiformes), the extent and role of fat deposition was studied in the Semipalmated Sandpiper (*Ereunetes pusillus*) during its autumn migratory pause at Long Point, Ontario.

METHODS

The study was conducted at Long Point, Ontario, a 32 km-peninsula running east from the north shore of Lake Erie. Since Semipalmated Sandpipers invariably stop over near the eastern extremity of Long Point (Page and Bradstreet, 1968) the easternmost 8 km of the south beach was selected as the study area. The study was conducted from July to October, 1966 to 1969.

In all four years of the study Semipalmated Sandpipers were trapped, banded, categorized as to size by measuring the wing length to the nearest millimeter, weighed to the nearest gram and, with the exception of 1966, color-marked with indelible ink on the breast, abdomen, and flanks. In 1969 Semipalmated Sandpipers were marked with one or two colors according to the date of capture and their estimated fat level. This permitted observers to determine how long sandpipers of differing fat levels remained on Long Point. Birds were captured in mist nets during the late afternoon and early evening to minimize possible diurnal weight variations, except in 1969 when a scarcity of sandpipers necessitated trapping around the clock.

During the last year of the study the fat-free weights of 69 Semipalmated Sandpipers (16 spring, 53 autumn) were determined in the following manner. Birds were frozen in liquid nitrogen, individually pounded into small pieces, and vacuum-dried. The fat was extracted from each dehydrated sandpiper with diethyl ether in a soxhlet apparatus for 24 hours. The fat-free weight was taken as the weight of the freshly killed bird minus the weight of the fat extracted in the soxhlet apparatus.

The determinations of the fat-free weights made on the 16 birds collected in the spring of 1969 were used as a basis to estimate the fat levels in live birds for color-marking. However, in the analysis of the data the fat determinations of the 53 autumn specimens were used to estimate the fat levels of the sandpipers. The method is described in a subsequent section of this paper.

In this study two statistical techniques were used to analyze most of the data, the Student's *t* test for the difference between means and Regression and Correlation for the relationship between two variables (Chapters 5, 9, and 10 respectively, Steel and Torrie, 1960). A method of partitioning variability, outlined in Alder and Roessler (1964, p. 160), was used to determine the amount of body weight variation resulting from the variation in the weight of the bird's fat depots.

OCCURRENCE OF THE SEMIPALMATED SANDPIPER AT LONG POINT

During the autumn migration most adult Semipalmated Sandpipers occur at Long Point from mid-July until the end of August, but a few individuals are present until mid-September. The immature sandpipers (birds-of-the-year) occur between mid-August and mid-October. Since there is only a limited overlap in the occurrence of adult and immature birds at Long Point (Fig. 1), most adult and immature sandpipers must migrate separately at this location.

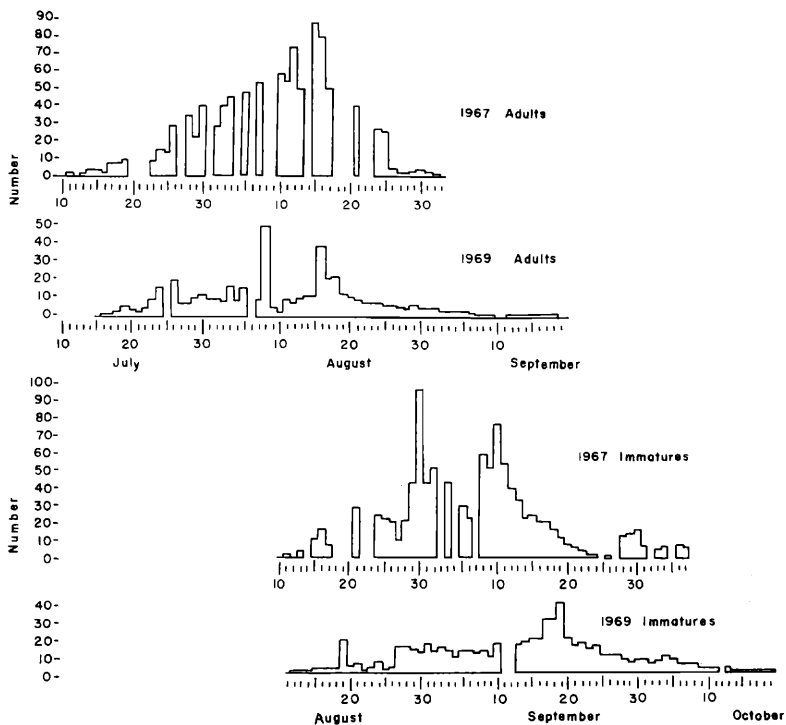


FIGURE 1. Occurrence of adult and immature Semipalmated Sandpipers at Long Point, 1967 and 1969.

STABILITY OF THE FAT-FREE WEIGHT

Although there is considerable body weight variation within a passerine species, there is relatively little variation in the fat-free weight (Odum, 1965). Intraspecific variation in the latter can be correlated with body dimensions such as wing length or sex (Connell, Odum, and Kale, 1960; Rogers and Odum, 1964; Helms *et al.*, 1967; Child, 1969). However, when males and females of similar wing lengths are compared, fat-free weight differences are usually small or insignificant (Odum, 1960; Rogers and Odum, 1964; Helms *et al.*, 1967; Child, 1969). The fat-free weight of many small passerines is from one to two grams heavier in the spring than in the fall (Odum and Perkinson, 1951; Connell, Odum, and Kale, 1960; King, 1963; Child, 1969). Very little intraspecific variation of the fat-free weight is related to the bird's age or the amount of fat in its depots (Odum, Rogers, and Hicks, 1964; Child, 1969).

As with passerines, variation of the fat-free weight in Semipalmated Sandpipers was correlated with wing length and was largely independent of the bird's age, sex, and fat reserves. In the 53 autumn migrants for which fat-free weights were determined, the fat-free weight was positively correlated with wing length ($P < 0.01$) increasing by 0.31g per mm increase of wing length (Fig. 2). The fat-free weight increases of 0.21 and 0.39g per mm increase of wing length, calculated for adult and immature birds respectively, were not significantly different from each other ($P > 0.05$). Likewise the mean wing lengths (adults 94 mm, immatures 95 mm) and fat-free weights (adults 20.8g, immatures 20.6g) between adult and immature birds did not differ significantly ($P > 0.05$), and there was no correlation between the bird's fat-free weight and the amount of fat extracted. Although female sandpipers had significantly longer wing lengths and heavier fat-free weights than the males ($P < 0.05$), the significance disappeared when males and females of similar wing length were compared. The fat-free weights of the Semipalmated Sandpipers differed ($P < 0.05$) between the spring and the autumn, the fat-free weights of the 16 spring specimens averaging 2.3g heavier than the 53 autumn specimens.

BODY FAT LEVELS

In the Semipalmated Sandpiper, 80 per cent of the total weight variation resulted from variation in the weight of the bird's fat depots. The fat-free weights of the 53 autumn specimens ranged from 17.4 - 24.8 g, whereas the amount of fat extracted varied from 0.7 - 15.9 g. Variations of these magnitudes occur in the Golden Plover (*Pluvialis dominica*) (Johnston and McFarlane, 1967), and in some passerine species (Odum, 1960; Hicks, 1967).

In order to determine the fat levels of sandpipers stopping at Long Point, the following method was devised to estimate the fat levels of birds in the field from their wing lengths and body weights. The fat-free weights of the 53 fall specimens were estimated from the regression of their fat-free weights (FFW) on their wing lengths (WL), $FFW = -9.0513 + .3134 (WL)$. The "estimated per cent

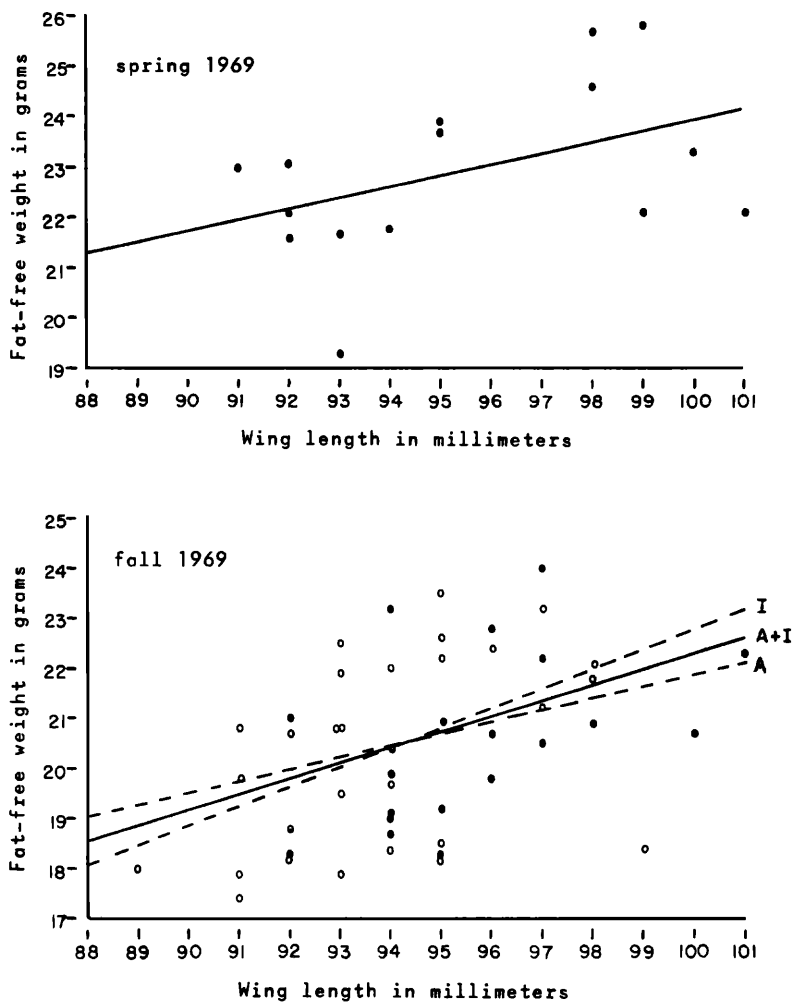


FIGURE 2. Regression of fat-free weight on wing length for adult and immature Semipalmated Sandpipers at Long Point in the spring and fall of 1969. A (●) is adult and I (○) is immature.

fat" (EPF) was calculated from $EPF = 100 \left(\frac{WT - FFW}{WT} \right)$ where WT is the total body weight. Although the actual and estimated per cent fat differed by as much as 15 per cent in individual birds (Fig. 3-A), the means and the 95 per cent confidence intervals of the actual and estimated per cent fat of small sandpiper samples were in general agreement (Fig. 3-A).

Although there was considerable variation in the fat levels of the sandpipers in this study, some birds achieved fat levels that would provide sufficient fuel for very long flights. The amount of fat in

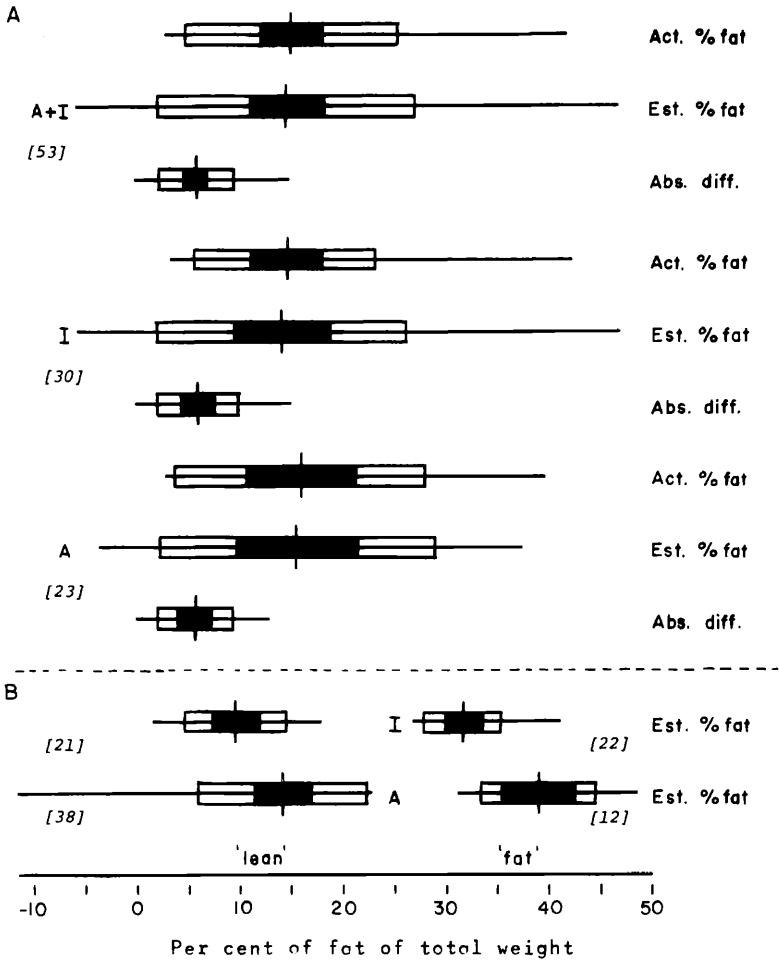


FIGURE 3.-A: Actual (Act.) and estimated (Est.) per cent fat of 53 Semipalmated Sandpipers analyzed for fat content in 1969. B. Estimated per cent fat of "lean" and "fat" Semipalmated Sandpipers color-marked at Long Point in 1969. A (adult), I (immature) and Abs. diff. (absolute difference). Horizontal line is range, vertical line is mean, open rectangle is 1 standard deviation and solid rectangle is 95 per cent confidence interval. Sample sizes are in parentheses.

the 53 fall specimens analyzed in 1969 varied from 4.6 per cent of the body weight (a level similar to that found in non-migrating birds) to 42.1 per cent, a level common in long-distance migrants (Odum and Connell, 1956; Odum, 1965). In 1966, 1967, and 1968 the adult sandpipers that were banded averaged between 28 and 34 per cent fat as compared with 16-20 per cent fat for the immatures (Fig. 4).

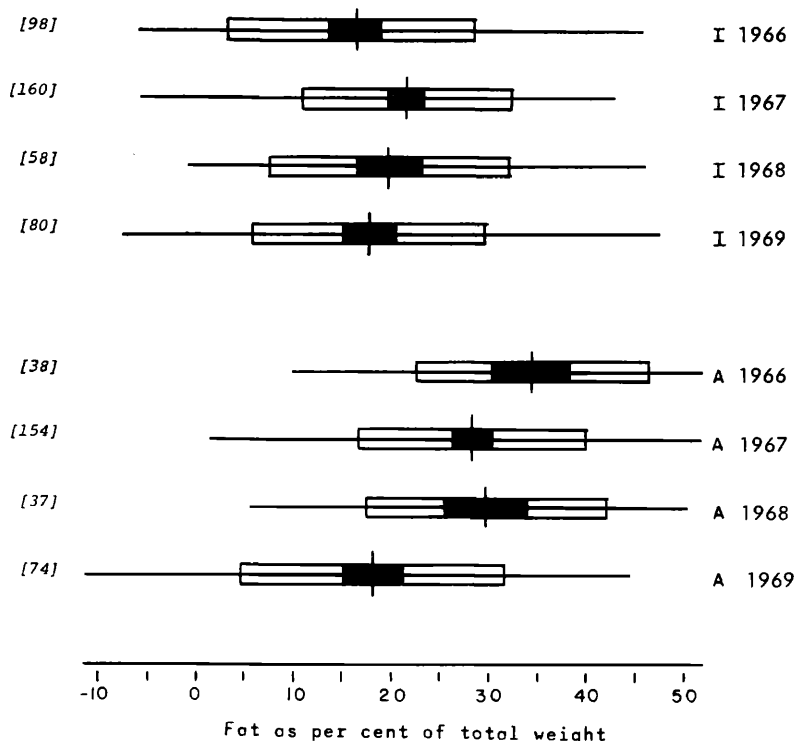


FIGURE 4. Estimated per cent fat of Semipalmated Sandpipers according to age and year at Long Point, 1966 to 1969. Symbols and abbreviations as in Fig. 3.

However, in 1969 the average fat level was approximately 18 per cent for both adults and immatures (Fig. 4). Some individuals had an estimated 50 per cent fat, a level probably sufficient for flights of at least 2000 miles (Odum, Connell, and Stoddard, 1961; McNeil, 1969).

FAT ACCUMULATION DURING MIGRATORY PAUSE

The weight changes of Semipalmated Sandpipers probably reflect changing fat levels because body weight variation was strongly correlated with the amount of fat in their depots. Birds recaptured one or two days after banding generally had lost weight, but the weight increases of birds recaptured from three to 16 days after banding indicated that subsequent to the initial weight loss the sandpipers steadily supplemented their fat deposits (Fig. 5). Small weight gains occurred in birds recaptured more than 16 days after banding, suggesting that some factor unrelated to fat deposition governed the duration of very long stops. Except for the time intervals, the observed pattern of weight loss followed by weight gain in the Semipalmated Sandpiper is very similar to that de-

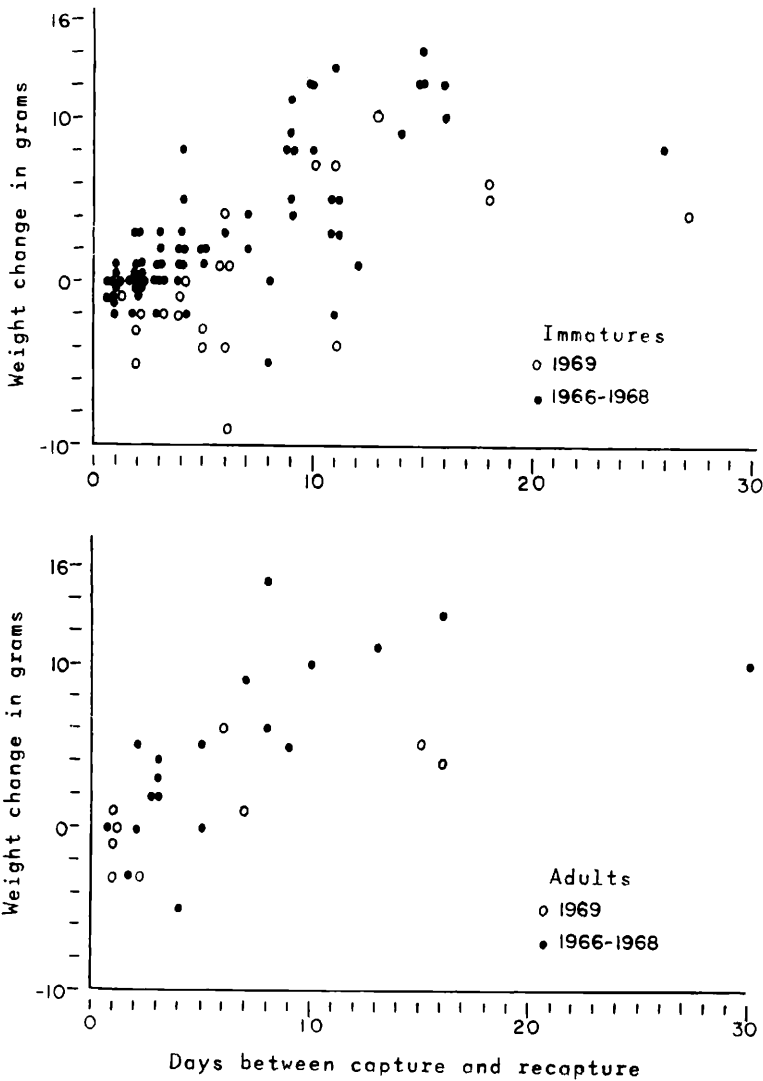


FIGURE 5. Weight changes of adult and immature Semipalmated Sandpipers retrapped at Long Point, 1966 to 1969.

scribed for the Blackpoll Warbler (*Dendroica striata*) (Nisbet, Drury, and Baird, 1963), the Dunlin (*Calidris alpina*) (Mascher, 1966) and the Swainson's Thrush (*Hylocichla ustulata*) (Mueller and Berger, 1966). Mueller and Berger (1966) attributed the weight loss that follows banding to the handling of the birds by the captor. By contrast, Mascher (1966) believed weight loss to be a natural phenom-

enon related to the recent completion of a migratory flight. Nevertheless, during their migratory pause at Long Point, Semipalmated Sandpipers generally increased their fat levels.

To check whether the fat levels within the depots affect the resumption of migratory flight, the departure from Long Point of "lean" (<24 EPF) and "fat" (> 26 EPF) sandpipers was compared during 1969. Subsequently, "lean" adults were found to average 14.2 EPF as compared to 39.0 EPF for the "fat" adults. Similarly, immature birds when separated into "lean" and "fat" groups averaged 9.6 EPF and 31.6 EPF respectively (Fig. 3-B). Adult birds that arrived at Long Point before the immatures (prior to August 11) did not stop for long in the study area (Fig. 6) and had relatively small fat deposits. The later-migrating adult sandpipers, arriving after August 11, remained longer in the study area than did the earlier-migrating adults (Fig. 6) and exhibited a wide range of fat levels. There was no obvious tendency for the late-migrating adults in the "fat" group to stop at Long Point for less time than the late-migrating adults in the "lean" group.

By contrast to the adults, the "fat" immature birds did stop in the study area for shorter periods than their "lean" counterparts, but the difference averaged only 1.4 days. The small differences observed between the departure time of the relatively "lean" and "fat" sandpipers, the lengthy stops shown by "fat" birds, and the rapid passage of the early-migrating "lean" adults, suggest that the magnitude of fat deposits had little effect on the resumption of migratory flights by the Semipalmated Sandpiper from Long Point in the autumn.

DISCUSSION

Semipalmated Sandpipers might normally undertake long, unbroken flights, since they migrate overland from northern Canada to the Great Lakes and the seaboard of the southeastern United States, and have occurred in Great Britain (Smith, 1968). In addition to their suspected long flights, short flights might also figure prominently in the migration of this species. For example, in our study 30 color-marked birds were relocated within 100 km of Long Point. Twenty-eight birds had moved east along the north shore of Lake Erie, one moved to the west and the other to the southwest of Long Point (Page, 1970).

Helms and Smythe (1969) suggested that the independence of migratory movements from the accumulation of large fat reserves might have energetic advantages by permitting birds to move limited distances without the energetic cost of carrying extra fuel. On the other hand, certain species must complete long flights over environments with limited food resources and must, therefore, carry heavy fat deposits. Thus although large fat reserves are apparently unnecessary for the initiation of migratory flight in certain species (King and Farner, 1963; Lofts, Marshall, and Wolfson, 1963; Yarbrough and Johnston, 1965), heavy fat reserves must be essential for the initiation of successful migratory flights by birds that have to cross large inhospitable areas.

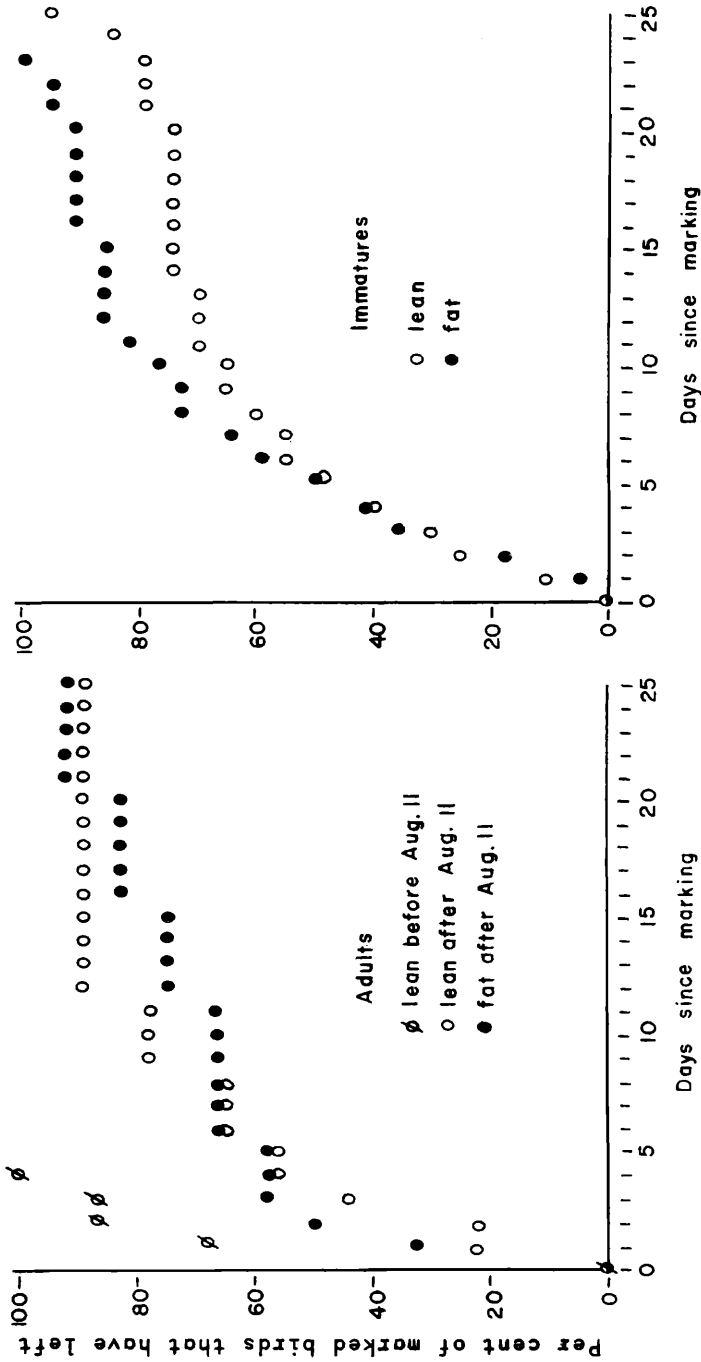


FIGURE 6. Departure rate of "lean" and "fat" adult and immature, color-marked Semipalmated Sandpipers from Long Point, 1969. Within a given group each point represents the per cent of color-marked birds that had left the study area by a given period after marking.

At Long Point many Semipalmated Sandpipers were apparently not yet embarking on long, non-stop flights since many flew short distances eastward to other points on the north shore of Lake Erie. Many of the birds did not accumulate large fat reserves. Thus, based on our evidence, there was no reason to believe that Semipalmated Sandpipers required large fat reserves to initiate their migration from Long Point. However, it would be interesting to compare the Long Point data with data collected in the breeding area and at migratory stopover points in the north (Hope and Shortt, 1944). In the latter locations perhaps heavy fat deposits must be accumulated as a part of the migratory stimulus. By the time the birds reach Long Point, they have presumably completed long, nonstop flights from their breeding grounds or more northerly migratory stopover points, and could reach their final winter destinations by a series of relatively short flights. Until further evidence is available, the precise role of fat in governing migration of the Semipalmated Sandpiper remains unknown.

SUMMARY

Fat deposition was studied during the autumn migratory pause of the Semipalmated Sandpiper at Long Point, Ontario between 1966 and 1969. Fat-free weight increased by 0.31 g per mm increase of wing length. There were no significant age or sex differences in fat-free weight when sandpipers of similar wing length were compared. Fat levels varied between 4.6 per cent and 42.1 per cent of total body weight in the sandpipers that were analyzed for fat content and probably exceeded 50 per cent in some individuals that were banded. Weight increases of birds recaptured after banding indicated that subsequent to a one or two day period of weight loss, individuals remaining in the study area increased the amount of fat in their depots. There was no evidence that the departure of Semipalmated Sandpipers from Long Point was related to specific fat levels in the birds.

ACKNOWLEDGMENTS

The field work was supported by the National Research Council of Canada through grant A3911 to Dr. Middleton and by the Canadian National Sportsmen's Show through grants to Long Point Bird Observatory. Many participants of Long Point Bird Observatory and particularly Mike Bradstreet aided in the collection of the data at Long Point. Dr. A. Salvadori, Department of Mathematics and Statistics, University of Guelph provided invaluable assistance in the computer analysis of the data.

LITERATURE CITED

- ALDER, H. L., and E. B. ROESSLER. 1964. Introduction to probability and statistics. W. H. Freeman and Company, San Francisco, 3rd ed.
- CHILD, G. I. 1969. A study of nonfat weights in migrating Swainson's Thrushes (*Hyalocichla ustulata*). *Auk*, **86**: 327-338.
- CONNELL, C. E., E. P. ODUM, and H. KALE. 1960. Fat-free weights of birds. *Auk*, **77**: 1-9.
- HELMS, C. W., W. H. AUSSIKER, E. B. BOWER, and S. D. FRETWELL. 1967. A biometric study of major body components of the Slate-colored Junco, *Junco hyemalis*. *Condor*, **69**: 560-578.
- HELMS, C. W., and R. B. SMYTHE. 1969. Variation in major body components of the Tree Sparrow (*Spizella arborea*) sampled within the winter range. *Wilson Bull.*, **81**: 280-292.
- HICKS, D. L. 1967. Adipose tissue composition and cell size in fall migratory thrushes (Turdidae). *Condor*, **69**: 387-399.
- HOPE, C. E., and T. M. SHORTT. 1944. Southward migration of adult shorebirds on the west coast of James Bay, Ontario. *Auk*, **61**: 572-576.
- JOHNSTON, D. W. 1966. A review of the vernal fat deposition picture in overland migrant birds. *Bird-Banding*, **37**: 172-183.
- JOHNSTON, D. W., and R. W. McFARLANE. 1967. Migration and bioenergetics of flight in the Pacific Golden Plover. *Condor*, **69**: 156-168.
- KING, J. R. 1963. Autumnal migratory-fat deposition in the White-crowned Sparrow. *Proc. XIII Intern. Ornithol. Congr.*, 940-949.
- KING, J. R., and D. S. FARNER. 1963. The relationship of fat deposition to Zugunruhe and migration. *Condor*, **65**: 200-223.
- LOFTS, B., A. J. MARSHALL, and A. WOLFSON. 1963. The experimental demonstration of pre-migration activity in the absence of fat deposition in birds. *Ibis*, **105**: 99-105.
- MASCHER, J. W. 1966. Weight variations in resting Dunlins (*Calidris a. alpina*) on autumn migration in Sweden. *Bird-Banding*, **37**: 1-34.
- MCNEIL, R. 1969. La détermination du contenu lipidique et de la capacité de vol chez quelques espèces d'oiseaux de rivage (Charadriidae et Scolopacidae). *Can. J. Zool.*, **47**: 525-536.
- MUELLER, H. C., and D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. *Bird-Banding*, **37**: 83-112.
- NISBET, I. C. T., W. H. DRURY, JR., and J. BAIRD. 1963. Weight-loss during migration. Part I: Deposition and consumption of fat by the Blackpoll Warbler (*Dendroica striata*). *Bird-Banding*, **34**: 107-159.
- ODUM, E. P. 1960. Lipid deposition in nocturnal migrant birds. *Proc. XII Intern. Ornithol. Congr.*, 563-576.
- . 1965. Adipose tissue in migrating birds. In *Handbook of Physiology*, Section 5, Am. Physiol. Soc., Washington, D. C., p. 37-43.
- ODUM, E. P., and C. E. CONNELL. 1956. Lipid levels in migrating birds. *Science*, **123**: 892-894.
- ODUM, E. P., C. E. CONNELL, and H. L. STODDARD. 1961. Flight energy and estimated flight ranges of some migratory birds. *Auk*, **78**: 515-527.
- ODUM, E. P., and J. D. PERKINSON, 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.
- ODUM, E. P., D. T. ROGERS, and D. L. HICKS. 1964. Homeostasis of the nonfat components of migrating birds. *Science*, **143**: 1037-1039.
- PAGE, G. 1970. The relationship between fat deposition and migration in the Semipalmated Sandpiper. M. S., Thesis, Department of Zoology, University of Guelph. 49 p.
- PAGE, G., and M. BRADSTREET. 1968. Size and composition of a fall population of Least and Semipalmated Sandpipers at Long Point, Ontario. *Ontario Bird-Banding*, **4**: 82-88.

- ROGERS, D. T., JR., and E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. *Auk*, **81**: 505-513.
- SMITH, F. R. 1968. Report on rare birds in Great Britain in 1967. *Brit. Birds*, **61**: 329-365.
- STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York.
- YARBROUGH, C. G., and D. W. JOHNSTON. 1965. Lipid deposition in wintering and premigratory Myrtle Warblers. *Wilson Bull.*, **77**: 175-191.

*Point Reyes Bird Observatory,
Mesa Road, Bolinas, California 94924, and
Department of Zoology, University of Guelph, Guelph, Ontario*

Received 19 March 1971, accepted 11 February 1972.