ARCTIC INSTITUTE OF NORTH AMERICA

TECHNICAL PAPER NO. 12

THE DYNAMICS OF CONDITION FACTORS IN CANADA GEESE AND THEIR RELATION TO SEASONAL STRESSES

By

HAROLD C. HANSON

PUBLISHED DECEMBER 1962

THE ARCTIC INSTITUTE OF NORTH AMERICA

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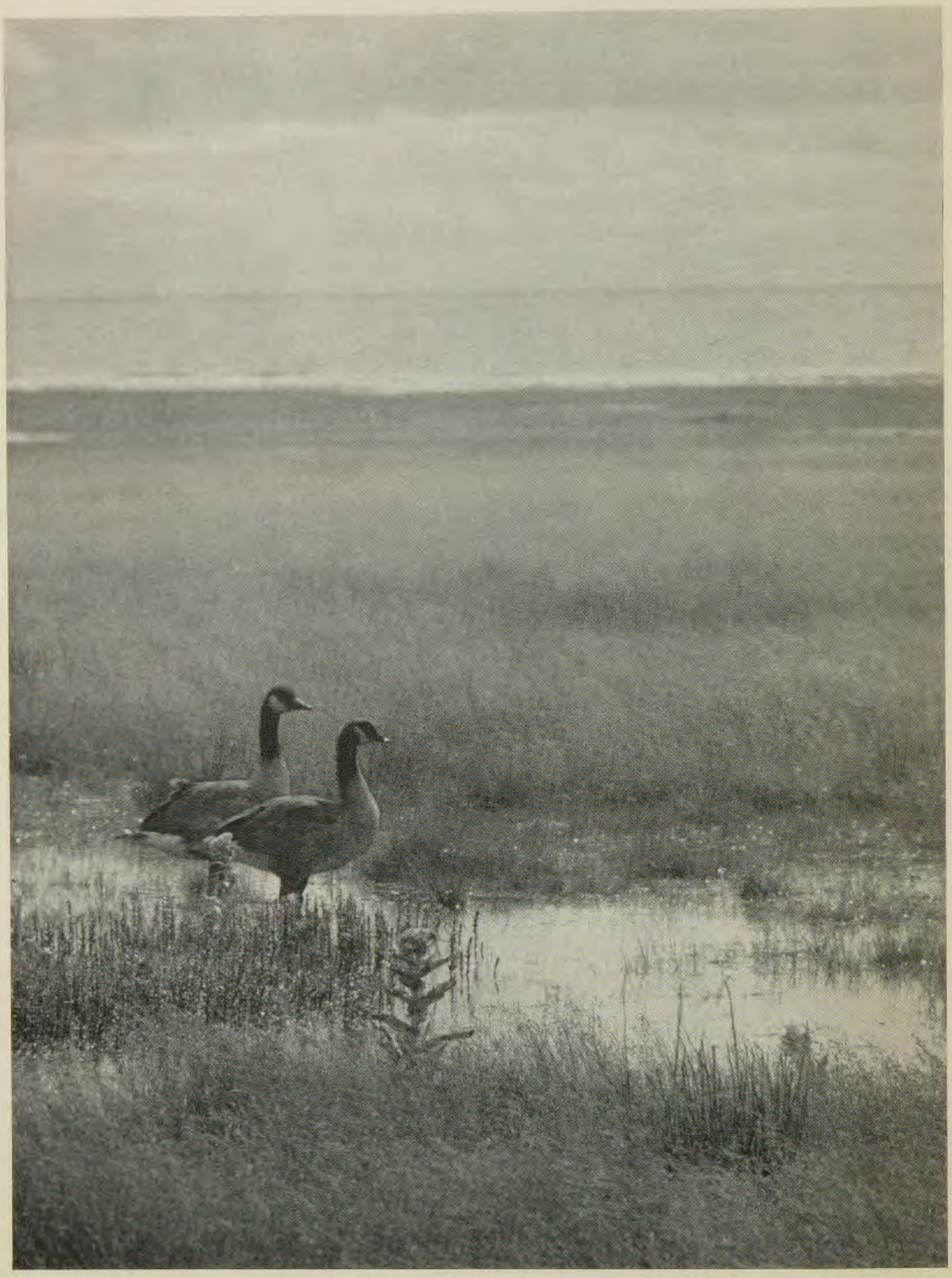

Plate 1. Immature Canada Geese on the south shore of Akimiski Island, N.W.T.

THE DYNAMICS OF CONDITION FACTORS IN CANADA GEESE AND THEIR RELATION TO SEASONAL STRESSES[1]

Harold C. Hanson[2]

As reduction of wildlife habitat and increased hunting pressure stimulate more intensive management of wildlife populations, the physical welfare of these populations will necessarily receive greater attention. Students of big game populations particularly have been keenly aware of the relation of condition factors to population dynamics. Condition factors in small migratory birds—especially that of body fat—have received intensive investigation by ornithologists studying the physiology of migration. Waterfowl, on the other hand, have been little studied in this regard, although the need has been great and the opportunity they provide for gaining new insights into basic avian biology is possibly unmatched.

The history of the Canada Goose (*Branta canadensis interior*) population in the Mississippi Flyway during the last decade clearly demonstrates the extra dividends in the form of population increase gained from management practices. Studies by Hanson and Smith (1950) have shown that the long-term population trends depend upon conditions on the wintering grounds—not on the breeding grounds. Unlike the breeding grounds of prairie nesting ducks, which are subjected to ever increasing inroads by agriculture, the muskeg breeding grounds of the Canada Goose in the Hudson Bay Lowlands of northern Ontario do not appear threatened in the foreseeable future. Furthermore, it would appear that the breeding grounds could readily support several times the flyway populations of recent years which have been as high as a quarter of a million birds. Consequently, management on the wintering grounds must be concerned not only with how many geese current refuges can support but also with the health of the birds during the winter period.

A long-term study of the physiology and biochemistry of the Canada Geese in the Mississippi Flyway was initiated in 1954 with studies of the weights of the visceral organs of geese wintering in southern Illinois. In 1958 and 1959 studies were carried out on Akimiski Island in James Bay and in a subarctic area of northern Ontario adjacent to Hudson Bay. Objectives were two-fold: (1) to establish normal values for the various physiological parameters; and (2) to determine what factors can be used in evaluating "condition" in Canada Geese and how these vary during the course of the life cycle. The present paper is one of a series under preparation on the physiology, biochemistry, endocrinology, and organ weights of Canada Geese throughout their life cycle. For some of the background information on this population of Canada Geese, see the six papers marked by asterisks in the references.

[1]Based in part on a portion of a doctoral thesis submitted to the University of Illinois.

[2]Illinois Natural History Survey, Urbana.

Acknowledgments

Collection of the data reported here was made possible by the support of many agencies. Foremost among these was the Arctic Institute of North America, which through a research grant made it possible for the investigator to spend the summers of 1958 and 1959 on Akimiski Island in James Bay, N.W.T., and the spring of 1959 at Hawley Lake and along the Sutton River, northern Ontario. The scope of the field operations was possible only through the splendid logistic support of the Ontario Department of Lands and Forests. In this regard, Dr. C. H. D. Clarke, Mr. Harry G. Lumsden, and Mr. W. Campbell Currie are mentioned with gratitude. I am also deeply indebted to Wing-Commander George Moir, R.C.A.F., commanding officer at the Winisk Air Base in 1959, for many courtesies extended to me. For kind hospitality, and assistance while in the field, Mr. Michael Pasco, Mr. John Campbell, and Mr. Don Paterson of the Hudson's Bay Company are gratefully remembered. Permission to take geese on Akimiski Island for study was extremely important to the success of the work, a concession which was kindly granted by Mr. Winston Mair, Chief of the Canadian Wildlife Service. Nets for live-trapping Canada Geese on Akimiski Island were generously supplied by the U.S. Bureau of Sports Fisheries and Wildlife.

The success of the day-to-day field work literally hinged on the knowledge, abilities, and good friendship of the Indian guides employed. At Hawley Lake six weeks were spent living and travelling with the families of Joseph and Louis Chokomoolin. On Akimiski Island Antoine and Onesime Wheesk of Attawapiskat gave the field work whole-hearted assistance.

Facilities were provided at the Horseshoe Lake Game Refuge by the Illinois Department of Conservation. Mr. George Arthur, Mr. Otha Hart, and Mr. Gene Hart of the Department were most helpful throughout the study.

Dr. Thomas G. Scott, Head of the Section of Wildlife Research at the Illinois Natural History Survey, provided the encouragement and personal support that made the study possible. For a critical review of the manuscript and helpful suggestions, the author is indebted to Dr. Scott, Dr. Ralph Yeatter, and Dr. Robert Hiltibran of the Illinois Natural History Survey, and to Dr. S. Charles Kendeigh, Dr. R. E. Johnson, Dr. Fred A. Kummerow, and Dr. Elwood F. Reber of the University of Illinois.

Dr. Horace W. Norton of the University of Illinois provided helpful advice on statistical computations which were carried out under a more general program of support from the National Science Foundation. Digital computor facilities were afforded by the Graduate College of the University of Illinois.

MATERIALS AND METHODS

This paper is concerned chiefly with body weight, weight of sternal muscles, weight of muscles of the tibiotarsus, and estimation and weights of body fat of Canada Geese. Liver weights were also included as they proved to be helpful in interpreting the various physiological states.

Body weights recorded here generally represent geese with empty or nearly empty digestive tracts. The weights of bagged geese represent geese shot before 9.00 a.m.; most geese trapped in autumn and winter were held overnight before being banded and weighed. In any event, disturbance and excitement probably accelerated loss of intestinal contents. Canada Geese weighed at Horseshoe Lake prior to 1957 were weighed on scales graduated in pounds and

ounces and in pounds and tenths of pounds. Prior to the conversion of these data to grams, they were first averaged to pounds and hundredths of pounds and subsequently rounded off to pounds and tenths of pounds. Conversion[1] of the latter to grams (Tables 1–6) has led to some inconsistencies and, seemingly, errors, but these do not significantly affect weight relationships or the conclusions drawn from them.

The muscles of the sternum which were weighed were the *pectoralis*, *supracoracoideus*, and *corabrachialis*. The weights obtained by unilateral excision of the pectoral muscles were doubled in computing their relation to total body weight. To obtain tracings of the cross-sectional area of the pectoral muscles for the purpose of illustrating condition types, the sternum and the intact half of these muscles were transected by a cut originating at the sterno-coracoidal process and at right angles to the anterior carinal margin.

The muscles of the tibiotarsus weighed included all which originated on this bone and were attached by long tendons to the lower extremities. Before removing these muscles the *semimembranous*, which originates on the femur, was excised close to its insertion on the tibiotarsus, and then the leg was excised at the articulation of the femur and the tibiotarsus.

Fat deposits in Canada Geese were classified into four categories that were useful in appraising condition: (1) the *subcutaneous deposits* that adhere to the skin of the breast and belly; (2) the *axillary deposit*, a roughly triangular deposit attached to that part of the body underlying the axillary feathers; (3) the "*knee patch*", an elongated strip of fat, usually roughly triangular in cross-section, that is loosely attached to the skin and lies adjacent to the anterior face of the distal portion of the femur and the proximal portion of the tibiotarsus; and (4) *visceral* fat lying principally posterior to the gizzard. In making dissections, these fat depots were appraised on a scale ranging from 0 to 5, and measurements of fat thickness and weights of various deposits were made.

Prior to weighing each liver, the gall bladder was excised, and all clotted blood in exposed sections of the major veins was removed.

All geese studied were divided into sexes and classified in one of five age groups. Young geese of the year studied on the breeding grounds were classified as *goslings* up to and after reaching the flying stage. Upon reaching the wintering grounds, goslings were classified as *immatures*; immatures of the previous winter were classified as *yearlings*, and all older geese as *adults*. Immatures returning to the breeding grounds were classified as *yearlings*; yearlings of the previous winter were classified as *2-year-old adults*, and all older geese as *adults*. In the present report, data on the last two age classes have been combined. Criteria for the recognition of these age classes have been presented (Hanson, 1949, 1959, and 1962b). Incubating females were also recorded separately. Females classified as *incubating* were shot at the nest. Females collected in July and August that had nested that spring could be readily separated from those that had not by the incubation patch (Hanson, 1959).

Information on weights of Canada Geese during the moult was obtained both from captives and from wild geese trapped on Akimiski Island. At the time of handling and weighing, the primary wing feathers of each goose were measured along their anterior edge, from the point of insertion to the tip of the shaft. The stage of the moult, that is, regrowth of the primaries, was then

[1]See Appendix for conversion of grams to pounds and tenths of pounds.

computed in terms of the percentage of the total length of all growing primaries, as compared with the average total length of all primaries of a sample of geese of the same age-sex class in winter (Hanson, unpublished).

For readers not familiar with the range limits of the Canada Geese of the Mississippi Flyway, it should be pointed out here that three refugees in Illinois, the Horseshoe Lake Wildlife Refuge in Alexander County, the Union County Wildlife Refuge, and the Crab Orchard National Wildlife Refuge in Williamson County, form the winter termini of the bulk of the flyway population. The breeding grounds of these geese lie in the muskeg of northern Ontario west of James Bay and south of Hudson Bay and on Akimiski Island, N.W.T., in James Bay. Hawley Lake, Ontario, mentioned above, lies 40 miles south of Hudson Bay and 90 miles west of James Bay. It is drained by the Sutton River.

BODY WEIGHTS

Because of their labile character, body weights in birds have particular significance; but, for the same reason, weight changes require careful analysis and interpretation. Nice (1938) has pointed out that body weights of birds may fluctuate 4.6–10.8 per cent or more throughout the day. During the migration period, fat passerine birds (Wolfson, 1954) and Mourning Doves (Hanson and Kossack, 1957) may weigh as much as 35 per cent more than individuals of the same age and sex carrying no body fat. The temporary growth of the ovary and oviduct at laying time increases the body weight of female Ringed Turtle Doves (*Streptopelia roseogrisea*; see Vaurie, 1961 for justification of specific name) by 2–3 per cent (Riddle and Braucher, 1934). Although the weight of most birds is usually at an annual minimum during the moult, this is not true for some species (Richdale, 1947). Finally, there are the normal seasonal trends in weight which reflect over-all metabolic activity and special energy demands (Baldwin and Kendeigh, 1938; Kendeigh, 1949).

The life cycle of Canada Geese can be divided into nine sub-periods or categories of physiological activity: (1) wintering; (2) spring migration; (3) nest-building and egg-laying; (4) incubation; (5) growth stage in goslings; (6) the nonflying portion of the moult in older geese; (7) late moult period and early flight; (8) pre-migration period; and (9) autumn migration. The wintering period is used here as an inclusive term for autumn and winter; the other eight periods are largely or wholly confined to spring and summer. No weight data were obtained for period 8, and period 9 is represented only by weights of geese at the end of their migration in Illinois.

Body weights in autumn and winter

Elder (1946) studied monthly trends in body weights of shot and live-trapped Canada Geese at Horseshoe Lake in 1941–3. His findings on body weights of immatures are summarized in Tables 1 and 2. Weights obtained by the writer of trapped geese and geese shot by hunters are contained in Tables 1–12. Body weights for immatures obtained by the writer compare fairly closely with Elder's averages for the same period. In general, they show (Table 10) that in late fall and winter yearling geese weigh 400–480 grams or

about a pound more than immatures, while adults weigh 130–150 grams or about one-third of a pound more than yearlings, the differences between age classes being about the same for both sexes.

Elder's (1946) data probably portray normal seasonal gains and losses of a wintering population of Canada Geese having access to a fairly adequate food supply. The geese arriving at Horseshoe Lake Refuge in autumn find an abundance of food available, chiefly corn and pasture. Together with mild weather, this permits them to make rapid gains in weight. As food supplies on the refuge become exhausted, the birds fly to surrounding fields to feed on waste grain. In mid-winter, however, their food supply has to be supplemented daily by several hundred bushels of corn.

The seasonal trends in average body weights of geese live-trapped by the writer during the winters of 1943–4 and 1945–6 are shown in Table 10. The numbers of geese in the Horseshoe Lake area in relation to the amount of food produced on the refuge combine to affect average weight. This was clearly shown in the winters of 1943–4 and 1944–5. In 1943–4 the peak number of geese using the Horseshoe Lake Refuge was about 50,000 (Hanson and Smith, 1950); in 1944–5 the peak number was about 35,000 birds. In 8 of the 12 comparisons possible between weights for the months of November and December 1943 and 1944 for the six age and sex classes, the geese averaged somewhat heavier in 1944 than in 1943, Tables 1–6.

A comparison of smaller samples of geese bagged by hunters shows no important change in the average weight of immatures between 1943 and 1957, Tables 8 and 9. While only limited meaning can be attached to these figures because of differences in sample size and variation in the age of the immatures due to different average hatching dates, there is no indication that there has been a consistent upward trend in average weight due to refuge management practices *per se*. The low in body weights of immatures in 1953 can be attributed to poor food conditions at the Horseshoe Lake Refuge that year as a result of drought. Many geese died that autumn from food impaction of the esophagus as a result of eating the dry leaves and stems of plants and soybeans.

Personnel guiding farming practices on refuges for Canada Geese bear a particularly heavy responsibility as, either on or off the refuges, native plants are usually of minor importance. How closely refuge food supplies may affect body weight in geese is demonstrated by weights of immature geese obtained in November and December 1957 at the Horseshoe Lake Refuge and at the Union County Refuge (Table 11). The two areas lie only about 15 miles apart. At both refuges large acreages are planted to forage crops (wheat and rye in late summer; grasses and legumes in spring for permanent pasture). When Canada Geese first arrive at the refuges, forage crops constitute the principal food; later, as the quality and quantity of this food is reduced and the geese become less wary, they feed in cornfields that remain unpicked. In 1957 at Horseshoe Lake, heavy autumn rains prevented removal of any of the corn; at Union County, which unlike much of the Horseshoe Lake Refuge was share-cropped at that time, the tenant farmers picked the great bulk of the corn crop, leaving little for the geese.[1]

[1]This situation arose from the fact that much of the share of corn normally allotted to the refuge for the use of geese was taken to pay for the cost of fertilizers bought at tenant expense.

The 1957 fall population of Canada Geese at the Horseshoe Lake Refuge was unusually large, around 125,000 in November, and the migration unusually early. The Union County Refuge, on the other hand, had only about a third as many geese, but a larger acreage of forage crops to support them. Hence it had relatively greater food resources early in the fall of 1957 than Horseshoe Lake Refuge; by late fall it had markedly less because of the standing corn crop in the Horseshoe Lake Refuge. It is not too surprising therefore that immature geese at Union County had significantly higher weights in November than the birds at Horseshoe Lake, and that in December this relationship was reversed, Table 11.

Terminal starvation weights in winter

In dry autumns, some of the geese in the Horseshoe Lake area become "crop bound" from ingesting dry, unpalatable foods (Hanson and Smith, 1950). The dry roughage forms a bolus in the extensible esophagus which, although permitting drinking, prevents all food from entering the lower digestive tract. The result is death from slow starvation. The lining of the esophagus usually becomes necrotic, but this seemingly does not hasten death. In 1953, the mortality from this cause was estimated to have been as high as 1–2 per cent of the population. Durant (1956) has reported on mortality from this cause in the Canada Geese of the Eastern Prairie Flyway that stop over at the Swan Lake National Wildlife Refuge in Missouri.

In November 1953 a large number of geese that died of starvation from impaction of the esophagus were weighed after first removing the bolus of food, which was usually of considerable size and weight. The body weights obtained provided starvation data which may even be superior to information from captives as these birds were living under natural conditions. The terminal death weights obtained are summarized in Table 12.

The percentage of body weight presumed to have been lost by crop-bound geese was calculated by using the body weights of geese shot by hunters in November, Table 7, as a base for initial autumn weights, the assumption being that both samples represented a normal cross-section of the population within each sex and age group. The weight losses of the various age and sex samples of the "crop-impacted" geese, computed to be from 43–46 per cent of assumed average initial weights, are given in Table 10 (data for yearling females were inadequate).

Benedict and Lee (1937), in their study of fasting domestic geese, found that young geese had lost about 35 per cent of their initial weight at the time of death, and that adult geese could lose a similar percentage. Although many of the adults they studied were killed before death from starvation was permitted to occur, they noted that "the ravages of fasting were more severe with the young birds" (p. 90). The data on Canada Geese, Table 12, support this observation only in the case of the immature females. Condition of plumage in autumn and parasitological infections (Hanson and Gilford, 1961) have often suggested that immature females tend to be less "thrifty" and resistant than immature males. Extremes of temperature in either direction shorten the survival period of fasting birds (Kendeigh, 1945 and 1949).

Starvation studies of penned Mallards (*Anas platyrhynchos*) showed that death occurred from the twelfth to the twenty-sixth day (Jordan, 1953). Mortality of males was found to be twice that of females during the spring breeding

season. Latham (1947), in an experimental study of starvation, also found survival of females to be superior to males in Mallards, and in Ring-necked Pheasants (*Phasianus colchicus*) and Ruffed Grouse (*Bonasa umbellus*), all polygamous species, but inferior in Bobwhite (*Colinus virginianus*) and Gray Partridge (*Perdix perdix*), both monogamous species.

Jordan (1953) reported the greatest average loss of weight of Mallards that were starved and later recovered to be about 44 per cent, a figure which agrees closely with those obtained for Canada Geese. Trautman *et al.* (1939) in their study of several hundred ducks that died from starvation and severe winter weather at the western end of Lake Erie weighed 25 birds comprising eight species. They found that the most emaciated ducks were more than 50 per cent below compiled "normal weight" range. Hagen (1942), in a study of 1,152 grouse (*Tetranidae*) in Norway, found that the average difference between the lowest and highest weights recorded was 42.6 per cent which he considered to be near the maximum loss that could be survived. Kendeigh (1945) correlated greater resistance to starvation in House Sparrows (*Passer domesticus*) with higher initial weights, the ability to lose more weight, and to lose it at a slower rate. Benedict and Lee (1937) have stressed the importance in withstanding starvation of the initial status of protein reserves as well as fat stores; some of the inter-relationships of fat, protein, and carbohydrate stores involved will be pointed out in the discussion.

Body weights in spring and summer

Body weights obtained of Canada Geese of the Mississippi Flyway in the Hudson Bay–James Bay region during spring and summer of 1958 and 1959 represented 5 sub-periods or categories of physiological activity.

Spring migration

Body weight and other condition factors during spring migration are based on geese collected at Hawley Lake, northern Ontario, from 2–12 May 1959. This place had several advantages: (1) the area is one of the most northern parts of the breeding range and therefore the condition of geese arriving there can be considered to be typical of the conclusion of spring migration; and (2) the current keeps the Sutton River, flowing out of the north end of Hawley Lake, open for several miles, which attracts geese to the region in considerable numbers and at an early date. In evaluating the data, it should be remembered that during the migration period most of the northern parts of the muskeg country lie under two to four feet of snow. Between May 2–12, a total of 123 geese killed by the local Indians at Hawley Lake was studied; prior to this time, between April 7, when the first migrant was seen, and May 2, only 17 geese had been killed by the Indians for food. The data, therefore, cover the main migration period and can be considered to be representative of the condition of the geese that spring, and, in all probability, of most springs.

In Tables 13 and 14, weights of 70 geese shot at Hawley Lake are given for comparison with a summary of body weights during the life cycle (goslings excepted). It will be noted that individuals of this population of Canada Geese may attain their peak body weight during spring migration. The fatness of most individuals was such that it seemed unlikely that there could have been an important loss of weight and fat during the final stages of migration over

the heavily forested country. In terms of weight gains over averages for the wintering period, gains for the various age-sex classes were: yearling males, 14.7 per cent; yearling females, 26.7 per cent; adult males, 10.0 per cent; and adult females, 17.9 per cent. The basis for higher gains by females of both age classes than by males will be considered in the discussion.

The spring kill at Hawley Lake unexpectedly showed that the migrant geese did not arrive in flocks of moderate size and that the age and sex classes did not arrive in a random sequence. Instead, daily kills by the Indians suggested that their flight was stratified, beginning with old mated adults arriving as single pairs, followed by pairs two years of age, yearling males and, finally, yearling females. While the successive arrival of these age groups dove-tailed into one another, the sequential character of the basic pattern was evident. The migration of Canada Geese through northern Ontario will be the subject of a subsequent paper. Noteworthy, as far as we are concerned here, is that the sample of yearling females shot could be divided into two categories: (1) fat birds whose arrival merged with and succeeded the yearling males, and (2) nearly fatless birds that arrived the concluding two days of the spring flight. These latter yearlings averaged 424 grams or nearly a pound less than the immediately preceding flight of yearling females.

Nest-building and egg-laying period

Only a few geese were collected in this period: a pair shot along the Sutton River, the female of which contained an egg in the oviduct, and four yearlings (Tables 13 and 14). The mated adults, shot two weeks after the close of the migration period, were still exceptionally fat and heavy and, in the case of the female, its weight was due in part to the advanced development of the ovary and oviduct. The yearlings, on the other hand, collected along the lower Sutton River 3 to 3½ weeks after the close of migration, had lost 6–10 per cent of their weight during this period. This weight loss consisted almost wholly of fat as predicted in advance by my Indian guides who said that by June 7–10 the geese would carry no fat and that by the time the first new growth of grass would be appearing the geese would again begin to put on fat.

Incubation period

A total of eight incubating females was collected. The weights of these were closely grouped and averaged 21.5 per cent less than adult females at the end of migration. This weight loss can be ascribed chiefly to loss of fat. Reduced food intake and heat losses already incurred during the early stages of incubation undoubtedly further accelerated weight loss.

Moulting period–nonflying stages

The anatomical, metabolic, and histological changes taking place in Canada Geese (and undoubtedly in most geese and ducks) during the moult period constitute a series of related episodes as dramatic and as interesting as any in our knowledge of avian biology, the elucidation of which is certain to lead to new insights into basic physiology. These changes include changes in body weight, body fat, organ weights, chemistry of the blood and tissues, size and histology of the endocrine glands, and porosity of the long bones of the legs (osteoporosis) (Hanson, 1958), subjects which will be covered in forthcoming

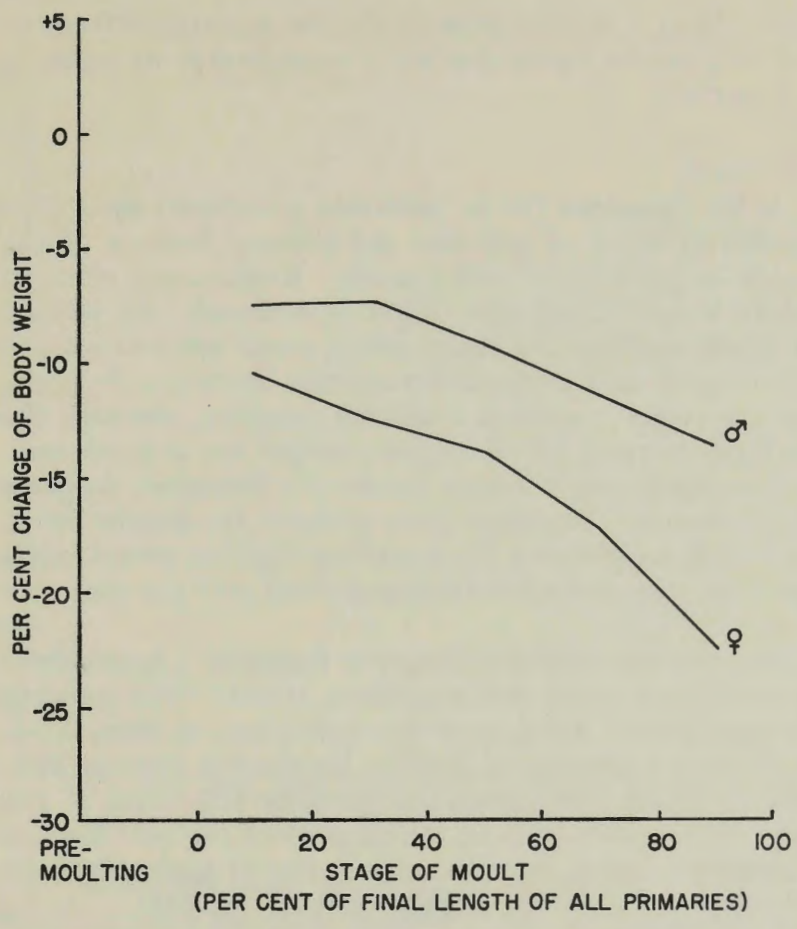

Fig. 1. Relation of body weight changes in caged male and female Canada Geese to moult and growth of the primary feathers of the wing.

papers. We are concerned here only with changes in body weight and in the size and weight of the principal muscle groups. Body weights during this period reach their minimums for the respective age-sex classes (allowing for the continuing physical maturation of the yearlings), Tables 13 and 14, indicating that the moult period is perhaps the period of greatest stress in the life of the Canada Goose. At this time, males average 4 and 12 per cent less and females 13 and 20 per cent less in weight, yearlings and adults, respectively, than at the time of their arrival on the breeding grounds. Greater initial fat deposits account for the relatively greater loss of weight in females and, in the case of the adult females, reflect the stresses of reproduction.

Prior to studies on the breeding grounds, weight changes were measured during the moult in 12 males and 7 females, both sex groups containing yearlings and adults. While the data obtained on these caged geese were not as complete and detailed as was desirable, they demonstrated a steady loss of body weight during the moult and, as in the case in the wild, the percentage loss in weight was greater in females than in males, Fig. 1.

In view of the above findings on weight loss in wild and penned moulting geese, Moffitt's (1931, p. 236) observation made in California while capturing wild moulting Canada Geese for banding is of interest: "All the old geese were quite thin; but the females were in exceptionally poor flesh, being much thinner than the males." Consequently there can be little doubt that the stress of the moult is particularly heavy on females, following the energy demands of egg

laying and caring for the young. *It seems possible that the apparent differential stress of moult may be a primary reason for the preponderance of males in populations of adult waterfowl.*

Moulting period—flying stages

Data on growth of the primaries (to be published elsewhere) show that Canada Geese are capable of flight by the time the primary feathers of the wing have achieved only 85 per cent of total growth. Replacement of neck, head, and body feathers is accelerated after flight is achieved. As will be shown below, Canada Geese in these late stages of the moult attained a significantly different physiological and anatomical condition from the flightless, moulting geese and are therefore treated as a distinct category, although the entire moult and the accompanying physiological changes are a continuum. During the flying stages, a gain in weight occurs for the first time since the geese arrived on the breeding grounds. Yearlings (data available for females only) showed a 4–5 per cent gain in weight over the preceding flightless period; adult males showed a 10 per cent gain; and adult females showed a 13 per cent gain in weight.

Davis (1945), who observed moulting Emperor Penguins (*Aptenodytes forsteri*) both in Antarctica and under pen conditions, stated: "The growing of new feathers is a most severe strain upon the individual, at times more detrimental than the temporary absence of food." He further remarks that, "In the course of these molts the birds refused to eat their full ration of fish during the latter stages of the transformation, the stage when the new feathers are in the process of forming. Other activities, such as that of pacing the cage in single file and occasionally swimming, largely ceased." (p. 144).

Richdale (1947) found that the Yellow-eyed Penguins (*Megadyptes antipodes*) reached their minimum weight for the year on completion of the moult. He also cited several other species in which weight losses did *not* occur during the moult but in most species studied—domestic fowl, Song Sparrow (*Melospiza melodia*) (Nice, 1938), Ring-necked Pheasant (Kirkpatrick, 1944; Kabat, *et al.*, 1950 and 1956), Blue-winged Teal (*Anas discors*) (Bennett, 1938), and Redhead (*Aythya americana*) (Weller, 1957)—minimum annual weights were recorded near the end of the moult.

BODY WEIGHT VERSUS CONDITION FACTORS

The role of refuges in maintaining adequate nutrition for wintering geese has been the underlying theme of much of the foregoing discussion. With the increase of Canada Geese in the Mississippi Flyway from about 40,000 in 1945–6 to a peak of about a quarter of a million birds in recent years, the question as to what constitutes "condition" in geese has become more pressing. In the fall of 1957, therefore, a series of investigations was initiated to explore more fully this question.

What are the factors involved in "condition"? It obviously cannot be assumed that the heaviest (fattest?) birds are in the "best condition", although body weight is ultimately linked to any evaluation of condition. Does any one

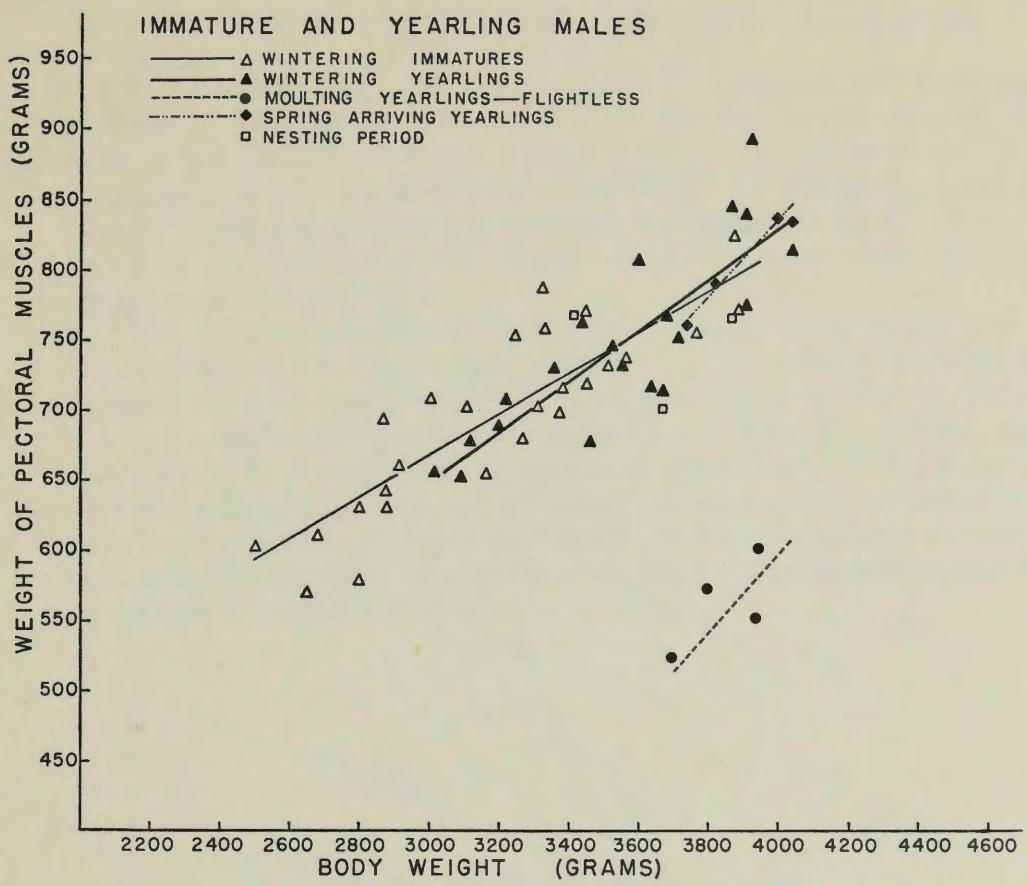

Fig. 2. Relation of weight of pectoral muscles to body weight in immature and yearling male Canada Geese.

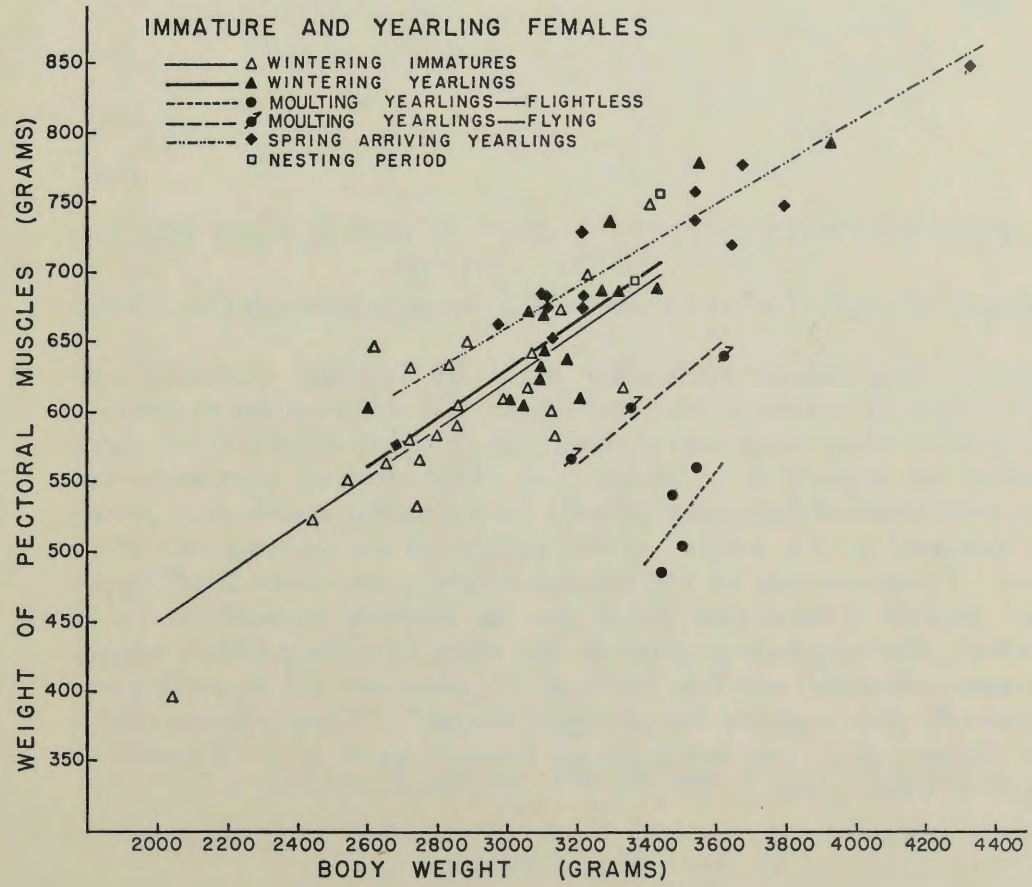

Fig. 3. Relation of weight of pectoral muscles to body weight in immature and yearling female Canada Geese.

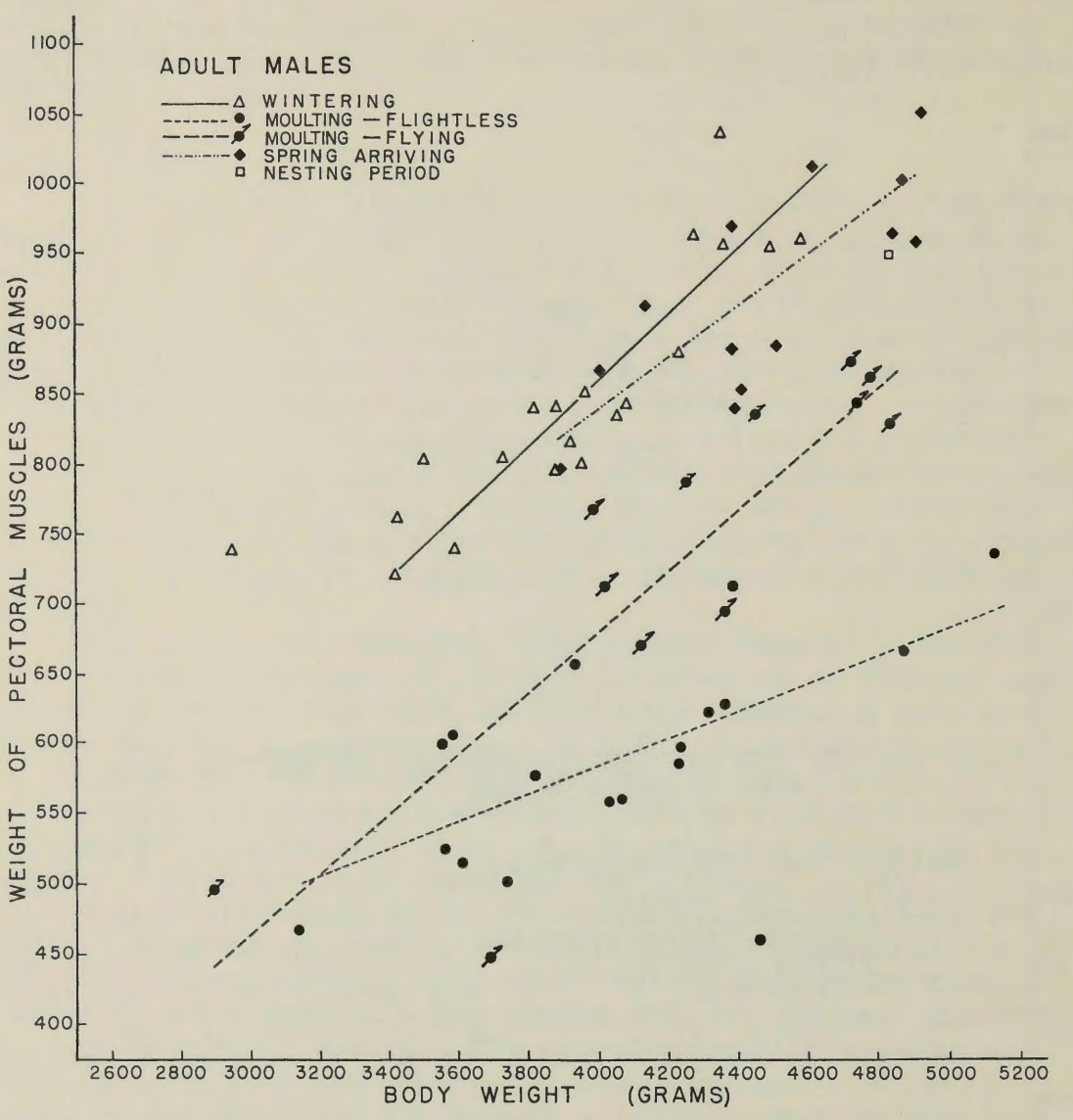

Fig. 4. Relation of weight of pectoral muscles to body weight in adult male Canada Geese.

constituent of the blood provide a subtle but definitive clue? Probably not—at least investigators in farm animal research are not able to point to one.

The present study sought to appraise physiological condition by direct assessment of the physical status of the bird. This involved quantitative and subjective evaluations of the amount of body fat and similar appraisals of protein stores as indicated by the weights of the muscles of the sternum and of the tibiotarsus. Tissue analyses of the muscles of the geese studied will, when complete,[1] provide a correction factor for the invisible intracellular fat of muscle tissue. Carbohydrate reserves do not enter into this problem importantly because as Benedict and Lee (1937, p. 57) point out, the domestic goose "has a relatively poor capacity for glycogen storage". These authors further state that the respiratory quotient in fasting domestic geese descends rapidly to the fat level in a few hours.

[1]Triplicate 10-gram samples of pectoral muscle, leg muscle, and liver from geese in all categories are being analysed for about a dozen constituents.

In December 1957 and January 1958, 79 immature and adult geese were autopsied. This sample comprised geese shot by hunters as well as trapped geese killed for this particular study and included birds in as widely different nutritive states as were obtainable at the time. The following autumn, a total of 36 yearling geese, randomly selected, was taken for study. Data from the breeding grounds (Akimiski Island, N.W.T.) were obtained during the summers of 1958 and 1959.

The wintering bird, the "basal goose", appeared to be the best standard for comparison for a variety of reasons: (1) its physical activities are more balanced between flying and walking than at any other time of the year; (2) it is under no metabolic stress such as prolonged flying (migration), egg laying, moulting, or in an immediate recovery stage therefrom; (3) the wintering goose does not generally undergo any prolonged climatic stress as winters in southern Illinois are generally mild and short; and (4) a food shortage—at least in terms of its complete absence for several weeks—is not experienced by geese wintering on refuges in southern Illinois.

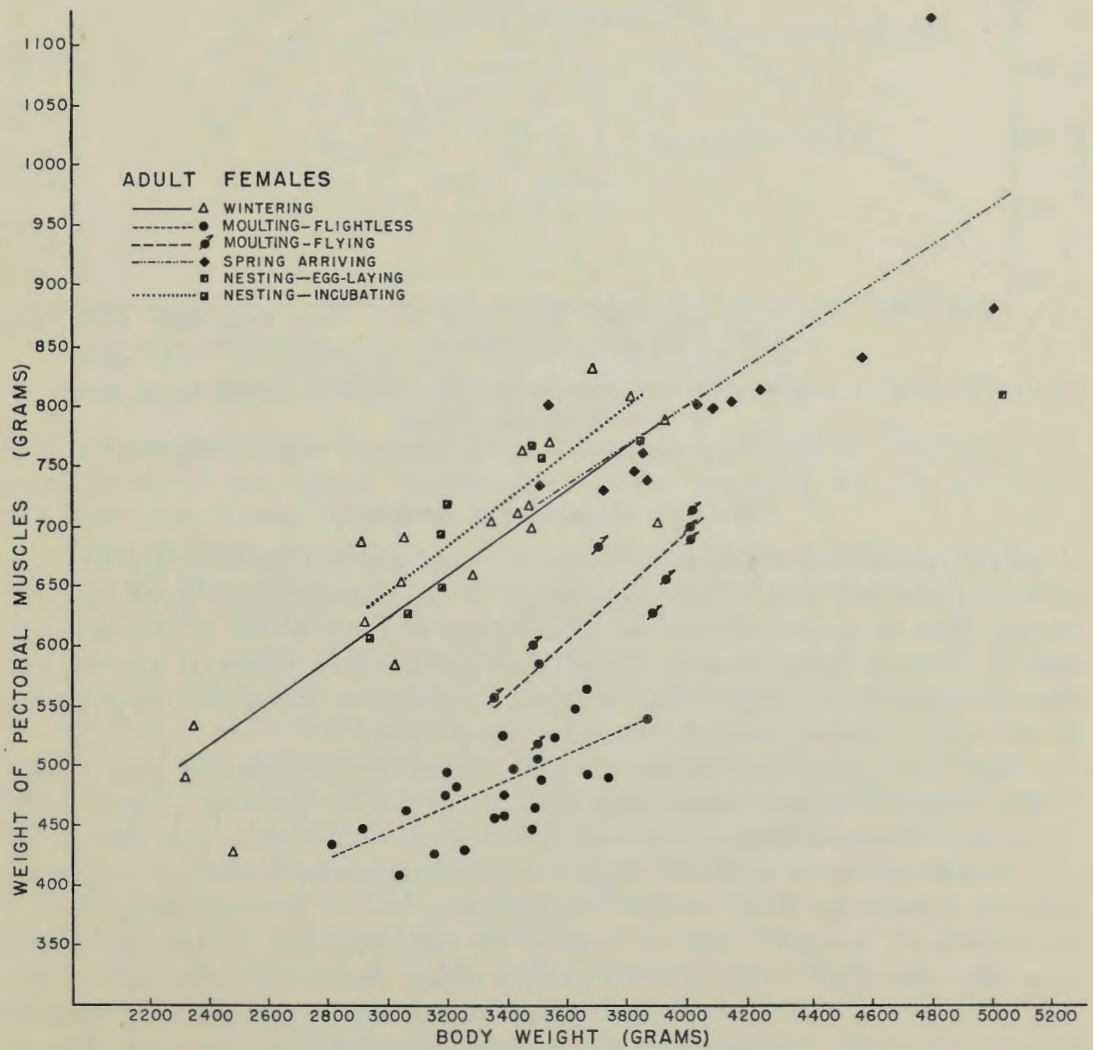

Fig. 5. Relation of weight of pectoral muscles to body weight in adult female Canada Geese.

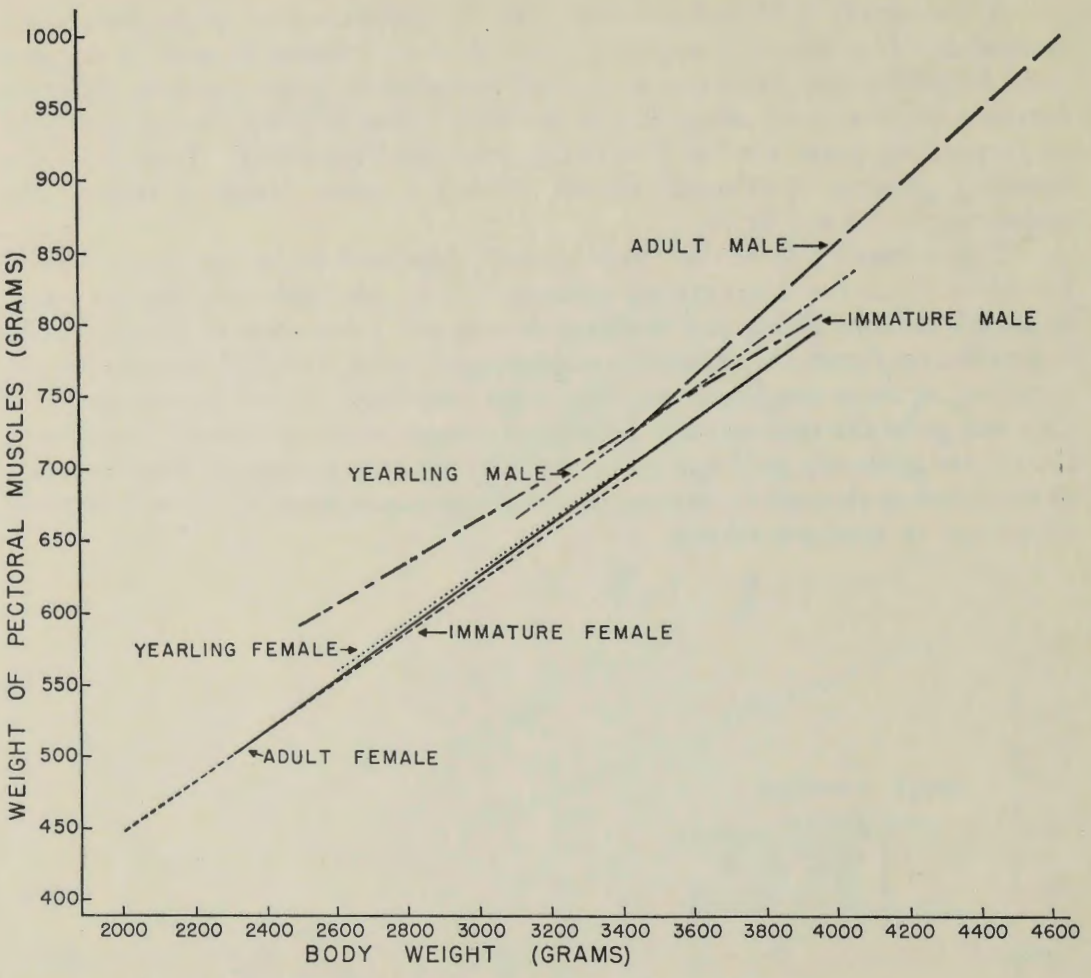

Fig. 6. Relation of weight of pectoral muscles to body weight in Canada Geese wintering at Horseshoe Lake, Illinois.

Weight of pectoral muscles

The dynamic aspect of the effects of sexual maturation with age and the various seasonal stresses on the physiology of the Canada Geese were brought sharply into focus as data on the relationship of the weight of the pectoral muscles to body weight accumulated. In Figs. 2–5 and Tables 15 and 16, the dramatic shifts in weights of these muscles according to the relative importance of their physical and metabolic function are evident.

Our first concern in understanding the status of the wintering bird is with proportional differences rather than absolute values for pectoral muscle mass. Are there differences between age and sex classes as well as those directly related to differences in body weight? Figure 6 shows regression curves of weight of pectoral muscles on body weight for wintering birds. No significant differences between the age classes of females are indicated, but the curves for the three age classes of males show a graded series, immature males having the smallest pectoral muscles and adult males having the largest pectoral muscles per unit of body weight, with the yearling males falling between, Fig. 6, Table 15. The significance of these findings, first reported in Hanson (1958), will be deferred to the discussion. These differences in wintering geese and

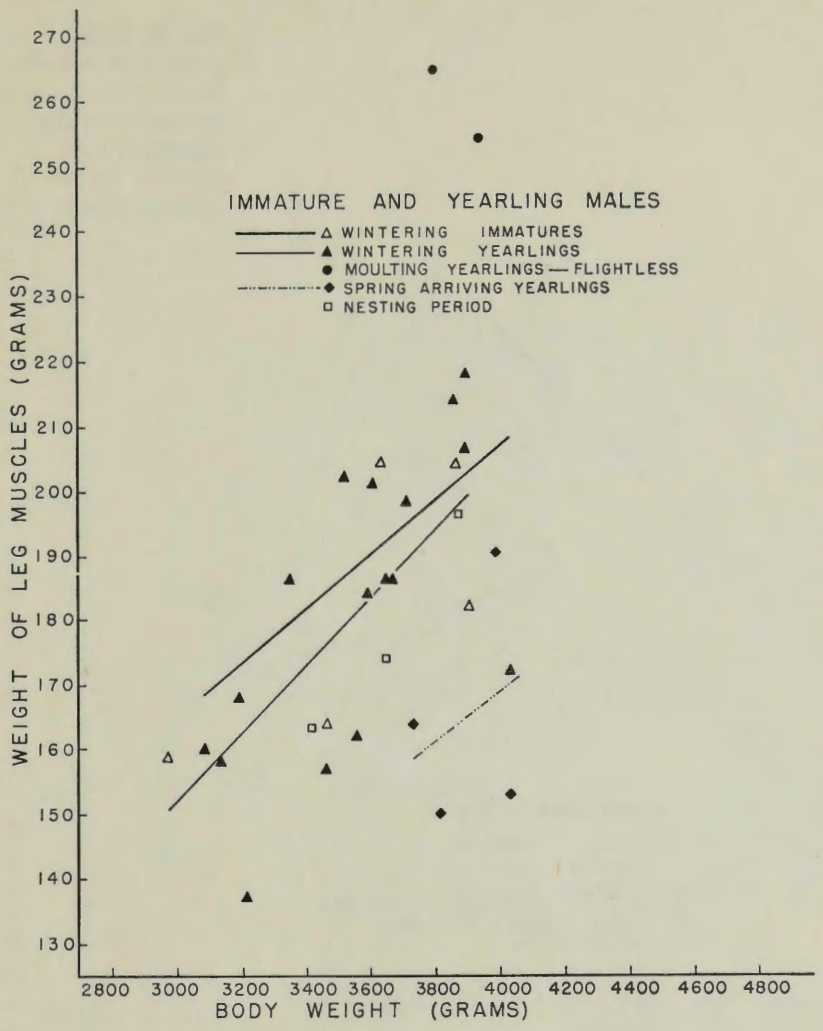

Fig. 7. Relation of weight of muscles of the tibiotarsus to body weight in immature and yearling male Canada Geese.

the percentage changes involved are summarized in Table 17. Similar comparisons within sex classes between the various stages in the life cycle are summarized in Tables 18 and 19.

The data from the tables show: (1) as a result of the exercise of migration, the pectoral muscles become enlarged 13–16 per cent in the yearling class and in adult females, but only 6 per cent in the case of sexually mature males which have an 8–9 per cent advantage in this respect prior to migration (Tables 18 and 19); (2) these gains are rather quickly lost in the ensuing few weeks, and the pectoral muscles more closely approach the size they had in winter; (3) the onset of the moult brings about marked atrophy of the muscles of the sternum, the reduction over the migration period being 30 and 36 per cent in males, 25 and 41 per cent in females, for yearlings and adults respectively, the data for the adults having the greater statistical reliability; and (4) when flight is resumed, although the moult is not yet complete, the weight of the pectoral muscles for all sex-age groups has markedly increased, attaining 17 per cent of body weight as compared with 14–15 per cent during the flightless period.

Weight of muscles of tibiotarsus

A study of the weights of the muscles of the tibiotarsus (Pl. 2A) showed that they underwent equally dramatic changes in mass during the course of the

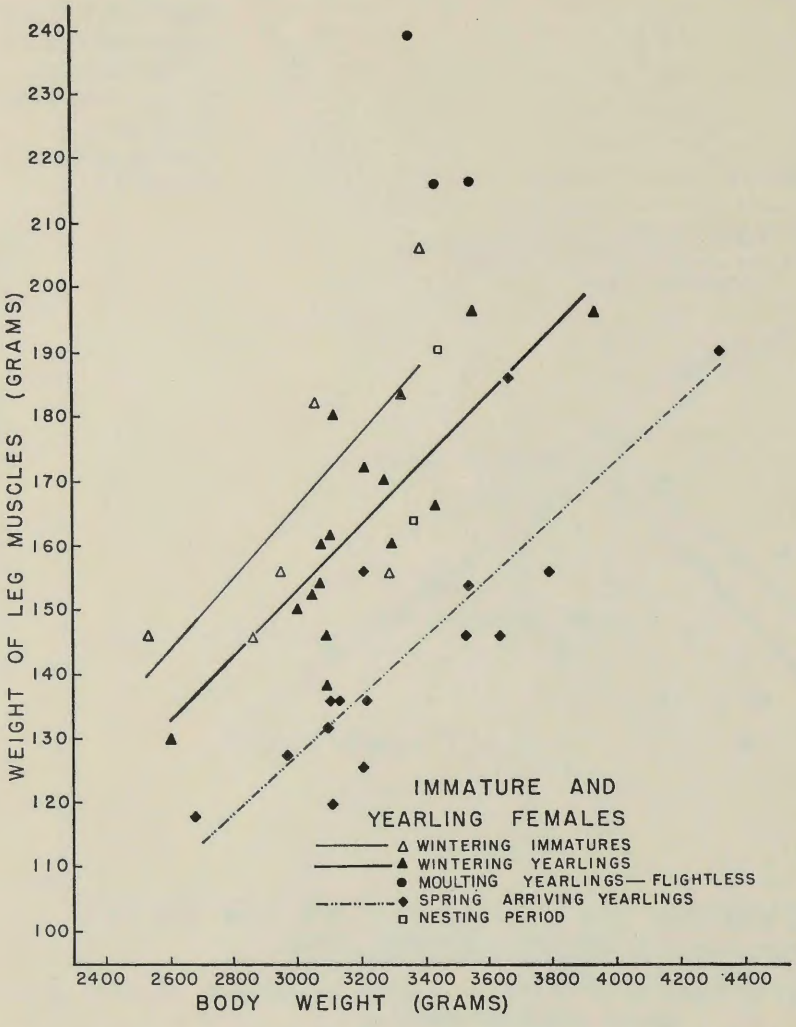

Fig. 8. Relation of weight of muscles of the tibiotarsus to body weight in immature and yearling female Canada Geese.

life cycle (Pl. 2 and Figs. 7–10). Statistical findings are given in Tables 20 and 21 and the relationships of their weights per unit of body weight shown graphically in Figs. 7–10. Changes in the collective weights of these leg muscles with successive stages of the life cycle are presented in Tables 18 and 19. From these data it appears: (1) that there is an inverse relationship between the size of the pectoral muscles and the size of the leg muscles; (2) during migration, the leg muscles, which are relatively little used, become reduced in size, both absolutely and relatively—markedly in the case of yearlings (9–13 per cent) and to a less extent in the case of the adults (3–7 per cent); (3) an increase to "wintering size" occurs during the few weeks following spring migration; (4) there is a very marked increase in size during the flightless period, at which time the average weight of the muscles of the tibiotarsus is 41–57 per cent higher than at the end of migration, Pl. 2; followed by (5) a gradual return of the leg muscles to wintering or "basal size".

Reciprocal relationships of the muscles of locomotion

It is believed that the changes in size of the two sets of muscles studied accurately reflect the relative functional importance of the two sets of appendages from the standpoint of both locomotor and metabolic function. From

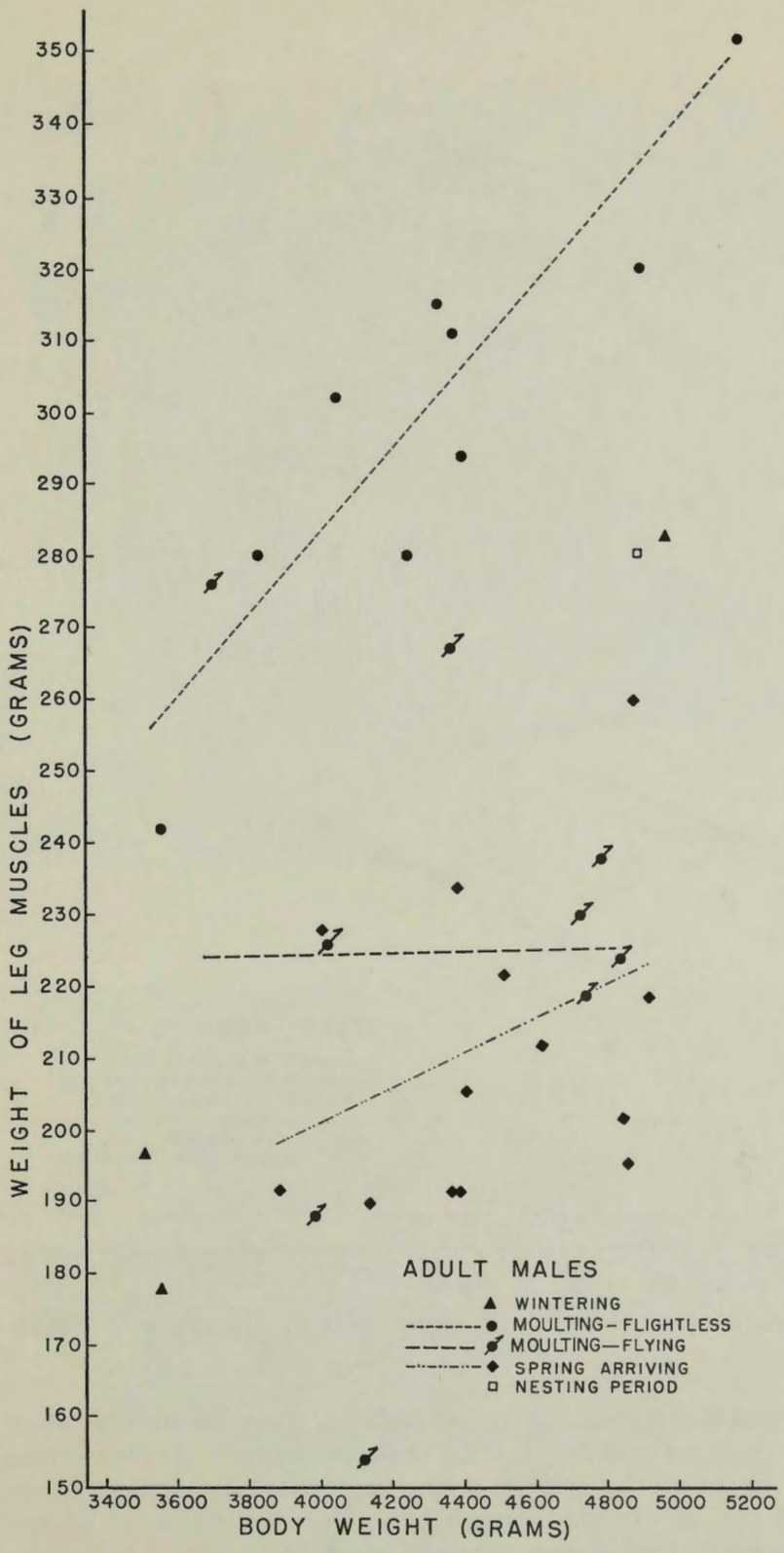

Fig. 9. Relation of weight of muscles of the tibiotarsus to body weight in adult male Canada Geese.

Tables 22 and 23, which give average values for weight of leg muscles expressed as a percentage of weight of the pectoral muscles, the over-all significance of

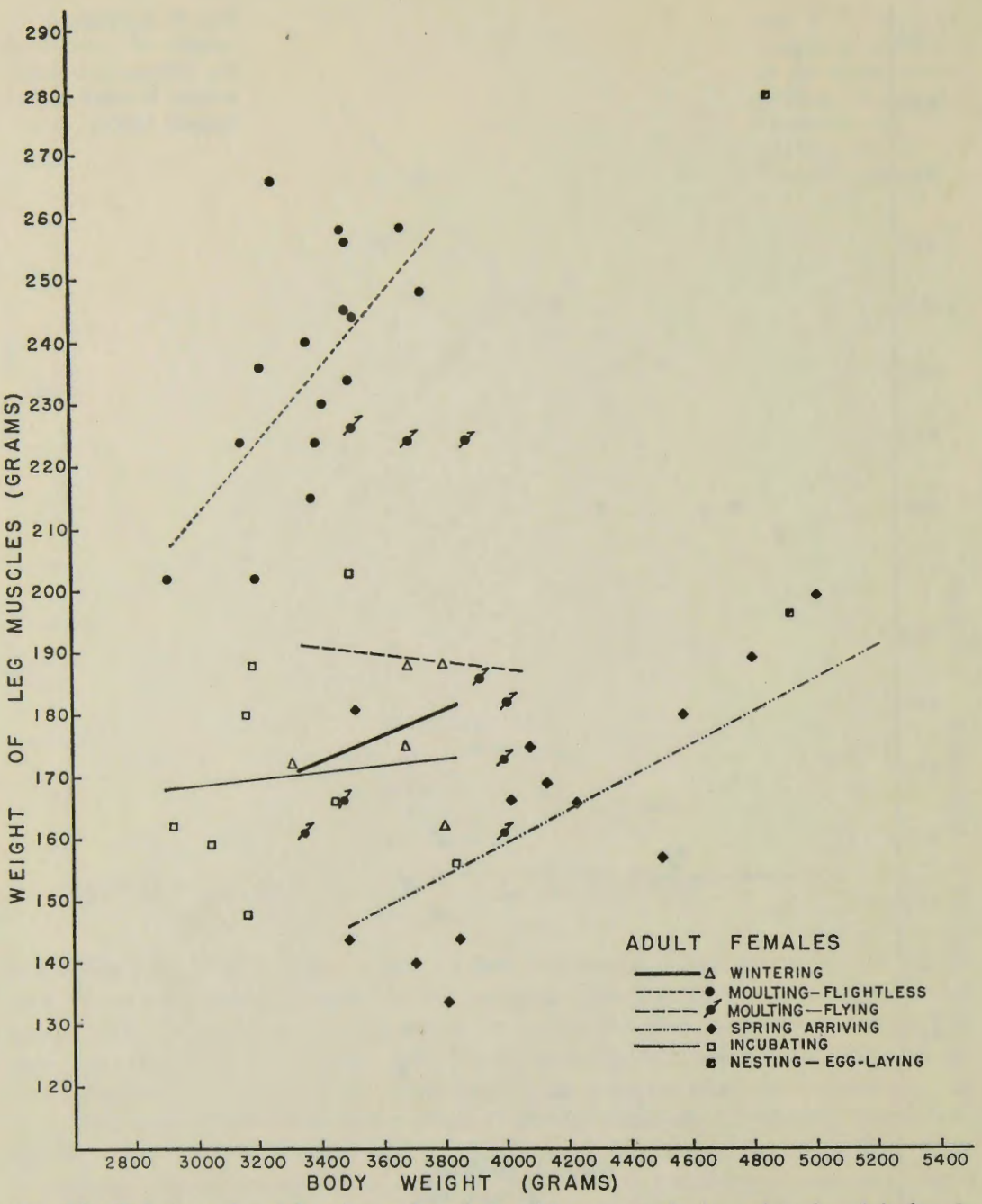

Fig. 10. Relation of weight of muscles of the tibiotarsus to body weight in adult female Canada Geese.

muscle hypertrophy and atrophy can be easily realized. For instance, relative to the weight of the pectoral muscles, the leg muscles annually increase more than twice as much between the end of spring migration and the flightless portion of the moult period. In this remarkable transformation most of the increase and return to normal takes place in a period of 40–50 days, i.e., mainly the duration of the moult. Enlargement of the leg muscles is undoubtedly initiated in breeding geese soon after the young have hatched and flying largely ceases. Moult begins when the young are 10–14 days old. Figure 11 shows

Plate 2. A. Tibiotarsus sector of leg showing muscles excised for weighing. From Canada Goose wintering at Horseshoe Lake, Illinois. B. Leg of an adult male Canada Goose in the moult showing extreme hypertrophy of muscles; Akimiski Island, N.W.T.

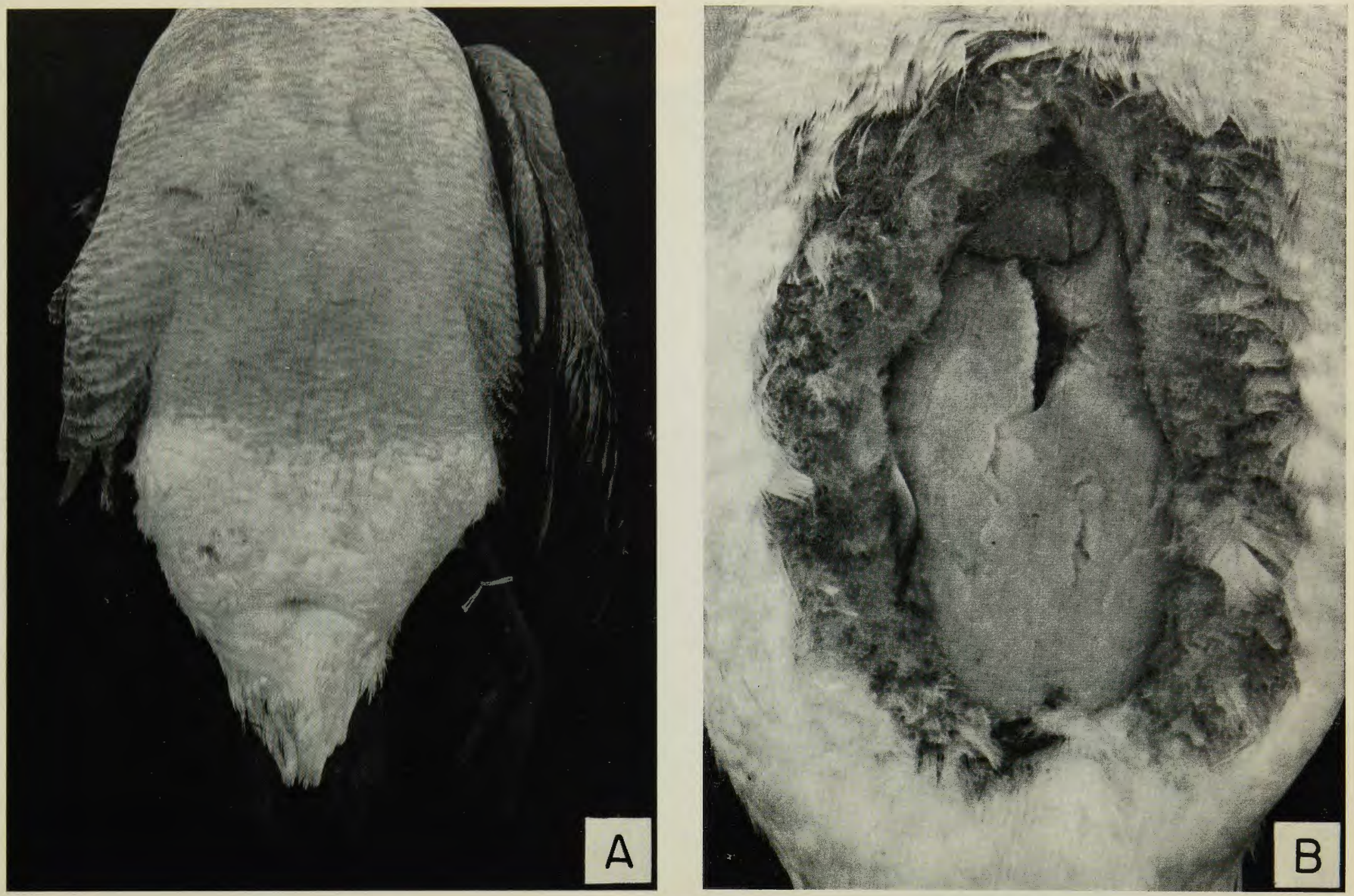

Plate 3. An adult female Canada Goose weighing 5,005 gm., shot on 8 May 1959, at Hawley Lake, Ontario. A. Ventral view to show the massive enlargement of the belly area due to excessive fat depots, enlarged liver, and the presence of enlarged ova. B. View of belly area with skin removed to show heavy fat layer. Fatty liver (200 gm.) is seen protruded well beyond posterior edge of sternum.

the relationship of these muscles to the progress of the moult, as measured by the degree of completion of the growth of the primary feathers of the wing. Although data could not be collected for the entire moult period, there is little question that the data obtained and the projected portions of the curve adequately portray this dynamic relationship.

Relation of fat reserves to body weight

One of the objectives of the study had been to determine total fat reserves by chemical processing of the entire carcass. Lack of funds at the time, however, made it necessary to resort to measurements and estimates of visible fat deposits. Nevertheless, the findings provide a useful rule-of-thumb appraisal of fatness and a realistic and basic understanding of the relationship between fat reserves and body musculature. With chemical processing the invisible intracellular fat would have been recorded as well as the visible fat. The relative amounts of intracellular fat in muscle may somewhat alter the picture of hypertrophy and atrophy of the protein component of muscle tissue, but

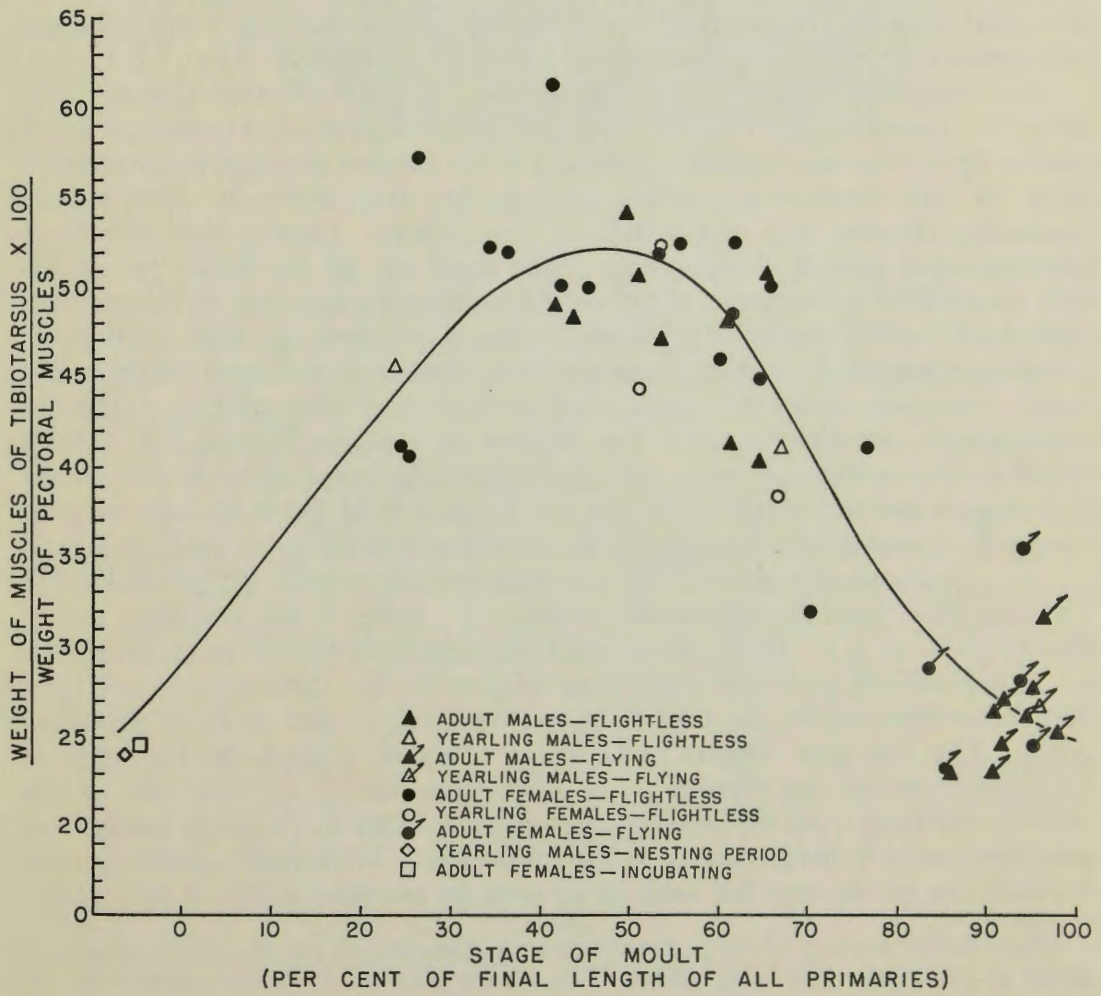

Fig. 11. Complementary relationship of weight of muscles of the tibiotarsus to weight of pectoral muscles of Canada Geese during the replacement of the primary feathers of the wing.

10-gram samples of leg and pectoral muscles which are being analysed for fat and other constituents, will provide a correction factor.[1]

What constitutes a fat bird, and how can we describe a thin or lean bird? These terms are often misleading. A heavy bird is usually fat and a light bird generally has little fat reserve. Under some circumstances, however, heavy geese may carry relatively little fat and "thin" birds considerable amounts of fat. Before proceeding to a review of the cyclic changes in the balance between protein and fat reserves, it is desirable to describe four basic, extreme types.

a. *Maximum protein and fat reserves* (*"heavy and fat"*). Geese of this type were observed under two circumstances: (1) at the end of spring migration, Pl. 3, and (2) caged birds in spring with unlimited food. Reports from some areas of the Mississippi Flyway on the condition of geese during the fall migration, as well as experience with caged and wild geese at Horseshoe Lake, indicate this condition is repeated in the autumn. Photographs taken of cross-sections[2] of a caged goose killed in March, Pls. 4–6, illustrate this type. The goose, an adult male, is reasonably typical of the majority of the migrants arriving at Hawley Lake, Ontario, in the first ten days in May. In geese having maximum development of the pectoral muscles, the portion of these muscles adjacent to the carina becomes flat in *rigor mortis*, whereas to either side of this area, the arrangement of the muscle fibres causes the tissue to become ridged, Pl. 7.

b. *Maximum protein and little or no visible fat reserves* (*"heavy and fatless"*). Geese in this condition may still have considerable amounts of intracellular lipids, but nevertheless represent a fairly distinct physical and condition type. It was observed in yearling geese in late May and early June, and in incubating females, but particularly in the former. During this immediate post-migration period, the yearlings make rapid use of the heavy fat depots with which they arrived, but at the same time they are also able to secure sufficient food (berries from the previous autumn, *Equisetum* sp., basal portions of grasses and sedges, etc.) from along the rivers and scattered open places in the muskeg as to prevent inroads from being made on their body protein. Geese in this condition are also found in late autumn in southern Illinois, but in both situations it is a transitory type, the individual usually being either in the process of losing or gaining weight. Figure 12, K, of a wild goose in late summer, essentially demonstrates this type, as do wintering geese, Fig. 12, A–C (less fat).

c. *Minimum protein reserves and moderate fat reserves* (*"light and fat"*). The atrophied state of the pectoral muscles of a goose in this condition immediately classifies it as "thin" in common language, but dissection revealed that the individual still possessed a moderate amount of fat. Examples of this type have been observed in late autumn in southern Illinois and in caged moulting geese. The first case appears to be the product of a particular sequence of food condition on the refuges—great abundance during the first part of the autumn and then rapid depletion of supplies due either to the large numbers of geese present or to inadequate food for the winter. With food supplies greatly reduced, the goose must fall back on its own fat reserves, which in many cases

[1]Analyses of samples of the pectoral muscles and muscles of the tibiotarsus were completed as this report was being edited. The results, obtained in collaboration with Dr. Robert E. Johnson of the Department of Physiology, University of Illinois, substantiate the original appraisal in the field that variations in the fat content of these muscles could account for only a small part of their gross weight changes with successive seasonal stresses.

[2]Prepared in conjunction with a study of cross-sectional anatomy of the Canada Goose.

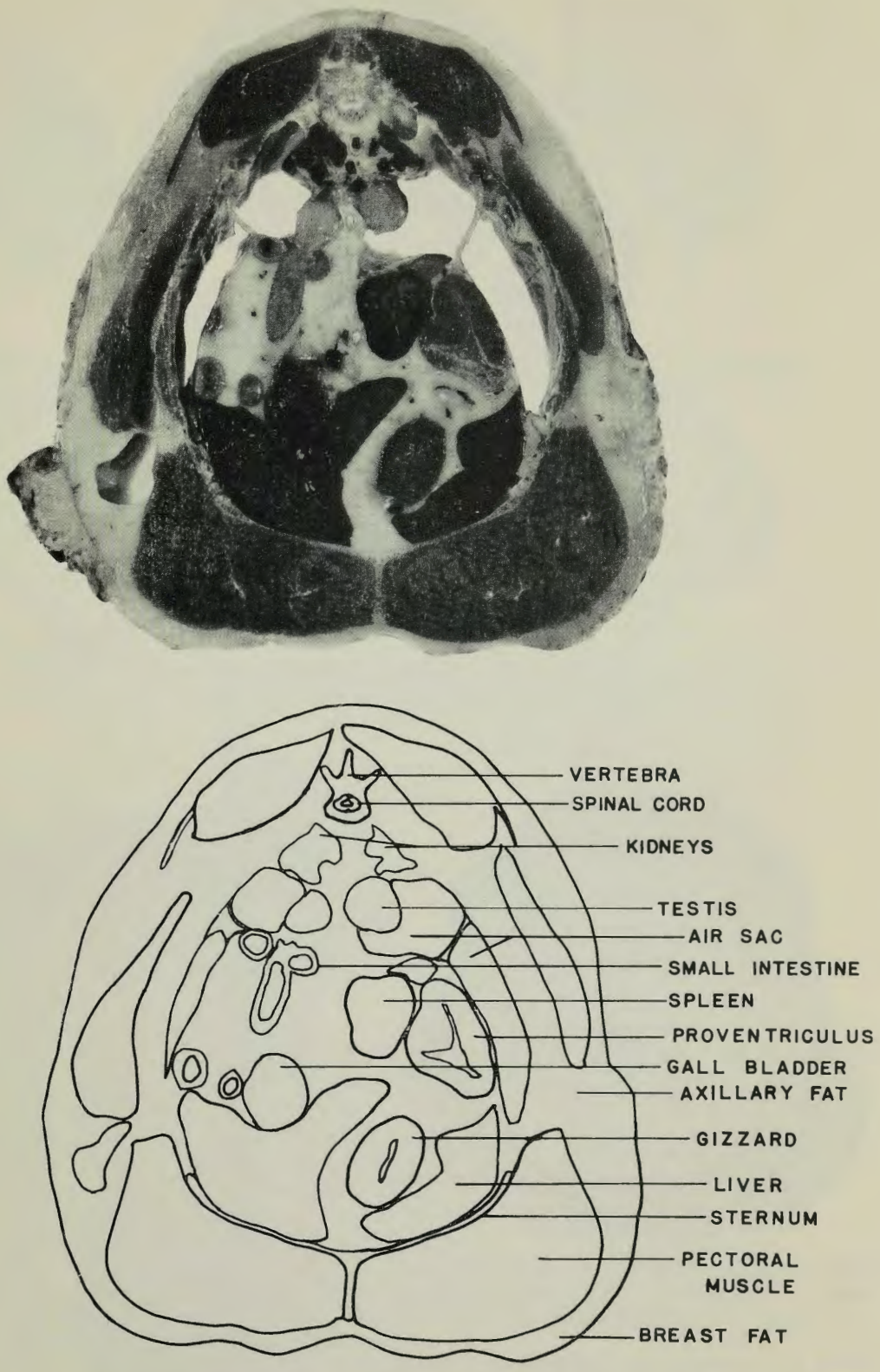

Plate 4. Cross-sectional view of the region of the testes of an excessively fat adult male Canada Goose that had been held in captivity and killed in mid-March. Arteries were injected with yellow latex and thus can readily be distinguished from the veins. A key to the organs is given below.

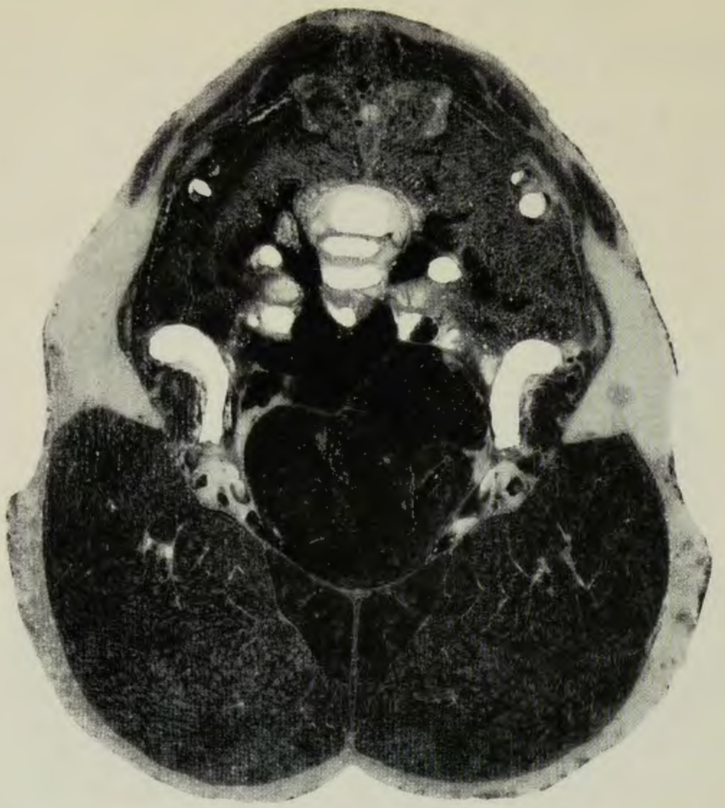

Plate 5. Cross-sectional view of the same adult male as Pl. 4 in the region of the heart. Axillary fat depots are those lying immediately above the dorso-lateral edge of the pectoral muscles.

Plate 6. Cross-sectional view of the same adult male as Pl. 4 through the posterior portion of the body traversed by the large intestines.

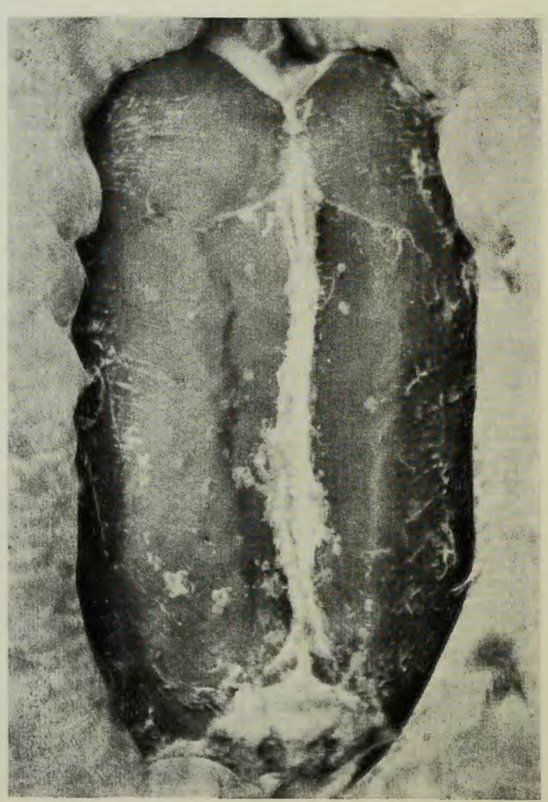

Plate 7. Ventral view of pectoral muscles in *rigor mortis* of an adult female Canada Goose rated as being in excellent state of protein nutrition. Note flattened area of muscles to either side of the keel and the ridged condition of the tissue on the periphery.

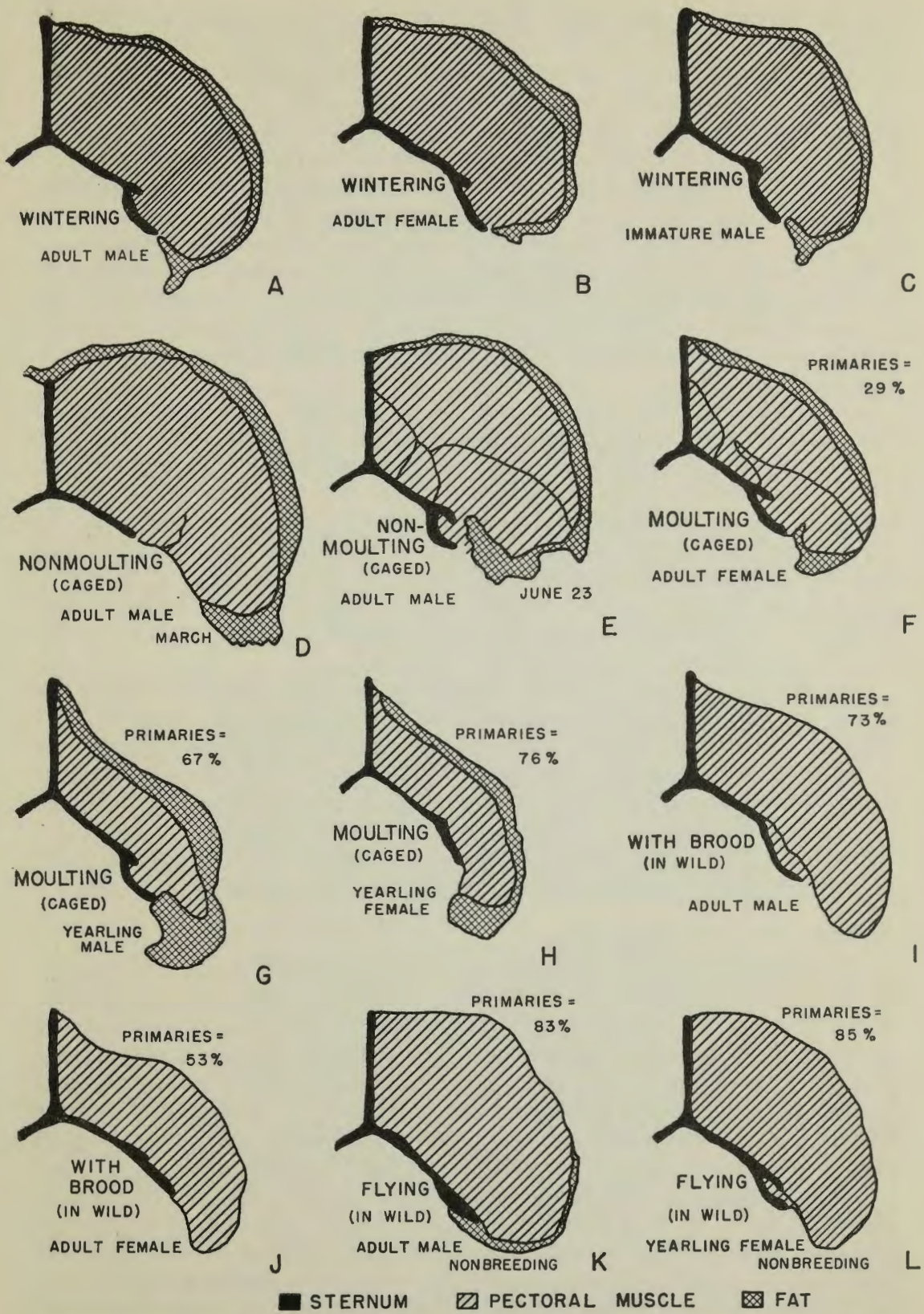

Fig. 12. Unilateral, cross-sectional tracings of pectoral muscles of Canada Geese at various stages of the life cycle. Sections A–C represent geese in good to excellent condition during the wintering period.

may be exceptional, but to do this normal metabolism requires an intake of carbohydrates. If they are not available, the individual must make inroads on its own protein reserves to secure the necessary oxalacetate directly or indirectly via alpha-ketoglutarate for degradation of its fat. This apparent synchronous degradation of fat and protein was forcibly brought to my attention in the course of routine dissection to obtain weights of the pectoral muscles.

Caged moulting geese showed this condition, but for somewhat different reasons. As the result of an unlimited food supply, little exercise or climatic stress, and, initially in spring, a favourable hormone balance, these geese became very fat prior to the onset of the moult. However, the metabolic demands of the moult were such that they suffered loss of muscle tissue, their intake of food apparently being insufficient alone to satisfy the need for protein for rapid feather growth. Cross-sectional profiles of this physical type are shown in Fig. 12, F, G, and H.

d. *Minimum protein and little or no fat reserves.* Extreme examples of this condition were found in geese that had died of starvation resulting from "crop impaction". These geese were greatly emaciated and had used virtually every vestige of fat. Less extreme examples of this condition were found in the wild in adult flightless geese that had nested and were accompanied by their young when collected for study, Fig. 12, I and J. Non-breeding yearlings and adult geese undergo the moult with apparently less stress, Fig. 12, K and L, and had less severely depleted pectoral muscles than the successfully breeding adults at a comparable moult stage and, in the case of yearlings, carried as much as a 3-millimetre layer of fat over the breast.

A variety of factors combine to produce the unique physical type of the moult period (atrophied pectoral muscles, hypertrophied leg muscles): (1) disuse of pectoral muscles due to loss of flight feathers, and complete dependence on legs for locomotion (captives in cages 6 feet by 18 feet develop atrophied pectoral muscles but show no enlargement of leg muscles); (2) the high demand for amino acids, particularly the sulphur-containing amino acids which are required in relatively large amounts for the synthesis of feather keratin; and (3) the use of unemployed pectoral muscles as a dynamic store of protein.

Fat reserves in wintering geese

The determination of condition in wintering geese is a problem of primary concern in management. As shown early in this report, refuge food supplies *do* affect condition, and the long-term prospect is that goose populations will be increasingly dependent upon refuges for survival. Assessment of condition of a flock during the hunting season can be made easily from body weights of bagged birds, Table 24, and inspection of carcasses at picking and dressing stations. The obvious alternative approach would be to weigh trapped geese and, if desirable, to kill a representative number for study.

The condition of immature geese should always be interpreted with caution. Hatching dates can vary considerably from year to year and from place to place and consequently so can the size, weight, and condition of the individuals. The summer of 1960 was notable for this: in flights in northern Ontario over the breeding grounds of the Mississippi Flyway population, observations made by H. G. Lumsden and the writer indicated an unusually late average date of hatching; on nearby Akimiski Island in James Bay, which also contributes geese

to the Mississippi Flyway, the growth stage of the goslings appeared to be about normal for the time of the year (late July). On the whole, as much as 2–3 weeks may have separated the average dates of hatch for the two nesting populations. The net result was evident in autumn at Horseshoe Lake; a large component of immatures had unusually undeveloped plumage, causing those engaged in dressing geese for hunters to comment that they had never seen such numerous pin feathers; the older component of immatures were robust and mature in plumage, possessing adult-type feathers over the entire breast. The corollary of the above is that the late-hatched geese are less physically developed than the early-hatched geese and usually tend to have less fat.

Appraisal of condition in adult geese must naturally be approached with caution if the condition of a flock as a whole is to be interpreted in the light of the body weight of a few individuals. Two adult females killed on 1 February 1961, illustrate this point. One, a bird with a small skeletal frame, weighed 3,320 grams, had a 3-millimetre layer of breast fat, and carried 42 grams of visible internal fat; the second had a large frame, weighed 3,690 grams, had scarcely a definable layer of fat under the breast skin, and carried 36 grams of fat internally.

What are desirable condition standards of wintering geese? It is axiomatic that they be in an excellent state of protein nutrition. As Benedict and Lee (1937) have pointed out, it is those geese in the best state of protein nutrition that can best tolerate a period of food shortage—an observation with which our findings are in agreement. What significance should be attached to fatness in wintering geese? A reasonable supply of fat is requisite to help sustain a bird in time of stress, and large depots are probably of vital importance to survival in the north in the spring; but, in the wintering goose, because of metabolic and hormonal relationships, there appear to be definite limits to its ability to store fat. As pointed out earlier, female geese in spring tend to put on relatively more fat than males. This factor, probably combined with a slightly lower rate of metabolism in females—characteristic of various species of birds that have been studied—may account for the reported ability of females of some species (Mallard, Ring-necked Pheasant, and Ruffed Grouse) to withstand starvation much longer than males.

Canada Geese, on reaching Horseshoe Lake, have often appeared to have a voracious appetite ("hyperphagia"), and the data clearly show that they are still capable of making notable weight gains. By mid-December, however, a decrease in weight generally occurs. This can be attributed in part to a reduction in forage supplies, but corn is freely available as the result of the refuge feeding program. Data recently published by Friley (1960) indicate a similar autumn weight cycle for Canada Geese stopping at a Michigan refuge. The impression was often gained that the appetite of the geese was less in mid-winter than in autumn. Whatever the true explanation, the geese are *seldom* more than moderately fat in February and March and *usually* carry little fat. One explanation may be that they are in a "refractory period" in so far as excessive fat deposits are concerned, as recently shown for the White-throated Sparrow (*Zonotrichia albicollis*) (Shank, 1959). Excessive fat would be of little value to the bird as the cytoplasm of the fat cells is extremely active metabolically (Wertheimer and Shafrir, 1960). To maintain these fat cells unnecessarily would only increase food requirements.

With these considerations in mind, an attempt was made to define various condition classes of wintering geese, the weights given being for *Branta canadensis interior*, Table 24. For those who may wish to make use of this table as a guide to management practices for wintering geese, it should again be emphasized that geese representing a wide variation of condition are usually found in a wintering flock. Furthermore, the definition of condition classes must necessarily be somewhat subjective. For example, throughout the wintering period, the immatures are continuing their physical maturation and consequently increasing their average basic weight.

Fat reserves in migrating geese

The extreme fatness of geese at the termination of their spring migration has been previously pointed out; at this time their body weight reaches the annual maximum. In Table 24, the fatness of spring migrants is compared with wintering geese.

Elder's (1946) data (Tables 1 and 2) show that the weights of the geese wintering at Horseshoe Lake undergo only a slight upturn in March. A limited sample of geese weighed by the writer on 6 March 1958 indicated that no appreciable gain in weight had taken place by that time. An aerial survey made on the same date revealed that there were still large numbers of geese present on the Horseshoe Lake and Union County refuges. Normally, by March 10–15 nearly all of the geese have left on their northward flights. From this we can conclude that these Canada Geese normally have initiated migration before putting on appreciable fat reserves. Once migration has begun, however, fat reserves are put on quite rapidly. In 1955, an Illinois State game warden brought me a number of geese found dead in early April on a farmer's field near Vandalia, Illinois, 150 air miles north of Horseshoe Lake. These individuals were part of a flock of about 25 that possibly had been killed by lightning. All were in an excellent state of nutrition and carried considerable fat. The rapid accumulation of fat in Canada Geese may be dependent to an important degree on the availability of new green vegetation over a period of several weeks. The principal fat gain in spring is probably made while the geese are using the Horicon National Wildlife Refuge and vicinity in Dodge County, Wisconsin. In most years, the major portion of the geese wintering in southern Illinois spends from March 15 to April 20–24 in this area (Richard Hunt, biologist, Wisconsin Conservation Department, personal communication). One to two weeks after the latter dates, the bulk of the population is on the breeding grounds.

In autumn, similar relationships appear to hold true, but at present adequate data are not available. In 1947, Indians at York Factory told me that they preferred Lesser Canada Geese (*Branta canadensis parvipes*) to Canada Geese in the autumn because of the much greater fatness during the migration period of the former, which were already on their way south from their breeding grounds in the Arctic, whereas the local Canada Geese were still lean at this time. In 1960, Indians at a number of posts in northern Ontario were questioned as to whether the geese they shot were fatter in spring or in autumn. In lieu of technical data, their responses do suggest that once either migration has begun, the geese generally carry large amounts of fat. Although the condition of the geese may be similar during the two migration periods, the northern Indians

definitely prefer eating geese shot in spring to geese shot in fall. This probably relates to the flavour of these geese, resulting from their diet of domestic crops during the previous winter.

Weight data reported for Canada Geese at various areas in Wisconsin in autumn (Tables 8 and 9) cover too long a period of time to indicate the condition of geese after they first arrive from the breeding grounds. However, in mid-October, 1961, the writer examined about a hundred Canada Geese trapped at the Horicon Marsh National Wildlife Refuge, apparently recently-arrived migrants. These birds were found to be very thin; geese in similar condition in mid-winter in southern Illinois would have been cause for alarm and the initiation of supplemental feeding. It can therefore be concluded that, at least in some years, the Canada Geese leave their breeding grounds in the Hudson Bay Lowlands without putting on large amounts of fat—or at least a sufficient amount to last until they arrive at their first major stopping area. This period of stress and undernutrition, however, is in itself a likely factor which would permit rapid compensatory gains in weight and fat to be made shortly thereafter (see "Management implications" in the discussion).

Fat reserves during the nesting period

During the egg-laying period, in late May, both adult males and females still retain much fat, if the single pair collected can be regarded as typical. By the onset and during the early stages of incubation, however, the fat reserves are rapidly depleted, superficial fat under the skin being metabolized first, with the remnant of visceral fat the last to be used.

A yearling male shot on 26 May 1959, carried about a 3-millimetre layer of fat under the breast skin and a small amount of internal fat; two shot on June 6 were nearly devoid of visible fat. A yearling female shot on June 3 was also virtually without visible fat depots.

Fat reserves of moulting geese

During the flightless stages of the moult, both sexes of adults carry some body fat, particularly the adult males which are under much less stress during the nesting periods than are the females. The various depots were rated "3" in most males, whereas in females were rated only "1" or "2", and in several cases "0" (see page 7). During the latter part of the moult, the flight stage, adults of both sexes are again largely devoid of fat, whereas yearlings carry moderate amounts of fat throughout the moult period.

LIVER WEIGHTS

Changes in weight of the livers of the Canada Geese studied are of interest mainly for the insight they provide into the metabolic stresses involved rather than as a reflection of condition *per se*. Because of its central role in intermediary metabolism, the liver can be expected to be particularly responsive to shifts in metabolism.

Liver weights obtained in the course of the study are summarized in Tables 25 and 26. The constancy of the relation of liver weight to body weight for the two sexes in each age class is notable.

Weights of the livers of males at the end of northward migration average 25–50 per cent less than in wintering geese. Adult females, on the other hand, have somewhat larger livers at the end of spring migration than they do in winter, while yearlings show no important change. Relative to body weight, the livers of immatures in late autumn averaged somewhat larger than in older geese (Hanson, 1962a). Because of the investigator's desire to record extreme liver weights attained by some adult females, the data in Table 26 are not entirely random. Not included in the average is the exceptional liver weight of 200 grams recorded for one adult female. It should be noted that the liver weights of five of the other seven adults vary only from 51 to 64 grams (51, 53, 62, 64, 64, 109, and 123 grams). The largest livers were tan in colour because of their high fat content. This presumably can be ascribed to the action of estrogen (Sturkie, 1954, p. 334) and the "adipokinetic" substances produced by the pituitary (Rudman *et al.*, 1962).

The livers of two yearling males shot on 6 June 1959, at least three weeks after their arrival on the breeding grounds, were nearly 50 per cent above the average weight for livers of this age-sex class in winter, whereas the liver weights of two yearling females were only slightly larger than in winter. The metabolic stress of egg laying is indicated by the liver weights of incubating females which were markedly less than at the end of migration and averaged 28 per cent less than the average for this age-sex class during the wintering period.

The livers of both sexes of adults shot during the nonflying stages of the moult were closely similar to those taken in winter, but during the flying stages of the moult, the livers of yearlings (1 male only) and both sexes of adults shot were 61 and 88 per cent heavier than during the flightless stage, males and females respectively, Tables 25 and 26.

Recent findings by Fisher and Bartlett (1957) showed that the overnight loss of weight of the liver in Redwinged Blackbirds (*Agelaius phoeniceus*) is of the magnitude of 30 per cent in males and 12 per cent in females. While these unexpectedly large overnight losses indicate the need for care in obtaining data that are comparable, as the authors point out, it is doubtful that they invalidate comparisons of adequate samples taken during the same periods of the day. It would also appear likely that small birds, because of their higher metabolic rate, may have more variable liver weights over a 24-hour period. The relatively high metabolism of small birds is reflected in the relative size of the liver—5 per cent of body weight for Starlings (*Sturnus vulgaris*) (Stegman, 1954) as compared with 1.43 to 1.79 per cent for wintering Canada Geese.

Findings reported here are in agreement with those of Oakeson (1953 and 1956) on White-crowned Sparrows (*Zonotrichia leucophrys*) who found that the liver weights of female White-crowned Sparrows exceeded males in spring only. (For further discussions of the weights of visceral organs in Canada Geese, see Hanson (1962a)).

DISCUSSION

It is concluded that there are four main complexes of factors that determine muscle size, and protein and fat reserves: (1) use and disuse; (2) interrelationships between hormones and rates of secretion; (3) relation of protein and fat to intermediary metabolism, and (4) ecological factors. A brief discussion of these factors is requisite to a general understanding of condition in Canada Geese.

Relation of muscle size to use and disuse

In mammals, the hypertrophy and atrophy of muscle groups resulting from use and disuse is common knowledge, but similar muscular changes apparently had not been documented in free-living birds. The enlargement of the pectoral muscles during the migration period would seem to be at least in part a case of hypertrophy from use; while the muscles of the legs being little used in migration become smaller. The reduction of the pectoral muscles in wild geese during the flightless period does not represent primarily a case of disuse, as geese held in cages (approximately 6 x 18 x 2 feet) were similarly affected during the moult. It would further appear that the hypertrophy of the leg muscles during the flightless period is purely a result of extensive use; leg muscles of caged geese do not undergo enlargement during this period. The atrophy of the breast muscles during the moult, on the other hand, appears to be an evolutionary adaptation of important survival value whereby these temporarily inactive muscles can be drawn on for vital constituents (see below), thereby maintaining a rapid rate of feather growth.

Relation of protein and fat reserves to hormones

Hormones have an important influence on condition factors in Canada Geese. The differences between age classes of males in the regression of the weight of the pectoral muscles on body weight as compared with females can be attributed to the well-documented anabolic action of the androgens on the skeletal musculature of mammals and birds (Kochakian and Tillotson, 1956; see Sturkie, 1954; Dorfman and Shipley, 1956, for additional reviews of the subject). Immature males in winter, which had the same regression as females, were only 5–8 months of age, possessed undeveloped sex organs, and presumably were producing a minimal output of androgen. However, this situation changes markedly during the first spring migration—immatures, now termed yearlings, on their return to the breeding grounds have enlarged gonads and a penis that shows development nearly comparable with that of breeding adults (Hanson, 1962b). This hormonal stimulation in the nonbreeding but still sexually immature yearling is reflected the following autumn (now 17–18 months of age) by the more highly developed pectoral musculature. The older, sexually mature adults (2½ or more years of age in autumn), having lived through at least one additional spring and its accompanying stimuli, have an even more marked enlargement of the pectoral muscles per unit of body weight. It can, therefore, be concluded that the nitrogen-conserving effect of the androgen probably stimulates the development of all striated muscle in male Canada Geese. In mammals, it is the muscles of service which are reported to be primarily influenced by the male sex hormone (Russell and Wilhelmi, 1960, p. 150).

Other hormones may at times have an effect on protein metabolism. According to Pitt-Rivers and Tata (1959), the catabolic action of thyroid hormones on protein metabolism is indisputable. White (1956) points out that the quantity of a hormone that is available and the relative balance of other endocrine factors determine whether a specific hormone will have an anabolic or catabolic effect.

The lipogenic effect of the estrogens in birds is well documented (Sturkie, 1954). Entenman, Lorenz, and Chaikoff (1940, p. 495) state that "A distinctive feature of the lipid metabolism of the bird is its response to estrogenic activity." Mitchell, Card, and Hamilton (1926, p. 113) found that pullets fatten at a much more rapid rate than either cockerels or capons, noting that pullets between 5 and 6 pounds contained over twice as much fat as 7- to 8-pound cockerels. It can be assumed that the production of estrogen is at or near the annual maximum in adult female geese completing their spring migration, i.e., just prior to nesting. At this time the ovary and oviduct are greatly enlarged and the latter may contain a partially developed egg. Concomitantly, as discussed earlier, maximum fatness is achieved by the adult females at this time, in which respect they outrank other age-sex classes. Breitenbach, Meyer, and Nagra (unpublished data cited in Nagra and Buss, 1959) and Breitenbach and Meyer (1959) found that fat reserves in the hen pheasant are at a maximum in spring prior to egg laying. Similarly, Kabat *et al.* (1956) report that the hen pheasant reaches its maximum weight in April, and its survival time under applied stress was the highest for the year.

King and Farner (1956) have attributed increased rates of fat deposition in White-crowned Sparrows in spring to hyperphagia induced by increased photoperiod, but probably mediated by a hypothalamo-hypophyseal system. King, Mewaldt and Farner (1960), on the basis of further studies and those of Shank (1959), have suggested that the gonadotrophic and metabolic functions of this latter system may be basically independent of one another and, reasoning from mammalian studies, express the belief that lipogenesis and high rate of turnover of depot fat may be linked to the hypophyseal-adrenal axis. Additional data on the "adipokinetic" substances, including ACTH, isolated from the pituitaries of mammals (Rudman *et al.*, 1962; Cantarow and Schepartz, 1962, p. 525) make it seem likely that similar substances will be found to play a part in lipid metabolism in birds. Moreover, it is becoming increasingly obvious that the physiological preparation of a bird for migration and subsequent breeding, admittedly under the control of increased photoperiod in spring, is the result of increased secretion of many of the hormones of the pituitary gland.

The photoperiod and ambient temperatures do, of course, affect hormone secretion via the hypothalamus and pituitary, but a discussion of these relationships would not be of immediate concern here. In summary, it appears that the gonadal hormones confer on each sex a distinctive metabolic advantage in terms of survival: the males, because of greater initial protein stores and the nitrogen-conserving influence of the androgens, apparently undergo the moult with less ill effect than the females; the latter, on the other hand, can probably more readily survive most times of starvation stress because of superior fat reserves—the result of the influence of estrogens and, presumably, a lower metabolic rate.

There is no need at this point to detail the endocrine background of the mobilization of body reserves for the production of eggs and the expenditure

of energy in incubation, but the net result in Canada Geese is a loss of nearly all visible fat reserves by the time incubation is under way.

The onset of moult in birds has hormonal origins, but there has not been general agreement as to the hormone chiefly involved. Höhn (1950) has expressed the belief that the moult follows a period of increased activity of the thyroid, and Assenmacher (1958) has suggested that the thyroid hormone is the most important in producing the moult. Preliminary studies of the histology of the thyroids of Canada Geese, however, revealed that these birds are in a marked hypothyroid state during the moult (Hanson and St. Clair, unpublished), and Tanabe *et al.* (1957) were unable to detect an increased rate of secretion of I^{131} from the thyroid either in the moulting or premoulting period. The latter believed that in the hen the moult is induced by a decrease in ovarian activity, an opinion in agreement with the more widely held belief that the moult is induced by a decrease in the level of gonadal hormones.

Insulin must be presumed to play an important role in the incorporation of amino acids into protein in geese, as has been demonstrated in rats, but its exact role, although apparently independent of increased glucose utilization, is not known with certainty (Manchester and Young, 1960). At present, insulin is believed to facilitate the entry of amino acids into the cell. In the opinion of Chain (1960, p. 52), "Insulin appears to exert a specific stimulating effect on the energy-requiring synthetic reactions occurring in the cells on which it acts, such as glycogen, fat and protein synthesis." A study of the pancreas and insulin secretion of normal and moulting geese might provide some further insights into protein synthesis.

Relation of protein and fat reserves to metabolism

Protein metabolism

While the concept of a protein or nitrogen reserve in animals has been frequently debated (György, 1959, p. 1,212; Allison, 1959), the question appears to be partially one of semantics. Until recently, on the basis of studies by Schoenheimer and associates, it has been generally agreed that amino acids from the diet "form a common pool with the amino acids which have been derived from breakdown of tissue proteins and that the pool is utilized or destroyed without regard to a recognition of its origin" (Hoffman, 1954, pp. 13–14). Mitchell (1959), nevertheless, is of the opinion that tracer studies have not invalidated a more general concept of exogenous and endogenous proteins and that tissue proteins are relatively stable. This opinion has received support in recent studies (Lipkin, Almy, and Quastler, 1961). The uncertainty of either concept has been discussed by Tarver (1954). In times of starvation or protein deprivation, liver and intestinal proteins are the most labile, with muscle tissue proteins next (Fisher, 1954). Plasma proteins are degraded only under extreme duress, the other tissues being sacrificed to maintain normal plasma protein levels. For this reason, plasma protein levels are believed to be a poor indicator of protein nutrition (Keys *et al.*, 1950). Plasma amino acid nitrogen levels, however, appear to reflect nutritional states (Albanese, 1959b)[1]. Wallace (1959,

[1]The amino acid composition of plasma, pectoral muscle, muscles of the leg, and of liver from both wintering and moulting geese are currently being studied in collaboration with Dr. James D. Jones, Department of Biochemistry, Mayo Clinic, Rochester, Minnesota.

p. 1,126) has firmly stated that "on a fat-free basis the nitrogen content is remarkably constant in all mammalian species", and that "Even starvation or surfeit feeding do not appear to alter the nitrogen content of the body to a degree that is significant for the interpretation of balance data." Wallace maintains that the relative quantity of nitrogen in the lean body is quite fixed. In this respect Benedict and Lee's (1937, p. 40) remark is pertinent: ". . . one may conclude that the increases in body weight of adult geese above the normal adult weight are chiefly additions of water and fat and are not accompanied by a corresponding increase in protein." Nevertheless, a dynamic free pool of intracellular amino acids does exist, whether they are available for the function of enzymes or destined to be used in the formation of new protein (Glass, 1955). It should be emphasized, however, that this is a transient pool, as it is generally recognized that there is no permanent storage of excess amino acids (Hoffman, 1954). "Deposit protein" is not a specialized storage product, but the cytoplasm itself (Fisher, 1954).

An understanding of current concepts on protein metabolism is desirable here as the theory has been advanced that the pectoral muscles of geese serve as a dynamic source—or reserve in a more limited sense—of protein that is used during the moult period for the accelerated formation of new feather keratin. The dominating position of the synthesis of keratins in protein metabolism has been stressed by Mitchell (1959, p. 38): "The continued growth and regeneration of these protective proteins against environmental stress are sufficiently important to the body that, in case the food supply is inadequate to support them, the protoplasmic tissues of the body are raided to supply the amino acids, particularly methionine-cystine, needed, *via* the metabolic pool." An inadequate intake rather than an inadequate supply of food appears to be the explanation of loss of pectoral muscle tissue in moulting Canada Geese, whether wild or caged, despite, in the latter case, duck pellets, with an average protein content of 24 per cent, being freely available. In either situation, the goose apparently is unable or lacks appetite to consume sufficient food to meet the demands of feather synthesis and maintenance of body weight. The feathers of the White Leghorn chicken contain over 20 per cent of the crude protein in the total carcass (Mitchell *et al.*, 1931); in all probability, because of proportionately larger wing feathers and a heavier insulation of body feathers, the figure is higher for Canada Geese. The chick has a high requirement for methionine, cystine, and arginine (Mitchell, 1959), and a high percentage of its sulphur amino acid intake is diverted to the synthesis of feathers—which may contain as much as 10 per cent cystine (Almquist, 1959). A recent analysis of the amino acid composition of normal feathers of the fowl revealed that cystine and methionine constitute 9 per cent of the normal fowl feather (Krimm, 1960).

The markedly low liver weights of females in the early stages of incubation are suggestive of the stress of mobilization of body resources for the production of eggs. Sturkie (1954) points out that the protein content of a hen's egg is equivalent to the total circulating plasma protein of the hen. The pectoral and leg muscles, however, are not reduced in size below wintering levels to supply this protein need.

The moult appears to involve two periods of stress, each of a somewhat different metabolic nature, protein rather than fat being the chief nutrient involved. During the nonflying stages, the liver approximates normal wintering

size but, as pointed out above, the pectoral muscles which normally constitute about 20 per cent of body weight become greatly depleted. During the final stages of the wing moult, when the growth rate of the primaries is slowed, the pectoral muscles rapidly enlarge to normal size. It would thus appear that the function of the liver, during the period of rapid growth of the rectrices and catabolism of the pectoral muscles, must differ markedly from its function during the period when the synthesis of new muscle tissue and replacement of the contour feathers of the body is the major metabolic stress.

Growth of new protein tissue, as in the redevelopment of the pectoral muscle, requires an increased intake of food, particularly carbohydrates, as the necessary source of energy to form new proteins. In the metabolism of carbohydrates, the liver plays the predominant role (Popper and Schaffner, 1957). Even to maintain a normal turnover of protein, Tarver (1954, p. 1,292) has pointed out that "it is no doubt necessary to supply energy, and a significant fraction of the basal metabolism may represent heat evolved owing to the persistence of this process."

With normal food supplies available, the nitrogen-sparing action of carbohydrates would hold. This mechanism has been interpreted by Miller, Burke and Haft (1955) in terms of a liver L-glutamic acid dehydrogenase system coupled with alpha-ketoglutaric-amino acid transaminases, a concept with which Braunstein (1958) is in agreement.

The use of tissue amino acids for feather synthesis can be accounted for by the process of deamination and transamination (A. Meister, 1955). Birds and reptiles (snakes) differ from mammals in having a much greater ability to carry out deamination of amino acids *via* L-amino oxidases (Braunstein, 1958). The amino acid oxidases are probably present in greatest concentration in the liver and kidney whereas transaminase reactions may occur in a variety of tissues including muscle. Hence, there is also biochemical support for the concept that liver function is not involved to an exceptional degree in the metabolic processes requisite for feather growth.

The marked increase of the standard metabolic rate of fowl and small birds during the moult period, as compared with rates at other times (see King and Farner, 1960), is further indication that the moult period is indeed the period of greatest stress in the life of birds. An inability of immature Mourning Doves to maintain a normal rate of increase of lean body weight during the peak of the moult was previously detected (Hanson and Kossack, 1957), but this tendency was obscured where food conditions permitted unusual gains in body fat. Koch and de Bont (1944) noted a large increase in the metabolism of a fringillid (*Fringilla coelebs*) during the replacement of the rectrices, while during the replacement of the contour feathers the metabolic rate returned to normal. It might be presumed from the physical measurements presented above that a comparable relationship exists in moulting geese, which rapidly attain normal body musculature as the growth rate of the primaries becomes slowed near the end of their growth and their powers of flight are attained. Renewal of powers of flight is then followed by a marked acceleration in the moult of the contour feathers of the body (Hanson, 1959).

King and Farner (1960) have calculated from various published data that House Sparrows need only increase their energy intake by about 7.6 per cent in order to produce the winter plumage. This figure, however, may be a very

unrealistic appraisal of the metabolic stress of the moult as it does not take into account the fact that the growth of feather keratin is a *selective* metabolic process (in regard to amino acids) and one which has *priority* over other metabolic activities, even to the extent of raiding the body tissues to meet the nutritional requirements.

A study by Ackerson and Blish (1925), read belatedly after completion of the current report, also asked the question (p. 165): "Is the increased endogenous metabolism of nitrogen [in the moulting hen] partially due to the breaking down of body proteins in an effort to secure a sulphur containing nucleus for the synthesis of keratin?" They then effectively demonstrated the key role of cystine in the metabolism of the moulting hen in an experiment in which they held 12 Rhode Island Red chickens on a nitrogen-free diet; in 6 of these the diet was supplemented with cystine calculated to furnish 5 per cent of their endogenous nitrogen loss. They found that the controls lost 239 mg. per kg. of body weight of nitrogen per day compared with a loss of 137 mg. per kg. by the birds receiving 150 mg. of cystine per day. It was calculated that an intake of 15–19 mg. of cystine daily prevented the loss of 65 grams of muscle protein. They concluded (p. 165) that "The cystine fed exerted a protein sparing effect out of proportion to its nitrogen content."

Sulphur and sulphur amino acids may be involved in another aspect of the physiological stress of moult. The marked changes that the major muscle masses of Canada Geese undergo during the moult are also accompanied by a transitory osteoporitic condition of the long bones of the leg, particularly the tarsusmetatarsus. (A large series of microscopic sections of leg bones from Canada Geese collected for the present investigation are currently under study.) According to W. Meister (1951, p. 4), whose pioneering study of osteoporosis in moulting birds was based primarily on waterfowl, ". . . a more or less pronounced osteoporosis takes place by enlargement of the Haversian and Volkmann's canals." The physiological basis for this event is yet unclear, but the cause is undoubtedly related to the nutritional need of the moulting bird.

Calcium *per se* is neither an important constituent nor a requisite for feather growth and, in the case of the population of geese under review, is readily available in the form of snail shells and calciphilous plants. The latter are characteristic of the Hudson Bay Lowlands, which are underlain by limestone (Hustich, 1957). Furthermore, a calcium deficiency is seldom considered as a possible cause of osteoporosis (McLean and Budy, 1959; Urist and Deutsch, 1960b). The possible role of the nutritional need for sulphur in the development of osteoporosis in birds, however, does not appear to have been considered.

In laying hens, the osteoporosis brought about by the production of eggs is intensified by the moult. The only mineral common in relatively large amounts to both eggs and feather keratin (Kahn and Goodridge, 1926) is sulphur. Sulphur comprises 15.2 per cent of the mineral contents of the hen's egg, being concentrated principally in the albumen where it is the most abundant mineral (Romanoff and Romanoff, 1949). The sulphur is bound to organic compounds, probably entirely to the amino acids, cystine, and methionine (Marlow and King, 1936). Protein is the chief dietary source of sulphur for the hen (Romanoff and Romanoff, 1949). It is significant that a hen exceeding a rate of egg production of 50 per cent comes into negative sulphur balance (Holman, Taylor and Russell, 1945).

According to Pritchard (1956, p. 7), "The presence of a cementing medium for the collagen fibers of bone matrix is generally accepted". He further states (p. 8) that "in cartilage, where a similar histological masking of collagen fibers takes place in development, large quantities of the acid mucopolysaccharide, chondroitin sulfate, can be demonstrated chemically and histochemically." Studies with S^{35} have indicated that calcification is associated with an accelerated turnover of chondroitin sulphate (Dixon and Perkins, 1956). It would seem reasonable to make the corollary conclusion: that if during the moult a selective degradation of chondroitin sulphate occurred, decalcification of the bone would ensue. However, doubt has been expressed, on the basis of current evidence, whether demineralization of bone is dependent on an attack on the organic matrix (Neuman and Neuman, 1958).

The problem of osteoporosis in chickens has been extensively investigated by Urist and his collaborator (Urist and Deutsch, 1960 a, b, c). These studies have stressed the positive influence of ACTH and cortisone in producing avian osteoporosis. Androgen, however, counteracts the effects of cortisone and, as in the case of muscle tissue, has an anabolic effect. Although Urist and Deutsch (1960b) report that atrophy of the adrenal cortex is associated with avian osteoporosis, the adrenal glands of Canada Geese increase 25 per cent in weight during the moult (Hanson, unpublished). The hormones of the adrenal cortex are believed to inhibit the metabolism of acid mucopolysaccharides, apparently by depressing the incorporation of sulphate in the chondroitin-sulphuric acid (Dorfman and Schiller, 1958). Also, enzymatic involvement in osteoporosis, possibly via a sulphatase, is suggested by the fact that in chickens administered cortisone the cortex of the long bones may be resorbed without formation of osteoclasts (Urist and Deutsch, 1960c). According to Haas (1956, p. 795), "sulfatases which split sulfate from chondroitin sulfate esters are not conspicuous in mammalian tissues. The absence of enzymes of this class should not divert attention from the problem of removal of the acidic matrix mucopolysaccharides. There is no evidence that they pass from the calcified matrix of cartilage to adjacent osteoid matrix at the epiphyseal line. These compounds must either be degraded, resorbed, or converted to something else prior to, during, or after calcification." Evidence that chondrosulphatase is present in mammals (and presumably birds) is indicated by the fact that "$S^{35}O_4^{2-}$ ions are liberated from S^{35}–labeled chondroitin sulfate administered to rats." (see Roy, 1960 and Young and Maw, 1958.) Discussions by Neuman and Neuman (1958) underline the possibly dominant role of the chondroitin sulphate in calcification.

The finding by Gordon and Sizer (1955) that inorganic sodium sulphate ($Na_2S^{35}O_4$) will stimulate growth and normal feather development in chickens on a sulphur-deficient diet has considerable relevance here. They also confirmed earlier studies that the largest uptake of radio sulphate occurs in the chondroitin sulphate matrix of cartilage—"the mucopolysaccharide-mucoprotein 'organic' sulfate fractions isolated from connective tissues." While, they point out, inorganic sulphate cannot replace dietary cystine or methionine for protein synthesis, sulphate appears to "spare" the sulphur amino acids for protein synthesis.

Holman, Taylor and Russell (1945) showed that the moulting hen is in negative sulphur balance, but this is the case only when the old, moulted feathers

are included in the calculations. If these are not included, the hen in the process of growing new feathers is actually in positive sulphur balance. The involvement of a sulphur deficiency during the moult in producing osteoporosis would, therefore, seem to be a possibility.

The underlying theme of this discussion of the relation of protein metabolism to the life cycle of the Canada Goose can be expressed no better than a statement made by Tarver (1954, p. 1,285): "It is evident that these changes in protein content of organs and tissues, and the fluctuations in their enzymatic constitution must be related to the turnover of the proteins; in fact it appears that the lability of the body protein and hence of the enzymatic activity of tissues must represent one mechanism which allows the organism to cope with changes in its external environment."

Fat metabolism

The fat metabolism of migratory birds has probably received more attention in recent years than any other factor in studies of the physiology of wild birds. It would, nevertheless, also appear that the metabolism of the fat depots is sometimes poorly understood and therefore misinterpreted. Frequently discussions of data imply continued adherence to the once-held concept that an animal deprived of food first uses its glycogen reserves, then its fat reserves, and finally its own body tissues. Recent studies of intermediary metabolism, however, have shown that the degradation of these basic food types is interlinked. Early studies led to the analogy that fats are burned in the flame of carbohydrate; more recently, Braunstein (1958, p. 70), in a review of the chemical integration of nitrogen metabolism, paraphrased this adage, stating that "Proteins are consumed in the fire of carbohydrate." The cornerstone of the present discussion is a further modification of the original analogy, namely, that in the starving bird, or one on inadequate diet, fats must necessarily be metabolized hand in hand with the breakdown products of protein degradation, i.e., in the starving animal "fats are burned in the flame of proteins", a truism that completes the circle and cancels any special significance of any of the three analogies.

A bird cannot reduce its fat depots during migration or during a period of starvation without simultaneous reduction of its protein "pool". According to Benedict and Lee (1937, p. 4), "there is a fairly constant draft upon protein representing usually about 10 per cent of the total katabolism." It has commonly been assumed that weight lost at the end of a flight or period of stress consists wholly of fat. While their studies on the domestic goose were carried out prior to current-day concepts of intermediary metabolism, Benedict and Lee (1937) correctly assessed this metabolic relationship of these components of food: (p. 106) "the mere presence of a large amount of fat in the body is by no means assurance of ability to withstand fasting until the fat depots are nearly exhausted. Indeed, the situation is quite the contrary, and the cause of death after prolonged fasting must be ascribed to something other than absence of previously deposited fat, from which energy can be derived." Further, (p. 92) "Studies of the goose and of the fat mouse, however, emphasize the fact that the ability to withstand fasting is not dependent exclusively upon the storage of body fat. . . . The resistance to fasting is frequently associated with the nutritive condition at the start of the fast. The normal nutritive condition is usually considered to be that obtaining when the animal has not previously

been depleted of its protein reserves and has a proportion of body fat normal for the goose species."

It was noted above that in making dissections of geese which had been wintering under conditions of food shortage that even very thin geese usually possessed moderate stores of visible fat. This observation was in agreement with Benedict and Lee (1937, p. 106) who wrote: "In most instances there was a liberal supply of fat in the bodies of these geese, even after prolonged fasting." An unexpectedly high ratio of fat to protein tissue was also found in caged moulting geese. These geese entered the moult in a very fat condition and were of excellent weight; during various stages of the moult, they had greatly reduced pectoral muscles but still retained a heavy layer of fat under the breast skin, Fig. 12, F–H.

These findings can be explained in the light of current knowledge of metabolic pathways. The final oxidation of carbohydrates, proteins, and fats involves the same chemical pathways, i.e., the citric acid or Krebs cycle. Carbohydrates and proteins can be metabolized in this chain of chemical reactions independent of prior breakdown products of proteins and fats. Fatty acids, on the other hand, are reduced to two-carbon fragments before entering this cycle, and to be metabolized must be condensed with oxalacetate, a four-carbon chain compound produced as one of the reactants in the citric acid cycle when carbohydrates and proteins are degraded.

In geese—and probably most birds—the glycogen reserves are short-lived when food is not available, lasting only about 24 hours (Benedict and Lee, 1937). When glycogen stores are depleted the fat stores are drawn upon, but these cannot be metabolized completely without a concurrent supply of oxalacetate normally accruing from the metabolism of glycogen—and to a minor extent, from the glycerol portion of the neutral fats. To meet this deficit, the glucogenic amino acids of the body protein must be drawn upon to supply the necessary carbon chain. The net result is that, in the absence of glycogen reserves, body fat reserves are reduced and metabolized hand in hand with protein. Hence, with equal validity, it can be said that under conditions of starvation fats are burned in the flame of protein. (For particularly lucid expositions of these relationships, the reader is referred to Dickman (1958) and to discussions in Cantarow and Schepartz (1962)).

George and Naik (1958a) have reported that two types of fibres are found in the pectoral muscles of pigeons; a narrow type which are fat-loaded, and a broad type which are glycogen-loaded. The former are also reported to be exceptionally rich in mitochondria (George and Naik, 1958b) and lipase occurs chiefly in them (George and Scaria, 1958). George and Naik (1958a) have hypothesized that the glycogen-loaded fibres are adapted for short flights, the fat-loaded fibres for long flights. A similar relationship may hold true for Canada Geese. No physical basis was found to indicate that migration flights *per se* constitute a stress of very great significance. Fatty acids released for metabolism from the depots of neutral fats may be transported to the liver and there degraded to ketone bodies which studies have shown are readily oxidized by muscle (Fruton and Simmonds, 1953). It is reasonable, therefore, to suppose the pectoral muscle of geese is similarly capable, and these products of fat degradation in the liver may be an important energy source in the migrant bird. However, direct oxidation of long-chain fatty acids in the pectoral

muscles during flight is also likely (Reynold *et al.*, 1960). Therefore the relation of liver size in spring migrants to metabolic rates would be masked in the case of adult females by the heavy deposition of fat.

The eggs of waterfowl contain less water and more fat than eggs of land birds (Romanoff and Romanoff, 1949). According to these authors, the contents of the egg of the goose (presumably domestic) is composed of 13 per cent lipids and 14 per cent protein. The depletion of fat resources in female Canada Geese in the early stages of incubation probably reflects both the mobilization of fat for egg production and the use of fat for energy during a period of reduced food intake.

Relation of protein and fat reserves to ecological factors

The winter period is a time of actual or potential food shortage for many species of wildlife in northern regions. Most present-day populations of the larger races of Canada Geese are in large measure independent of naturally fluctuating food supplies and instead are dependent on refuge crops and farming practices. Cover as such is not a factor in the welfare of wintering geese, and, with food and water available, extreme lows in temperature are tolerated well.[1] Consequently, the welfare of wintering geese is largely related to farming practices and is therefore eminently subject to management. An example of how farming practices affect condition, i.e., body weight, was cited in detail earlier. The relative simplicity of the ecology of wintering geese is, of course, one of the chief reasons they afford such excellent opportunity for management.

In the wilderness areas of the north, the Canada Goose can be said to revert to ecological type. In spring, weather conditions are the dominating influence affecting migration (Hanson, unpublished data). Late snowstorms sometimes force several retreats of migrating flocks before the final flight is made. Feeding opportunities are limited by the snow cover, and the foods which are available can be termed "stored foods", for example, berries and basal portions of grasses and sedges of the previous year (Hanson, unpublished data).

It has been the concensus of students of the physiology of migration that in small birds premigratory fat depots serve the purpose of fuelling the successive stages of migration and that fat depots laid down immediately prior to each flight are prerequisite to the initiation of each stage of migration. This rapid deposition of lipid in spring is photoperiodically controlled, but is directly accomplished through the induction of "hyperphagia". However, in more recent years data have been accumulated to show that this relationship does not hold true for migrants which make relatively leisurely migrations, for example, the Mourning Dove (Hanson and Kossack, 1957) and Slate-coloured Junco (Johnston, 1962). Even long-range migrants of small size may not have exhausted their fat depots by the time of their arrival on the breeding grounds. Irving (1960) in his studies at Anaktuvuk Pass, Alaska, found that only a small proportion of the species of migratory birds arriving in spring were in the lowest category of fatness. Possibly, as more species are studied, the phenomena of fattening and migration will be found to be as frequently concurrent as they are sequential.

Canada Geese, in their pattern of fattening, conform more closely with

[1]In a subsequent publication it will be shown that the distribution of the various races of Canada Geese in winter is inversely related to temperature, thus, contrary to current belief, is in accordance with Bergman's rule.

that shown by species which migrate leisurely. As pointed out earlier, they *initiate* their northward migration from southern Illinois *prior* to making substantial fat gains. In this race, fat depots, aside from their use in flight, appear to have an additional important role—*namely that of supplying energy from the time of their arrival on the breeding grounds until the snow cover has left and new plant growth is again available.*

Freuchen and Salomonsen (1958) state that wild geese are frequently lean on their arrival on the Canadian arctic islands in the spring. Data on arctic races of the Canada Goose and on other species of geese indicate, however, that this is not the rule for goose populations nesting on the mainland of arctic Canada. The Lesser Canada Goose, *Branta canadensis parvipes*, arrives in the Perry River region (Hanson, Queneau, and Scott, 1956) and Adelaide Peninsula (Macpherson and Manning, 1959) still retaining considerable amounts of body fat. This appears to hold true for Blue and Lesser Snow Geese, *Anser caerulescens caerulescens*, and White-fronted Geese, *Anser albifrons frontalis* (Hanson, Queneau, and Scott, 1956).

Both Irving and McCabe (1943) have noted a rapid decline in weight and loss of fat in small birds after their arrival in the north. Irving (1960) thinks that fat reserves may be important to male birds during the intense period of courtship and maintenance of territory. Yet he has pointed out at considerable length that in arctic birds the stages preparatory to nesting are greatly compressed and highly synchronized. Irving (1960) implies that the female is under relatively little stress during mating and incubation, and the fact that females of several species do not show a decline in weight and fat until after the young have hatched is given as evidence that egg laying imposed no stress. If we can project our findings on Canada Geese, it would seem likely that a close study of other northern birds would show that the females arrive on the breeding grounds differentially fatter than the males, and, for this reason, females retain their fat stores longer as noted by Irving. Certainly in arctic areas nesting geese of either sex or geese with newly hatched broods are virtually depleted of visible fat reserves (Hanson, Queneau, and Scott, 1956; Macpherson and Manning, 1959). Courtship is not a stressful activity of Canada Geese in northern Ontario in late spring as they are mated on their arrival on the breeding grounds.

Because the breeding season in the High Arctic is considerably shorter than in subarctic areas, the possibility exists that the smaller geese breeding in the far north complete their wing moult in a shorter period of time than do the larger subspecies nesting at lower latitudes.[1] If, as seems likely, the rate of growth of the wing feathers is the same for both large and small forms, the small forms would complete the moult more rapidly, and we have one possible explanation why a south to north cline in reduction of size has evolved in related forms of geese in the northern hemisphere. The Greater Snow Goose (*Anser caerulescens atlantica*) is, of course, an exception to the general rule. The shorter incubation and fledging periods of the small high arctic forms of geese also reduce the length of time these birds must reside at high latitudes.

[1]Data recently obtained by the writer for six species and subspecies of geese support this concept. This factor together with a shorter incubation period and shorter fledging period in smaller geese are believed to explain the relation of size to climate and latitude in the *summer* distribution of the various species and races of geese. Data on these relationships and those relating to winter distribution cited in a previous footnote will be presented and discussed more fully in a forthcoming paper on factors affecting evolution in geese.

MANAGEMENT IMPLICATIONS

Findings from the present study have suggested a number of steps that can be taken to improve the welfare of geese on the wintering grounds, the primary area where practical management is now possible. The importance of an adequate food supply is self-evident, and its direct relationship to condition in geese has been clearly shown.

The *quality* of the food available to wintering geese must, however, be a further consideration. Corn, various grasses, and clovers probably provide wintering geese with a reasonably well-balanced ration, but, by mid-winter, little forage remains, and the available corn and waste soybeans are not the ideal foods. This is particularly true for immature geese, many of which in some years have not replaced the contour feathers of the body nor most of the tail feathers by the time they arrive on the wintering grounds. In order to supply the sulphur amino acids (methionine and cystine) in greater amounts, the planting of dwarf varieties of sunflowers on refuges is suggested. (Small experimental plantings have been made on the Illinois state refuges in recent years by George C. Arthur, biologist in charge, and this is an important step in the right direction.) Sunflower seed oil meal contains 46.8 per cent crude protein as compared with 11 per cent for corn meal. In respect to methionine, sunflower meal contains 1.6 per cent, corn only 0.3 per cent (Boucher, 1956), a five-fold difference. Special techniques may be necessary to make the seeds of even dwarf forms of sunflowers readily available to the geese—perhaps initial mechanical harvesting.

Both quantity and quality of refuge food supplies could be greatly augmented by the use of pelleted food when winter feeding is desirable. To have forage at a desirable height at the time the geese arrive in autumn, pastures planted for geese should be clipped several times during the summer. The resulting yield could be made available to wintering geese if it were pelletized. A few crude trials by the writer have indicated that palatability is a problem. The pellets should have a fairly high corn content supplemented by molasses to increase palatability and to furnish a binder and make the pellets more weather resistant.

Numerous studies of livestock have shown that a period of moderate undernutrition during growth is followed, on resumption of normal feeding, by a period of compensatory growth, the rate of which greatly exceeds the normal for the respective age (Wilson and Osbourn, 1960). While several factors influence this relationship, the basic findings have many implications in our understanding and management of wildlife populations. For example, a mid- to late-winter decline in weight is a common phenomenon in birds, but, unless excessive, it should not, in the case of geese subject to management measures, be cause for concern. Instead it is possible that a weight loss in late winter partly sets the stage for, and to an unrealized extent may be associated with, increased appetite and rapid gains in weight and fat made prior to, or in the course of, spring migration. By further analogy from findings on domestic stock, summarized by Wilson and Osbourn, when it is desirable to provide supplementary food for geese in late winter, there may be some advantage in feeding large amounts of grains at moderately spaced intervals rather than in

giving a daily ration: "Not only will it allow short periods of retardation to be followed by *ad libitum* feeding and short periods of compensatory growth, but it will reduce the competition between the animals. . . .

"It has been shown that restricted and re-alimented animals invariably finish growth with a higher proportion of body fat than continuously grown controls." (Wilson and Osbourn, 1960, p. 153).

The importance of maintaining wintering geese in a reasonably good state of nutrition is evident from the studies of Herman, Steenis and Wehr (1955) who found that protein malnutrition among Canada Geese wintering on the Pea Island National Wildlife Refuge, North Carolina, was apparently partly responsible for serious losses from parasite infections.

SUMMARY

1. In determining condition in Canada Geese, the following aspects were studied: (a) body weight; (b) weight of sternal muscles (*pectoralis*, *supracoracoideus*, and *corabrachialis*); (c) weight of muscles of the tibiotarsus; (d) extent of fat depots; and (e) liver weight.

2. Body weight in wintering geese was found to be directly affected by management practices on refuges, food supplies, and the relative size of the wintering population.

3. Body weights of various age-sex classes of Canada Geese that died from starvation as a result of impaction of the esophagus were 43–46 per cent less than average weights of geese collected in November.

4. Body weights of Canada Geese at or near the end of spring migration exceed that attained at any other period of the year, with possible exception of the fall migration period. At the end of spring migration body weights of yearlings exceed winter weights by 14.7 and 26.7 per cent; adults by 10.1 and 17.9 per cent, males and females respectively.

5. Yearling geese lose 6–10 per cent of their body weight in the first 3 to 3½ weeks after their arrival on the breeding grounds; the bulk of this weight loss consists of fat.

6. Incubating females weigh about 22 per cent less than their average weight on arrival on the breeding grounds. This weight loss consists largely of fat, but a reduction in the weight of muscles and the reduced size of the ovary and oviduct also contribute to the over-all reduction in body weight.

7. Minimum body weight is attained during the nonflying stages of the moult. For males the reduction in weight below migration weight is about 6 and 12 per cent; for females, 13.5 and 20 per cent, yearlings and adults respectively. Data from both wild and caged geese reveal a differentially heavier loss of weight by the females.

8. Geese that have regained the power of flight, but are still completing growth of the wing feathers and in the process of replacing the contour feathers, show a gain in body weight of from 10 and 13 per cent in adults (males and females) over the nonflying stage and about 4 per cent in yearlings (females) which underwent a smaller weight loss during the preceding stage.

9. Pectoral muscles and muscles of the tibiotarsus undergo large changes in size during various activity periods; changes in the two muscle masses are usually reciprocal.

10. The most notable changes in the weights of these muscle groups occur during the flightless period of the moult. At this time the weight of pectoral muscles is 30 and 36 per cent less in males and 25 and 41 per cent less in females, for yearlings and adults respectively, than the average weights of these muscles at the end of migration. The enlargement of the leg muscles, on the other hand, during the flightless portion of the moult ranged from 41–57 per cent above average weights for the various age-sex classes at the end of migration.

11. Consideration of the protein reserve (muscle tissue) and fat depots showed that a goose in good condition is not one that merely has considerable amounts of depot fat, but one which also has a maximum or near maximum protein reserve.

12. In determining condition, not only body weight and body fat must be considered, but protein reserves (size of muscle groups) which also affect body weight must be included in an over-all evaluation, because in times of starvation stress, the extent of use of fat reserves may depend on the extent of protein reserve since both must be degraded simultaneously.

13. In the course of a year, various stresses produce the following four "conditions" or physiological types in a population of Canada Geese: geese that have (1) maximum protein and fat reserves ("heavy and fat"); (2) maximum protein and little or no usable fat reserves ("heavy and fatless"); (3) minimum protein reserves and moderate fat reserves ("light and fat"); and (4) minimum protein and little or no fat reserves ("light and fatless").

14. Maximum fat reserves are found during migration; minimum fat reserves are found in moulting geese. Maximum and minimum protein reserves are found during the same respective periods. "Type 2" above is exemplified by yearling geese on the breeding grounds in early June just prior to the emergence of new vegetation and also later by geese at the end of the moult period. "Type 3" is found in wintering geese that have undergone starvation which usually occurs during a period of excessive cold and snowfall.

15. The dynamic changes in protein and fat reserves that are found annually in Canada Geese (and doubtless paralleled by most other waterfowl) can be largely explained by four sets of factors: (1) relative use and disuse of flight (pectoral) and walking (leg) muscles, (2) changing hormone production, (3) metabolic pathways of protein and fat degradation, and (4) ecological factors.

16. Enlargement of pectoral muscles during migration and enlargement of leg muscles during the moult appear to be the result of a temporal use-adaptation; the reduction of leg muscles during migration is believed to reflect relative disuse. The reduction of the pectoral muscles during the moult, however, appears to be an evolutionary development whereby the protein can be degraded and the amino acids used to support rapid feather growth.

17. Relative enlargement of the pectoral muscles in male Canada Geese with age is associated with relative sexual maturity and the production of nitrogen-conserving androgens. Factors affecting increased fat deposition

may be associated with undernutrition followed by hyperphagia as well as increased secretion of a complex of pituitary hormones.

18. Metabolic interrelationships are best exemplified by (1) undernourished or starving geese in which muscle protein must be degraded in order to metabolize fat reserves; and (2) moulting geese in which the pectoral muscle proteins are presumed to be degraded to increase the availability of amino acids, *particularly the sulphur amino acids—cystine and methionine—for the synthesis of feather keratin.* Growth of leg muscles may also to a considerable degree be dependent upon the common pool of amino acids derived from the degradation of pectoral muscle proteins.

19. Liver weights appeared to reflect relative metabolic activity and metabolic pathways rather than condition *per se.* High liver weights in migrating adult females were attributed to the effects of increased rates of secretion of estrogen; low liver weights in incubating females were attributed to the mobilization of body reserves, particularly fat, for the production of eggs. Normal liver weights during the flightless stages of the moult suggested that this organ is not directly stressed in transamination reactions involving the use of pectoral muscle tissue for feather growth. Large livers in geese during the flying stage of the moult are associated with accelerated food intake for formation of new protein and the increased energy required for flying.

20. Extensive fat depots noted in the Canada Geese in spring are believed to have, aside from the function of providing energy for migration, the important adaptive function of sustaining the geese for several weeks after their arrival in the north while the country is still under several feet of snow and food is limited.

21. The present study of the physiological effects of the moult on Canada Geese revealed that females are stressed to a greater extent than males. Thus the combined effects of the moult and the reproductive period would seem to be the primary reasons why sex ratios of adult waterfowl in the autumn are usually heavily weighted in favour of males.

22. It is suggested that a shorter moult period combined with a shorter incubation period may be the basis for the evolutionary selection of small races and species of geese in high latitude in the northern hemisphere.

23. The use of pelleted domestic hays (grasses and legumes) combined with corn and other cereal grains is suggested as a means of increasing the output of food on refuges. The planting of sunflowers for geese is recommended.

Table 1. Body weights in grams of immature male Canada Geese trapped at Horseshoe Lake, Illinois, 1942–6.

Season	*October*			*November*			*December*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1942–3[a]	—	—	—	(65)	(3311 ± 37)	(295)	(91)	(3547 ± 37)	(349)
1943–4	—	—	—	77	3388 ± 38	336	206	3479 ± 22	318
1944–5	10	3484 ± 134	422	43	3411 ± 50	327	58	3520 ± 46	349
1945–6	—	—	—	9	3393 ± 95	286	—	—	—
Total or average	10	3484 ± 134	422	129	3397 ± 29	331	264	3488 ± 20	327
	January			*February*			*March*		
1942–3[a]	(61)	(3293 ± 35)	(277)	(69)	(3316 ± 44)	(367)	(46)	(3361 ± 55)	(376)
1943–4	—	—	—	—	—	—	—	—	—
1944–5	37	3615 ± 52	318	14	3552 ± 74	277	—	—	—
1945–6	—	—	—	—	—	—	—	—	—
Total or average	37	3615 ± 52	318	14	3552 ± 74	277	—	—	—

[a]Data from Elder (1946); they are not included in total or average.

Table 2. Body weights in grams of immature female Canada Geese trapped at Horseshoe Lake, Illinois, 1942–6.

Season	*October*			*November*			*December*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1942–3[a]	—	—	—	(41)	(3007 ± 39)	(249)	(77)	(3071 ± 33)	(290)
1943–4	—	—	—	69	2826 ± 31	254	196	2939 ± 20	286
1944–5	8	3057 ± 80	227	37	2912 ± 44	268	40	2994 ± 47	299
1945–6	—	—	—	20	2744 ± 61	274	—	—	—
Total or average	8	3057 ± 80	227	126	2840 ± 24	268	236	2948 ± 19	290
	January			*February*			*March*		
1942–3[a]	(57)	(2903 ± 32)	(240)	(57)	(2862 ± 46)	(345)	(49)	(2939 ± 54)	(381)
1943–4	—	—	—	—	—	—	—	—	—
1944–5	35	3071 ± 41	249	9	3026 ± 54	163	—	—	—
1945–6	—	—	—	—	—	—	—	—	—
Total or average	35	3071 ± 41	249	9	3026 ± 54	163	—	—	—

[a]Data from Elder (1946); they are not included in totals or average.

Table 3. Body weights in grams of yearling male Canada Geese trapped at Horseshoe Lake, Illinois, 1943–6.

Season	*November*			*December*			*January*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1943–4	9	3837 ± 106	318	15	3756 ± 86	331	—	—	—
1944–5	7	4096 ± 87	231	13	3878 ± 82	295	7	3960 ± 94	249
1945–6	16	3946 ± 82	327	—	—	—	—	—	—
Total or average	32	3951 ± 56	318	28	3815 ± 61	322	7	3960 ± 94	249

Table 4. Body weights in grams of yearling female Canada Geese trapped at Horseshoe Lake, Illinois, 1943–6.

Season	*November*			*December*			*January*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1943–4	5	3379 ± 117	263	8	3447 ± 141	399	—	—	—
1944–5	15	3243 ± 39	150	4	3397 ± 166	331	4	3466 ± 157	313
1945–6	12	3461 ± 165	572	—	—	—	—	—	—
Total or average	32	3361 ± 44	249	12	3429 ± 113	392	4	3466 ± 157	313

Table 5. Body weights in grams of adult male Canada Geese trapped at Horseshoe Lake, Illinois, 1943–6.

Season	*November*			*December*			*January*			*February*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1943–4	8	3915 ± 123	349	5	4128 ± 101	227	—	—	—	—	—	—
1944–5	22	4051 ± 91	426	34	4060 ± 87	508	31	4069 ± 55	304	9	3828 ± 80	240
1945–6	19	4064 ± 82	358	—	—	—	—	—	—	—	—	—
Total or average	49	4037 ± 56	395	39	4069 ± 78	485	31	4069 ± 55	304	9	3828 ± 80	240

Table 6. Body weights in grams of adult female Canada Geese trapped at Horseshoe Lake, Illinois, 1943–6.

Season	*November*			*December*			*January*		
	Number	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*	*Number*	*Mean*	*Standard deviation*
1943–4	11	3538 ± 74	245	9	3261 ± 77	231	—	—	—
1944–5	16	3470 ± 73	290	24	3515 ± 69	340	10	3561 ± 85	268
1945–6	24	3724 ± 85	417	—	—	—	—	—	—
Total or average	57	3611 ± 60	381	33	3488 ± 58	334	10	3561 ± 85	268

Table 7. Body weights in grams of Canada Geese at Horseshoe Lake, Illinois, in November and December, 1953. All geese were shot by hunters and nearly all during the early morning hours before they had had opportunity to feed.

Age and sex	*Number*	*Average weight*	*Standard deviation*	*Coefficient of variation*
Immature male	44	3338 ± 44	290	8.7 ± 0.9
Yearling male	14	3878 ± 93	349	9.0 ± 1.7
Adult male	18	4046 ± 84	358	8.8 ± 1.5
Immature female	37	2944 ± 54	331	15.0 ± 1.7
Yearling female	10	3075 ± 50	159	5.2 ± 1.2
Adult female	23	3343 ± 84	403	12.1 ± 1.8

Table 8. Weights in grams of immature male Canada Geese examined in hunters' bags in the Mississippi Flyway, 1942–57.

Year	*Locality*	*Inclusive dates*	*Number*	*Average*	*Range*
1942[a]	Horseshoe Lake, Ill.	Nov. 1–Nov. 30	164	3583	2722 – 4491
1943	Horseshoe Lake, Ill.	Oct. 29–Nov. 14	21	3583	2404 – 3992
1944	Horseshoe Lake, Ill.	Oct. 30–Nov. 3	19	3447	2767 – 4128
1950[b]	Wisconsin[c]	Oct. 14–Dec. 7	74	3447	2676 – 4899
1953	Horseshoe Lake, Ill.	Oct. 30–Nov. 24	44	3357	2540 – 4218
1956[d]	Wisconsin[e]	Oct. 1–Dec. 9	303	3810	2268 – 5171
1957	Horseshoe Lake, Ill.	Nov. 9–Nov. 30	45	3583	2903 – 4173

[a] From Elder (1943); in unpublished summary of data in Illinois Natural History Survey files.
[b] From Jahn *et al.* (1951).
[c] All but two from areas near Horicon Marsh and Rock Prairie refuges.
[d] From Jahn *et al.* (1957).
[e] All from the Horicon Marsh National Wildlife Refuge.

Table 9. Weights in grams of immature female Canada Geese examined in hunters' bags in the Mississippi Flyway, 1942–57.

Year	*Locality*	*Inclusive dates*	*Number*	*Average*	*Range*
1942[a]	Horseshoe Lake, Ill.	Nov. 1–Nov. 30	120	3130	2449 – 4218
1943	Horseshoe Lake, Ill.	Oct. 29–Nov. 14	11	3221	2903 – 3583
1944	Horseshoe Lake, Ill.	Oct. 30–Nov. 3	11	2948	2676 – 3130
1950[b]	Wisconsin[c]	Oct. 14–Dec. 7	115	3221	2223 – 4491
1953	Horseshoe Lake, Ill.	Oct. 30–Nov. 24	37	2948	2177 – 3992
1956[d]	Wisconsin[e]	Oct. 1–Dec. 9	580	3221	1361 – 4627
1957	Horseshoe Lake, Ill.	Nov. 7–Nov. 30	44	3084	2449 – 3629

[a] From Elder (1943); in unpublished summary of data in Illinois Natural History Survey files.
[b] From Jahn *et al.* (1951).
[c] All but four from areas near Horicon Marsh and Rock Prairie refuges.
[d] From Jahn *et al.* (1957).
[e] All from the Horicon Marsh National Wildlife Refuge.

Table 10. Summary of body weights in grams of Canada Geese trapped at Horseshoe Lake, Illinois, arranged to show differences between age classes in winter, 1943–6. Data from Tables 1 to 6.

Age and sex	*November*		*December*		*January*		
	Number	*Mean*	*Number*	*Mean*	*Number*	*Mean*	*Average of means*
Immature male	129	3397	264	3488	37	3615	3500
Yearling male	32	3951	28	3815	7	3960	3905
Adult male	49	4037	39	4069	31	4069	4058
Immature female	126	2840	236	2948	35	3071	2953
Yearling female	32	3361	12	3429	4	3466	3419
Adult female	51	3611	33	3488	10	3561	3553

Table 11. Body weights in grams of immature Canada Geese at the Horseshoe Lake and Union County refuges in November and December, 1957.

Refuge	*Month*	*Number*	*Average weight*	*Range*	*S.D.*	*V.*
Males						
Horseshoe Lake	November	45	3583 ± 45	2903 – 4264	408	11.4
Union County	November	81	3856 ± 45	2631 – 4218	318	8.2
Total or average	November	126	3765 ± 45	2631 – 4218	272	7.2
Horseshoe Lake	December	13	3583 ± 91	2948 – 3946	318	8.9
Union County	December	36	3357 ± 91	2722 – 4218	408	12.2
Total or average	December	49	3402 ± 45	2722 – 4218	363	10.7
Females						
Horseshoe Lake	November	44	3084 ± 45	2449 – 3269	272	8.8
Union County	November	77	3266 ± 45	2087 – 3720	272	8.3
Total or average	November	121	3221 ± 14	2087 – 3720	181	5.6
Horseshoe Lake	December	16	3039 ± 45	2631 – 3447	227	7.5
Union County	December	17	2858 ± 91	2087 – 3673	363	12.7
Total or average	December	33	2948 ± 45	2087 – 3673	318	10.8

Table 12. Body weights in grams of Canada Geese at Horseshoe Lake, Illinois, that died in autumn from starvation due to impaction of the upper digestive tract.

Age and sex	*Number*	*Average*	*Range*	*Calculated average % loss of weight*[a] *%*
Immature male	19	1901	1633 – 1951	43.0
Yearling male	5	2241	2087 – 2731	42.2
Adult male	16	2286	1950 – 2858	43.5
Immature female	23	1588	1361 – 1905	46.1
Yearling female	3	2009	1678 – 2404	34.7
Adult female	8	1887	1678 – 2132	43.6

[a] Percentage loss calculated from difference in average body weights in this table and average weights presented in Table 7.

Table 13. Body weights of male Canada Geese in the Mississippi Flyway at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. body weight (gm.)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	5–8 mo.	(430)	3500[a]	—	—
Yearling	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	17–20 mo.	(67)	3905[a]	—	—
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	+29 mo.	119	4058[a]	—	—
Yearling	Hawley Lake, Ont.	Migrating	May 2–12	10–11 mo.	6	4010 ± 87	3735 – 4280	214 ± 62
Adult	Hawley Lake, Ont.	Migrating	May 2–10	+35 mo.	22	4472 ± 30	3880 – 5080	141 ± 21
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 26–June 6	10–11 mo.	3	3645 ± 132	3410 – 3865	228 ± 93
Adult	Sutton River, Ont.	Egg-laying period	May 25	+35 mo.	1	4865	—	—
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 16–21	12–13 mo.	18	3853 ± 43	3425 – 4065	180 ± 30
Yearling	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 7–14	12–13 mo.	3	4592 ± 61	4485 – 4770	105 ± 43
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–Aug. 7	+24 mo.	45	3946 ± 61	3140 – 5135	129 ± 14
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 10–14	+24 mo.	18	4349 ± 118	2890 – 4870	500 ± 83

a. From Table 10.

Table 14. Body weights of female Canada Geese in the Mississippi Flyway at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. body weight (gm.)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	5–8 mo.	(397)	2953[a]	—	—
Yearling	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	17–20 mo.	(48)	3420[a]	—	—
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 1–Dec. 31	+29 mo.	(94)	3553[a]	—	—
Yearling	Hawley Lake, Ont.	Migrating (early)	May 2–12	10–11 mo.	16	3742 ± 107	2970 – 4375	427 ± 75
Yearling	Hawley Lake, Ont.	Migrating (late)	May 2–12	22–23 mo.	8	3318 ± 179	2680 – 4320	506 ± 127
Adult	Hawley Lake, Ont.	Migrating	May 2–12	+34 mo.	18	4188 ± 109	3495 – 5005	463 ± 77
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 30–June 3	10–11 mo.	2	3395	3360 – 3430	—
Adult	Sutton River, Ont.	Egg-laying period	May 25	+35 mo.	1	4930	—	—
Adult	Sutton River, Ont.	Incubating	May 28–June 6	+23 mo.	8	3287 ± 105	2925 – 3840	296 ± 74
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–27	12–13 mo.	20	3235 ± 48	2965 – 3545	214 ± 34
Yearling	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 6–7	12–13 mo.	2	3485 ± 60	3350 – 3620	85.1 ± 43
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 12–Aug. 8	+24 mo.	30	3349 ± 49	2815 – 3870	268 ± 35
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 10–14	+24 mo.	12	3786 ± 75	3350 – 4180	259 ± 53

a. From Table 10.

Table 15. Weight of pectoral muscles of male Canada Geese at various ages and periods of the life cycle and the relation of pectoral muscle weight to body weight.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. wt. of pectoral muscles (gm.)*	*Range*	*Standard deviation*	*Wt. of pectoral muscles / body wt. %*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 13–Jan. 4	5–8 mo.	(430)[a]	715[b]	578 – 824[c]	—	20.4
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–Jan. 1	17–20 mo.	20	745.6 ± 14.2	650 – 880	63.5 ± 10.0	21.1
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 20–Jan. 15	+29 mo.	(119)[a]	870[d]	396 – 1034[d]	—	21.4
Yearling	Hawley Lake, Ont.	Migrating	May 2–10	10–11 mo.	4	808.0 ± 16.4	762 – 840	32.8 ± 11.6	20.8
Adult	Hawley Lake, Ont.	Migrating	May 2–9	+23 mo.	13	922.2 ± 20.2	796 – 1050	72.9 ± 14.3	20.7
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 26–June 6	10–11 mo.	3	746.7 ± 21.4	704 – 768	37.0 ± 15.1	20.8
Adult	Sutton River, Ont.	Nesting period (nonbreeding)	May 25	35 mo.	1	954.0	—	—	19.6
Gosling	Akimiski Id., N.W.T.	Growth (nonflying)	Aug. 7	8.5 wk.	3	450.3 ± 23.4	406 – 485	40.4 ± 16.5	12.8
Gosling	Akimiski Id., N.W.T.	Growth (flying)	Aug. 10	9–10 wk.	1	442.0	—	—	16.2
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 16–21	12–13 mo.	4	563.5 ± 14.7	524 – 604	29.3 ± 10.4	14.7
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–Aug. 8	+24 mo.	18	588.6 ± 17.7	462 – 734	75.2 ± 12.5	14.6
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 10–14	+24 mo.	12	734.8 ± 38.7	448 – 872	133.8 ± 27.3	17.3

[a] From Table 10.
[b] From Fig. 10 by interpolation from body weight in last column in Table 10.
[c] From actual observations, Fig. 5.
[d] From Fig. 7 by interpolation from body weight in last column in Table 10.

Table 16. Weight of pectoral muscles of female Canada Geese at various ages and periods of the life cycle and the relation of pectoral muscle weight to body weight.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. wt. of pectoral muscles (gm.)*	*Range*	*Standard deviation*	*Wt. of pectoral muscles / body wt. %*
Immature	Horseshoe Lake, Ill.	Wintering	Nov.–Jan. 15	5–8 mo.	(397)[a]	613[b]	394 – 746[c]	—	20.8
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–20	17–20 mo.	16	666.0 ± 14.4	602 – 790	57.4 ± 10.1	20.9
Adult	Horseshoe Lake, Ill.	Wintering	Nov.–Jan. 15	+29 mo.	(94)[a]	723[b]	428 – 830[d]	—	20.4
Yearling	Hawley Lake, Ont.	Migrating	May 2–12	10–11 mo.	15	711.7 ± 15.9	573 – 850	61.7 ± 11.3	21.3
Adult	Hawley Lake, Ont.	Migrating	May 2–12	23 mo.	13	820.5 ± 27.7	736 – 1136	100.1 ± 19.6	20.1
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 30–June 3	10–11 mo.	2	727.0 ± 30.3	696 – 758	42.7 ± 21.4	21.4
Adult	Sutton River, Ont.	Egg-laying period	May 25	35 mo.	1	796	—	—	16.1
Adult	Sutton River, Ont.	Incubating	May 28–June 6	+23 mo.	8	702.1 ± 21.6	610 – 776	61.0 ± 15.3	21.4
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–Aug. 8	12–13 mo.	4	537.5 ± 15.6	486 – 562	31.1 ± 11.0	15.0
Yearling	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 6–7	12–13 mo.	3	603.0 ± 16.9	566 – 640	29.3 ± 12.0	17.8
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 14–27	24 mo.	25	486.2 ± 8.7	410 – 590	43.6 ± 6.2	14.4
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 8–11	24 mo.	9	642.1 ± 21.6	520 – 718	64.8 ± 15.3	17.0

[a] From Table 10.
[b] From Fig. 6 by interpolation from body weight in last column of Table 10.
[c] From actual observations, Fig. 6.
[d] From Fig. 8 by interpolation from body weight in last column in Table 10.

Table 17. Differences in body weight and weights of pectoral muscles and of muscles of tibiotarsus between age classes and sex classes of Canada Geese wintering at Horseshoe Lake, Illinois.

Age and sex classes compared	*Differences in body weight*		*Differences in weight of pectoral muscles*		*Differences in weight of muscles of tibiotarsus*	
	(*gm.*)	(%)	(*gm.*)	(%)	(*gm.*)	(%)
Males						
Yearling to immature	405	11.6	30.6	4.3	−0.5	0.1
Adult to yearling	153	3.9	124.4	16.7	37.6	20.6
Adult to immature	558	15.9	155.0	21.7	37.1	20.3
Females						
Yearling to immature	467	15.8	53.0	8.6	1.9	1.1
Adult to yearling	133	3.8	57.0	8.6	13.4	7.0
Adult to immature	600	20.3	110.0	17.9	11.5	8.2
Immatures						
Male to female	547	18.5	102.0	16.6	17.3	10.5
Yearlings						
Male to female	485	14.2	79.0	11.9	18.7	11.4
Adults						
Male to female	505	14.2	147.0	20.3	42.9	24.3

Table 18. Changes in total body weight and weights of pectoral and leg muscles of male Canada Geese with various stresses in the life cycle.

Age — activity categories compared	*Change in body weight*[a]		*Change in weight of pectoral muscles*[b]		*Change in weight of leg muscles*[c]	
	(*gm.*)	(%)	(*gm.*)	(%)	(*gm.*)	(%)
Migrating yearling to wintering immature	+510	+14.6	+93.0	+13.0	−18.1	−9.9
Migrating adult to wintering adult	+414	+10.2	+52.2	+6.0	−7.0	−3.2
Yearling (nesting period) to migrating yearling	−365	−9.1	−72.0	−8.9	+21.0	+12.8
Moulting yearling (nonflying) to migrating yearling	−157	−3.9	−244.5	−30.3	+94.5	+57.4
Moulting adult (nonflying) to migrating adult	−526	−11.8	−333.6	−36.2	+86.9	+40.9
Moulting adult (flying) to moulting adult (nonflying)	+403	+10.2	+146.2	+24.8	−74.9	−25.0

[a] Based on data in Table 13.
[b] Based on data in Table 15.
[c] Based on data in Table 20.

Table 19. Changes in total body weight and weights of pectoral and leg muscles of female Canada Geese with various stresses in the life cycle.

Age — activity categories compared	*Change in body weight*[a]		*Change in weight of pectoral muscles*[b]		*Change in weight of leg muscles*[c]	
	(*gm.*)	(%)	(*gm.*)	(%)	(*gm.*)	(%)
Migrating yearling to wintering immature	+789	+26.7	+99.0	+16.2	−21.1	−12.8
Migrating adult to wintering adult	+635	+17.9	+97.5	+13.5	−11.9	−6.7
Yearling (nesting period) to migrating yearling	−347	−10.2	+15.3	+2.1	+32.8	+22.7
Incubating adult to migrating adult	−901	−21.5	−118.4	−14.4	+5.4	+3.3
Moulting yearling (nonflying) to migrating yearling	−507	−13.5	−174.2	−24.5	+71.8	+49.8
Moulting yearling (flying) to moulting yearling (nonflying)	+250	+7.7	—	—	—	—
Moulting adult (nonflying) to incubating adult	−114	−3.4	−215.9	−30.8	+66.0	+38.8
Moulting adult (nonflying) to migrating adult	−839	−20.0	−334.3	−40.7	+71.4	+43.3
Moulting adult (flying) to moulting adult (nonflying)	+437	+13.0	+155.9	+32.1	−47.1	−19.9

[a] Based on data in Table 14.
[b] Based on data in Table 16.
[c] Based on data in Table 21.

Table 20. Weight of muscles of tibiotarsus of male Canada Geese at various ages and periods of the life cycle and the relation of weight of leg muscles to body weight.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Average wt. leg muscles (gm.)*	*Range*	*Standard deviation*	*Wt. leg muscles / body wt. (%)*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 20–Dec. 19	5–8 mo.	5	182.6 ± 8.5	159 – 204	19.1 ± 6.0	5.1
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–20	17–20 mo.	17	182.1 ± 5.4	137 – 218	22.2 ± 3.8	5.1
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 21–Jan. 12	+29 mo.	3	219.7 ± 26.6	178 – 284	46.1 ± 18.8	5.4
Yearling	Hawley Lake, Ont.	Migrating	May 2–10	10–11 mo.	4	164.5 ± 8.1	150 – 191	16.2 ± 5.7	4.2
Adult	Hawley Lake, Ont.	Migrating	May 2–9	+23 mo.	13	212.7 ± 5.6	190 – 260	20.1 ± 3.9	4.8
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	June 6	10–11 mo.	3	178.3 ± 9.8	164 – 197	17.0 ± 6.9	4.9
Adult	Sutton River, Ont.	Egg-laying period	May 25	+23 mo.	1	280.0	—	—	5.8
Gosling	Akimiski Id., N.W.T.	Growth (nonflying)	Aug. 7	8–9 wk.	3	219.0 ± 6.4	202 – 218	11.0 ± 4.5	6.1
Gosling	Akimiski Id., N.W.T.	Growth (flying)	Aug. 10	9–10 wk.	1	152	—	—	5.6
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 21–27	12–13 mo.	2	259.0 ± 5.0	254 – 264	7.1 ± 3.6	6.7
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–Aug. 2	+24 mo.	9	299.6 ± 9.7	242 – 352	29.2 ± 6.9	7.0
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 10–11	+24 mo.	9	224.7 ± 11.7	154 – 276	35.0 ± 8.3	5.2

Table 21. Weight of muscles of tibiotarsus of female Canada Geese at various ages and periods of the life cycle and the relation of weight of leg muscles to body weight.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Average wt. leg muscles (gm.)*	*Range*	*Standard deviation*	*Wt. leg muscles / body wt. (%)*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 20–Jan. 14	5–8 mo.	6	165.3 ± 8.9	146 – 206	21.8 ± 6.3	5.5
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–20	17–20 mo.	16	163.4 ± 4.8	130 – 196	19.0 ± 3.4	5.1
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 20–Jan. 13	+29 mo.	5	176.8 ± 5.0	162 – 188	11.2 ± 3.5	4.9
Yearling	Hawley Lake, Ont.	Migrating	May 2–12	10–11 mo.	15	144.2 ± 5.4	118 – 190	20.8 ± 3.8	4.3
Adult	Hawley Lake, Ont.	Migrating	May 2–11	+23 mo.	13	164.9 ± 5.3	134 – 199	19.3 ± 3.8	4.0
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 30–June 3	10–11 mo.	2	177.0 ± 13.0	164 – 190	18.4 ± 9.2	5.2
Adult	Sutton River, Ont.	Egg-laying period	May 25	+35 mo.	1	196.0	—	—	4.0
Adult	Sutton River, Ont.	Incubating	May 28–June 6	+23 mo.	8	170.3 ± 6.1	148 – 203	17.3 ± 4.3	5.2
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 18–21	12–13 mo.	3	216.0 ± 8.0	216 – 240	13.9 ± 5.7	6.5
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 18–27	+24 mo.	16	236.3 ± 4.6	202 – 258	18.8 ± 3.3	6.9
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 8–11	+24 mo.	9	189.2 ± 8.8	161 – 226	26.3 ± 6.2	5.0

Table 22. Relation of weight of muscles of tibiotarsus to weight of pectoral muscles of male Canada Geese at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. wt. of leg muscles / Av. wt. of pectoral muscles (%)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 20–Dec. 19	5–8 mo.	5	24.2 ± 0.8	22.1 – 26.3	1.7 ± 0.5
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–20	17–20 mo.	17	23.2 ± 5.6	19.4 – 28.0	2.3 ± 0.4
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 21–Jan. 12	+29 mo.	3	24.7 ± 1.5	24.1 – 26.8	2.6 ± 1.1
Yearling	Hawley Lake, Ont.	Migrating	May 2–10	10–11 mo.	4	20.4 ± 1.1	18.3 – 22.7	2.1 ± 0.7
Adult	Hawley Lake, Ont.	Migrating	May 2–9	+23 mo.	13	23.1 ± 0.6	20.1 – 26.3	2.1 ± 0.4
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 26–June 6	10–11 mo.	3	23.9 ± 1.4	21.4 – 25.7	2.3 ± 1.0
Adult	Sutton River, Ont.	Nesting period	May 25	+35 mo.	1	29.4	—	—
Gosling	Akimiski Id., N.W.T.	Growth (nonflying)	Aug. 7	8.5 wk.	3	47.5 ± 3.9	41.5 – 53.7	6.6 ± 2.8
Gosling	Akimiski Id., N.W.T.	Growth (flying)	Aug. 10	9–10 wk.	1	34.4	—	—
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 18–27	12–13 mo.	2	44.1 ± 2.0	42.1 – 46.0	2.8 ± 1.4
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 10–Aug. 2	+24 mo.	9	47.6 ± 1.5	41.2 – 54.1	4.4 ± 1.0
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 10–11	+24 mo.	9	31.8 ± 4.0	23.0 – 61.6	12.1 ± 2.9

Table 23. Relation of weight of muscles of tibiotarsus to weight of pectoral muscles of female Canada Geese at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Time of year*	*Approximate age*	*Number*	*Av. wt. of leg muscles / Av. wt. of pectoral muscles (%)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	Nov. 20–Jan. 14	5–8 mo.	6	26.9 ± 1.0	22.8 – 28.7	2.3 ± 0.7
Yearling	Horseshoe Lake, Ill.	Wintering	Dec. 8–20	17–20 mo.	16	24.5 ± 0.5	21.6 – 28.3	1.9 ± 0.3
Adult	Horseshoe Lake, Ill.	Wintering	Nov. 20–Jan. 13	+29 mo.	5	22.8 ± 0.5	20.9 – 24.2	1.3 ± 0.4
Yearling	Hawley Lake, Ont.	Migrating	May 2–12	10–11 mo.	15	20.2 ± 0.4	18.5 – 23.9	1.6 ± 0.3
Adult	Hawley Lake, Ont.	Migrating	May 2–11	23 mo.	13	20.2 ± 0.5	16.6 – 22.5	1.8 ± 0.4
Yearling	Sutton River, Ont.	Nesting period (nonbreeding)	May 30–June 3	10–11 mo.	2	24.4 ± 0.7	23.6 – 25.1	1.0 ± 0.5
Adult	Sutton River, Ont.	Egg-laying period	May 25	35 mo.	1	24.6		
Adult	Sutton River, Ont.	Incubating	May 28–June 6	+23 mo.	8	24.4 ± 0.9	20.3 – 26.6	2.5 ± 0.6
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	July 18–21	12–13 mo.	3	45.0 ± 4.5	38.4 – 52.2	7.6 ± 3.2
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	July 18–27	24 mo.	16	49.5 ± 1.5	39.7 – 61.4	5.9 ± 1.0
Adult	Akimiski Id., N.W.T.	Moulting (flying)	Aug. 8–11	24 mo.	9	29.6 ± 1.9	23.2 – 41.1	5.8 ± 1.4

Table 24. Relation of condition classes to body weight and fat categories in wintering and migrant Canada Geese.

Age—sex class and condition factors	*Av. terminal starvation weight (from Table 12) (gm.)*	*Condition class*				
		Poor (negligible fat)	*Fair (little fat—borderline condition)*	*Good (moderately fat)*	*Excellent (fat)*	*Migratory (fat to very fat)*
Immature males	1901					
Weight bracket (gm.)		Under 3000	3000–3200	3200–3500	Over 3500	Over 3700
Internal fat (gm.)		Under 15	15–25	20–40	40–80	40–115
Breast skin fat (mm.)		0–1	1–2	3–4	4–6	3+
Adult males	2286					
Weight bracket (gm.)		Under 3500	3500–3800	3800–4200	4200–4500[a]	4350–4900[b]
Internal fat (gm.)		Under 20	20–30	30–50	50–80	122–250
Breast skin fat (mm.)		0–1	1–2	3–4	4–6	4–8
Immature females	1588					
Weight bracket (gm.)		Under 2700	2700–2900	2900–3200	3200–3400	3200–4300
Internal fat (gm.)		Under 15	15–40	30–60	40–140	—
Breast skin fat (mm.)		0–1	1–3	3–4	4–5	3–5
Adult females	1887					
Weight bracket (gm.)		Under 3100	3100–3350	3350–3600	3600–3850	Over 3800[c]
Internal fat (gm.)		Under 15	15–20	15–40	40–70	155–205
Breast skin fat (mm.)		0–1	1–2	3–4	4–6	5–8

[a] An adult male held in captivity at Horseshoe Lake in January 1960 weighed 5,330 gm. and had 345 gm. of visceral fat.
[b] Approximately 85 per cent of individuals.
[c] Approximately 80 per cent of individuals.

Table 25. Weight of liver of male Canada Geese at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Number*	*Av. wt. of liver (gm.)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	44	57.8 ± 1.3	40 – 81	8.9 ± 0.9
Yearling	Horseshoe Lake, Ill.	Wintering	13	55.3 ± 1.7	41 – 69	6.2 ± 1.2
Adult	Horseshoe Lake, Ill.	Wintering	12	68.0 ± 6.7	51 – 88	23.5 ± 4.8
Yearling	Hawley Lake, Ont.	Migrating	4	45.8 ± 3.6	37 – 53	7.2 ± 2.6
Adult	Hawley Lake, Ont.	Migrating	13	45.1 ± 2.0	32 – 60	7.4 ± 1.5
Yearling	Sutton River, Ont.	Nesting period	2	79.5	75 – 84	6.3 ± 2.0
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	1	56.0	—	—
Yearling	Akimiski Id., N.W.T.	Moulting (flying)	1	113.0	—	—
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	6	71.5 ± 5.4	62 – 103	15.4 ± 3.9
Adult	Akimiski Id., N.W.T.	Moulting (flying)	8	108.4 ± 7.1	68 – 140	20.0 ± 5.0

Table 26. Weight of liver of female Canada Geese at various ages and periods of the life cycle.

Age class	*Locality*	*Activity or Period*	*Number*	*Av. wt. of liver (gm.)*	*Range*	*Standard deviation*
Immature	Horseshoe Lake, Ill.	Wintering	37	52.8 ± 1.9	33 – 89	11.6 ± 1.3
Yearling	Horseshoe Lake, Ill.	Wintering	10	44.7 ± 2.5	26 – 101	8.1 ± 1.8
Adult	Horseshoe Lake, Ill.	Wintering	17	52.5 ± 5.7	36.9 – 136	23.2 ± 4.0
Yearling	Hawley Lake, Ont.	Migrating	12	49.9 ± 6.0	37 – 111	20.7 ± 4.2
Adult	Hawley Lake, Ont.	Migrating	7	75.1 ± 10.8	51 – 123	28.7 ± 7.7
Yearling	Sutton River, Ont.	Nesting period	2	58.0	57 – 59	—
Adult	Sutton River, Ont.	Incubating	8	37.7 ± 1.6	32 – 46	4.6 ± 1.2
Yearling	Akimiski Id., N.W.T.	Moulting (nonflying)	1	58.0	—	—
Adult	Akimiski Id., N.W.T.	Moulting (nonflying)	11	58.1 ± 3.3	43 – 80	11.0 ± 2.3
Adult	Akimiski Id., N.W.T.	Moulting (flying)	5	109.4 ± 2.7	85 – 141	6.4 ± 2.0

APPENDIX

Table for conversion of gram weights to pounds and tenths of pounds.

Grams	*Pounds*	*Grams*	*Pounds*	*Grams*	*Pounds*
2268	5.0	3357	7.4	4445	9.8
2313	5.1	3402	7.5	4491	9.9
2359	5.2	3447	7.6	4536	10.0
2404	5.3	3493	7.7	4581	10.1
2449	5.4	3538	7.8	4627	10.2
2495	5.5	3583	7.9	4672	10.3
2540	5.6	3629	8.0	4717	10.4
2586	5.7	3674	8.1	4763	10.5
2631	5.8	3720	8.2	4808	10.6
2676	5.9	3765	8.3	4853	10.7
2722	6.0	3810	8.4	4899	10.8
2767	6.1	3856	8.5	4944	10.9
2812	6.2	3901	8.6	4990	11.0
2858	6.3	3946	8.7	5035	11.1
2903	6.4	3992	8.8	5080	11.2
2948	6.5	4037	8.9	5126	11.3
2994	6.6	4082	9.0	5171	11.4
3039	6.7	4128	9.1	5216	11.5
3084	6.8	4173	9.2	5262	11.6
3130	6.9	4218	9.3	5307	11.7
3175	7.0	4264	9.4	5352	11.8
3221	7.1	4309	9.5	5398	11.9
3266	7.2	4355	9.6	5443	12.0
3311	7.3	4400	9.7	—	—

REFERENCES

Ackerson, C. W. and M. J. Blish. 1925. "The effect of cystine on the endogenous metabolism of moulting hens". *Poul. Sci.* Vol. 5, pp. 162–5.

Albanese, Anthony A. 1959a. Ed. 'Protein and amino acid nutrition'. Academic Press, New York: 604 pp.

1959b. "Criteria of protein nutrition" pp. 297–347 *in* Albanese, A. A. (1959a).

Allison, James B. 1959. "The efficiency of utilization of dietary proteins" pp. 97–116 *in* Albanese, A. A. (1959a).

Almquist, H. J. 1959. "The amino acid requirements of animals" pp. 349–80 *in* Albanese, A. A. (1959a).

Assenmacher, I. 1958. "La mue des oiseaux et son déterminisme endocrinien". *Alauda*, Vol. 26, pp. 242–89.

Baldwin, S. Prentiss and S. Charles Kendeigh. 1938. "Variations in the weight of birds". *Auk*, Vol. 55, pp. 416–67.

Benedict, Francis G. and Robert C. Lee. 1937. 'Lipogenesis in the animal body, with special reference to the physiology of the goose'. *Carnegie Inst. Wash. Publ.* No. 489, 232 pp.

Bennett, Logan J. 1938. 'The Blue-winged Teal. Its ecology and management'. Collegiate Press, Ames, Iowa: 144 pp.

Boucher, R. V. (Chairman of Committee). 1956. 'Composition of concentrate byproduct feeding stuffs'. *Nat. Acad. Sci.—Nat. Res. Council Publ.* 449, Washington, D.C.: 126 pp.

Bourne, Geoffrey H. 1956. Ed. 'The biochemistry and physiology of bone'. Academic Press, New York: 875 pp.

Braunstein, A. E. 1958. "Some aspects of the chemical integration of nitrogen metabolism". *Proc. Fourth Internat. Congr. Biochem.* Vienna, 1958. Vol. 14, pp. 63–88. *I.U.B. Symposium Series*, Vol. 16.

Breitenbach, Robert P. and Roland K. Meyer. 1959. "Effect of incubation and brooding on fat, visceral weights and body weight of the hen pheasant (*Phasianus colchicus*)". *Poul. Sci.* Vol. 38, pp. 1,014–26.

Cantarow, Abraham and Bernard Schepartz. 1962. 'Biochemistry', 3rd. Ed. W. B. Saunders Co. Philadelphia: 938 pp.

Chain, E. B. 1960. "Some observations on the mode of action of insulin" pp. 49–63 *in* Young, F. G., W. A. Broom and F. W. Wolff (1960).

Davis, Malcolm. 1945. "The molt of the Emperor Penguin". *Auk*, Vol. 62, p. 144.

Dickman, Sherman R. 1958. "Why we store fat". *Amer. Scientist*, Vol. 46, pp. 285–93.

Dixon, T. F. and H. R. Perkins. 1956. "The chemistry of calcification" pp. 287–307 *in* Bourne, G. H. (1956).

Dorfman, Albert and Sara Schiller. 1958. "Effects of hormones on the metabolism of acid mucopolysaccharides of connective tissue" pp. 427–53 *in* Pincus, G. (1958).

Dorfman, Ralph I. and Reginald A. Shipley. 1956. 'Androgens. Biochemistry, physiology, and clinical significance'. John Wiley, New York: 590 pp.

Durant, A. J. 1956. "Impaction and pressure necrosis in Canada Geese due to eating dry hulled soybeans". *J. Wildl. Mgt.* Vol. 20, pp. 399–404.

Elder, William H. 1946. "Age and sex criteria and weights of Canada Geese". *J. Wildl. Mgt.* Vol. 10, pp. 93–111.

Engle, Earl T. and Gregory Pincus. 1956. Eds. 'Hormones and the aging process'. Academic Press, New York: 323 pp.

Entenman, C., F. W. Lorenz and I. L. Chaikoff. 1940. "The endocrine control of lipid metabolism in the bird. III: The effects of crystalline sex hormones on the blood lipids of the bird". *J. Biol. Chem.* Vol. 134, pp. 495–504.

Fisher, Harvey I. and Lawrence M. Bartlett. 1957. "Diurnal cycles in liver weights in birds". *Condor*, Vol. 59, pp. 364–72.

Fisher, R. B. 1954. 'Protein metabolism'. Methuen and Co. London: 198 pp.

Freuchen, Peter and Finn Salomonsen. 1958. 'The arctic year'. G. P. Putnam's, New York: 438 pp.

Friley, Charles E., Jr. 1960. "The Canada Geese of Michigan's Swan Creek Highbanks, 1953–1957". *J. Wildl. Mgt.* Vol. 24, pp. 97–9.

Fruton, Joseph S. and Sofia Simmonds. 1953. 'General biochemistry'. John Wiley, New York: 940 pp.

George, J. C. and R. M. Naik. 1958a. "Relative distribution and chemical nature of the fuel store of the two types of fibres in the pectoralis major muscle of the pigeon". *Nature*, Vol. 181, pp. 709–11.

1958b. "Relative distribution of the mitochondria in the two types of fibres in the pectoralis major muscle of the pigeon". *Nature*, Vol. 181, pp. 782–3.

George, J. C. and K. S. Scaria. 1958. "Histochemical demonstration of lipase activity in the pectoralis major muscle of the pigeon". *Nature*, Vol. 181, p. 783.

Glass, Bentley. 1955. "Summary" pp. 950–1,032 *in* McElroy, W. D. and H. B. Glass (1955).

Gordon, Richard S. and Irwin W. Sizer. 1955. "Ability of sodium sulfate to stimulate growth of the chicken". *Science*, Vol. 122, No. 3183, pp. 1,270–1.

György, Paul. 1959. Chairman of "Symposium on protein requirement". *Fed. Proc.* Vol. 18, pp. 1,125–231.

Hagen, Yngvar. 1942. "Totalgewichts—Studien bei norwegischen Vogelarten". *Archiv. für Naturgeschichte*, Vol. 11, pp. 133–73.

*Hanson, Harold C. 1949. "Methods of determining age in Canada Geese and other waterfowl". *J. Wildl. Mgt.* Vol. 13, pp. 177–83.

* 1958. 'Studies on the physiology of Canada Geese (*Branta canadensis interior*)'. Ph.D. Thesis, Univ. of Ill.

* 1959. "The incubation patch of wild geese: its recognition and significance". *Arctic*, Vol. 12, pp. 139–50.

* 1962a. 'Some comparative aspects of organ weights in Canada Geese (*Branta canadensis interior*)'. *Ill. Acad. Sci. Bull.* Vol. 55. In press.

* 1962b. 'Characters of age, sex, and sexual maturity in Canada Geese'. *Ill. Nat. Hist. Surv. Biol. Notes*, No. 49, 15 pp.

Hanson, Harold C. and James H. Gilford. 1961. "The prevalence of some helminth parasites in Canada Geese wintering in southern Illinois". *Ill. Acad. Sci. Trans.* Vol. 54, pp. 41–53.

Hanson, Harold C. and Charles W. Kossack. 1957. "Weight and body-fat relationships of Mourning Doves in Illinois". *J. Wildl. Mgt.* Vol. 21, pp. 169–81.

Hanson, Harold C., Paul Queneau, and Peter Scott. 1956. 'The geography, birds, and mammals of the Perry River region'. *Arctic Inst. North Amer. Spec. Publ.* No. 3, 96 pp.

*Hanson, Harold C. and Robert H. Smith. 1950. 'Canada Geese of the Mississippi Flyway with special reference to an Illinois flock'. *Ill. Nat. Hist. Surv. Bull.* Vol. 25, pp. 67–210.

Hass, George M. 1956. "Pathological calcification" pp. 767–810 *in* Bourne, G. H. (1956).

Herman, C. M., J. H. Steenis and E. E. Wehr. 1955. "Causes of winter losses among Canada Geese". *Trans. Twentieth North Amer. Wildl. Conf.* pp. 161–5.

Hoffman, William S. 1954. 'The biochemistry of clinical medicine'. The Year Book Publishers, Chicago: 681 pp.

Höhn, E. O. 1950. "Physiology of the thyroid gland in birds: a review". *Ibis,* Vol. 92, pp. 464–73.

Holman, Ralph T., M. Wight Taylor and Walter C. Russell. 1945. "The sulfur balance of the non-laying, molting and laying hen". *J. Nutrition,* Vol. 29, pp. 277–81.

Hustich, I. 1957. 'On the phytogeography of the Hudson Bay Lowland'. *Acta Geogr.* Vol. 16, No. 1, 48 pp.

Irving, Laurence. 1960. 'Birds of Anaktuvuk Pass, Kobuk and Old Crow. A study in arctic adaptation'. *U.S. Nat. Mus. Bull.* 217, 409 pp.

Jahn, L. R., J. G. Bell and R. Russell. (1957). 'Results of the 1956 Horicon Marsh managed waterfowl hunt'. *Wis. Cons. Dept.* (Multilith), 28 pp.

Jahn, L. R., A. J. Ruesch and R. A. Hunt. 1951. "1950 Wisconsin goose studies". *Wis. P-R Quart. Prog. Rept.* Vol. 10, No. 1, pp. 27–81.

Johnston, David W. 1962. "Lipid deposition and gonadal recrudescence in response to photoperiodic manipulation in the Slate-colored Junco". *Auk,* Vol. 79, pp. 387–98.

Jordan, James S. 1953. "Effects of starvation on wild Mallards". *J. Wildl. Mgt.* Vol. 17, pp. 304–11.

Kabat, Cyril, R. K. Meyer, Kenneth G. Flakas, and Ruth L. Hine. 1956. 'Seasonal variation in stress resistance and survival in the hen pheasant'. *Wis. Cons. Dept. Tech. Wildl. Bull.* 13, 48 pp.

Kabat, Cyril, Donald R. Thompson, and Frank M. Kozlik. 1950. 'Pheasant weights and wing molt in relation to reproduction with survival implications'. *Wis. Cons. Dept. Tech. Wildl. Bull.* 2, 26 pp.

Kahn, Max and Frederic G. Goodridge. 1926. 'Sulfur metabolism. A review of the literature'. Lea and Febiger, Phil. and New York: 831 pp.

Kendeigh, S. Charles. 1945. "Resistance to hunger in birds". *J. Wildl. Mgt.* Vol. 9, pp. 217–26.

1949. "Effect of temperature and season on energy resources of the English Sparrow". *Auk,* Vol. 66, pp. 113–27.

Keys, Ancel, Josef Brozek, Austin Henschel, Olaf Mickelsen and Henry Longstreet Taylor. 1950. 'The biology of human starvation'. Univ. of Minn. Press, Vols. 1 and 2, 1,385 pp.

King, James R. and Donald S. Farner. 1956. "Bioenergetic basis of light-induced fat deposition in the White-crowned Sparrow". *Proc. Soc. Exp. Biol. Med.* Vol. 93, pp. 354–9.

1960. "Energy metabolism, thermoregulation and body temperature" pp. 215–88 *in* Marshall, A. J. (1960).

King, James R., L. Richard Mewaldt and Donald S. Farner. 1960. "The duration of postnuptial metabolic refractoriness in the White-crowned Sparrow". *Auk,* Vol. 77, pp. 89–92.

Kirkpatrick, C. M. 1944. "Body weights and organ measurements in relation to age and season in Ring-necked Pheasants". *Anat. Record,* Vol. 89, pp. 175–94.

Koch, H. J. and A. F. de Bont. 1944. "Influence de la mue sur l'intensité du métabolisme chez le pinson, *Fringilla coelebs coelebs* L." *Ann. Soc. Roy. Belg.* Vol. 75, pp. 81–6.

Kochakian, Charles D. and Carol Tillotson. 1956. "Hormonal regulation of muscle development" pp. 63–74 *in* Engle, E. T. and G. Pincus (1956).

Krimm, S. 1960. "Structure of frizzle mutant feather keratin". *J. Molecular Biol.* Vol. 2, pp. 247–9.

Latham, Roger M. 1947. "Differential ability of male and female game birds to withstand starvation and climatic extremes". *J. Wildl. Mgt.* Vol. 11, pp. 139–49.

Lipkin, M., T. P. Almy and H. Quastler. 1961. "Stability of protein in intestinal epithelial cells". *Science,* Vol. 133, pp. 1,019–21.

Macpherson, A. H. and T. H. Manning. 1959. 'The birds and mammals of Adelaide Peninsula, N.W.T.' *Nat. Mus. Can. Bull.* 161, 63 pp.

Manchester, K. L. and F. G. Young. 1960. "Insulin and incorporation of amino acids into protein" pp. 113–25 *in* Young, F. G., W. A. Broom and F. W. Wolff (1960).

Marlow, H. W. and H. H. King. 1936. "Sulfur in eggs". *Poul. Sci.* Vol. 15, pp. 377–80.

Marshall, A. J. 1960. 'Biology and comparative physiology of birds'. Academic Press, New York: Vol. 1, 518 pp., Vol. 2, 468 pp.

McCabe, T. T. 1943. "An aspect of collector's technique". *Auk,* Vol. 60, pp. 550–8.

McClean, Franklin C. and Ann M. Budy. 1959. "Connective and supporting tissues: bone". *Ann. Rev. Phys.* Vol. 21, pp. 69–90.

McElroy, William D. and H. Bentley Glass. 1955. 'A symposium on amino acid metabolism'. *McCollum-Pratt Instit. Contrib.* No. 105. The Johns Hopkins Press, Baltimore: 1,048 pp.

Meister, Alton. 1955. "General reactions of amino acids" pp. 3–32 *in* McElroy, W. D. and H. B. Glass (1955).

Meister, Waldemar. 1951. "Changes in the histological structure of the long bones of birds during the molt". *Anat. Rec.* Vol. 111, pp. 1–22.

Miller, Leon L., William T. Burke and David E. Haft. 1955. "Interrelations in amino acid and carbohydrate metabolism. Studies of the nitrogen sparing action of carbohydrate with the isolated perfused rat liver". *Fed. Proc.* Vol. 14, pp. 707–16.

Mitchell, H. H. 1959. "Some species and age differences in amino acid requirements" pp. 11–43 *in* Albanese, A. A. (1959a).

Mitchell, H. H., L. E. Card and T. S. Hamilton. 1926. 'The growth of White Plymouth Rock chickens'. *Univ. Ill. Agr. Exp. Sta. Bull.* 278, pp. 71–132.

1931. 'A technical study of the growth of White Leghorn chickens'. *Univ. Ill. Agr. Exp. Sta. Bull.* 367, pp. 83–139.

Moffitt, James. 1931. "Banding Canada Geese in California in 1931". *Condor,* Vol. 33, pp. 229–37.

Nagra, Clarence L. and Irven O. Buss. 1959. "Change in body weight associated with onset of ovarian recrudescence and oviposition in pheasants". *Condor,* Vol. 61, pp. 348–50.

Neuman, William F. and Margaret W. Neuman. 1958. 'The chemical dynamics of bone mineral'. Univ. Chicago Press: 209 pp.

Neurath, Hans and Kenneth Bailey. 1954. 'The proteins. Chemistry, biological activity, and methods'. Academic Press, New York: Vol. 2, Pt. B, 1,418 pp.

Nice, Margaret M. 1938. "The biological significance of bird weights". *Bird-Banding,* Vol. 9, pp. 1–11.

Oakeson, Barbara B. 1953. "Cyclic changes in liver and spleen weights in migratory White-crowned Sparrows". *Condor,* Vol. 55, pp. 3–16.

1956. "Liver and spleen weight cycles in non-migratory White-crowned Sparrows". *Condor,* Vol. 58, pp. 45–50.

Pincus, Gregory. 1958. Ed. 'Recent progress in hormone research'. Academic Press, New York: Vol. 14, 582 pp.

1962. Ed. 'Recent progress in hormone research'. Academic Press, New York: Vol. 18, 535 pp.

Pitt-Rivers, Rosalind and Jamshed R. Tata. 1959. 'The thyroid hormones'. Pergamon Press, New York: 247 pp.

Popper, Hans and Fenton Schaffner. 1957. 'Liver: structure and function'. McGraw-Hill Book Co. New York: 777 pp.

Pritchard, J. J. 1956. "General anatomy and histology of bone" pp. 1–25 *in* Bourne, G. H. (1956).

Reynold, Albert E., Albert I. Winegrad, Bernard Jeanrenaud and Donald B. Martin. 1960. "Suggested importance of adipose tissue as a site of insulin action and as a major site of metabolic interrelations between carbohydrates and fats" pp. 153–64 *in* Young, F. G., W. A. Broom and F. W. Wolff (1960).

Richdale, L. E. 1947. "Seasonal fluctuations in weights of penguins and petrels". *Wilson Bull.* Vol. 59, pp. 160–71.

Riddle, Oscar and Peta Fay Braucher. 1934. "Studies on the physiology of reproduction in birds". *Amer. J. Physiol.* Vol. 107, pp. 343–7.

Romanoff, Alexis L. and Anastasia J. Romanoff. 1949. 'The avian egg'. John Wiley and Sons, New York: 918 pp.

Roy, A. B. 1960. "The synthesis and hydrolysis of sulfate esters" pp. 205–35 *in* 'Advances in enzymology' Vol. 22, Interscience Publishers, New York.

Rudman, Daniel, Robert L. Hirsch, Forrest E. Kendall, Floyd Seidman and Stanley J. Brown. 1962. "An adipokinetic component of the pituitary gland: purification, physical, chemical, and biologic properties" pp. 89–116 *in* Pincus, G. (1962).

Russell, Jane A. and Alfred E. Wilhelmi. 1960. "Endocrines and muscle" pp. 141–98 *in* Bourne, G. H., Ed. 'The structure and function of muscle. Vol. II. Biochemistry and physiology'. Academic Press, New York: 593 pp.

Shank, Max C. 1959. "The natural termination of the refractory period in the Slate-colored Junco and in the White-throated Sparrow". *Auk,* Vol. 76, pp. 44–54.

Stegman, Leroy C. 1954. "Variation in a flock of the European Starling". *Auk,* Vol. 71, pp. 179–85.

Sturkie, Paul D. 1954. 'Avian physiology'. Comstock Publ. Ass., Cornell Univ. Press, Ithaca: 423 pp.

Tanabe, Y., K. Himeno and H. Nozaki. 1957. "Thyroid and ovarian function in relation to molting in the hen". *Endocrin.* Vol. 61, pp. 661–6.

Tarver, H. 1954. "Peptide and protein synthesis. Protein turnover" pp. 1,199–296 *in* Neurath, H. and K. Bailey (1954).

Trautman, Milton B., William E. Bills and Edward L. Wickliff. 1939. "Winter losses from starvation and exposure of waterfowl and upland game birds in Ohio and other northern states". *Wilson Bull.* Vol. 51, pp. 86–104.

Urist, Marshall R. and Nancy Marie Deutsch. 1960a. "Influence of ACTH upon avian species and osteoporosis". *Proc. Soc. Exper. Biol. and Med.* Vol. 104, pp. 35–9.

1960b. "Osteoporosis in the laying hen". *Endocrin.* Vol. 66, pp. 377–91.

1960c. "Effects of cortisone upon blood, adrenal cortex, gonads, and the development of osteoporosis in birds". *Endocrin.* Vol. 66, pp. 805–18.

Vaurie, Charles. 1961. 'Systematic notes on palearctic birds, No. 49 Columbidae: the genus *Streptopelia*'. *Amer. Mus. Novitates,* 2058, 25 pp.

Wallace, William M. 1959. "Nitrogen content of the body and its relation to retention and loss of nitrogen". *Fed. Proc.* Vol. 18, pp. 1,125–30.

Weller, Milton W. 1957. "Growth, weights, and plumages of the Redhead, *Aythya americana*". *Wilson Bull.* Vol. 69, pp. 5–38.

Wertheimer, Ernst and Eleazar Shafrir. 1960. "Influence of hormones on adipose tissue as a center of fat metabolism" pp. 467–90 *in* Pincus, G. 'Recent progress in hormone research'. *Proc. Laurentian Hormone Conf.* 1959, Vol. 16. Academic Press, New York: 608 pp.

White, Abraham. 1956. "Effects of hormones on protein metabolism" pp. 127–46 *in* Engle, E. T. and G. Pincus (1956).

Wilson, P. N. and D. F. Osbourn. 1960. "Compensatory growth after undernutrition in mammals and birds". *Biol. Reviews,* Vol. 35, pp. 324–63.

Wolfson, Albert. 1954. "Weight and fat deposition in relation to spring migration in transient White-throated Sparrows". *Auk,* Vol. 71, pp. 413–34.

Young, F. G., W. A. Broom and F. W. Wolff. 1960. 'The mechanism of action of insulin. A symposium'. Charles C. Thomas, Springfield, Ill.: 320 pp.

Young, Leslie and George A. Maw. 1958. 'The metabolism of sulphur compounds'. Methuen and Co., London: 180 pp.

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