MOLT PATTERNS AND WEIGHT CHANGES OF THE AMERICAN WOODCOCK

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FEW data are available on the timing and extent of molts in the American Woodcock (*Philohela minor*). Pettingill (1936) described the plumages, pterylae, and certain aspects of the molt sequence. Martin (1964) studied flight feather molt and developed a rapid aging technique, while Sheldon (1967) provided molt data for 13 birds. Numerous workers have reported weights of male and female woodcock from various geographical areas at different times of the year (Blankenship, 1957; Glasgow, 1958; Goodrum and Reid, 1952; Lynch, 1952; Liscinsky, 1972; Mendall and Aldous, 1943; Pettingill, 1936; and Tufts, 1940). However, only Greeley (1953) in Wisconsin, Sheldon (1967) in Massachusetts, and Marshall (1970) in Minnesota presented weight data by age and sex classes. Seasonal changes in body weights could indicate periods of stress and might be useful in understanding the timing of such biological events as molt and migration.

A detailed investigation of molt and body weights of woodcock was initiated in 1969. The study was primarily conducted in Maine, although late fall and winter weights of woodcock were obtained in New Jersey, Mississippi, and Louisiana. This paper discusses (1) the sequence, duration, and intensity of molt, (2) seasonal changes in body weights, and (3) the relationships between molt, weight change, fat deposition, and migration.

METHODS

General.—We examined most woodcock in conjunction with various banding programs. In Maine, the birds sampled included those caught on singing-grounds in the spring, on summer fields at night, trapped during the summer in diurnal covers, and shot during the fall hunting season. Woodcock in New Jersey were captured by night-lighting on nocturnal fields during fall migration. In Mississippi and Louisiana, wintering birds were captured by night-lighting. The age and sex of each woodcock handled was determined according to Martin (1964). Adults include all after-hatching-year birds while immatures are hatching-year woodcock. Molt data were collected from June through November, 1969 and 1970. Most of the woodcock were weighed in 1970 and 1971, although a few spring weights date back to 1961.

Molt Study.—Eight hundred and fifty woodcock, captured in the summer or shot during the fall in Maine, were examined. Molt information from 33 areas of the body (Pettingill, 1936; Holmes, 1966) was recorded from 319 birds. The following areas were examined for molt: malar region, frontal region, coronal region,* temporal region, auricular region, occipital region, anterior cervical region,* interscapular region,* dorsal region,* pelvic region, humeral tract, posterior cervical region, axillar region, sternal region,* abdominal region, femoral tract,* crural tract,* primaries,* under greater primary coverts,* under lesser primary coverts, upper greater primary coverts, upper middle primary coverts,

secondaries,* under greater secondary coverts,* under middle secondary coverts,* under lesser secondary coverts,* upper greater secondary coverts,* upper middle secondary coverts,* upper lesser secondary coverts,* marginal coverts, rectrices,* under tail coverts, upper tail coverts. The extent of molt, ranging from 0 (no molt) to 3 (heavy molt) was recorded for the 33 areas on 176 birds, while only the presence (+) or absence (–) of molt on these areas was noted for the remaining 143 woodcock. The number of molting primaries, secondaries, and rectrices was counted on all 319 woodcock. Summer banding crews examined selected areas, indicated by asterisks above, on an additional 531 birds. Although these data were not quantitative they were useful in interpreting the August sample, a period when birds were difficult to capture. The termination of flight feather molt was determined by examining 2,629 wings from woodcock shot during 1970 in Maine. The wings were obtained from the Wing Collection Survey of the U.S. Fish and Wildlife Service.

The beginning, ending, and peak of molt did not differ significantly between sexes, nor between years, so the data were combined and expressed only by age and weekly collection periods. We defined the duration of molt for a particular area on the body as the length of time between the first and last occurrence of molt on that area in the total sample of birds examined. Frequency histograms were drawn for each area expressing the percentage of birds molting in each weekly sample and the period of maximum intensity was noted. Figures for particular feathers or areas were combined when they had approximately the same duration and period of highest intensity.

We calculated a molt index for each bird by multiplying the average weight of feathers from each of 33 areas by the degree of molt observed (0–3) on each area and summing all 33 values. In doing this we assumed that the energy needed to renew feathers on each area was proportional to the weight of the feathers from that area (Holmes, 1966). Average feather weights for individual areas were obtained from four woodcock by plucking, oven drying, and weighing feathers to the nearest 0.001 g. This sample was comprised arbitrarily of two males and two females which had completed their molt.

Weight Study.—More than 2,100 woodcock were weighed. Birds were weighed during every month of the year except December, February, and March. Most woodcock were weighed alive, although some October and November weights were of shot birds. Weights were determined with spring scales having a capacity of 300 grams. Spring scales were periodically checked against a more sensitive balance to insure accuracy within two grams. Average weights were calculated by age and sex according to time periods. The chronology of weight change was not significantly different between the summers of 1970 and 1971. We obtained a fat index for 116 birds by recording the degree of deposition, ranging from 0 (no fat) to 3 (very fat) on seven areas and averaging the values. The areas examined were: furcula region, sternal line, pectoral feather tract, an area running from the pectoral tract dorsally behind the humerus to the scapula region, abdominal region, rump, and thigh.

A probability level of 0.05 was required for significance in all statistical tests.

RESULTS

Postnuptial Molt.—The adult postnuptial molt was a complete molt, beginning in June and ending by mid-October. In all cases, the percentage of birds molting particular areas throughout the summer exhibited a normal distribution with very few individuals molting at the extremes. Feather replacement usually started with the loss of the first and second primaries in

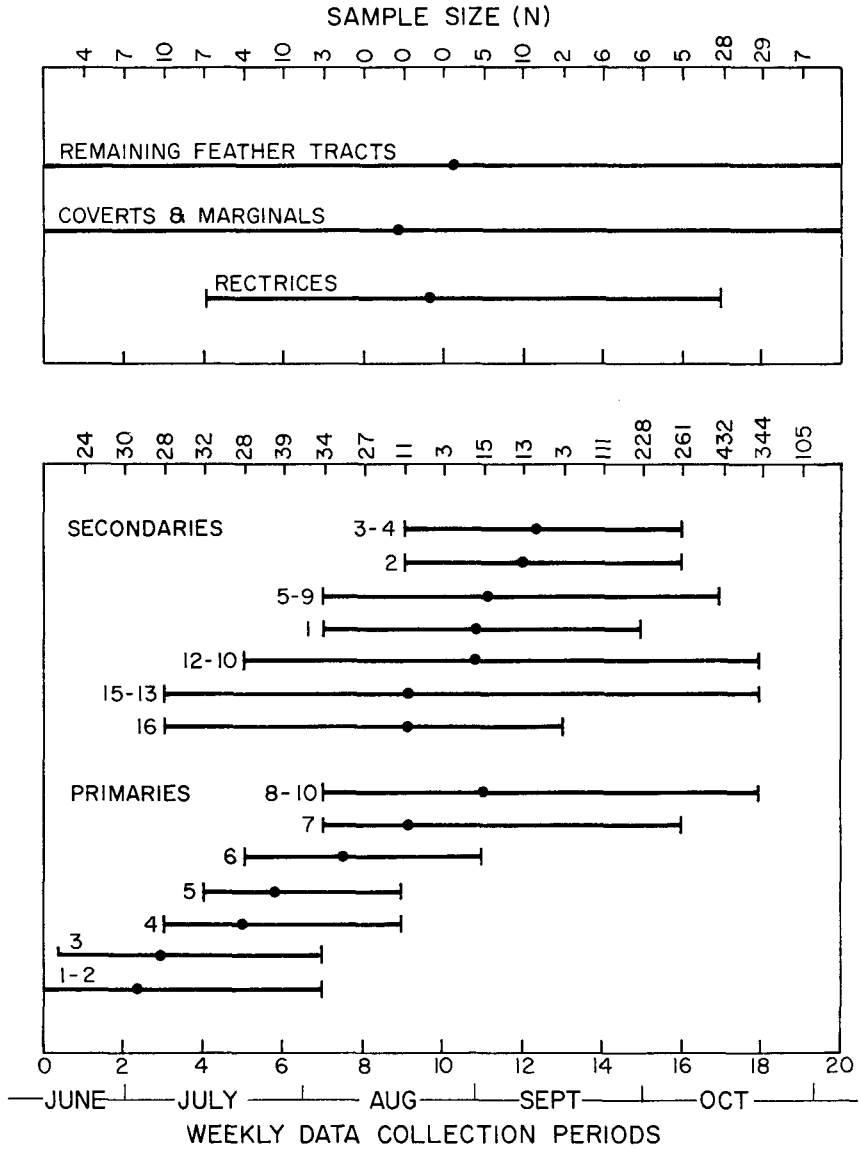


FIG. 1. Chronology of molt of adult Woodcock, 1969–1970. Each dot represents the time of highest intensity of molt.

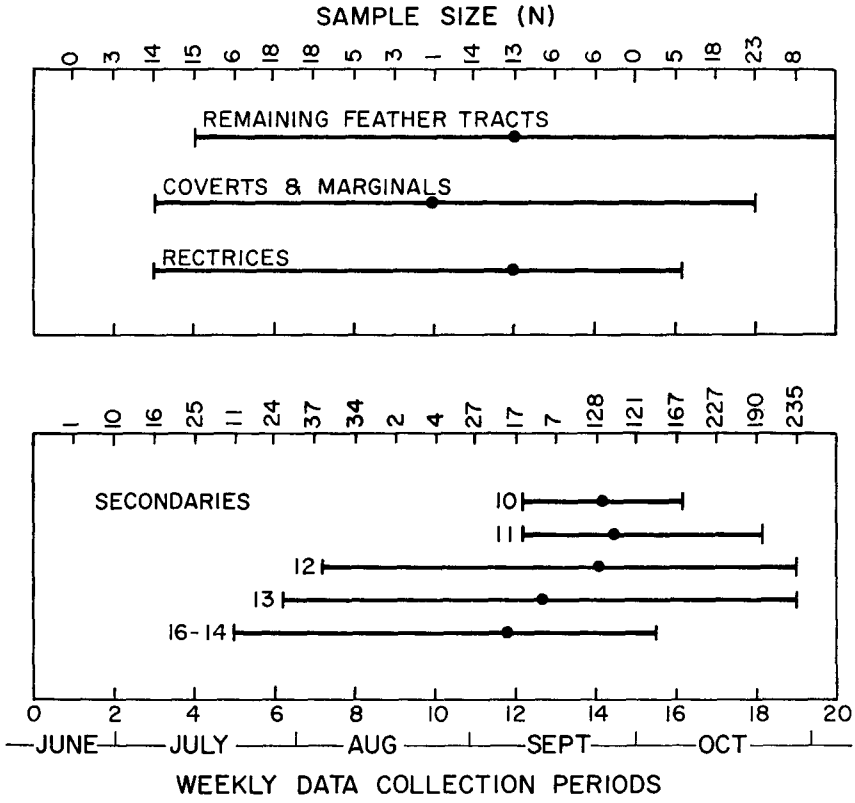


FIG. 2. Chronology of molt of immature Woodcock, 1969–1970. Each dot represents the time of highest intensity of molt.

late June or early July (Fig. 1). Primaries one through eight were dropped sequentially with the emergence and partial growth of one feather before the next was lost. The molt of the first and second primaries tended to overlap while the modified primaries eight through ten were generally dropped simultaneously.

Ability to fly was apparently retained throughout the summer with the majority of the primaries replaced before the secondaries started molting (Fig. 1). The secondary molt exhibited more overlap than did that of the primaries, but like the primaries, the innermost secondaries were molted first. As the molt progressed from the proximal end towards the center of the feather tract, the distal secondaries were also replaced. This resulted in feathers being replaced in sequence from both ends of the feather tract.

TABLE 1

FREQUENCY DISTRIBUTION OF THE LAST SECONDARY REPLACED BY IMMATURE WOODCOCK, 1970

Last Secondary Molted:	1–7	8	9	10	11	12	13	14	15–16
Number of Young Birds:	0	1	6	11	52	87	43	3	0
Percent Distribution:	0	1	3	5	25	42	23	1	0

Welty (1962) noted that a similar pattern of flight feather molt is common in passerine species. Several adult females caught in late August renewed all secondaries simultaneously. Perhaps these birds were late nesters or re-nesters which caused delayed initiation of molt. Simultaneous loss of feathers could be a physiological mechanism whereby the secondary molt is accelerated. Based on studies of recaptured birds, individual primaries and secondaries required from 14 to 20 days to fully develop. Pettingill (1936) indicated that all retrices were replaced simultaneously. While we found this to be a common pattern, considerable variation between birds did occur.

The capital, ventral, spinal, humeral, femoral, and crural tracts exhibited a prolonged molt extending from late June through October (Fig. 1). The molt period of the coverts and marginals corresponded closely with flight feather replacement. As each primary was molted, the corresponding upper greater primary covert was also replaced. There was a tendency for all secondary coverts in an individual tract to be molted simultaneously, with the under greater secondary coverts being molted last.

Postjuvenal Molt.—Several young birds captured in late June were still undergoing the postnatal molt. The postjuvenal molt generally began in late July and, similar to the adults, ended in mid-October. However, unlike the postnuptial molt, the postjuvenal molt was incomplete. Immature woodcock did not molt primary feathers and replaced only the proximal secondaries (Fig. 2), as reported by Pettingill (1936) and Martin (1964).

Possibly, the number of secondaries molted was related to the time of hatching (Table 1). If woodcock re-nest, then the young from re-nests might renew fewer secondaries when compared to immatures hatched earlier. Re-nesting was not indicated by the data since the frequency distribution was continuous and not bimodal. The body molt of the young birds was complete as was the replacement of the retrices. As in adults, the duration of molt was longest for the major feather tracts.

Seasonal Weight Changes.—A total of 1,469 woodcock were weighed in Maine between June and November. Sample sizes generally exceeded ten birds weekly for each of the four age-sex classes except during late September

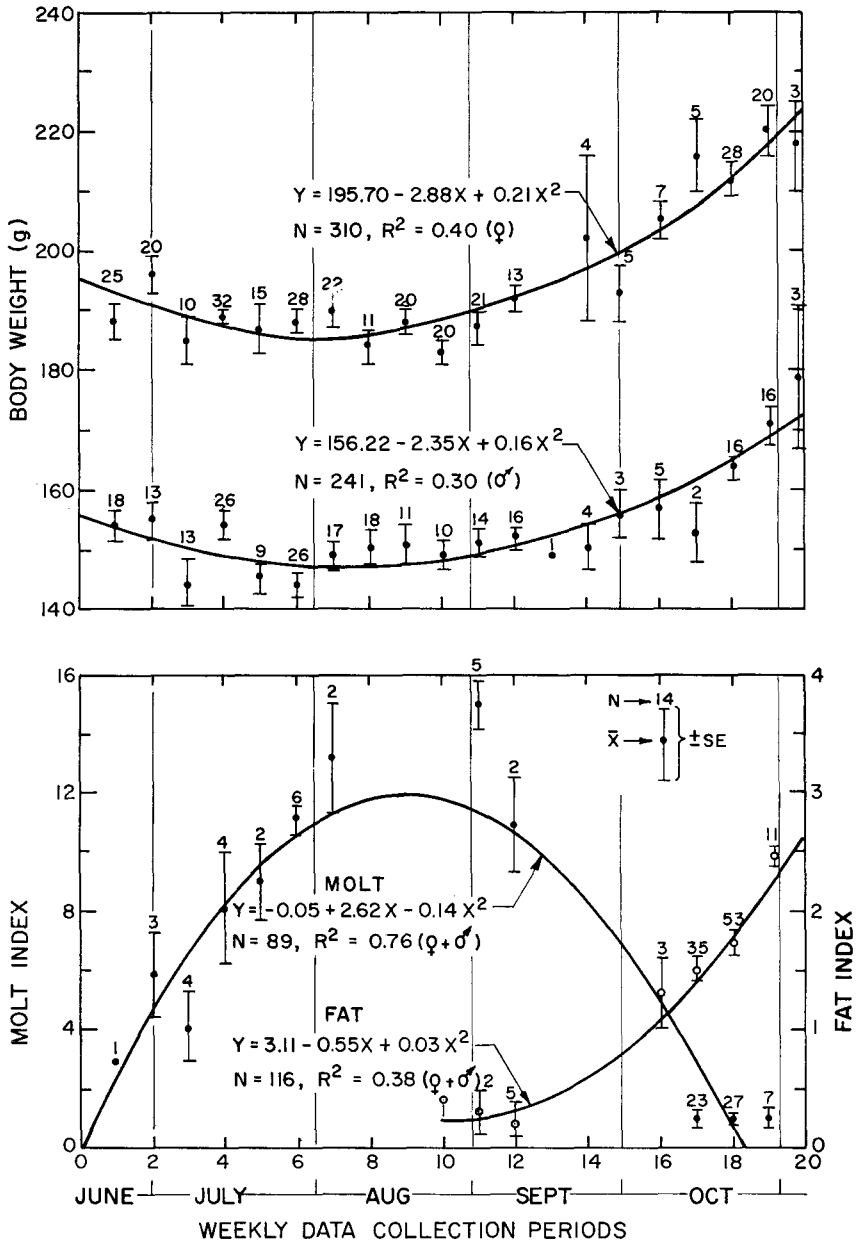


FIG. 3. Relationships between molt, body weight, and fat deposition of adult male and female Woodcock.

TABLE 2

LATE FALL THROUGH SPRING WOODCOCK BODY WEIGHTS BY SEX, LOCATION AND ACTIVITY

Date	Location	Activity	Male		Female	
			$\bar{x} \pm$ S.E.	(N)	$\bar{x} \pm$ S.E.	(N)
15–29 November (1970–1971)	New Jersey	Migrating	166 ± 1	(110)	205 ± 2	(94)
18–28 January (1971)	Mississippi–Louisiana	Wintering	155 ± 1	(111)	192 ± 1	(95)
April (1965–1970)	Maine	Reproducing	135 ± 1	(94)	217 ± 4	(8)
May (1961–1970)	Maine	Reproducing	137 ± 1	(115)	213 ± 5	(9)

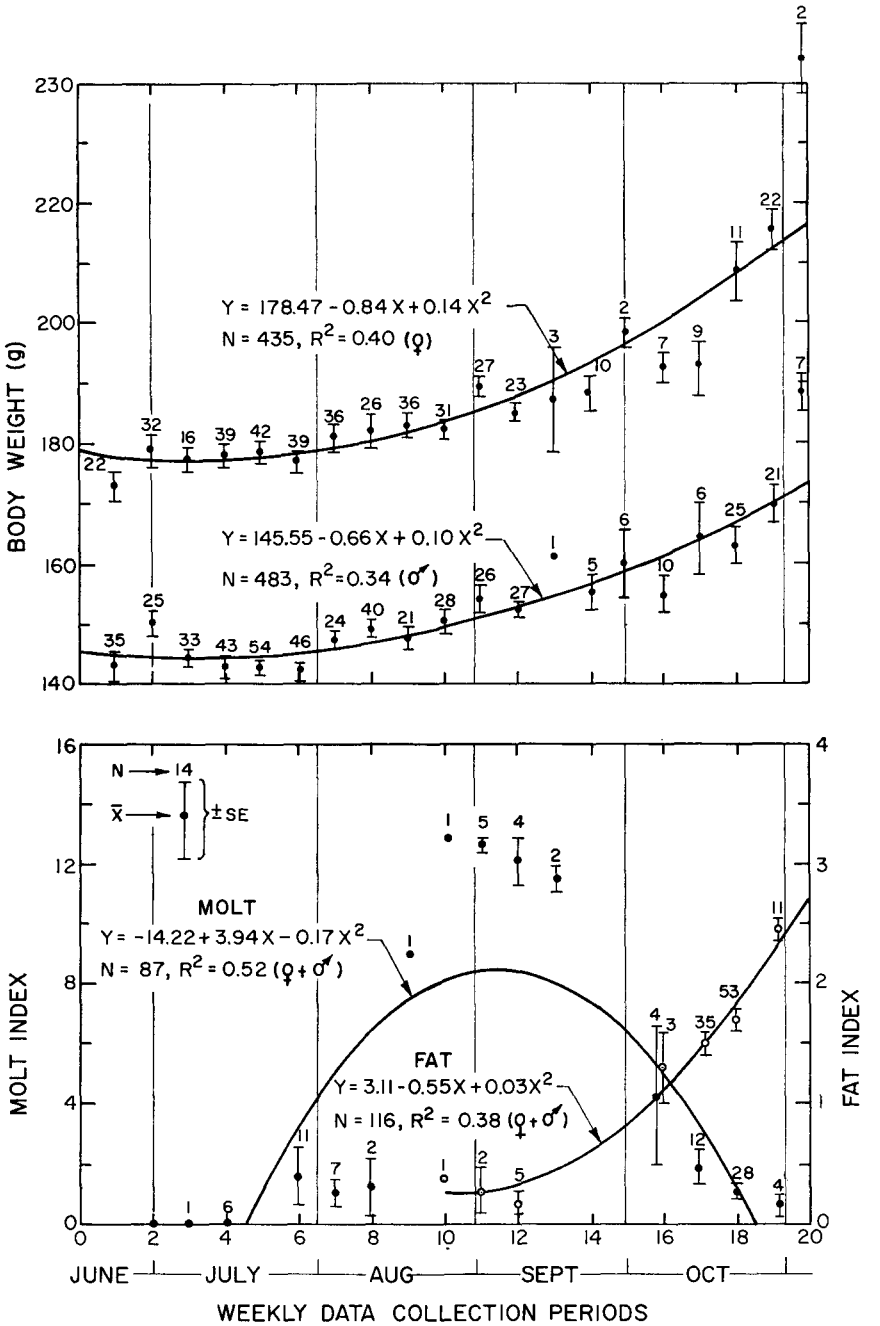
and early October, when preseason banding had ceased and few specimens were submitted by hunters.

Adults lost weight in early summer but by the middle of September were rapidly regaining weight. In contrast, immatures steadily grew heavier during June and July with the rate accelerating in August and September. Immatures of both sexes weighed as much as adults by late August and females of both age classes were significantly heavier than males throughout the entire summer.

Six hundred and thirty-six woodcock were weighed between late November and May (Table 2). Data for age classes were combined because differences were insignificant. Woodcock in Maine reached peak weights in late October and early November (Fig. 3, Fig. 4). Migrating birds captured at Cape May, New Jersey, were about five per cent lighter than the Maine birds (Table 2). Woodcock wintering in Mississippi and Louisiana were approximately six percent lighter than the fall migrants at Cape May. In the spring, early arriving males in Maine were at their lowest point in their annual weight cycle but gradually gained weight during May and June, before decreasing again during the summer molt period. Limited data on the spring weights of females indicated that these birds were lighter than birds during the fall pre-migratory period (Fig. 3, Fig. 4) but were heavier than fall migrants in New Jersey and wintering birds (Table 2). The relatively high body weights of females in spring were probably due to ovarian development.

DISCUSSION

The interrelationships between molt, fat deposition, and body weight of adult woodcock are shown in Figure 3. Peak molt coincided with a period of weight loss in both sexes and was probably related to the increased energy


BODY WEIGHT (g)
Y = 178.47 - 0.84 X + 0.14 X²
N = 435, R² = 0.40 (♀)
Y = 145.55 - 0.66 X + 0.10 X²
N = 483, R² = 0.34 (♂)
N → 14
X̄ → ±SE
MOLT
Y = -14.22 + 3.94 X - 0.17 X²
N = 87, R² = 0.52 (♀+♂)
FAT
Y = 3.11 - 0.55 X + 0.03 X²
N = 116, R² = 0.38 (♀+♂)
MOLT INDEX
FAT INDEX
JUNE
JULY
AUG
SEPT
OCT
WEEKLY DATA COLLECTION PERIODS

demand of plumage replacement. As the intensity of molt decreased in late September, birds commenced accumulating fat and rapidly gained weight.

Immatures gradually gained weight throughout the summer without a weight loss during the peak of molt (Fig. 4). The postjuvenal molt occurred later, and although not as intensive, ended at approximately the same time as the adult postnuptial molt. Apparently the abbreviated molt of young woodcock is less energy demanding, thus enabling them to gradually gain weight throughout the summer and attain adult size by late summer.

It is generally recognized that birds of the north temperate region store fat immediately prior to migration. In the present study, fat was deposited during the fall by adult and immature woodcock at the same rate. A significant negative correlation ($P < 0.001$) was found between fat deposition and molt index indicating that fall deposition of premigratory fat in woodcock does not start until after the peak molt has passed. Fall weight gain was also directly correlated ($P < 0.001$) with fat deposition in both sexes. Holmes (1966) concluded that during periods of rapid migration of the Red-backed Sandpiper (*Calidris alpina*) molt was suspended, although some body molt did occur during the initial "drifting" phase of migration. Molt, premigratory fattening, and migration are all energy demanding events and are generally sequenced to enable a bird to maintain a positive energy balance (West, 1960). The data presented here on the molt, fat deposition, and weight gain indicate that woodcock in Maine were not physiologically prepared to migrate until mid-October. This finding is in general agreement with Mendall and Aldous (1943), who felt that the migration in Maine did not start until October with the bulk of the migrants passing through the New England region throughout October.

Assuming that weights reflect physical condition, the data presented here indicate that the spring is a time of great stress and possible mortality to male woodcock. Spring is the time of migration, courtship, and reproduction. These strenuous activities, often occurring in sub-freezing temperatures, consume much energy while ice or snow threaten to make food unavailable. F. W. Martin (pers. comm.) found that annual mortality rates of woodcock banded in Louisiana appeared higher for adult males than adult females. Sheldon (1967) has postulated that males, migrating north first, have a shorter life expectancy than females because they are subjected to more severe weather and stress. Weight data suggested that a second but less intense period of stress for adults occurred during the peak of the molt in August. Presumably

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FIG. 4. Relationships between molt, body weight, and fat deposition of immature male and female Woodcock.

weight loss then was not critical because earthworms are generally plentiful during the summer, except perhaps during prolonged droughts.

SUMMARY

A study of molt and changes in body weight of American Woodcock was conducted to better understand the summer and fall behavior of these birds and to indicate periods of physiological stress. The postnuptial molt of adults was a complete molt beginning in late June and ending by the middle of October. In contrast, the postjuvenal molt was a less intensive partial molt beginning in mid-July but also extending to the middle of October. Both male and female adult birds experienced weight loss in August during peak molt. Young birds gradually gained weight throughout the summer. Fat deposition was negatively correlated with molt while fall body weights were positively correlated with fat deposition. The data indicated that the majority of Maine woodcock are not physiologically prepared for migration until mid-October. Weights of adult males during the spring suggested that this is an important period of stress for these birds.

ACKNOWLEDGMENTS

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NEW LIFE MEMBER

A recent addition to the list of Life Members of the Wilson Society is Maurice Broun, who needs no introduction to the hosts of ornithologists and birders who have gathered each fall at the Hawk Mountain (Pa.) Sanctuary to study the southbound raptor flight. From 1934 until his retirement in 1966 Mr. Broun was Curator of the Sanctuary. His early year experiences there were reported in the classic book, "Hawks Aloft." Since his retirement Mr. Broun has managed his own private 60-acre wildlife refuge, and busies himself making a bird and plant inventory of that area near New Ringgold, Pennsylvania. He is also a competent botanist and has authored a work on North American ferns. In 1952 Muhlenberg College awarded him an honorary D.Sc. degree for his conservation work. Mr. Broun is a member of the A.O.U., the D.V.O.C., the American Fern Society, and both the Eastern and Northeastern Bird-Banding Associations. He is married with no children.