BODY AND ORGAN MASS AND BODY COMPOSITION OF POSTBREEDING FEMALE LESSER SCAUP

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ABSTRACT.—Changes in body and organ mass and body composition of postbreeding female Lesser Scaup (*Aythya affinis*) were investigated in the prairie-pothole region of southwestern Manitoba. Body mass was lowest during the wing molt and peaked during the migratory period. Most digestive organs gradually increased in mass through the postbreeding season. Lipid reserves remained relatively constant from the preflightless through the postflightless periods ($\bar{x}$ = 43 g). The marked increase in lipids in the migratory period ($\bar{x}$ = 183 g, $P <$ 0.05) corresponded with premigratory hyperphagia. Time spent feeding explained 87% of the variation in lipid levels during the postbreeding season. Protein reserves declined with the onset of wing molt ($P < 0.001$) and increased during the postflightless period ($P < 0.05$). Breast muscle mass followed a similar pattern and was strongly correlated with molt intensity ($r = 0.799$, $P < 0.001$). Protein reserves, in particular the breast muscles, provide at least part of the protein required for feather production. Low body mass and lipid reserves during molt may not indicate energetic or nutritional stress but, alternatively, may be part of a postbreeding strategy to minimize energy demands and to reduce the length of the flightless period. *Received 12 September 1986, accepted 5 May 1987.*

ANATIDS often reach an annual low in protein and lipid reserves near the end of breeding efforts (Korschgen 1977, Drobney 1980, Brown 1981, Reinecke et al. 1982, Hohman 1986). Immediately after breeding most anatids undergo a complete molt of body, tail, and wing feathers that may be costly in terms of time, energy, and nutrients (Blackmore 1969, Payne 1972, Dolnik and Gavrilov 1979). Following the molt and before fall migration, lipid reserves increase.

Physiological aspects of the recovery from breeding efforts, molt and its associated energetic and nutritional costs, and preparation for fall migration are not well known in anatids. Postbreeding studies of Mallards (*Anas platyrhynchos*; Young 1981) and Redheads (*Aythya americana*; Bailey 1981) indicated that males were able to meet the nutritional and energetic demands of molt following breeding. Lipid levels in both Mallards and Redheads increased from breeding into the early periods of prebasic molt, then temporarily declined during the flightless period. In Mallards protein levels declined from breeding through the flightless period, whereas in Redheads it started to increase before the flightless period. Nonbreeding Redheads maintained higher protein levels from breeding through late molt than birds that had bred previously.

Changes in body condition of females immediately following breeding are largely unknown. The investment of time, energy, and nutrients in reproduction differs from that in males. The breeding period for females is often longer than that for males because of the brood period, which may shorten the time available for molt and premigratory preparation. In female American Black Ducks (*Anas rubripes*; Reinecke et al. 1982), general patterns of lipid levels and mass of the flight muscles following breeding were similar to those seen in Mallard and Redhead males (Young and Boag 1982, Bailey 1985); however, protein content remained constant. This study may represent an incomplete picture of the changes just before and during molt because sample sizes were small and classification (postlaying, molting, and fall periods) provided less detailed differentiation of postbreeding birds than the studies of males.

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We report changes in body and organ mass and body composition of female Lesser Scaup during the period immediately following breeding (July–October), which includes the wing molt and early fall migration. Results were evaluated with regard to changes in molt, activities, and feeding ecology.

STUDY AREA AND METHODS

The study was conducted in the prairie-pothole region near Erickson, Manitoba, 240 km west-northwest of Winnipeg and 35 km north of Minnedosa. The study area included approximately 4,700 ha near Erickson and other ponds within 32 km to the west (Austin 1983). Wetlands studied included shallow ephemeral ponds, seasonal or semipermanent ponds, and permanent lakes (for details see Rogers 1964, Sunde and Barcia 1975, Austin 1983, Afton 1983). Lesser Scaup are among the most common waterfowl species breeding in the area and are also common during postbreeding and migration periods.

Birds were collected from mid-July through October 1981–1982, and in July 1984. In addition, 8 flightless birds were obtained from the Long Island Bay area of Lake Winnipegosis in August 1982. These birds did not differ significantly in body or organ mass or molt scores (Austin and Fredrickson 1986) from birds collected in the Erickson area (Mann-Whitney test, $P > 0.05$), and, therefore, data from both areas were pooled.

Females were classified into 4 molt periods: (1) preflightless birds that had completed or terminated breeding efforts but had not yet lost flight feathers; (2) flightless birds with soft, growing primary feathers; (3) postflightless birds with new primary feathers, not part of migratory flocks but capable of flight; and (4) migratory scaup in flocks staging or migrating through the area. Preflightless females were distinguished from incubating or brood females by behavioral observations (e.g. inactivity for long periods, associations with other female Lesser Scaup, absence of a mate or brood) and, in some birds, the presence of incoming feathers in the brood patch. Most postflightless birds were collected before the numbers of scaup in the area increased with fall migration, and some birds were identified by the presence of soft primaries.

Birds were weighed to the nearest 5 g on a Pesola spring scale for total body mass, corrected for food content. Total body length and the lengths of the wing, tarsus, and keel were recorded to the nearest millimeter. Internal organs, right breast muscles (pectoralis, supracoracoideus, and coracobrachiolis), right leg muscles with their insertion or origin on the femur or tibiotarsus, and right leg bones (femur, tibiotarsus, and fibula) were weighed to the nearest 0.01 g. All adhering fat and contents of the digestive tract were removed before weighing. Lengths of the esophagus-proventriculus and intestine were determined to the nearest 5 mm. Eviscerated mass included the mass of feathers, lungs, and kidneys. Visceral and peritoneal fat deposits were removed and weighed to the nearest 0.1 g.

For composition analysis, feathers were clipped with commercial sheep shears; remaining feathers were plucked by hand. An entire carcass, including all internal organs, was ground to a homogenate in a commercial food grinder by passing the body through the grinder at least 6 times. A random sample was removed after the final homogenation and frozen for analysis. Composition analyses were performed by the University of Missouri Agriculture Experiment Station Chemical Laboratories following AOAC procedures (Horowitz 1980). Results were expressed as grams of total body mass. Protein content refers to ash-free lean dry mass.

Data from 1981 and 1982 were pooled because only total body mass showed a significant difference between years (*t*-test, $P < 0.05$; Conover 1980). Birds collected in July 1984 differed from 1981 and 1982 birds in several measurements (fresh body mass, molt intensity, new feather index, and mass of oviduct and breast muscle) (*t*-test, $P < 0.05$). The 1984 birds were collected 20 days earlier than birds in other years, however, and the body and molt measurements strongly indicate that they represented the earliest part of a continuum of the preflightless period. Because 1984 birds can be classified as preflightless, based on behavior and wing molt, the data from these birds were pooled with 1981 and 1982 birds to more completely represent the conditions occurring in the preflightless period. Differences among periods were analyzed using Kruskal-Wallis tests (Conover 1980) because of their heterogeneous variances and the small, unequal sample sizes among periods.

RESULTS

Body mass.—Changes in total body mass (TBM) and eviscerated body mass (EBM) were similar during the postbreeding season (Table 1), although changes in EBM were more marked. Birds reached their lowest EBM in the flightless period ($P < 0.001$) and subsequently increased in the postflightless ($P < 0.05$) and migratory periods ($P < 0.001$). During the migratory period mass continued to increase as birds fed intensively and birds from northern areas arrived (Austin 1983). Lipid content explained 76.5% of the changes in EBM.

Gonads.—Ovaries and oviducts regressed rapidly during the preflightless period. These organs had lost over half of their original mass

TABLE 1. Mean body and organ mass for female Lesser Scaup in relation to postbreeding status.[a] Collection from Erickson, Manitoba, 1981–1982 and 1984. Values are means ± 0.05 confidence intervals. Numbers in parentheses are sample sizes.

Category	Preflightless (21)		Flightless (24)		Postflightless (8)		Migratory (32)
Total body mass (g)	688 ± 57.49	**	647 ± 17.9		693 ± 80.2	***	842 ± 29.1
Eviscerated body mass (g)	407 ± 11.51	***	506 ± 17.4	*	543 ± 37.5	***	661 ± 31.9
Organ mass (g)							
Esophagus-proventriculus	7.13 ± 0.94		7.79 ± 0.51		8.42 ± 0.74	***	6.91 ± 0.26
Intestine	24.74 ± 3.35		32.36 ± 2.88		36.65 ± 11.26		33.50 ± 2.37
Gizzard	29.23 ± 3.63	**	31.98 ± 1.93		35.54 ± 5.02		35.98 ± 2.40
Liver	21.67 ± 3.97		22.51 ± 1.20		24.22 ± 5.05		26.75 ± 2.19
Heart	6.39 ± 0.79	**	5.76 ± 0.24	***	7.34 ± 0.87		7.74 ± 0.28
Kidney	7.64 ± 0.95	**	9.12 ± 0.53		8.87 ± 0.92		9.55 ± 0.44
Oviduct	1.37 ± 0.87	**	0.781 ± 0.07		0.574 ± 0.12		0.600 ± 0.04
Ovary	0.40 ± 0.34	*	0.191 ± 0.02		0.177 ± 0.02		0.176 ± 0.02
Organ lengths (mm)							
Esophagus-proventriculus	219 ± 17.8		225 ± 6.5		236 ± 20.5		230 ± 6.5
Intestine	1,881 ± 96.1		1,827 ± 57.0	*	1,943 ± 175.0		1,947 ± 0.02
Right pectoral muscle (g)	57.22 ± 7.43	***	38.41 ± 2.07	***	48.56 ± 5.96	***	58.72 ± 1.52
Right leg muscles (g)	25.89 ± 2.29	**	27.51 ± 0.94		26.07 ± 2.38	***	22.68 ± 0.75
Right leg bones (g)	3.63 ± 0.18		3.52 ± 1.69		3.48 ± 0.20		3.51 ± 0.07

[a] Asterisks indicate significant differences between periods. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

($P < 0.01$) by the flightless period (Table 1), and mass continued to decline over the postbreeding season. Variation in mass was greatest during the preflightless period, indicating differences in recent breeding histories and timing among individuals. For example, birds collected in 1984 were shot an average of 20 days earlier and had significantly larger oviducts than birds collected in 1981 or 1982 ($P < 0.01$). Birds collected in 1984 probably represented the early portion of the preflightless period because of their molt scores (Austin and Fredrickson 1986) and larger reproductive organs.

Organ mass and length.—Most digestive organs gradually increased in mass during the postbreeding season (Table 1). Only changes in gizzard ($P < 0.01$) and esophagus-proventriculus ($P < 0.001$) mass were significant. Gizzard mass increased from the preflightless to the flightless period ($P < 0.01$). Esophagus-proventriculus length showed little change during the postbreeding season, whereas intestine length increased from the flightless to the postflightless period ($P < 0.05$)

Lipid reserves.—Lipid reserves remained relatively constant through the postflightless period ($P > 0.05$, $\bar{x} = 46.5$ g) but increased markedly from the postflightless to the migratory period ($P < 0.001$, $\bar{x} = 188.1$ g) (Table 2). Fat levels ranged from 5.5% to 33.5% during the migratory period, and later migrants generally were fatter than earlier migrants. Time spent

foraging (Austin 1987) was positively correlated with fat content ($r = 0.933$) and explained 87% of the variation in fat. This relationship closely follows that found for postbreeding male Redheads (Bailey 1985).

Mineral content.—Ash content of the carcass (Table 2) and mass of the right leg bones (Table 1) remained relatively constant through the postbreeding season.

Protein reserves.—Protein reserves were lowest during the flightless period ($P < 0.001$). After the birds regained flight, protein levels gradually increased over the postflightless ($P < 0.05$) and migratory periods, although protein content among individuals varied greatly during these periods (Table 2). Changes in breast muscle mass were similar to those of total protein content, including a decline of 28% (15 g) from the preflightless to the flightless period ($P < 0.001$). Leg muscle mass increased ($P < 0.01$) at the same time that breast muscle mass declined and was lowest ($P < 0.001$) in the migratory period.

DISCUSSION

The increases in organ mass during the earlier periods of the postbreeding season may reflect, at least in part, a recovery from the low levels reached during breeding. Low feeding activity and high nutritional demands during breeding result in low metabolic reserves and small digestive organs among breeding females

TABLE 2. Carcass composition and mean mass of fat depots of female Lesser Scaup collected during the postbreeding season, July–October 1981–1982 and 1984.[a] Values shown are means ± 0.05 confidence intervals. Protein content refers to ash-free dry mass.

	Preflightless		Flightless		Postflightless		Migratory
Composition (g)							
Water	467 ± 34	**	432 ± 31		462 ± 61		463 ± 32
Lipid	50.7 ± 31.9		37.2 ± 14.5		46.5 ± 21.6	***	188.1 ± 82.7
Ash	31.3 ± 5.5		29.2 ± 5.2		31.4 ± 7.4		30.2 ± 6.0
Protein	147.6 ± 8.6	***	134.4 ± 6.9	*	144.6 ± 18.9		149.4 ± 11.3
Fat depots (g)							
Abdominal	0.9 ± 1.3		0.7 ± 0.5	*	2.0 ± 1.5	***	15.9 ± 4.6
Visceral	1.9 ± 2.7		1.3 ± 0.8		1.9 ± 1.6	***	13.0 ± 3.0

[a] Asterisks indicate significant differences between periods. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(Ankney 1977, Korschgen 1977, Brown 1981, Reinecke et al. 1982, Drobney 1984). Increased mass of digestive organs also may reflect increased alimentary efficiency (Kirkpatrick 1944, Anderson 1972, Ankney 1977) during periods of high molt intensity (preflightless, flightless, and postflightless periods) (Austin and Fredrickson 1986). Digestive efficiency may increase because metabolic reserves are minimal, food intake (foraging time) is low (Austin 1987), and energetic and nutritional requirements have increased for feather synthesis (Payne 1972, Dolnik and Gavrilov 1979). The significant increase in esophagus-proventriculus mass can be related to its role in protein digestion and to high protein demands during feather synthesis (Dolnik and Gavrilov 1979). Food quality (Pendergast and Boag 1973, Moss 1974, Miller 1975, Ankney 1977) probably had little influence on changes in digestive organs in this study because the composition of *Gammarus*, the primary food item of scaup in the study area (Rogers 1964, Austin 1983), remained relatively constant during the postbreeding season (Mathius et al. 1982).

The gizzard was the only digestive organ that increased from the preflightless to the flightless period. A similar increase in gizzard mass was observed in male Redheads between the late premolt and early (wing) molt periods (Bailey 1981) and in Black Ducks between postlaying and flightlessness (Reinecke et al. 1982). The gizzard is believed to be a source of protein for egg formation during the breeding period (Korschgen 1977, Ankney 1977, Krapu 1981); however, the continued gradual increase in mass from the flightless through the migratory period indicates that this organ is not a major protein source for feather formation.

The decline of breast muscle mass may be related at least in part to atrophy from disuse during flightlessness. Breast muscle mass increased in the last third of the flightless period, however, and was positively correlated with molt intensity ($r = 0.799, P < 0.001$). A similar, but curvilinear, relationship between molt and breast muscle mass was found in flightless male Redheads (Bailey 1985). In molting Common Chaffinches (*Fringella coelebs*), changes in protein catabolism were identical to changes in the rate of feather regeneration (Dolnik and Gavrilov 1979). In postbreeding American Black Ducks, breast muscle mass declined during the molt, although total protein content remained constant (Reinecke et al. 1982). These findings indicate that protein demands for feather synthesis are related to molt intensity, and that catabolism of breast muscle provides at least part of the protein requirements of molt (Hanson 1962, Hanson and Jones 1976, Bailey 1985). The lack of mass loss in other potential protein reserves such as the gizzard or leg muscles suggests that these protein demands probably are not very great in molting birds.

Leg muscle mass increased at the same time that breast muscle mass declined. Other studies have attributed such an increase to greater muscle activity (Hanson 1962, Hay 1974, Ankney 1979, Young and Boag 1982). Bailey (1985) attributed the increase in muscle mass to anticipated needs for power rather than use, and found no evidence that locomotory activities involving these muscles were directly responsible for the changing size of these muscle masses. Although scaup leg muscle mass was highest in the flightless period, scaup actually spent less time swimming or diving while flightless than in other periods (Austin 1987). Leg muscle mass was lower ($P < 0.001$) in the migratory period, when birds were most active

in feeding and swimming (Austin 1987), than in the flightless period.

Strategies of postbreeding Lesser Scaup.—Scaup did not increase metabolic reserves before molt or increase feeding during the most intensive period of molt. The concept of nutritional or energetic stress for these birds is difficult to support because of the abundance of foods available during the postbreeding season and the decline in the time spent feeding. Average spring densities of *Gammarus* reach 1,500 animals/m^2 (Mathius et al. 1982). *Gammarus* abundance remains high throughout the ice-free season, even during drought years (Mathius and Pabst 1981, Austin 1983). The time available for foraging during the postbreeding season was not constrained by other activities, as it is in the breeding season when birds devote a large proportion of time to courtship activities. Scaup could have obtained additional foraging time by decreasing resting activities, which were highest during the flightless and postflightless periods (Austin 1987).

Low body mass and lipid reserves during the molt may not indicate energetic or nutritional stress but, alternatively, may be part of a postbreeding strategy to minimize overall energy demands and to reduce the length of the flightless period. By maintaining low body mass during the remige molt, birds would reduce wing loading and regain flight earlier (Douthewaite 1976, Owen and Ogilvie 1979). Also, large metabolic reserves are costly to maintain and are not necessary in a predictable environment where food resources are sufficient (Evans and Smith 1975). Birds molting in July and August, the warmest months of the year, therefore may require only minimal metabolic reserves because they would not have to anticipate high energy demands, e.g. from cold weather or migration. Birds molting in early fall, however, such as females with late broods, may require a different strategy of higher metabolic reserves and a shorter molt period (Austin 1983).

The low level of feeding during the period of high molt intensity and the declining mass of breast muscle and total protein reserves suggest that scaup may incur a negative protein balance during the simultaneous wing molt and associated body molt. Feather production is a relatively inefficient process that requires larger amounts of energy and protein than are contained in the final plumage (Dolnik and Gavrilov 1979, Murphy and King 1984). Mobilization of muscle protein may be a means to balance

the benefits of maintaining low body mass with the nutritional requirements of molt, particularly during the intensive period of the simultaneous wing molt (Bailey 1985).

Decreased foraging activity during molt also results in lower energy intake. Birds appear to compensate for the lower energy levels by reducing the energy expenditures of activities. The time spent resting was greatest when molt intensity was highest (flightless and postflightless periods) (Austin and Fredrickson 1986) and energy-expensive activities (swimming, flying, diving) were lowest (Austin 1987). In postbreeding male Redheads, low daily energy expenditures (DEE) compensated for estimated increases in DEE of molt and resulted in relatively stable total DEE for the postbreeding season (Bailey 1981). The similarity of activity patterns of postbreeding scaup and Redheads suggests that scaup follow a similar strategy.

Ankney (1979) dismissed the theory of nutritional stress of molt as suggested by breast muscle atrophy in Snow Geese (*Chen caerulescens caerulescens*). Juveniles and molting adults had similar diets, but juveniles had nutritional demands of growth as well as those of feather synthesis. In female Lesser Scaup, however, food consumption of adults during molt may be less than that of growing, molting juveniles. Females with broods spend little time feeding (Afton 1983) and often have only a short period of time to regain the metabolic reserves expended during breeding before the onset of the remige molt. Catabolism of muscle protein for feather production may be most important in birds that have low metabolic reserves when they begin to molt and little time in which to complete the flightless period (Austin 1983).

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