

PROTEIN RESERVE DYNAMICS IN POSTBREEDING ADULT MALE REDHEADS

ROBERT O. BAILEY

ABSTRACT.—Labile protein reserve dynamics were studied in postbreeding adult male Redheads (*Aythya americana*) at Lake Winnipegosis, Manitoba, from 1974 to 1977. Changes in tissue masses were related to molt and behavioral activity. Total body protein fluctuated seasonally but tended to increase from breeding to late fall. Redheads did not increase foraging time to meet the nutritional demands of the simultaneous wing molt. Protein Reserve Index (PRI) increased from the late premolt period to the first half of the flightless phase each year. Losses in breast muscle from late premolt to early wing molt were not compensated by the increasing weight of leg muscles. Breast protein may have shifted to growing feathers or other concurrent tissue growth. Breast muscle gained weight over the latter half of the flightless phase in 1977. Changes in locomotor muscle size were related to overall PRI, foraging time, and anticipated seasonal use rather than simply use-disuse phenomena. Non-breeding male Redheads maintained significantly higher PRI from breeding to late molt and appeared to more easily meet seasonal protein requirements than birds which had bred previously.

Protein reserves are maintained by many birds, not as a specialized storage product (Fisher 1954) but as muscle sarcoplasm (Kendall et al. 1973), and may be used for breeding (Jones and Ward 1976, Milne 1976, Korschgen 1977), or molt (Hanson 1962, Newton 1968, Hanson and Jones 1976). The timing of accumulation and utilization of protein reserves in waterfowl appears to have evolved with temporal predictability of food supplies, time constraints on foraging, and predation pressure. Arctic-nesting geese have adapted to food shortage through almost total reliance upon reserves during nesting (Barry 1962, Ankney and MacInnes 1978, Raveling 1978). Goslings and adult females can thereby take advantage of temporarily abundant food and continuous daylight for rapid growth and reserve replenishment (Harwood 1975). In contrast, most ducks breed at lower latitudes, are smaller, and rely much more on dietary protein (Krapu 1974, 1981; Swanson et al. 1974; Serie and Swanson 1976; Drobney 1982). Heavy predation on nests has led to complete dependence on internal protein for successful reproduction in Common Eiders (*Somateria mollissima*; Milne 1976).

Little is known about mobility of protein reserves outside the breeding season. The simultaneous remigial molt is alluded to as a period of great stress in waterfowl because many species weigh the least at this time (Weller 1957, Hanson 1962, Hanson and Jones 1976). Conversely, Ankney (1979) and Raveling (1979) have shown that female Lesser Snow Geese (*Chen caerulescens caerulescens*)

and Canada Geese (*Branta canadensis*) are lightest during incubation and Ankney has argued that having less tissue is adaptive during molt because large reserves need not be maintained in view of a highly predictable, protein-sufficient diet. Hanson (1962) attributed leg hypertrophy during molt of Canada Geese to increased use but suggested that breast muscle atrophy results from the transfer of essential sulfur-containing amino acids (cystine, methionine) from temporarily unneeded breast muscle to growing remiges. Hanson and Jones (1976) found that the mass of the leg muscle increases before the flightless phase. They proposed that reciprocal changes in muscle groups do not result from use-disuse phenomenon, but are evolutionary adaptations to the flightless phase. Ankney (1979) suggested that diet of molting Lesser Snow Geese is not deficient in protein, and attributed compensatory changes in muscle groups to use-disuse. Harwood (1977) considered the arctic food supply to be nutrient-poor for Snow Geese and found variations in feeding behavior which were a compromise between maximizing daily protein intake and brood survival. Raveling (1979) concluded that both hypotheses could have validity in explaining similar changes in molting Cackling Geese (*B. c. minima*). He also suggested that the phenomenon occurs mainly in males because females eat enough to meet protein requirements.

At the center of this controversy is the question of whether birds lack protein during molt (Ankney 1979). It is difficult to demonstrate a deficit when average baseline levels are un-

known. Changes in tissue weight resulting from the use-disuse phenomenon imply that physiological functions have evolved a conservative nature. Organs and tissues decrease in size when their function is temporarily reduced because reduced tissue masses are less costly to maintain (Moss 1974, Ankney 1977, Raveling 1979). A protein deficit would exist if protein reserves were significantly below those normally maintained over the same time period.

Dynamics of muscle masses and other body tissues are virtually unknown in ducks during the postbreeding season. Hay (1974) and Young (1977) recorded reciprocal weight changes between leg and breast muscles in Gadwalls (*Anas strepera*) and Mallards (*A. platyrhynchos*), respectively. Fundamental differences in the ecology, morphology, and mating systems of ducks and geese predispose them to different ways of building up post-reproductive reserves. This paper describes the pattern of protein reserve dynamics in postbreeding Redheads (*Aythya americana*) as indicated by selected morphometric variables. I studied Redheads because their behavior could be observed throughout the postbreeding season and they were available for physiological and molt studies. The reserve cycle was examined in light of concurrent physiological events and constraints of the postbreeding environment. Fortuitous circumstances provided an opportunity to monitor physiological changes under two fundamentally different environmental states. Severe drought over the winter of 1976–1977 drastically curtailed Redhead breeding the following spring. Consequently, comparisons were made for 1974–1976 breeders and 1977 non-breeders.

STUDY AREA AND METHODS

I studied postbreeding male Redheads from 1974–1977 at Long Island Bay, Lake Winnipegosis, Manitoba. The bay is a large (72-km²) shallow basin on the ecotone between aspen parkland and boreal forest and is an important gathering area for male Redheads during the wing molt (Bartonek 1965, Bergman 1973, Bailey 1982). The alkaline marl substrate supports lush stands of algae (*Chara* spp.) and a few submergent macrophytes.

I shot a total of 239 adult male Redheads; 154 were taken during breeding years (1974–1976) and 85 in 1977. Birds were collected every week from the breeding season (May–June) to fall departure (mid-October–November). I made a special effort to obtain samples of flightless drakes. All flightless birds were approached by boat and were given an opportunity to fly or dive.

Protein reserves were monitored using sea-

sonal weights of the principal proteinaceous body tissues and organs. "Protein reserve index" (PRI) was the combined wet weight of the esophagus-proventriculus, gizzard, small and large intestine, caecae, heart, and one-half the leg and breast muscles. Liver was not included because it could contain large, labile stores of fat and glycogen (Fisher and Bartlett 1957). "Breast muscle" was the wet weight of one-half of the sternal muscles. "Leg muscle" was the wet weight of all muscles of the femur and tibiotarsus plus these bones because fluctuations in weight of these bones would be only a small proportion of the total weight measured (4–5 g). Visceral organs were prepared in a standard manner before weighing wet (i.e., empty and free of visible adhering fat).

Fluctuations in the wet weight of muscle masses were taken as a directly proportional change in the major constituents (water, protein, lipid, ash). Organ and tissue weights for flightless birds were compared by classifying birds according to the total length of growing primary remiges. "Total primary length" was the combined length of intact primaries 5, 9, and 10 on the right wing.

Seven categories were established corresponding to periods (treatments) for statistical analysis of weight changes. These were: *breeding*—Redheads collected from 1 May to 30 June; *early premolt*—between 1 and 20 July; *late premolt*—birds taken between 21 July and 8 August, provided the bird could fly; *early molt*—flightless, with total primary length <209 mm; *late molt*—flightless, with total primary length >208 mm; *early fall*—flying birds, between 1 September and 7 October; *late fall*—birds collected on or after 8 October.

I collected time-budget data using the instantaneous scan technique (Altmann 1974) to record activities of individuals. This method consisted of scanning entire flocks of Redheads with a telescope and instantly determining behavior of individuals according to one of five categories for each sex. Time-budgets for early and late premolt periods were combined. Statistical analyses were performed using the Statistical Analysis System (S.A.S.) developed by Barr et al. (1976). Two-way analyses of variance were conducted using the GLM procedure for unequal group sizes, and Type IV sums of squares. All means were tested by Duncans Multiple Range Test.

RESULTS

SEASONAL CHANGES IN BREAST AND LEG MUSCLE MASSES

Breast muscle weight varied significantly among periods ($F = 93.24$, $P < 0.0001$) and was highest during breeding and before fall

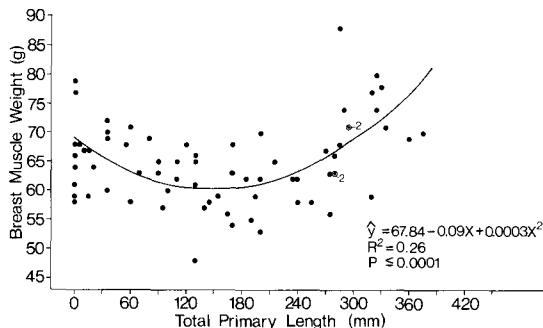


FIGURE 1. Curvilinear regression of breast muscle weight ($\frac{1}{2}$) of flightless adult male Redheads on total primary length.

departure (Table 1). These weights declined throughout the premolt each year then dropped dramatically in the early molt. Losses from breeding to early molt were 28 and 29% for 1977 and 1974–1976 birds, respectively. Breast muscle in flightless birds increased significantly from early to late molt in 1977, but not in 1974–1976. Breast muscles enlarged rapidly following the remigial molt to early fall, (24% in 1974–1976 and 26% in 1977 birds) and peaked before migration. Two-way ANOVA showed that breast muscles in 1977 were significantly heavier than those of preceding years. The heavier breast muscles of males in spring 1977 persisted until early fall.

Leg muscle weights varied significantly among periods, but not among years. Leg muscles were heavier for male Redheads in 1974–1976 breeding periods than in 1977 (Table 1). A drop in weight followed breeding to early premolt in 1974–1976 (14%) and 1977 (10%). In 1974–1976 a further 8% decrease occurred in the late premolt whereas no change was recorded in 1977. Weights were similar in the early molt each year, but 1974–1976 birds had to gain twice as much (20% vs. 9%) to achieve this level. Leg muscle weight dropped 9% ($P < 0.01$) before the end of the molt in 1974–1976, and remained at this level throughout fall. A 13% weight loss followed the late molt in 1977. In general, fall leg muscle weights were similar to those of the premolt whereas leg muscles of breeding and flightless birds were about the same size.

Fluctuations in breast and leg muscle weights were examined for compensatory patterns that might indicate protein transfer between these organs. Each year there was a net loss of breast muscle from breeding to early molt. The protein balance shifted half-way through the flightless period as breast muscle gained weight to late fall. Leg muscle weights did not follow this basic pattern. In normal years, the amount of breast muscle lost (g) from breeding to early

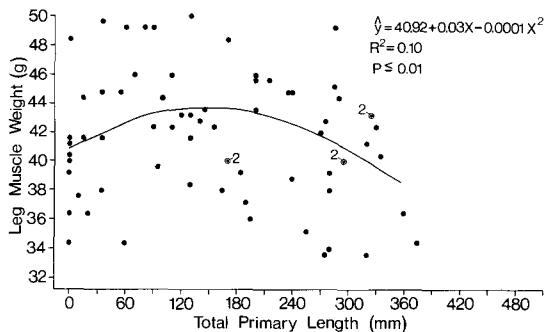


FIGURE 2. Curvilinear regression of leg muscle weight ($\frac{1}{2}$) of flightless adult male Redheads on total primary length.

premolt, then to late premolt, was matched by similar losses in leg muscle weight. From late premolt to early molt, 31.2 g were lost by the whole breast and 14.0 g were gained by the legs, followed into late molt with a 4.6 g increase in breast and a 7.4 g decrease in the leg muscle. In 1977, the whole breast muscle lost 40.8 g from late premolt to early molt whereas the legs gained 6.8 g. However, PRI increased from late premolt to early molt each year because of large increases in other proteinaceous tissues. Breast muscle increased 9.8 g during the 1977 flightless phase, but leg weight was constant. In the fall, breast muscle gained much weight while the legs remained a constant size.

BREAST AND LEG MASSES IN FLIGHTLESS BIRDS

Breast muscle size showed a significant curvilinear relationship (Fig. 1) to the length of growing primaries. The weight loss, which had started before the flightless phase, continued throughout the first half (total primary length 0–208 mm) of the molt. A rapid increase in breast muscle weight began at 260 mm total primary length, or about 1 week before regaining flight. Leg muscle weights decreased over the flightless phase (Fig. 2). Although leg muscle weight was significantly related to primary length, the low degree of variability explained (10%) indicated that other factors might be more important in determining the size of these muscles.

SEASONAL SHIFTS IN THE PROTEIN RESERVE INDEX

Protein Reserve Indices differed fundamentally between previously breeding and non-breeding male Redheads (Fig. 3). Two-way ANOVA indicated that PRI was significantly heavier ($F = 38.06$, $P < 0.001$) in 1977 birds from breeding to late molt, although differences were greatest in the early premolt and late molt. Significant increases occurred from

TABLE 1. Seasonal wet weights of 1/2 breast and 1/2 leg muscles of adult male Redheads at Long Island Bay, Manitoba, during 1974-1976 and 1977.

Year	Period						Year-period interaction
	Breeding	Early pre-molt	Late pre-molt	Early molt	Late molt	Early fall	
1974-1976	87.8 ² ± 1.2 NS ³ NS (15)	82.4 ± 1.4* NS (14)	77.5 ± 1.6** * (23)	Breast muscle		79.7 ± 1.4** ** (22)	97.0 ± 1.5 NS (31)
				61.9 ± 1.2 NS NS (26)	64.2 ± 1.9** * (9)		
1977	91.1 ± 1.8 NS	87.1 ± 1.9 NS (11)	85.7 ± 2.1** (6)	Leg muscle		88.6 ± 0.6 NS (7)	91.9 ± 2.2 (8)
				65.3 ± 1.2* (21)	70.2 ± 1.9** (15)		
1974-1976	43.3 ± 0.4** * (16)	37.5 ± 0.6** NS (12)	34.6 ± 0.6** ** (23)	Breast muscle		37.3 ± 0.6 NS NS (22)	37.2 ± 0.3 NS (31)
				41.6 ± 0.8** NS (26)	37.9 ± 1.4 NS ** (9)		
1977	40.8 ± 0.8**	36.9 ± 0.8 NS (12)	39.4 ± 2.3* (6)	Leg muscle		36.4 ± 0.8 NS (7)	36.8 ± 0.7 (8)
				42.8 ± 0.9 NS (21)	42.0 ± 0.9** (15)		
F-values							
						Year	Period
Breast muscle						17.17***	93.24***
Leg muscle						2.58 NS ⁴	18.47***
						Year-period interaction	2.76* 4.5***

¹ (n).

² Mean ± standard error (g).

³ Probability from a Duncan's Multiple Range Test that adjacent means are not statistically different, comparisons can be made vertically and horizontally.

* P < 0.05, ** P < 0.01, *** P < 0.001, NS = not significant.

⁴ P, F = 0.10.

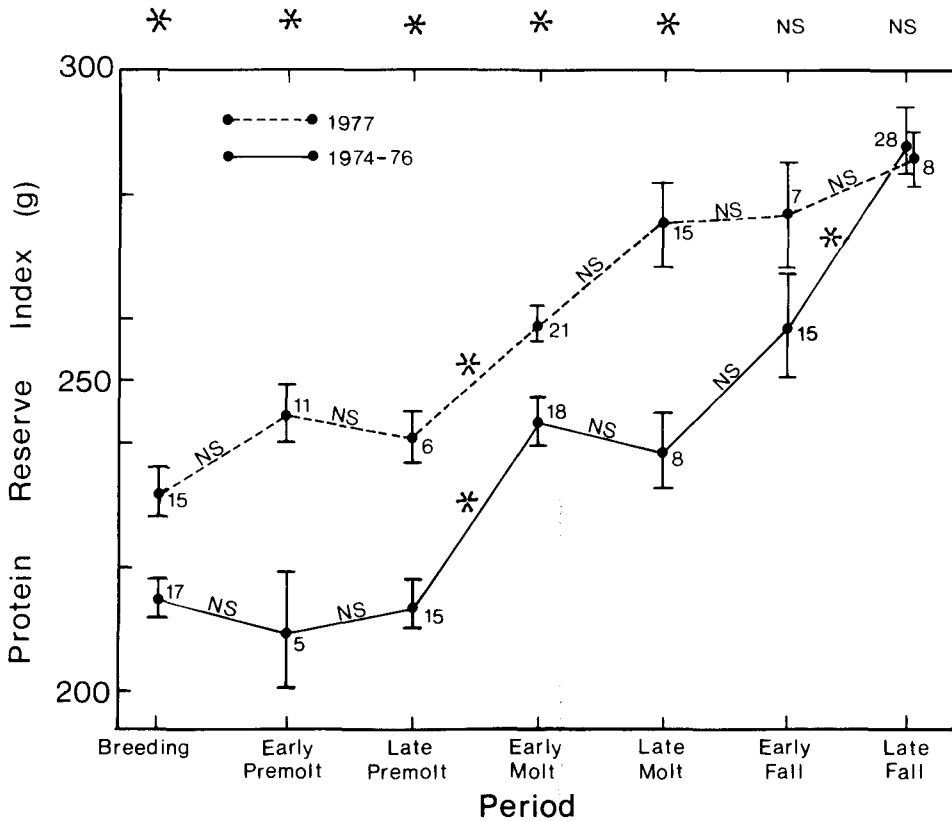


FIGURE 3. Protein reserve indices of adult male Redheads during each period in 1974–1976 and 1977. Statistical comparisons can be made among adjacent means or vertically as indicated across the top of the diagram. * = $P < 0.05$, NS = not significant.

late premolt to early molt in each year group. Protein reserves in 1974–1976 birds increased from late molt to late fall, although only the second increment was statistically significant. PRI increased gradually from early molt to late fall in non-breeders but overall gains were significant ($P < 0.05$).

I examined the distribution of protein (reflected by weight changes in eight proteinaceous tissues comprising PRI) for compensatory patterns within the reserve pool (Fig. 4). Differences between total weight gained and lost represented a surplus or deficit in the protein reserve balance. When net tissue gains exceeded losses, the difference must have been met through exogenous protein uptake. The magnitude of this disparity indicated the degree to which birds relied on dietary protein sources. Assuming the cost of plumage replacement to be the same each year, I could evaluate the relative “condition” of the two year groups with respect to the ability of birds to maintain and mobilize protein reserves.

A compensatory pattern of gains and losses in protein reserves was apparent (Fig. 4). Generally, 1977 birds were able to contribute quantities of protein from reserves which more

closely matched seasonal demands. However, if protein requirements for feather synthesis were added, the total demand would have been much larger and undoubtedly the difference had to be compensated through foraging. Nevertheless, higher reserve levels in 1977 lowered overall dependence on environmental sources. Protein reserves (mainly breast muscles) in 1974–1976 birds attained 1977 levels in late fall, but almost no endogenous protein contributed to the increase (Fig. 4).

INTEGRATION OF THE TIME-ACTIVITY BUDGET

Time spent foraging is important for understanding protein reserve dynamics. I determined time activity budgets from 107,917 individual observations of male Redheads taken in over 600 h of study (Fig. 5) (Bailey 1982). Male Redheads spent 32% more time foraging during the 1977 breeding season, than the previous years. Foraging time increased 25% from breeding to premolt in 1975–1976, whereas the already higher feeding rate of 1977 males went up another 30%. Time spent foraging was maintained from premolt to early molt by 1975–1976 birds but dropped 28% in the 1977

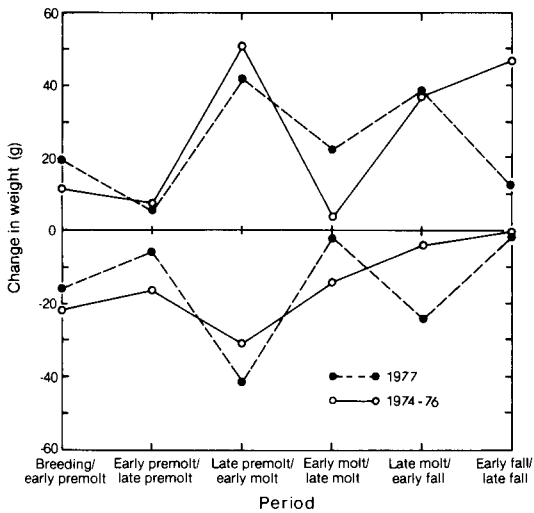


FIGURE 4. Weight gain and loss in eight proteinaceous tissues comprising the protein reserve index (PRI) of adult male Redheads for each period in 1974–1976 and 1977. Compensatory changes cannot be detected in the PRI.

group. Sleeping increased 36% in 1977 birds to replace foraging time. Foraging time increased 5% from early to late molt in 1975–1976, but sleeping went up 41% as time spent in all other activities greatly decreased. Foraging time decreased 20% in 1977 from early to late molt, and sleeping attained the maximum seasonal value. Foraging rates were highest for all birds in fall, when Redheads did very little other than forage and sleep.

Seasonal leg muscle weights (Table 1) were not correlated ($r = 0.47$, $P > 0.05$) with the combined percentage of time spent swimming and courting, indicating that size of these locomotor muscles was not related to their use.

DISCUSSION

SEASONAL BREAST AND LEG MUSCLE CHANGES

Seasonal changes in breast and leg muscle masses did not reveal a clear pattern of protein transfer between these tissues. The reciprocal relationships noted during the flightless phase accounted for only small amounts of muscle weight gained or lost at the time. Hanson (1962), Hay (1974), Hanson and Jones (1976), Young (1977), and Ankney (1979) all suggested that protein from degraded breast muscles may contribute to leg hypertrophy during molt. None of these authors, however, considered the large changes in other body tissues at this time. In view of the high protein demand from late premolt to early molt, I found little evidence that degraded breast muscle protein contributed exclusively to leg muscle hypertrophy rather than other rapidly enlarging tissue or growing feathers.

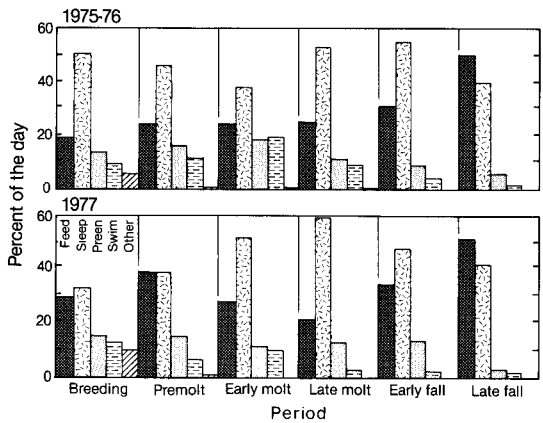


FIGURE 5. Percentage of the day spent in various activities from breeding to late fall for adult male Redheads in 1975–1976 and 1977.

Breast muscles were heaviest in spring and fall when birds were migrating or courting, and smallest during the flightless phase, which suggested that the size of these muscles may be related to use-disuse phenomenon as described by Ankney (1979). Time-budget data showed that Redheads spent a high proportion of time flying in the spring but this rapidly decreased after the breeding season. Foraging flights were common during summer, but feeding sites were usually near the roost so little time was spent flying. Later in October, as the pre-alternate molt ended and plumage was in prime condition, Redheads often slept and fed in the same place (Bailey 1982). The large size of fall pectoral muscles was concurrent with more flying, but was also correlated with: (1) decreased protein requirements for growth of other body tissues, (2) termination of remigial, body contour and down feather molt (Bailey 1982), (3) accelerated food intake, and (4) an imminent long migration.

Leg muscles were largest in spring and during the flightless phase, but smaller after breeding and in fall. This pattern suggested that leg muscle size was also related to use-disuse, but the lack of a significant correlation between leg weight and the actual amount of time spent in seasonal swimming and courtship activity did not support the hypothesis. Redheads feed almost exclusively by diving, yet during fall hyperphagia, leg size was significantly ($P < 0.01$) less than during breeding and early molt when feeding activity was lowest.

Seasonal changes in these muscle groups appeared to be related to anticipation of a need for increased power rather than actual use. Redheads on northern staging areas presumably require powerful pectoral musculature before departure in October. This implies that muscle size is not increased by migrating (use),

but in preparation for migration. Gains in leg muscle weight prior to and during the early molt may have resulted from the same phenomenon. Flightless Redheads swim in search of food and dive to escape predators. Leg muscle hypertrophy before the flightless phase assures enhanced swimming ability. Coincident high weights of leg and breast muscle in spring contribute to a male's ability to participate in vigorous aerial and underwater pursuit, typical of pairing and mate defense (Weller 1967).

Leg muscle hypertrophy in early molt was concurrent with a high protein demand from other tissues and feathers. Leg weights each year increased to the same size although 1974–1976 birds had to gain twice as much. This suggested strong selection for the greater leg muscle size in early molt.

The pattern of breast muscle growth from late molt to late fall was similar for each year group but there was considerable seasonal variation in size among years. Fall breast muscle size increased as protein demands from other tissues and plumage growth diminished. Replacement of the pre-alternate plumage was probably under photoperiodic control since it occurred at the same intensity in each year group (Bailey 1982). Fall breast muscle size was likely dependent upon the protein available or needed in other body tissues. Higher reserves in 1977 birds permitted an earlier increase to maximum breast muscle size.

These arguments do not preclude any influence of use-disuse, but I found no evidence that locomotor activity was directly responsible for initiating changes in the size of these muscle masses. Furthermore, differences in the total protein demand and supply from endogenous and exogenous sources appeared to modify the seasonal size of proteinaceous tissues. Circannual rhythms of seasonal change probably interacted with supply and demand for protein to determine size of these muscle masses. Consistent yearly patterns of seasonal change in leg and breast muscles support this hypothesis.

BREAST AND LEG MUSCLE MASSES IN FLIGHTLESS BIRDS

A significant increase in the breast muscle masses of flightless Redheads from early to late molt in 1977 and the curvilinear relationship between breast muscle weight and length of growing primaries in flightless Redheads support the contention of Hanson (1962) and Hanson and Jones (1976) that this muscle may be used as a source of protein for the growing feathers. The increase observed in breast muscle weight of flightless Redheads cannot be explained by the use-disuse hypothesis. The al-

ternative that breast muscle protein was shifted to other growing tissues cannot be excluded but changes in the size of these muscles more closely followed those of primary feather growth. Hay (1974) found that fasted Mallards continued to grow feathers at a normal rate despite a 19% weight loss.

Ankney (1979) suggested that Lesser Snow Geese did not rely on catabolism of body tissue during wing molt to obtain protein for feather growth. Nevertheless, the decrease in total protein (only breast and leg muscles) in male Snow Geese was significant from post hatch to early molt because the breast lost more tissue than the leg gained. A similar pattern was observed in male Redheads. The net loss in muscle tissue was 17.2 g in 1974–1976 and 34.0 g in 1977. Although 1977 birds lost nearly twice as much tissue, the remaining muscle masses equaled or exceeded those of 1974–1976 birds in weight. These muscles were significantly heavier (Table 1) during the premolt in 1977, indicating that they could contribute more protein while maintaining a satisfactory functional size.

Leg muscle weights were much more variable but tended to increase at the beginning of remigial molt, then decrease before regaining flight. Leg muscles of 1977 birds remained heaviest over the full flightless phase although these birds spent less time swimming, which suggested that more sufficient overall protein reserves spared extensive catabolism in the late molt.

SEASONAL SHIFTS IN ENDOGENOUS PROTEIN RESERVE

The concept of a labile protein reserve is broadly applicable to seasonal variability in the size of proteinaceous tissues of male Redheads (Swick and Benevenga 1977). Earlier work on passerines (Connell et al. 1960, Odum et al. 1964) suggested that fat-free carcass weight is constant. Body composition in Redheads was highly variable. Greater food intake tends to be correlated with increased protein synthesis and higher tissue weights, whereas lower intake coupled with increased protein demand caused a reduction in tissue masses. Skeletal muscles, particularly those of the sternum, contributed the largest amounts of protein to the reserve.

PRI was lowest in the breeding season and increased to a maximum in late fall each year (Fig. 3). Non-breeding Redheads spent 32% more time foraging during the usual breeding period than drakes actively involved in reproduction, and their PRI was significantly heavier. Breeding may place time constraints on foraging, perhaps initiating a long-term protein

deficit. Prebasic molt may also contribute to the protein deficit in birds which had bred previously because it started later but ended at the same time as in non-breeders (Bailey 1982).

Increases in the weight of the gizzard, small intestines, and leg muscles were mainly responsible for the significant gains in PRI from late premolt until early molt (Bailey 1982). These changes, plus growth of the regenerating feathers (Bailey 1982), imposed extremely high protein requirements at the beginning of the flightless phase. Despite these demands, time spent foraging did not increase in birds which had bred previously, and actually decreased 28% in non-breeders (Fig. 5). It was clear that reserves had to be drawn upon at this time to help meet protein requirements (Fig. 4). Endogenous protein could have satisfied 95% of the organ growth requirement in 1977 compared to 61% in 1974–1976, and breast muscle atrophy provided 97 and 98% respectively of the catabolized protein each year. Nevertheless, endogenous protein reserves can only buffer the Redheads' dependence on external sources.

ECOLOGICAL SIGNIFICANCE OF LABILE PROTEIN RESERVES

Time constraints on foraging and availability of food seem to play central roles in determining the feeding habits of waterfowl. Labile protein reserves have survival value where protein supplies are absent or limiting, or where they are unpredictable. In this case, protein reserves may buffer or replace inadequate dietary protein intake. On the other hand, labile protein reserves may be used to meet short-term high requirements. Arctic-nesting geese, breeding eider ducks, and molting waterfowl would appear to broadly represent these two situations.

The low feeding activity recorded (but not reported, as it should be) during molt suggests another condition under which dietary protein intake may be insufficient. It could be advantageous for birds to mobilize temporarily unneeded breast muscle to help meet protein requirements at the onset of molt, rather than to feed and simultaneously increase body lipid content. Total body lipid content was found to be a strong linear function of foraging time in male Redheads ($r = 0.90$, $P < 0.01$; Bailey 1982). Higher body weight may prolong the flightless phase (Owen and Ogilvie 1979), hence using breast muscle to supplement dietary protein could be part of a more important means of maintaining lower total lipid levels.

Apparently Redheads did not compensate their lower feeding rates by switching to a higher quality protein diet. Aquatic plants comprised

over 80% of their diet throughout the post-breeding season (Bailey and Titman 1984). Redhead drakes consumed more vascular plant material than algae during the flightless phase, but no major shifts in diet coincided with this molt. Algae comprised over 80% of the fall diet (Bailey and Titman 1984).

Protein reserves in male Redheads are replenished as demands for plumage and organ growth subside. Protein expenditure generally terminates when pectoral muscles (chief reserve) begin to be built up for migration.

Reproduction exerts substantial influence on the protein reserves in male Redheads. Previously breeding adult males showed a protein deficit from breeding throughout late molt when compared to a group of non-breeding males. Breeding apparently lowers protein intake by suppressing the amount of time spent feeding. Greater protein reserves in 1977 tended to minimize seasonal differences between losses and gains; hence, I conclude that non-breeding Redhead drakes were in better physiological condition with respect to protein reserves.

The protein deficit in 1974–1976 birds was equally large in the latter half of the wing molt and during the early premolt. It seems unreasonable to single out the wing molt as a season of greater nutritional stress in previously breeding Redheads, since the protein deficit was spread over a longer period. I found no basis to conclude that 1977 males were nutritionally stressed during any period. Undoubtedly, both body and wing molt demands contributed to the protein deficit in 1974–1976 birds, but were not necessarily the cause of it.

Some of the confusion surrounding discussions of the nutritional "stress" of molt may result from the question of "need" for catabolizing body tissues to meet protein requirements. The 1974–1976 data alone do not indicate a protein deficit, and these birds ended up in late fall with the same quantities of reserves as the 1977 birds. However, the fact that 1977 Redheads maintained significantly higher total protein levels during the same time period suggests that although higher PRI was not apparently "needed" in order for most of the birds to survive, it was nevertheless desirable and advantageous, i.e., closer to some established "optimal" level. Baseline levels of reserves in birds must be known in order to establish whether a protein deficit is present. The fact that total protein may increase significantly over a season does not preclude a protein deficit.

There are important, fundamental differences in foraging habits of male Redheads and geese during molt. Harwood (1975, 1977) showed that female Snow Geese spent 85% of

the daylight hours feeding after hatch but males foraged significantly less (77%) because they were alert more often. Body weight (protein) increased by 16% in females from late incubation to early molt but weights of males did not change (Ankney 1979). Raveling (1979) suggested that protein reserves were exhausted during incubation in female Canada Geese, whereas males have an opportunity to feed. Females fed constantly with their broods after hatch while males remained more alert.

Raveling (1979) concluded that female Canada Geese meet protein demands from the diet, but males probably use reserves to partially provide protein requirements after hatch. Derksen et al. (1982) have shown that Canada Geese and Black Brant (*Branta nigricans*), (unsexed) spend an average of 85 to 93% of the day feeding during wing molt.

Male Redheads averaged only 27% of the day ($n = 12,026$ of 44,022 instantaneous observations of individuals; range 22–28%) foraging during wing molt, which was lowest of all periods studied. Redheads, in contrast to geese, spend most of the day sleeping during molt. Relative inactivity during molt, coupled with the observed changes in proteinaceous tissues, strongly suggests that Redheads rely on catabolism of body tissues to meet protein requirements at this time. I agree with Raveling (1979) that this phenomenon appears to be more prevalent in male geese, since, as Ankney (1979) has suggested, females feed enough to replenish lost body weight and replace plumage, and goslings grow to adult size at the same time most years. Ducks and geese, however, have important, different ecological constraints. For example, because of their smaller body size and inability to meet nutrient requirements from reserves, most female dabbling ducks (*Anas* sp.) must feed during incubation (Afton 1979, Krapu 1981). These ecological differences make it difficult to predict the dynamics of protein reserves in ducks from the results of studies on geese. It is equally difficult to predict patterns of protein reserve use in female ducks based on those observed in males because of possible differences in time, energy, and nutrients devoted to reproduction among sexes.

ACKNOWLEDGMENTS

I thank R. D. Titman for advice during the study and review of the manuscript. C. D. Ankney and D. G. Raveling reviewed the manuscript and contributed many useful criticisms and comments. Support was provided by the North American Wildlife Foundation, Ducks Unlimited Foundation, Messers. Edson and Robert M. Gaylord, the Canadian National Sportmen's Show, and the Ontario Waterfowl Research Foundation, all administered through the Delta Waterfowl Research Station. Personal support

was supplied through postgraduate scholarships from the National Research Council of Canada and the Province of Quebec. The Canadian Wildlife Service contributed valuable time and financial resources to ensure completion of this work.

LITERATURE CITED

- AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. *Wilson Bull.* 91:42–49.
- ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227–267.
- ANKNEY, C. D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk* 94:275–282.
- ANKNEY, C. D. 1979. Does the wing molt cause nutritional stress in Lesser Snow Geese? *Auk* 96:68–72.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of Lesser Snow Geese. *Auk* 95:459–471.
- BAILEY, R. O. 1982. The postbreeding ecology of the Redhead Duck (*Aythya americana*) on Long Island Bay, Lake Winnepegosis, Manitoba. Ph.D. diss., McGill Univ., Montreal.
- BAILEY, R. O., AND R. D. TITMAN. 1984. Habitat use and feeding ecology of postbreeding Redheads. *J. Wildl. Manage.* 48:1144–1155.
- BARR, A. J., J. H. GOODNIGHT, J. P. SALL, AND J. T. HELWIG. 1976. A user's guide to S.A.S. Sparks Press, Raleigh, North Carolina.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19–26.
- BARTONEK, J. C. 1965. Mortality of diving ducks on Lake Winnepegosis through commercial fishing. *Can. Field-Nat.* 79:15–20.
- BERGMAN, R. D. 1973. Use of southern boreal lakes by postbreeding Canvasbacks and Redheads. *J. Wildl. Manage.* 37:160–170.
- CONNELL, C. E., E. P. ODUM, AND H. KALE. 1960. Fat-free weights of birds. *Auk* 77:1–9.
- DERKSEN, D. U., W. D. ELDRIDGE, AND M. W. WELLER. 1982. Habitat ecology of Pacific Black Brant and other geese moulting near Teshekpuk Lake, Alaska. *Wildfowl* 33:39–57.
- DROBNEY, R. D. 1982. Body weight and composition change and adaptations for breeding in Wood Ducks. *Condor* 84:300–305.
- FISHER, H. I., AND L. M. BARTLETT. 1957. Diurnal cycles in liver weights in birds. *Condor* 59:364–372.
- FISHER, R. B. 1954. Protein metabolism. Methuen and Co., London.
- HANSON, H. C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arct. Inst. N. Am. Pap. No.* 12.
- HANSON, H. C., AND R. L. JONES. 1976. The biogeochemistry of Blue, Snow, and Ross' Geese. III. *Nat. Hist. Surv. Spec. Publ. No. 1.* Southern Illinois Univ. Press, Carbondale.
- HARWOOD, J. 1975. The feeding strategies of Blue Geese, *Anas caerulescens*. Ph.D. diss., Univ. of Western Ontario, London.
- HARWOOD, J. 1977. Summer feeding ecology of Lesser Snow Geese. *J. Wildl. Manage.* 41:48–55.
- HAY, R. L. 1974. Molting biology of male Gadwall at Delta, Manitoba. M.Sc. thesis. Univ. of Wisconsin, Madison.
- JONES, P. J., AND P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea, *Quelea quelea*. *Ibis* 118:547–574.
- KENDALL, M. D., P. WARD, AND S. BACHUS. 1973. A protein reserve in the pectoralis major flight muscle of *Quelea quelea*. *Ibis* 115:600–601.
- KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. *J. Wildl. Manage.* 41:360–373.

- KRAPU, G. L. 1974. Feeding ecology of pintail hens during reproduction. *Auk* 91:278-290.
- KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98:29-38.
- MILNE, H. 1976. Body weights and carcass composition of the Common Eider. *Wildfowl* 27:115-122.
- MOSS, R. 1974. Winter diets, gut lengths and interspecific competition in Alaskan Ptarmigan. *Auk* 91:737-746.
- NEWTON, I. 1968. The temperatures, weights, and body composition of molting Bullfinches. *Condor* 70:323-332.
- ODUM, E. P., D. T. ROGERS, AND D. L. HICKS. 1964. Homeostasis of the nonfat components of migratory birds. *Science* 143:1037-1039.
- OWEN, M., AND M. A. OGLVIE. 1979. Wing molt and weights of Barnacle Geese in Spitsbergen. *Condor* 81:42-52.
- RAVELING, D. G. 1978. The timing of egg laying by northern geese. *Auk* 95:294-303.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96:234-252.
- SERIE, J. R., AND G. A. SWANSON. 1976. Feeding ecology of breeding Gadwalls on saline wetlands. *J. Wildl. Manage.* 40:69-81.
- SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. *J. Wildl. Manage.* 38:302-307.
- SWICK, R. W., AND N. J. BENEVENGA. 1977. Labile protein reserves and protein turnover. *J. Dairy Sci.* 60:505-515.
- WELLER, M. W. 1957. Growth, weights, and plumages of Redhead (*Aythya americana*). *Wilson Bull.* 69:5-38.
- WELLER, M. W. 1967. Courtship of the Redhead (*Aythya americana*). *Auk* 84:544-559.
- YOUNG, D. A. 1977. Characteristics of the molts in the male Mallard (*Anas platyrhynchos*). M.Sc. thesis, Univ. of Alberta, Edmonton.

Department of Renewable Resources, Macdonald College, Ste. Anne de Bellevue, Province of Quebec H9X 1C0, Canada. Present address: Canadian Wildlife Service, Ottawa, Ontario, Canada K1A 0E7. Received 26 April 1983. Final acceptance 23 April 1984.

The Condor 87:32

© The Cooper Ornithological Society 1985

RECENT PUBLICATIONS

The plovers, sandpipers, and snipes of the world.—Paul A. Johnsgard. 1981. University of Nebraska Press, Lincoln. 493 p. \$45.00. In recent years, the tireless Dr. Johnsgard has produced one after another comprehensive summaries on various families of non-passerine birds. Here he has turned his attention to the "relatively typical" charadriiforms from the Jacanidae through the Scolopacidae. The plan and design of the book are much the same as in his *Ducks, geese, and swans of the world* (noted in *Condor* 81:27). Added, however, are two overview chapters, one on taxonomy and evolutionary relationships and the other on reproductive biology. These are helpful introductions but do not delve as far as might be wished. Keys to families, genera and species are given. The species accounts are organized as to names, subspecies and ranges (with maps), measurements and weights, full description (both "in the hand" and "in the field"), and natural history (habitats, foods, social behavior, reproductive biology, status and relationships). They bring together an enormous amount of information from worldwide sources. This compilation is especially to be appreciated for those species that breed outside North America and the western Palearctic, regions whose shorebirds are already well covered in other books. The volume is illustrated with color and monochrome photographs, color paintings of downy young by Jon Fjeldså, and many pen-and-ink drawings by the author; these last include many plates of head profiles as aids to field identification. Glossary of scientific names, list of references, and index. Regrettably, Johnsgard offers little comparative discussion of shorebird biology, explaining that space considerations forced him to leave it out. His book is nevertheless an admirable guide for the identification of these birds and a source for specific information.

The bee-eaters.—C. H. Fry. 1984. Buteo Books, Vermillion, South Dakota. 304 p. \$47.50. Several species of bee-eaters have attracted much study owing to their foraging methods or their cooperative breeding behavior. In addition, the family as a whole is well suited for an investigation of speciation and radiation. While its 24 species—a manageable number—differ in details of appearance and habits, they constitute a distinctive and evidently closely-knit group. Fry has taken a strongly evolutionary approach in this book, thereby making his treatment far more interesting than the conventional catalog. Well-organized and comprehensive species accounts lay the groundwork for interpretive chapters on the origin of bee-eater species, their foraging, social, and reproductive habits, and differentiation within the family. A fascinating short chapter deals with the relations of the birds to bees and apiculture. All of this is written in an admirably clear, non-technical style, making the book accessible to biologically literate general readers as well as ornithologists. Eight fine color plates by the author depict most of the subspecies and a few immature plumages. They are placed together with the maps in order to emphasize the crucial relationship of systematics with geographical distribution, a reflection of Fry's thinking. Numerous sketches by John Busby throughout the book effectively show characteristic postures and actions of the birds. Appendices, references, index. This book is a small and modest production by comparison with its only predecessor, Dresser's century-old *Monograph of the Meropidae*. Thanks to its informative and insightful content, however, it is scientifically a far more valuable volume.