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NUTRITIONAL IMPLICATIONS OF MOLT IN MALE CANVASBACKS: VARIATION IN NUTRIENT RESERVES AND DIGESTIVE TRACT MORPHOLOGY[1]

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Abstract. Body composition and gut morphology of molting male Canvasbacks (*Aythya valisineria*) were investigated in central Alberta from termination of breeding activities until fall migration (May–October) in 1989–1990. During this postreproductive period, male Canvasbacks underwent prebasic, down, and partial prealternate molts. Protein, lipid, and mineral dynamics were analyzed to determine if male Canvasbacks relied on endogenous nutrient reserves to meet increased nutritional demands during molt. In addition, mass and length of digestive organs were analyzed to document changes in the digestive tract that could provide endogenous protein (i.e., via muscle tissue catabolism) and/or possibly enhance exogenous nutrient assimilation for molt. Ingesta-free body mass of male Canvasbacks reached its annual minima during remigial molt ($\bar{x}$ = 973.5 g) and fluctuated primarily in response to storage and catabolism of lipids. Body composition data indicated little reliance on endogenous fat, protein, and mineral to satisfy nutrient requirements for molt. Lipid reserves were not accumulated prior to molt, but instead were metabolized from arrival on molting areas through mid-remigial molt. Premigratory lipogenesis started during mid-remigial growth and occurred simultaneous to elevated molt intensity, indicating that energetic requirements for molt were met exogenously. Despite the relative stability of total body protein during postreproductive molts, there were marked shifts in the distribution of muscle tissue in molting birds. Pectoral muscles atrophied from arrival on molting habitat through mid-remigial molt, concurrent with hypertrophy of leg and some digestive tract tissues. Increased mass of the digestive tract during remigial molt originated principally from growth of the gizzard. The digestive tract returned to its original mass as birds regained the ability to fly and their diet reverted back to foods with lower fiber content. Because postreproductive molts were extended over six months, male Canvasbacks had relatively low daily nutritional demands that could be met by dietary intake.

Key words: nutritional ecology; molt; body composition; gut morphology; Canvasback; Aythya valisineria.

INTRODUCTION

Periodic molt in the annual cycle of birds increases energy and other nutritional requirements for production of epidermal keratins (Murphy and King 1991). Energy demands during molt originate from nutrient requirements to produce plumage and other epidermal keratins (e.g., feather sheaths, stratum corneum, and podotheca; Murphy and King 1986, King and Murphy 1990), increased body protein (Newton 1968, Dolnik and Gavrilov 1979) and mineral metabolism (Meister 1951), adjustments in somatic water balance (Chilgren 1977, Dolnik and Gavrilov 1979), increased blood volume (Chilgren and DeGraw 1977), and possibly increased costs of thermoregulation resulting from reduced insulative ability of growing plumage (King 1980, Young and Boag 1982). More significantly, however, the quantity of protein represented by plumage may equal or exceed 25% of the total protein content of a bird (Newton 1968, Chilgren 1977, Murphy and King 1991). Thus, the primary nutritional requirement during molt is an increased need for protein to supply amino acids used in formation of feathers and other epider-

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mal keratins (Murphy and King 1992). Mineral requirements for molt are usually small because ash content generally represents less than 4% of the dry mass of plumage (Hanson and Jones 1976, Murphy and King 1982).

During the postreproductive period, which extends from the end of breeding until fall migration, adult male Canvasbacks (*Aythya valisineria*) undergo a series of extensive molts (including. prebasic, down, and partial alternate molts; Thompson and Drobney 1995). Adaptive strategies that ducks (Anatinae) use to meet their nutritional demands during molt are not well understood (Hohman et al. 1992) and have been neglected relative to investigations of nutritional requirements for reproduction (see Alisauskas and Ankney 1992). This paucity of research is remarkable considering that postreproductive molts typically involve the most extensive production of somatic tissue in the annual cycle of adult birds (Walsberg 1983). Furthermore, molt is a critical period when malnutrition could have direct survival implications (i.e., malnourished birds may protract molt into less optimal times of the year and/or grow poorer quality plumage [Murphy et al. 1988]).

If energy, protein, or mineral demands during molt exceed dietary intake, birds have several options. They may (1) suspend or delay feather production until better conditions arise, (2) extend the duration of molt thereby lowering the daily rate of plumage production and corresponding nutrient demands, (3) continue plumage synthesis by catabolizing somatic nutrients, or (4) use a combination of these tactics (King and Murphy 1985). Male Canvasbacks molting on wetlands in northwestern Canada and Alaska typically do not have the option of delaying prebasic molt because feather wear is often so extensive in remigial tracts that their flight ability is impaired (J. Thompson, pers. observ.) and wetlands begin to freeze by late October. Therefore, Canvasbacks may either extend postreproductive molts to balance plumage growth rates with exogenous nutrient intake or catabolize somatic nutrient reserves. Most waterfowl can store nutrients as somatic tissue that can be used to meet daily nutritional demands if requirements can not be met by dietary intake (Alisauskas and Ankney 1992). We conducted this study to determine if male Canvasbacks catabolized endogenous nutrients to meet the nutritional requirements of postreproductive molts and to document changes in gut morphology that might provide endogenous protein and/or possibly enhance assimilation of exogenous nutrients during molt.

STUDY AREA AND METHODS

MOLT STATUS

Male Canvasbacks (n = 143) were collected by shooting along flight corridors and at foraging sites on Beaverhill Lake (53°27′N, 112°32′W) in central Alberta from late May to October in 1989–1990. Bradford (1990) provided a detailed description of the ecology and geology of the study area. To relate somatic nutrient dynamics and gut morphology of male Canvasbacks to their respective molt stage, specimens were categorized using the following terminology and plumage characteristics: (1) Early Preflightless (n = 32), early to intermediate stages of prebasic molt (≤ 50% basic plumage in capital and side/flank regions); (2) Late Preflightless (n = 28), advanced prebasic molt (> 50% basic plumage in capital and side/flank regions); (3) Flightless (n = 27), definitive basic plumage and immature remiges (< 80% of mature length); (4) Postflightless (n = 29), early to intermediate stages of prealternate molt (≤50% alternate plumage in the capital and side/flank regions) and remiges sufficiently mature for flight (≥80% of mature length); and (5) Staging (n = 27), advanced prealternate molt (>50% alternate plumage in capital and side/flank regions). Annual variation in chronology of molt stages is presented in Thompson and Drobney (1995; Table 1).

NECROPSY PROCEDURES

Male Canvasbacks were refrigerated at 4°C after collection and necropsied within 4–24 h to minimize post-mortem variation in tissue mass. Most birds were collected during early morning from 06:00–10:00 MST. Morphological measurements including lengths (0.01 mm) of the skull, culmen, tarsus, and keel were taken with digital calipers to correct nutrient reserve values for variation in body size (see below). Skull length was measured from the external occipital protuberance to the distal tip of the premaxilla. Culmen length was measured from the bottom of the V-point between the ceres to the distal tip of the premaxilla (culmen 1 measurement in Dzubin and Cooch 1992). Tarsal length extended from the proximal to distal end of the tarsometatarsus (tarsus bone measurement in Dzubin and Cooch

TABLE 1. Body mass and somatic nutrient dynamics of molting male Canvasbacks.[a]

Variable	Molt stage[b]								
	EP (n = 32)	P[c]	LP (n = 28)	P	FL (n = 27)	P	PF (n = 29)	P	ST (n = 27)
Body mass[d]	1,043.27	NS	1,054.82	*	973.51	***	1,116.96	*	1,207.38
	(12.18)		(18.72)		(18.12)		(12.76)		(21.03)
Lipid	112.66	NS	123.55	***	76.92	***	119.55	***	197.16
	(6.24)		(10.24)		(6.67)		(4.20)		(13.34)
Protein[e]	215.21	NS	216.61	NS	209.11	***	229.83	NS	233.98
	(1.88)		(2.59)		(2.22)		(1.74)		(3.29)
Breast[f]	219.80	NS	216.78	***	171.98	***	221.86	**	232.32
	(2.18)		(2.78)		(3.74)		(2.28)		(3.14)
Leg[g]	115.64	NS	112.36	***	124.88	NS	121.96	*	117.14
	(1.34)		(1.30)		(1.74)		(1.24)		(1.48)
Heart[h]	11.95	NS	11.82	***	10.32	***	12.53	NS	12.92
	(0.18)		(0.19)		(0.18)		(0.14)		(0.15)
Ash	48.77	NS	47.83	NS	49.15	NS	50.09	NS	51.30
	(0.74)		(0.79)		(0.75)		(0.68)		(0.69)

[a] Measurements are in g; means are presented with their corresponding SE below in parentheses.
[b] Molt periods include Early Preflightless (EP), Late Preflightless (LP), Flightless (FL), Postflightless (PF), and Staging (ST).
[c] Probability levels from t-tests between adjacent molt stages; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[d] Ingesta free body mass (wet).
[e] Ashfree lean dry mass.
[f] Wet mass of the left and right pectoralis and supra-coracoideus muscles.
[g] Wet mass of the femur and tibiotarsus and all muscle tissues attached to these bones from both legs.
[h] Wet mass.

1992). Keel length was measured from the anterior to posterior tip of the cranial process on the crest of the sternum (see Fitzgerald 1969) after removing the left breast muscles (see below).

To document changes in specific proteinaceous tissues, digestive tract organs (including liver and pancreas), left breast muscles (i.e., pectoralis and supra-coracoideus), left leg muscles (i.e., muscles attached to the femur and tibiotarsus), and heart were excised, stripped of adhering fat, blotted dry with a paper towel, and weighed wet (0.01 g). Masses of left breast and left leg muscles were doubled for analysis to represent the total tissue changes in pectoral and hind limb musculature. Leg muscle mass included femur and tibiotarsus bones because variation in mass of these bones could account for only a small fraction of total mass variation in this relatively large muscle group (Bailey 1985). The digestive tract was dissected into the upper digestive tract (esophagus and proventriculus), gizzard, small intestine, liver, pancreas, ceca, and large intestine. Ingesta was removed from organs before they were weighed. Total digestive tract mass was derived by summing masses of the emptied upper digestive tract, gizzard, small intestine, ceca, and large intestine. Lengths (1 mm) of the upper digestive tract, small intestine, ceca, and large intestine were measured using a meter stick. Gizzard length (0.01 mm) was measured from the proventricular junction to the most distal point using digital calipers. All measurements were made on unstretched digestive tract components before removal of ingesta to reduce variation in measurements associated with elasticity of these organs. Total digestive tract length was derived by summing lengths of the upper digestive tract, gizzard, small intestine, ceca, and large intestine.

CARCASS ANALYSES

When necropsies were completed, all excised organs and fat deposits were returned to the body cavity. The total body mass (0.1g) of the ingesta-free carcass was determined and the specimen was frozen for carcass composition analyses. Subsequently, thawed specimens were plucked and initially homogenized in a Hobart 1 HP meat grinder. Homogenate subsamples of approximately half of the plucked carcass mass (ca. 450 g) were extracted and oven-dried to constant mass at 90°C (Kerr et al. 1982). Dried samples were ground a second time in a Moulinex coffee grinder to ensure homogeneity. Cellulose thimbles dried to constant mass were filled with approximately 10 g of the dried homogenates and washed with petroleum ether in a modified Soxhlet apparatus to extract lipids (Dobush et al. 1985). Lean thimble contents were placed into Coors

porcelain crucibles and burned at 550°C in a muffle furnace for approximately 10 h to derive ash and ash-free lean (i.e., protein) content of the samples.

STATISTICAL ANALYSES

Nutrient reserves can show significant intraspecific variation due to individual body size (Alisauskas and Ankney 1987, Ankney and Afton 1988, Ankney and Alisauskas 1991). To eliminate this variation from our data, we performed principal components analysis of the correlation matrix (PROC PRINCOMP; SAS Institute Inc. 1985) derived from the four structural variables measured on each bird. The first principal components score (PC_1) for each bird was interpreted as a measure of body size because the loadings for all variables were positive (Pimental 1979), ranging from 0.36 to 0.58. PC_1 had an eigenvalue of 1.77 and explained 44% of the original variation in the data set.

To determine if nutrient reserves were related to body size, each variable including lipid, protein, and ash content was regressed (PROC REG; SAS Institute Inc. 1985) on PC_1. Carcass lipid ($F = 1.57$, df = 142, $P = 0.21$) and ash ($F = 0.34$, df = 142, $P = 0.56$) content were not related to structural size of the bird; however, protein content ($F = 30.14$, df = 142, $P = 0.0001$) was related to body size as:

$$\text{carcass protein} = 221.18 + 5.45(PC_1)$$
$$r^2 = 0.18$$

Body protein mass corrected for structural size (y_i) was determined for each specimen using the following equation (see Ankney and Alisauskas 1991):

$$y_i = y_{obs} - [a + b(PC_1)] + \bar{Y}_{obs}$$

where y_{obs} equals the unadjusted carcass protein mass for an individual bird and $\bar{Y}_{obs}$ equals the mean of unadjusted carcass protein mass for all specimens. Values of body protein corrected for body size were used in the ensuing analyses.

Effects of year and molt status and their interaction on nutrient reserves and gut morphology were investigated using analysis of variance (ANOVA) (PROC GLM; SAS Institute Inc. 1985) following tests to ensure normality of each data set (PROC UNIVARIATE NORM; SAS Institute Inc. 1985). Because two-way ANOVA indicated no significant ($P > 0.05$) interactions or differences in nutrient reserves or gut morphology between years, we investigated variation only in relation to stage of molt. Means for all variables were compared between sequential molt periods using t-tests (PROC TTEST; SAS Institute Inc. 1985). Unless noted otherwise, all differences indicated are significant at $P < 0.05$. To detect potential use of somatic nutrients during remigial molt, we regressed each nutrient against the combined lengths of primaries 6–10 (PROC GLM; SAS Institute Inc. 1985). Postflightless Canvasbacks that had completed remigial growth ($n = 5$) were not included in this analysis.

RESULTS

BODY MASS AND NUTRIENT DYNAMICS

Most variation in body mass of molting male Canvasbacks resulted from lipid storage and catabolism (Table 1). Ingesta-free body mass declined ($P \leq 0.05$) from the early and late preflightless periods to the flightless period as body lipids were metabolized. Body mass increased ($P \leq 0.001$) from the flightless to the postflightless period as birds accumulated fat and protein (Table 1). A subsequent increase ($P < 0.05$) in body mass occurred between the postflightless and staging periods as birds continued to store fat ($P < 0.001$). Staging birds had accumulated an average of 200 g of body fat and were at peak seasonal body mass ($\bar{x} = 1207.4$ g).

Protein content of male Canvasbacks was relatively stable during the postreproductive period (Table 1). The only significant change in total protein was an increase ($P \leq 0.001$) from the flightless to the postflightless period. Clearly, most of this gain in total body protein resulted from hypertrophy of the pectoral muscles (Table 1), which continued to grow through the postflightless and staging periods. Hind limb musculature hypertrophied ($P \leq 0.001$) from the late preflightless to flightless periods, but subsequently declined ($P \leq 0.05$) from the postflightless to staging periods. Heart mass of male Canvasbacks declined ($P \leq 0.001$) from the late preflightless to the flightless period, but rapidly recovered ($P \leq 0.001$) to pre-remigial molt mass in postflightless birds when they regained the ability to fly.

Somatic ash content did not differ between sequential molt stages (Table 1), but there was a gradual, albeit small increase ($P \leq 0.05$) in mineral reserves from the late preflightless period to the staging period, encompassing a time span of approximately three months.

NUTRIENT RESERVE DYNAMICS DURING REMIGIAL MOLT

Molt intensity and corresponding nutritional requirements for keratin synthesis were highest during the flightless and postflightless molt stages due to overlap in prebasic and prealternate molts (Thompson and Drobney 1995). To determine whether nutrient reserves were used during the most intense periods of molt, body protein, lipid, and ash content were regressed against the combined length of primaries 6–10 as they matured (Fig. 1). Our samples were somewhat skewed towards birds that had recently shed their flight feathers or were nearly completed with remigial molt. However, we suggest that the curvilinear relationships between nutrient reserve dynamics and primary growth in male Canvasbacks are supported by the specimens we collected and similar relationships documented for other waterfowl (Ankney 1979, 1984, Bailey 1985).

Male Canvasbacks accumulated endogenous protein, lipid, and mineral during remigial molt indicating that these birds did not experience a prolonged dietary deficiency of these nutrients during peak nutritional requirements for molt. Somatic protein (Fig. 1) exhibited a significant ($P = 0.0001$, $r^2 = 0.47$) curvilinear relationship with the length of growing primaries. Body protein declined slightly during early remigial molt, but increased rapidly in the latter stages of primary maturation. Synthesis of body protein began when the combined length of the distal primaries was approximately 300 mm (Fig. 1), before birds regained the ability to fly. Body lipid content of male Canvasbacks reflected a pattern similar to that of protein, decreasing during early remigial molt, but rapidly increasing when the distal primaries were approximately half grown (Fig. 1). Body ash content had only a weak relationship ($P = 0.03$, $r^2 = 0.13$) to primary growth (Fig. 1), indicating that little somatic mineral was catabolized during the highest mineral requirements for plumage synthesis. As with both protein and fat, ash content of the carcass dropped slightly during early remigial molt, but rapidly exceeded preflightless levels during latter remigial growth (Fig. 1).

GUT MORPHOLOGY

Morphology of the digestive tract varied considerably during the postreproductive molts (Table 2). Total digestive tract mass increased ($P \leq 0.01$) from the early to the late preflightless period and continued to grow until peak seasonal mass was attained during the flightless period. Mass of the gut subsequently declined from the flightless to the postflightless period ($P \leq 0.001$) and again before departure for fall migration ($P \leq 0.05$). Most variation in mass of the digestive tract was attributable to changes in gizzard mass (Table 2). Hypertrophy of gizzard tissue occurred during both early and late preflightless periods until peak seasonal mass was reached during the flightless period (Table 2). Gizzard mass declined ($P \leq 0.001$) from the flightless to the postflightless period and again ($P \leq 0.05$) from the postflightless to the staging period. Other digestive tract organs, with exception of the large intestine, exhibited similar patterns of variability in mass (Table 2).

Increases in pancreas and liver mass were initiated prior to lipogenesis in molting Canvasbacks. Pancreas mass initially increased from the early to late preflightless periods ($P \leq 0.05$), whereas liver mass originally increased between the late preflightless and flightless periods ($P \leq 0.001$). Both the pancreas and liver continued to increase ($P \leq 0.001$) in mass from the flightless to postflightless periods as birds accumulated additional premigratory lipid reserves (Table 1).

There was also variability in length of the total digestive tract and its components in molting male Canvasbacks (Table 2). Total digestive tract length increased ($P \leq 0.05$) from the early to late preflightless periods and remained longer throughout the remaining molt periods. Elongation of the digestive tract resulted primarily from growth in the upper digestive tract ($P \leq 0.01$), small intestine ($P \leq 0.05$), and ceca ($P \leq 0.05$). Of these organs, only the small intestine maintained similar length throughout the remaining molt periods (Table 2). From the late preflightless to the flightless period, the length of the upper digestive tract declined ($P \leq 0.05$), whereas the ceca ($P \leq 0.01$) and gizzard ($P \leq 0.001$) became more extended. The only subsequent change in length of the digestive tract was a reduction in length ($P \leq 0.001$) of the gizzard from the flightless to the postflightless period.

DISCUSSION

BODY COMPOSITION RELATIVE TO NUTRITIONAL REQUIREMENTS FOR MOLT

Lipid. Male Canvasbacks gradually catabolized somatic lipids remaining from the breeding sea-

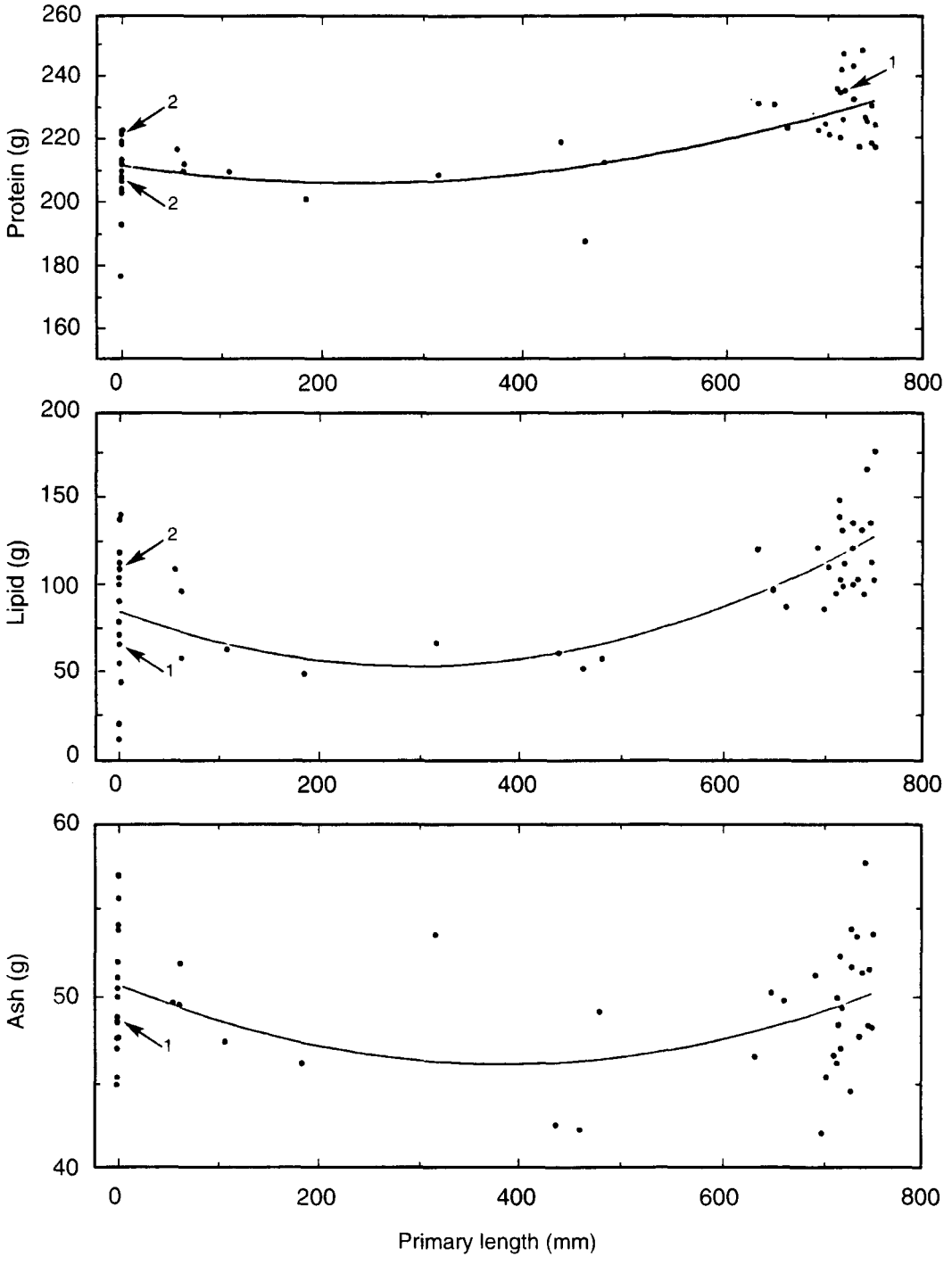

FIGURE 1. Curvilinear relationships between somatic protein, lipid, and ash and primary growth (i.e., combined length of primaries 6–10) in flightless and postflightless male Canvasbacks. Solid curved lines indicate the following equations describing the relationship between nutrient reserves and primary growth: protein $Y = 211.26 - 0.46x + 0.0001x^2$ ($r^2 = 0.47$, $P = 0.0001$), lipid $Y = 84.11 - 0.046x + 0.0004x^2$ ($r^2 = 0.43$, $P = 0.0001$), and ash $Y = 50.71 - 0.026x + 0.00003x^2$ ($r^2 = 0.13$, $P = 0.03$). Arabic numerals indicate the number and location of data points hidden due to overlap with another specimen.

TABLE 2. Digestive tract, liver, and pancreas morphology of molting male Canvasbacks.[a]

Variable	Molt stage[b] EP (n = 32)	P[c]	LP (n = 28)	P	FL (n = 27)	P	PF (n = 29)	P	ST (n = 27)
Mass:									
Total digestive tract[d]	56.48	**	63.35	***	76.17	***	66.11	*	61.85
	(1.38)		(2.47)		(2.28)		(1.31)		(1.39)
Upper digestive tract	9.33	NS	10.05	*	10.82	NS	10.80	*	10.17
	(0.21)		(0.24)		(0.20)		(0.22)		(0.20)
Gizzard	27.49	**	32.54	***	44.66	***	36.43	*	34.44
	(0.44)		(1.55)		(1.47)		(0.59)		(0.58)
Small intestine	16.94	NS	18.13	NS	18.10	**	16.25	NS	14.83
	(0.62)		(0.56)		(0.57)		(0.42)		(0.54)
Ceca	0.93	NS	0.99	NS	1.05	NS	1.05	NS	0.96
	(0.03)		(0.04)		(0.04)		(0.03)		(0.03)
Large intestine	1.79	NS	1.64	NS	1.54	NS	1.58	NS	1.45
	(0.08)		(0.08)		(0.04)		(0.05)		(0.04)
Liver	33.34	NS	32.35	**	37.19	***	48.37	NS	47.26
	(1.02)		(0.95)		(1.41)		(1.52)		(1.69)
Pancreas	2.91	*	3.20	NS	3.35	***	3.95	NS	4.03
	(0.09)		(0.11)		(0.08)		(0.10)		(0.12)
Length:									
Total digestive tract[e]	2,135.8	*	2,219.8	NS	2,255.8	NS	2,222.7	NS	2,211.2
	(2.11)		(3.02)		(2.51)		(2.11)		(2.03)
Upper digestive tract	344.4	**	352.7	*	347.5	NS	348.6	NS	350.1
	(0.20)		(0.19)		(0.21)		(0.18)		(0.18)
Gizzard	50.2	NS	52.7	***	59.2	***	53.0	NS	53.6
	(0.04)		(0.11)		(0.09)		(0.07)		(0.07)
Small intestine	1,366.8	*	1,426.5	NS	1,444.9	NS	1,415.3	NS	1,413.7
	(1.28)		(2.04)		(1.62)		(1.37)		(1.17)
Ceca	273.8	*	286.7	**	304.7	NS	304.2	NS	294.7
	(0.39)		(0.45)		(0.48)		(0.35)		(0.46)
Large intestine	100.6	NS	101.2	NS	99.5	NS	101.6	NS	99.1
	(0.20)		(0.23)		(0.11)		(0.14)		(0.15)

[a] Mass measurements (wet) are in g; length measurements are in mm; means are presented with their corresponding SE in parentheses below.
[b] Molt periods include Early Preflightless (EP), Late Preflightless (LP), Flightless (FL), Postflightless (PF), and Staging (ST).
[c] Probability levels from t-tests between adjacent molt stages; * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, NS = $P > 0.05$.
[d] Cumulative mass of the upper digestive tract, gizzard, small intestine, ceca, and large intestine.
[e] Cumulative length of the upper digestive tract, gizzard, small intestine, ceca, and large intestine.

son from arrival on molting habitat through mid-remigial molt. If it was necessary for Canvasbacks to rely on lipid reserves to meet their energy requirements during molt, fat reserves should have been stored during the early and late preflightless periods in anticipation of maximum molt intensity during the flightless and postflightless periods (Thompson and Drobney 1995). Conversely, lipogenesis began concurrent with intense molt activity during mid-remigial growth (Fig. 1) suggesting little relationship between endogenous lipid dynamics and the energetic requirements for molt. Therefore, Canvasbacks primarily rely on their diet to meet energetic requirements during molt. Similarly, studies on captive Japanese Quail (*Coturnix coturnix*) (Thompson and Boag 1976) and White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) (Murphy and King 1992) indicated that these species were able to satisfy their energy demands during molt from their diets.

Lipid dynamics in molting birds are not necessarily reflective of the energetic costs of plumage synthesis (Chilgren 1977). Newton (1968) reported that fat reserves of molting and nonmolting Bullfinches (*Pyrrhula pyrrhula*) captured during the same time intervals were indistinguishable suggesting no significant contribution of endogenous energy during molt. Lipid deposition during molt in some migratory passerines (Newton 1968, Chilgren 1977) has been attributed to photoperiodic stimulation of hyperphagia before fall migration (King 1972). Lipid accretion during remigial molt or extensive body

molt has also been reported in several nonpasserines including Blue-winged Teal (*Anas discors*) (Dubowy 1985) and Canada Geese (Mainguy and Thomas 1985, Gates et al. 1993). Similarly, Canvasbacks began to accumulate fat reserves during the latter half of remigial growth, probably in response to photoperiodic stimulation of fall hyperphagia. Reduced conductive heat loss resulting from improved insulative ability of new down and alternate plumage may have also facilitated lipid storage. Additionally, time constraints may partially regulate onset of lipid acquisition in migrant waterfowl. However, temporal constraints on premigratory lipogenesis are more apparent in species that migrate soon after remigial molt (e.g., Blue-winged Teal) than in male Canvasbacks, which may linger on molting habitats for more than a month following maturation of their remiges.

Lipid catabolism in male Canvasbacks during late prebasic molt coincided with elevated down plumage replacement (Thompson and Drobney 1995), therefore fat reserves may have been partially catabolized as a result of increased thermoregulatory costs originating from greater conductive heat loss to water. In general, however, we suggest that Canvasbacks do not need to accumulate or maintain extensive lipid reserves during prebasic molt given the typical abundance and predictability of food on molting habitats (Salomonsen 1968) and warm ambient temperatures during this period of the annual cycle.

It has been speculated that several species of dabbling ducks may rely on lipid reserves during remigial molt to reduce foraging time, thereby allowing birds to remain more vigilant against predators in their marsh molting habitats (Young and Boag 1982, Panek and Majewski 1990). Male Canvasbacks reduce foraging activity during wing molt (Thompson 1992), however, since they molt on open expanses of water and consequently are easily observed during remigial molt, fat catabolism does not serve to reduce visibility and subsequent predation rates during molt. Furthermore, during extensive time budget observations (Thompson 1992), we never observed a single predation attempt on flightless Canvasbacks, suggesting that predation rates are low during remigial molt. Finally, if fat reserves significantly improved survival of molting Canvasbacks or other waterfowl, then more extensive lipogenesis should occur prior to wing molt. Species that store lipids before remigial molt, including Mallards (*Anas platyrhynchos*) (Folk et al. 1966, Young and Boag 1982, Pehrsson 1987) and Gadwalls (*Anas strepera*) (Hay 1974), show only relatively small increases (11–15%) in their energy reserves suggesting that fat deposition is probably incidental and not critical to meeting the energetic requirements of their postreproductive molts.

Premigratory hyperphagia ensures anticipatory accumulation of lipid reserves to buffer birds from declining ambient temperatures and meet the energy requirements of extended flights to other migrational and wintering habitats. Lipogenesis occurred from mid-remigial molt through the staging period, during which birds accumulated an average of nearly 200 g of body fat. There are, however, some species of waterfowl that catabolize or maintain constant fat reserves through remigial molt. Lipid reserves decline throughout primary maturation in male and female Mottled Ducks (*Anas fulvigula*) (Moorman et al. 1993), which is predictable because this relatively sedentary species does not migrate following remigial molt. Ankney (1979) suggested that Lesser Snow Geese (*Chen caerulescens caerulescens*) do not store fat during remigial molt because food is abundant and readily available in their molting habitats and migration does not occur for another two months.

Most variation in body mass of molting Canvasbacks originated from changes in lipid reserves. Flightless male Canvasbacks in Alberta were at minimum seasonal body mass principally due to lipid catabolism during the late preflightless period and early remigial molt. Similarly, live body mass of flightless male Canvasbacks molting in Alaska was consistently low ($\bar{x} = 1105.1$ g, $n = 48$) (Yocum 1970). Reduced body mass during early remigial molt has prompted some researchers to regard molt as a stressful period in the annual cycle of birds (Weller 1957, Hanson 1962). We suggest that reduction of body mass in molting Canvasbacks is not indicative of nutritional stress, but instead reflects the abundance and availability of food on molting habitats, which negates the need to maintain extensive nutrient reserves during this portion of the annual cycle.

Reduced body mass of waterfowl during their simultaneous remigial molt also has been postulated as an adaptation that lowers wingloading, thereby allowing birds to fly at earlier stages of remigial growth (Douthwaite 1976, Owen and

Ogilvie 1979, Geldenhuys 1983, Austin and Fredrickson 1987, Pehrsson 1987). Body mass of male Canvasbacks declined during early remigial molt. However, somatic protein and fat accretion began before birds regained flight (Fig. 1), indicating that body mass did not decline to reduce the flightless period. Furthermore, predation on male Canvasbacks was apparently low during remigial molt (Thompson 1992), suggesting that there is little selective pressure to shorten the flightless period beyond the normal three to four week time span (Hochbaum 1944, Thompson and Drobney 1995).

Protein. Much debate exists over whether or not waterfowl (*Anseriformes*) experience a protein or specific amino acid deficiency during their postreproductive molts (Hanson 1962, Ankney 1979, 1984, Bailey 1985). Minimum annual body mass (Hanson 1962), rapid turnover and mobility of body protein (Bailey 1985), and reduced foraging (Austin and Fredrickson 1987) have been considered symptomatic of a dietary protein deficit during remigial molt in waterfowl. However, these same events have been argued to be adaptations to simultaneous remigial molt in relatively productive habitats where food is abundant, nutrient reserves are not needed, and maintenance of lower body mass reduces metabolic costs (Ankney 1979).

Molting birds may need to acquire elevated amounts of the sulfur amino acids cyst[e]ine and methionine, which are concentrated in plumage keratins (Newton 1968) but occur in relatively low concentrations in dietary and body proteins (Murphy and King 1992, Murphy 1994). Acquisition of these essential, but relatively limited substrates may limit the rate of molt in some species of birds (Murphy et al. 1988, Murphy and King 1992). Researchers have noted the disparity in concentrations of the sulfur amino acids in the plumage of birds and their diet and proposed a variety of resolutions to this apparent nutritional constraint. Hanson (1962) suggested that molting Canada Geese catabolized somatic protein to help resolve the difference in the sulfur amino acid content of their diet and plumage. More recently, reduced foraging in molting ducks was suggested to be a mechanism that triggered body protein catabolism to meet the amino acid demands of plumage growth in male Redheads (*Aythya americana*) (Bailey 1985) and female Lesser Scaup (*Aythya affinis*) (Austin and Fredrickson 1987). However, none of these studies evaluated the daily requirements for the sulfur amino acids in relation to seasonal plumage growth rates.

Estimated plumage growth rates of male Canvasbacks (Thompson 1992) suggest that the peak nutritional requirements for keratin synthesis occurred during overlap in contour plumage and remigial growth in the flightless and postflightless molt periods (0.8 g dry feather/day). Male Canvasbacks lost approximately 5.0 g (dry mass) of somatic protein during early remigial growth (Fig. 1). Amino acid profiles of Canvasback breast muscle and plumage revealed that the sulfur amino acid concentrations (cyst[e]ine + methionine) were 346 μm/g and 841.3 μm/g, respectively (amino acid concentrations [Thompson 1992] were corrected to μm/g of protein recovered; 78% of the sample mass was recovered in breast muscle tissue and 99.28% was recovered in the plumage assay). Assuming a 75% conversion efficiency of the sulfur amino acids in somatic protein to epidermal keratin, 5 g of catabolized breast muscle tissue would supply the cyst[e]ine and methionine content in only 1.5 g of dry feather tissue. This potential endogenous contribution would equate to production of less than 2% of the total plumage mass replaced by a male Canvasback during the postreproductive period.

Thus, male Canvasbacks met the majority of their protein demand for postreproductive molts from their diet. We suggest that reliance on exogenous protein is predictable given that postreproductive molts are extended over a 6 month period (Thompson and Drobney 1995), which reduces the per diem sulfur amino acid requirement to a level that can be met by dietary intake. Reliance on dietary protein during molt is further supported by categorical analysis (Table 1), which indicated that the only significant change in body protein was a 20 g increase between the flightless and postflightless period concurrent with the highest seasonal molt intensity (Thompson and Drobney 1995). Mallards (Young and Boag 1982, Heitmeyer 1988), American Black Ducks (*Anas rubripes*) (Reinecke et al. 1982), Canada Geese (Gates et al. 1993, Mainguy and Thomas 1985), Brant (*Branta bernicla*) (Ankney 1984), and Lesser Snow Geese (Ankney 1979) also rely principally on dietary protein to meet the amino acid requirements of feather production as indicated by stable carcass protein levels during elevated molt intensity in their annual cycles.

It should be noted that daily patterns of en-

dogenous protein utilization and synthesis in Canvasbacks would not have been detected by the extended molt period categorization used in our study. Molting passerines typically rely on dietary protein to synthesize plumage during the day when they are actively feeding, however, nocturnal synthesis of feather keratin, which proceeds at the same rate as when birds are feeding (Newton 1968), is maintained by small scale catabolism of somatic protein that is replaced when birds resume foraging the following day (Murphy and King 1990). A similar daily cycle of body protein catabolism and accretion to maintain consistency in plumage growth rates is less likely for waterfowl which commonly feed both diurnally and nocturnally (Swanson and Sargeant 1972, Pedroli 1982, McNeil et al. 1992). Furthermore, daylight is extended during summer in north temperate and subarctic habitats (i.e., $\geq$ 50° latitude) where male Canvasbacks typically molt.

Despite relatively little variation in total protein content of molting male Canvasbacks, there were dramatic shifts in the distribution of body protein between muscle masses (Tables 1 and 2). Canvasback breast tissue mass declined by 44.8 g (wet mass) from the late preflightless to flightless period, which is very similar to the 40 g (wet mass) loss in the pectoral muscles of molting Mallards (Young and Boag 1982). Additionally, heart mass in male Canvasbacks declined by 1.5 g (wet mass) as time spent in active behaviors (e.g., foraging and flying) was minimized in flightless birds (Thompson 1992). Converted to a dry weight basis (75% of muscle tissue is typically water [Maynard and Loosli 1969]), the cumulative loss in breast and heart tissue would represent catabolism of 11.6 g of somatic protein, however, there may be some slight error in this estimate due to potential loss of intramuscular lipids (Gaunt et al. 1990). Redistribution of body protein to support hypertrophy of the leg musculature and gizzard in flightless Canvasbacks could account for 6.3 g of the catabolized protein. This leaves only 5.3 g of body protein that is unaccounted for by increased protein mass in other body tissues, which is remarkably close to the 5 g loss of somatic protein during early remigial molt. This relatively small amount of catabolized protein may have been partially incorporated into feather keratin or oxidized during transfer to other muscle tissues.

Changes in mass of breast and leg muscles of molting waterfowl have been attributed to use-disuse phenomena (Ankney 1979), anticipatory changes (Hanson and Jones 1976, Ankney 1984), and use in growth of plumage (Hanson 1962, Bailey 1985, Austin and Fredrickson 1987). Kendall et al. (1973) reported that birds could catabolize breast muscle tissue to satisfy amino acid demands during periods of insufficient dietary intake. However, male Canvasbacks did not rely on catabolized breast protein to meet a significant component of the amino acid demands for molt. Furthermore, we found no evidence that endogenous protein mobility in male Canvasbacks was a mechanism that directly provided amino acids for plumage growth.

Elevated protein metabolism in molting Canvasbacks was essential for adaptive redistribution of body muscle tissue given the metabolic cost of maintaining relatively constant somatic protein mass over the postreproductive period. Pectoral muscles of Canvasbacks steadily atrophied as the birds spent less time flying (Thompson 1992). Disuse atrophy resulted in breast protein being gradually catabolized and apparently redistributed to growing leg and gizzard muscle tissues. Atrophy in breast muscles during reduced flight activity suggests that these tissues are maintained at their smallest functional size due to the relatively high metabolic cost of maintaining proteinaceous tissue. Conservative regulation of the mass of proteinaceous tissues is supported by studies on a variety of species of birds (Moss 1974, Ankney 1977, Raveling 1979).

Powerful leg muscles are important to flightless diving ducks because swimming and diving are essentially their only modes of locomotion and escape from predators. However, the small increase (12%) in leg mass of flightless Canvasbacks is not nearly as dramatic as the nearly 40% increase in leg mass documented in several species of molting geese (Ankney 1979, 1984). The marked increase in mass of leg tissue in terrestrial molting geese is attributable to increased use because these birds may walk considerable distances during remigial molt. Because time spent swimming or foraging did not increase in flightless Canvasbacks (Thompson 1992), hypertrophy of leg musculature was apparently an ultimate response to anticipated need of increased power rather than actual use. Bailey (1985) suggested a similar motivation for leg mass hypertrophy in molting male Redheads because he

found little evidence that increased locomotion was responsible for changes in leg muscle mass.

Mineral. Cyclic osteoporosis has been reported during molt in several genera of waterfowl (Meister 1951). However, there was no significant decline in body mineral content of male Canvasbacks during their postreproductive molts (Table 1). Furthermore, primary growth explained only 13% of the variability in carcass ash content (Fig. 1) suggesting only a weak relationship between body mineral content and mineral requirements for plumage growth. Similarly, Lesser Snow Geese (Ankney 1979) and Brant (Ankney 1984) did not rely on catabolized body minerals for feather growth during remigial molt. Furthermore, Hanson and Jones (1976) indicated that the mineral content of plumage in several species of geese reflected the mineral composition of their molting habitat suggesting that these birds acquired the mineral component of their plumage from their diet.

Meister (1951) argued that most feather minerals originated from bone catabolism even when there was no apparent dietary deficiency due to hormonal regulation of mineral deposition in plumage. However, we found no evidence of prolonged bone catabolism in molting Canvasbacks to meet plumage mineral requirements (Table 1). Assuming that the low mineral content of passerine plumage (0.86% of dry plumage mass; Murphy and King 1982) is similar for Canvasbacks, only 0.7 g of ash was required to complete prebasic and prealternate molts (Thompson 1992). Given this low total requirement for two molts that are extended over 6 months, it is unlikely that there is significant need for transfer of endogenous minerals to feather tissue.

GUT MORPHOLOGY DURING MOLT

Many studies of molting waterfowl have neglected to document changes in gut morphology that may have accounted for much of the catabolized breast protein presumed to be incorporated into feather tissue. Most variation in gut size of male Canvasbacks was related to increased organ mass and length before or during remigial molt and a return to preflightless organ size as birds regained the ability to fly (Table 2). Gizzard mass increased 37% in male Canvasbacks during remigial molt, which may have improved the grinding ability of this organ thereby enhancing protein assimilation from the hard-shelled sago pondweed (*Potamogeton pectinatus*) seeds that predominated in the diet of flightless birds (Thompson and Drobney 1996). This hypothesis is further supported by a rapid reduction in gizzard mass during the postflightless and staging periods as feather growth rates declined and readily metabolized pondweed tubers, which require less mechanical processing before digestion, comprised the bulk of the diet. Similarly, gizzard mass in molting male Blue-winged Teal increased when seeds became an important component in the diet (Dubowy 1985).

Gut morphology can be influenced by the volume (Ankney 1977) and quality (Moss 1974, Miller 1975, Paulus 1982, Drobney 1984) of foods, therefore variation in gut size may not be indicative of the need for endogenous protein storage or utilization (Gauthier et al. 1984). The volume of food consumed by Canvasbacks probably decreased during the wing molt as foraging activity declined (Thompson 1992); however, the digestive tract was at peak mass. The diet during remigial molt was predominately pondweed seeds, which represented a reduction in food quality from preceding or subsequent molt periods when pondweed tubers and rootstalks were the primary foods (Thompson and Drobney 1996). Kehoe and Ankney (1985) categorized diets consisting primarily of seeds as intermediate in dietary fiber, whereas tuber diets were regarded as low fiber or higher quality diets. A nutritional consideration that was as much or perhaps more important than fiber content was the low sulfur amino acid content of seeds relative to that of plumage and other foods (Thompson 1992). Lower food intake and a shift to poorer quality food during remigial molt would increase the need for efficient protein assimilation from foods consumed by molting birds.

Increased mass in the digestive tract of molting birds may have evolved to improve digestive efficiency (Anderson 1972, Ankney 1977, Austin and Fredrickson 1987). Hypertrophy of the upper digestive tract (including the gizzard) improved protein assimilation in passerines (Dolnik and Gavrilov 1979). Digestive tract hypertrophy during remigial molt occurred in Lesser Scaup (Austin and Fredrickson 1987), Redheads (Bailey 1981), and Black Ducks (Reinecke et al. 1982) concurrent with decreased foraging activity and increased protein requirements of molt. Austin and Fredrickson (1987) postulated that anatids may need to increase alimentary efficiency during remigial molt because somatic lip-

id and protein reserves are usually minimal, foraging time is typically reduced, and the energetic and nutritional demands for feather synthesis are high. Thus, it is likely that many of the modifications in gut morphology of molting Canvasbacks evolved to improve protein assimilation from their diet thereby minimizing or negating reliance on catabolized body protein.

The gizzard can be an important source of catabolized protein for clutch formation in waterfowl (Ankney 1977, Korschgen 1977, Raveling 1979, Krapu 1981), but it was not a significant source of protein during molt because it increased in mass during the periods of higher molt intensity (Thompson and Drobney 1995). Gizzard mass declined in the postflightless period as pectoral muscle mass increased (Tables 1 and 3), but remained heavier than premolt levels through fall staging. Likewise, gizzard protein was not catabolized by molting Lesser Scaup to meet feather growth requirements because there was a gradual increase in gizzard size throughout the postreproductive period (Austin and Fredrickson 1987).

Rapid changes in morphology of the digestive tract of molting male Canvasbacks support the hypothesis that birds should maintain the smallest functional organ size because smaller organs reduce metabolic energy expenditure (Moss 1974). As Canvasbacks returned to a low fiber diet (i.e., pondweed tubers) and the need for maximum digestive efficiency was reduced due to increased foraging activity and improved diet quality following wing molt, the mass of the digestive tract declined (Table 2). Furthermore, maintaining digestive organs at heavier masses through fall migration may conflict with other energetic adaptations including abdominal lipid storage and the need to minimize transportation and maintenance costs during extended migratory movements.

CONCLUSIONS

Somatic lipid, protein, and mineral dynamics of postbreeding male Canvasbacks indicated no long term deficit in nutrient reserves that could be directly attributed to the nutritional requirements for molt. Because male Canvasbacks extend their two annual molts over six months, their low daily nutrient requirements for molt can be met principally through their diet. Molting over an extended portion of the annual cycle minimizes any potential disparity between specific amino acid demands for plumage synthesis and the availability of these substrates in the diet (Murphy et al. 1988). Furthermore, if necessary, birds may have the capability to select foods that can satisfy specific protein or amino acid requirements (Murphy and King 1987).

Primary reliance on their diet to meet the nutritional requirements for molt is evidently a common strategy in birds. This nutritional dependency on their molting habitat explains in part why birds typically concentrate plumage replacement during segments of their annual cycle when food is predictable, abundant, and readily available (Newton 1968). Other than molting penguins (Sphenisciformes), which rely exclusively on endogenous nutrients to synthesize plumage during a prolonged fast (Williams et al. 1977), there are apparently few exceptions to this pattern.

Redistribution of body protein in molting Canvasbacks was likely adaptive given the metabolic cost of maintaining stable body protein mass over the postreproductive period. Catabolism of breast protein was apparently an adaptation to support leg and gizzard muscle hypertrophy in flightless birds. Increased leg mass was anticipatory to need for locomotion when birds could not fly. Modifications in gut morphology, specifically hypertrophy of the gizzard in flightless birds, possibly improved dietary metabolic efficiency thereby alleviating the need for significant catabolism of body muscle tissue to meet the protein demands of molt. Because birds must molt to survive and maintain the functional and structural roles of their plumage (Murphy and King 1991), dependence on dietary nutrients to meet the nutritional demands of molt emphasizes the strategic importance of postbreeding habitats in the annual cycle of Canvasbacks.

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