

THE ANNUAL MOLT CYCLE OF *BRANTA CANADENSIS INTERIOR* IN RELATION TO NUTRIENT RESERVE DYNAMICS¹

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Abstract. During July 1984–February 1987, we measured the duration and seasonal changes in intensity of prebasic molt in Canada Geese (*Branta canadensis interior*) of the Mississippi Valley Population (MVP). Temporal and geographic variations in molt intensity were examined in relation to lipid and protein reserve dynamics and the chronology of annual events. Wing- and body-molt intensities were greatest before fall migration, but limited body molt overlapped migration and continued into fall. Final stages of molt progressed with declining intensity through winter. Only the nesting season (May–June) was entirely free of molt. Molt in individual geese may have required ≥ 8 months (July–March) in at least 60% of the population. Temporal and geographic variation in molt intensity were associated with differences in lipid mass, but carcass protein had little apparent relationship with molt intensity. There was no evidence of net catabolism of nutrient reserves between hatching, wing molt, and post-molting periods. Lipid masses of breeding females and non-breeding geese declined during wing molt. Protein masses declined during wing molt only in breeding and non-breeding males, due to atrophy of breast muscles associated with flightlessness. Seasonal changes in molt intensity and lipid reserves indicated that geese allocated energy to emphasize molting before fall migration, and nutrient reserve deposition thereafter. The largest nutritional costs of molting probably were incurred during July–November. We propose that rate, intensity, and duration of body molt were influenced by the amount of productive energy geese were able to allocate to feather growth, without compromising replenishment of nutrient reserves after breeding or the deposition of reserves before winter. The simple, single molt of Canada Geese provides greater latitude in adjusting nutritional demands to environmental conditions than is possible for ducks that molt twice annually.

Key words: *Canada goose; Branta canadensis interior; molt cycle; nutrient reserves; bioenergetics; annual cycle; nutritional stress.*

INTRODUCTION

Timing of annual cycle events is an important aspect of energy allocation in birds (Payne 1972, Foster 1975, King and Murphy 1985). Molt increases energy and protein metabolism and imposes special nutritional demands (Newton 1968, Thompson and Boag 1976, King 1980, Walsberg 1983, Murphy and King 1984a, Heitmeyer 1988a). Increased energy and nutrient demands, low energetic efficiency of molting (Murphy and King 1984a), and loss of body mass have caused

some to suggest that molt is nutritionally stressful (Hanson 1962a, Dolnik and Gavrilov 1979). Nutritional stress implies conflict in allocating energy and nutrients that ultimately reduces fitness (Ankney 1979, King and Murphy 1985, Lovvorn and Barzen 1988). Consequently, the timing of avian molt is often thought to be constrained by nutritional conflicts with other energy or nutrient-demanding life history events. Many temperate breeding birds avoid nutritional conflicts by segregating molt from breeding, migration, or seasons of nutrient deposition (Payne 1972, Owen and Krohn 1973, King 1974, Chiltern 1977, Rimmer 1988).

Time constraints, food resources, and chronologies of migration and breeding may cause overlap of molting with periods of migration, courtship, nesting, or nutrient deposition in different species (Payne 1972, Rimmer 1988). Among species in which molt overlaps other nutritionally demanding events, prolonged low in-

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tensity molting reduces daily nutrient daily requirements (Blackmore 1969, Payne 1972), or endogenous reserves are mobilized to resolve nutritional conflicts (King 1980, King and Murphy 1985). Molting can overlap other life history events if their nutritional requirements are compatible and the abundance and quality of available food resources is adequate (Payne 1972, Heitmeyer 1988b, Zaias and Breitwisch 1990).

Understanding of proximate and ultimate factors affecting body molt in waterfowl is derived mostly from research conducted with ducks that molt body feathers twice annually (DuBowoy 1985, Heitmeyer 1987, 1988b, Lovvorn and Barzen 1988). The duration and seasonal intensity of body molt is less known for geese than other waterfowl (Delacour 1964, Hanson 1965, Palmer 1976, Owen 1980, Weller 1980). Ducks typically complete or suspend prebasic molt before nesting (Oring 1968, Wishart 1985, Lovvorn and Barzen 1988), and molt is often segregated from migration (Bluhm 1988). Female Mallards (*Anas platyrhynchos*) tend to initiate and complete prealternate and prebasic molts in sequences that alternate with migration, courtship, and nutrient deposition during fall and winter (Heitmeyer 1987, 1988b). However, body-molts at least partly overlap migration, pair formation, gonadal recrudescence, and periods of nutrient deposition in some species, populations, or age/sex/social groups of ducks (Paulus 1984, DuBowoy 1985, Wishart 1985, Miller 1986, Bluhm 1988, Lovvorn and Barzen 1988, Heitmeyer 1988b). Molts are also affected by variation in habitat and diet quality (Miller 1986, Heitmeyer 1987, Pehrsson 1987, Richardson and Kaminski 1992).

Geese and swans differ from ducks in several aspects that are important to understanding molt patterns of Anseriformes. Anserinae are perennially monogamous, exhibit biparental care of young, are sexually monochromatic, have delayed sexual maturity, and molt only once per year (Palmer 1976). Much of the work conducted on molting in Anserinae has focused on energetic stress and body condition associated with wing molt (Ankney 1979, 1984; Earnst 1992). Hanson (1962a) considered wing molt to be nutritionally stressful based on seasonally diminished body, lipid, and muscle masses in flightless Canada Geese.

Hanson's (1962a) work on Canada Geese focused attention on the issue of nutritional stress in wing-molting waterfowl. However, several

studies that followed Hanson (1962a) demonstrated little or no loss of nutrient reserves during wing-molt in waterfowl (Raveling 1979; Ankney 1979, 1984; Young and Boag 1982; Mainguy and Thomas 1985; Austin and Fredrickson 1987). Furthermore, mobilization of nutrient reserves does not necessarily indicate nutritional stress (King and Murphy 1985) and alternative interpretations of mass loss in molting waterfowl have been proposed (Douthwaite 1976, Austin and Fredrickson 1987, Pehrsson 1987, Panek and Majewski 1990).

We measured duration and seasonal changes in wing- and body-molt intensities in *B. c. interior* of the Mississippi Valley Population (MVP). Temporal and geographic differences in molt intensity were examined in relation to nutrient reserve dynamics and the chronologies of annual events. The potential influences of nutritional and other constraints affecting patterns and timing of molts in Canada Geese were examined. Nutritional stress associated with wing molt was addressed by comparing nutrient reserve masses before, during, and after the flightless period. Inferences were generalized to the population of *B. c. interior* that comprises >95% of MVP Canada Geese that winter in southern Illinois (Spitzkeit and Tacha 1986).

STUDY AREA AND METHODS

We measured molt intensities and nutrient reserves in 735 Canada Geese (564 adults, 171 juveniles) collected between July 1984 and February 1987 at several study sites spanning the annual range of the MVP. Wintering geese were collected at Union County Conservation Area ($n = 319$), Rend Lake Wildlife Management Area ($n = 19$), and Crab Orchard National Wildlife Refuge ($n = 26$) in southern Illinois during October–February. Migrant geese were obtained near Horicon National Wildlife Refuge in east-central Wisconsin during fall (October–December; $n = 125$) and spring migration staging (March–April; $n = 124$). Breeding and postbreeding geese were collected along the southern Hudson Bay coast in Ontario during nesting (April–June; $n = 66$), the middle of wing molt (July; $n = 36$), and before fall migration (late August–early September; $n = 21$) in 1984–1986. Ninth primary lengths and body composition were measured on an additional 65 wing-molting adult geese collected in northern Ontario during July 1988–1990. The ninth primary was measured because it is the

most distal feather tip when measuring the wing chord. Spatial, morphological, and behavioral cues (Caithamer et al. 1993) were used to determine social status or recent breeding history of collected geese. Combining data across years, geese were obtained at 11 different points in the annual life cycle that were separated by no more than 45 days.

Molt intensities were compared between geese collected at two locations during the falls of 1984 and 1985. Late fall migrant geese (Kennedy and Arthur 1974) were those collected in east-central Wisconsin during October–December. Geese collected concurrently in southern Illinois were considered early fall migrants to terminal winter ranges. Late migrants migrated to southern Illinois, usually by late December, and mixed with early migrants already present on our study sites.

Body composition was determined by standard proximate analysis techniques that measured total carcass ash, neutral lipid, and water masses (Gates 1989). These components were subtracted from total carcass mass (without feathers, feet, bill, and gastrointestinal contents) to obtain ash-free lean dry mass (AFLDM) that approximated carcass protein content (Milne 1976).

Presence of blood quills within individual feather tracts or within specialized feather groups (i.e., scapulars, axillars, wing coverts, etc.) was noted as feathers were hand-plucked from carcasses in preparation for body composition analyses. Molt intensity was scored for each of eight pterygiae; capital, ventral, spinal, femoral, humeral, alar, crural, and caudal. Molt intensity scores were assigned to each pterygia according to relative densities of active feather follicles (enlarged feather papillae, soft quills engorged with blood, and partially sheathed feathers). Down feathers were not considered separately from contour feathers. Scores of 0 were recorded for tracts with no evidence of molt, 1 for tracts with <5 growing feathers/6.2 cm², 2 for densities of 5–10 growing feathers/6.2 cm², and 3 for densities exceeding 10 growing feathers/6.2 cm². Special feather groups (scapulars, axillars, alulae, tertials, secondaries, primaries, and under-wing, greater, middle, lesser, and primary wing coverts) were assigned scores of 0–3 corresponding to evaluations of no molt (0% of feathers), light molt (1–25%), moderate molt, (26–50%) or heavy molt (>50%). Molt scores for all pterygiae except alar and humeral tracts were summed for each carcass to obtain a body-molt intensity index.

Scores for special feather groups associated with the wing (excluding scapulars and axillars) were summed to provide a wing-molt intensity index. Total molt intensity was the sum of scores for all pterygiae including the alar and humeral. The ninth primary of one wing was measured from tip to point of insertion in skin. Rectrices were examined for the presence of notched tips indicating a juvenile feather (Hanson 1962b). Missing rectrices or partially sheathed or blood-filled quills indicated a molting tail feather follicle. Variation in rate or duration of molting is largely a function of the interval of growth activation between successive feather follicles, rather than feather growth rates (Payne 1972, Chilgren 1977, Murphy and King 1984b). Consequently, we considered higher molt scores to indicate faster rates of plumage renewal.

Mean molt intensity scores and nutrient reserve masses were compared among seasons, years, locations, and/or age/sex/social groups with 1-way and factorial analyses of variance (ANOVA) using the General Linear Models (GLM) Procedure of SAS (SAS Institute, Inc. 1985). Pairwise contrasts of least squares means (LSMEANS PDIFF option) from factorial ANOVA models were used when interactions were significant (Milliken and Johnson 1984) because of unbalanced data. Student-Newman-Keuls (SNK) test separated differences among means from one-way ANOVA models.

Lipid, protein (AFLDM) and mineral (ash) reserve masses of 57 breeding and 38 non-breeding adult geese collected July 1984–1985 and 1988–1990 in northern Ontario were regressed on ninth primary lengths to examine changes in nutrient reserves associated with stage of wing molt. Data were pooled across years, and separate regressions were conducted for breeding and non-breeding geese of each sex. Initial regression analyses found no effect of year and the interaction year × ninth primary length on nutrient reserve masses of flightless geese. Consequently, simple linear regressions of nutrient reserve masses on ninth primary length were used to test changes in nutrient reserves associated with stage of wing molt.

Stepwise multiple regression analyses (SAS Institute, Inc. 1985) of total molt intensity scores for geese collected October–December 1984–1985 in southern Illinois and east-central Wisconsin were conducted to identify relationships between nutrient reserve (lipid and protein) masses and total molt intensity during fall. These analyses

tested the strength of association between nutrient reserves and total molt intensity against other independent variables that included year, month, location, and their interactions. Main effects of sex and age were also tested. Stepwise regressions (forward and backward elimination) were performed across and within months, with age/sex classes combined. Significance levels for entering and retaining independent variables in stepwise regression models and all other tests were $P \leq 0.05$.

RESULTS AND DISCUSSION

AGE, SEX, AND SOCIAL GROUP DIFFERENCES

Wing, body, and total molt intensities did not differ ($F_{1,674} \leq 1.4$, $P \geq 0.24$) between sexes within or across age groups. Juveniles had greater total molt intensities ($P < 0.001$, $df = 611$) than adults during late July when they were molting heavily in all wing feather groups and body feather tracts. Only the primaries, secondaries, and spinal feather tract of adults were molting heavily in late July. Juveniles were 4–5 weeks old in late July and were still replacing natal down with their first juvenile plumage, a process not completed until at least 5–6 weeks of age (Yocum and Harris 1965, Palmer 1976). Juvenile plumage was replaced with prebasic I plumage in early September when juveniles were about 10 weeks old. Except for March when juvenile molt intensity again exceeded adults ($P = 0.048$, $df = 611$), molt intensities were similar ($P \geq 0.100$, $df = 611$) between age groups after July.

Initiation of wing molt by adult geese may differ as much as 2–4 weeks depending on recent breeding status (unpaired, non-parent paired, parent) (Palmer 1976, Owen 1980). Wing and total molt intensities varied ($F_{2,411} \geq 3.29$, $P \leq 0.038$) among parent, non-parent paired, and unpaired adults, primarily due to greater wing-molt intensities in unpaired geese compared to parent and/or paired geese during July and September ($P \leq 0.030$, $df = 411$). Parents had more ($P < 0.001$, $df = 413$) growing rectrices ($\bar{x} = 3.0$, $SE = 0.6$, $n = 22$) than paired ($\bar{x} = 1.2$, $SE = 0.4$, $n = 22$) and unpaired geese ($\bar{x} = 1.5$, $SE = 0.5$, $n = 22$) in October, indicating a later tail molt in successful nesting geese.

MOLT CHRONOLOGY

Separate seasonal comparisons were made for adults and juveniles with sexes combined because monthly molt intensities differed between

ages and not sexes. Wing molt was predictably most intense when geese were flightless in late July (Tables 1 and 2), 35–40 days after peak of hatching near Winisk, Ontario (Bruggink 1992). Primary growth was about 50% complete in adults and 40% complete in juveniles during late July. Wing-molt intensity declined substantially between late July and early September as geese regained flight. Wing molt was nearly complete by early September, wing coverts showed evidence of minor molt through November in adults; juveniles completed molting of wing coverts before November.

Adult and juvenile body-molt intensity increased July–September, then declined through February (Tables 1 and 2). Cumulative monthly molt intensity scores indicated that nearly all of wing molt and almost half of body molt occurred in northern Ontario before fall migration in late September.

Molting feathers found in late winter or spring could represent a second partial molt, replacement of lost feathers, or continuation of molting that was begun the previous summer. There was no evidence to indicate that molting after early winter represented a second plumage generation. This conclusion, however, requires validation by more thorough examination of feather replacement in individual geese over time. We believe that the gradual decline in body-molt intensity represented a prolonged molt of the same feather generation through fall and winter. Replacement of lost feathers cannot be excluded as the source of body molt observed in late winter and spring (January–April). Our data indicate that prebasic molt in *B. c. interior* spanned a period of no less than 5–6 months; July–December in adults, and August–December in juveniles. The only entirely molt-free interval occurred from after spring migration through nesting (May–June). Individual geese may have had shorter molt periods than the population as a whole; however, >60% of geese examined showed some indication of molt through at least March. Chronological patterns of wing and body molt intensities differed, with most of body molt occurring after geese regained flight (see also Hanson 1962a). The seasonal pattern of molt intensity did not differ among individual body pterygiae; however, replacement of axillars and scapulars occurred concurrently with wing coverts.

Molt intensities during October–May were greater in 1985–1986 than in 1984–1985 for adults ($F_{1,410} = 20.3$, $P < 0.001$) and juveniles

TABLE 1. Monthly mean total wing- and body-molt intensity scores and numbers of growing rectrices in adult Canada geese collected July 1984–February 1987 in northern Ontario, southern Illinois, and east-central Wisconsin (sexes, years, and locations combined).

Molt score ^a	Month											
	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Wing	\bar{x} 17.3 A ^b SE (n) 1.7 (27)	5.1 B 1.9 (12)	0.8 C 0.2 (82)	1.2 C 0.3 (62)	0.3 C 0.1 (58)	0.2 C 0.1 (87)	0.4 C 0.1 (72)	0.2 C 0.1 (46)	0.2 C 0.1 (57)	0.0 C 0.0 (29)	0.0 C 0.0 (24)	
Body	\bar{x} 9.0 B SE (n) 0.9 (30)	13.8 A 0.8 (15)	8.4 B 0.6 (81)	7.5 B 0.5 (63)	4.4 C 0.5 (58)	2.4 D 0.3 (87)	2.1 DE 0.3 (72)	2.6 D 0.5 (45)	1.5 DE 0.3 (57)	0.1 E 0.1 (29)	0.3 E 0.1 (24)	
Rectrices	\bar{x} 4.9 B SE (n) 0.8 (30)	10.7 A 0.5 (15)	2.3 C 0.3 (79)	1.7 C 0.3 (64)	0.8 D 0.2 (58)	0.2 D 0.1 (86)	0.1 D <0.1 (69)	0.2 D 0.2 (45)	0.1 D 0.1 (55)	0.0 D 0.0 (29)	0.0 D 0.0 (24)	

^a Monthly means and standard errors (SE) of growing rectrices and molt scores (0–3) of individual wing and body feather tracts summed for each carcass.

^b Monthly means not sharing the same letter were significantly different ($P \leq 0.05$), Student-Newman-Keuls test.

TABLE 2. Monthly mean total wing- and body-molt intensity scores and numbers of juvenile rectrices in juvenile Canada geese collected July 1984–February 1987 in northern Ontario, southern Illinois, and east-central Wisconsin (sexes, years, and locations combined).

Molt score ^a	Month											
	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	
Wing	\bar{x} 25.8 A ^b SE (n) 0.5 (6)	8.2 B 4.6 (5)	0.8 C 0.4 (26)	0.6 C 0.2 (25)	0.3 C 0.2 (21)	0.1 C 0.1 (28)	0.5 C 0.2 (26)	0.0 C 0.0 (10)	0.4 C 0.2 (11)	0.0 C 0.0 (12)	0.0 C – (1)	
Body	\bar{x} 17.0 A ^c SE (n) 1.0 (6)	15.2 A 0.9 (5)	8.7 B 1.1 (26)	8.1 B 0.9 (24)	5.0 BC 0.8 (21)	2.8 BC 0.5 (28)	2.8 BC 0.7 (26)	5.2 BC 1.3 (10)	2.9 BC 1.2 (10)	0.1 C 0.1 (12)	0.0 C – (1)	
Rectrices	\bar{x} 17.8 A SE (n) 0.4 (6)	13.8 AB 1.2 (4)	12.5 ABC 1.4 (26)	12.4 ABC 0.7 (24)	8.0 BCD 1.1 (21)	10.7 ABC 1.0 (28)	9.0 BCD 1.0 (26)	4.1 CD 1.5 (10)	9.4 BCD 1.3 (10)	5.4 BCD 0.7 (12)	2.0 D – (1)	

^a Monthly means and standard errors (SE) of juvenile rectrices and molt scores (0–3) of individual wing and body feather tracts summed for each carcass.

^b Monthly means not sharing the same letter were significantly different ($P \leq 0.05$), Student-Newman-Keuls test.

($F_{1,122} = 11.3$, $P = 0.001$) (Fig. 1). Molt intensity was highest in October, then declined steadily through April during 1984–1985. In contrast, total molt intensity in adults increased ($P = 0.002$, $df = 410$) October through November, then declined ($P < 0.001$, $df = 410$) November through January in 1985–1986. There was indication of a second molt intensity peak during spring 1986 ($P = 0.055$, $df = 410$). A similar pattern was evident in juveniles during 1985–1986 when total molt intensity declined ($P < 0.001$, $df = 122$) November–January, then increased ($P = 0.037$, $df = 122$) January–March. We concluded that more of prebasic molt occurred after fall migration in 1985–1986 compared to 1984–1985. During 1985–1986, molt intensity declined in winter, but increased again during February and March, allowing completion of prebasic molt before the breeding season.

GEOGRAPHIC DIFFERENCES

Total molt intensities differed ($F_{1,229} = 5.12$, $P = 0.025$) between early migrants in southern Illinois and late migrants in east-central Wisconsin (age groups combined). There were no differences between locations in fall 1984 (Table 3), but seasonal trends in molt intensity differed between locations during fall 1985, the year that more of body molt occurred after fall migration. During 1985, molt intensities remained relatively high throughout fall in southern Illinois, while molt intensity was lower ($P = 0.002$, $df = 229$) in Wisconsin during October, peaked at a level similar ($P = 0.237$, $df = 229$) to southern Illinois in November, then declined below ($P = 0.001$, $df = 229$) southern Illinois again in December.

Differences in molt intensity and stage of rectrix molt between early and late migrants indicated that geese spending fall in east-central Wisconsin (late migrants) arrived from Ontario in a more advanced stage of molt and replaced body feathers within a shorter time period than geese in southern Illinois (early migrants) during fall 1985. Late migrant juveniles retained fewer juvenile rectrices, ($P = 0.039$, $df = 54$) and late migrant adults had more growing rectrices ($P = 0.029$, $df = 176$), than early migrants during October 1985 (Table 3). These differences must have originated in northern Ontario because geese were collected shortly after peak arrival dates in Wisconsin and Illinois; however, we could not explain the source of these differences. Early and

late migrants to terminal winter ranges in southern Illinois are not separate subpopulations of the MVP that can be identified on the basis of breeding location or fidelity to fall or winter use sites (Tacha et al. 1988).

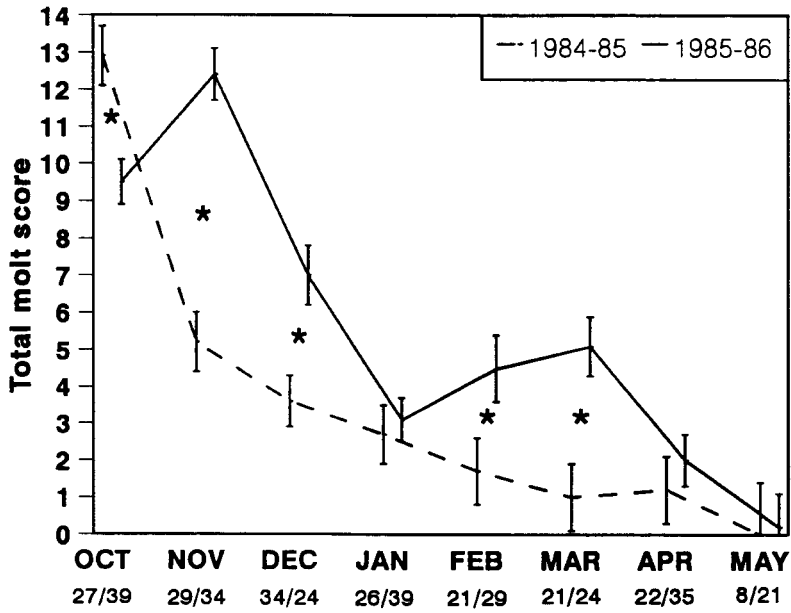
MOLTING AND NUTRIENT RESERVE DYNAMICS

Seasonal trends. Lipid reserves increased in adults during post-breeding (July–September; $P = 0.001$, $df = 627$) and in adults and juveniles after fall migration (October–December; $P < 0.001$, $df = 627$) when molt intensities were relatively high (Fig. 2). Protein reserves of adults and juveniles increased ($P \leq 0.017$, $df = 625$) during post-breeding, concurrent with intense wing and body molts. AFLDM levels varied over relatively narrow ranges after fall migration in mid-September and had no consistent relationship with total molt intensity in either age class. Lipid reserves declined in adults ($P < 0.001$, $df = 627$) during winter (December–February) when molt intensities were low. Prebasic molt was completed during spring migration (February–April) when adults and juveniles deposited large lipid and/or protein reserves.

Post-breeding. Lipid and protein masses of breeding geese were at the lowest levels of the annual cycle during hatching. Wing molt apparently did not prevent replacement of nutrient reserves after nesting because lipid and protein reserves of breeding females increased through hatching, wing-molt, and pre-fall migration periods (Table 4). Lipid reserves of breeding males also increased during these time periods, but protein reserves did not change. In contrast to breeding geese, lipid reserves of non-breeding females and males declined between hatching and wing molt, then recovered between wing molt and pre-fall migration (Table 5). Protein reserves of non-breeding geese (both sexes) did not change through hatching, wing molt, and fall migration.

Regression of nutrient reserves on ninth primary lengths of flightless geese indicated net catabolism of nutrient reserves during the first half of wing molt (Figs. 3 and 4). Lipid reserves declined as ninth primary length increased in breeding females ($F_{1,25} = 3.54$, $P = 0.072$, $r^2 = 0.124$), non-breeding females ($F_{1,18} = 8.81$, $P = 0.008$, $r^2 = 0.329$), and non-breeding males ($F_{1,16} = 7.20$, $P = 0.016$, $r^2 = 0.310$). Protein reserves declined with primary growth in breeding ($F_{1,28}$

Adults



Juveniles

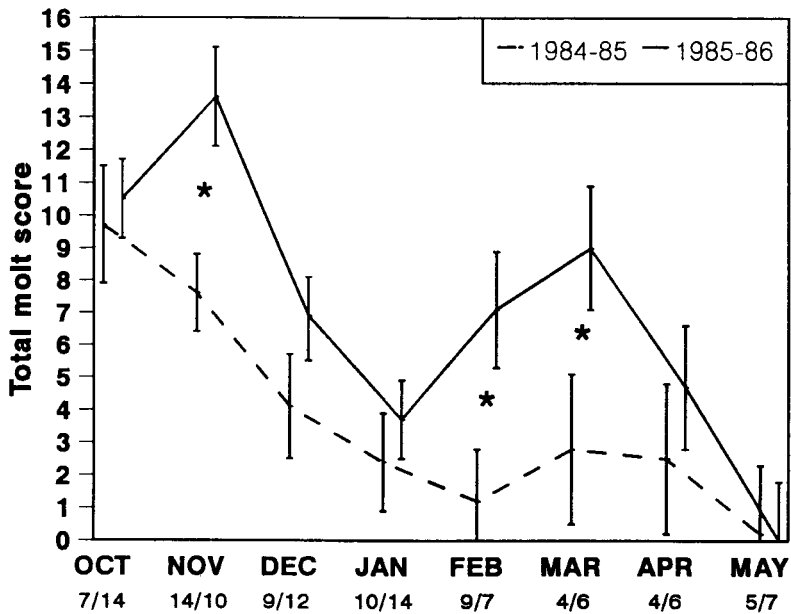


TABLE 3. Mean total molt intensity scores, number of growing retrices, and proportion of juvenile retrices for Canada geese (sexes and ages combined) collected October–December, 1984–1985 in southern Illinois (SI) and east-central Wisconsin (ECW).

Year Month	Total molt score		Number of retrices ^a				
	SI	ECW	Growing		Juvenile		
			SI	ECW	SI	ECW	
1984							
Oct	\bar{x}	11.3 A ^b	11.7 A	2.1 A	1.7 A	16.5 A	9.0 A
	SE (<i>n</i>)	1.5 (15)	1.6 (17)	0.6 (11)	0.5 (15)	2.3 (4)	3.2 (2)
Nov	\bar{x}	5.6 B	7.3 B	1.6 A	1.6 A	13.7 A	10.2 A
	SE (<i>n</i>)	1.1 (23)	1.3 (20)	0.5 (14)	0.6 (15)	1.8 (9)	2.1 (5)
Dec	\bar{x}	3.4 B	4.4 B	0.7 A	0.4 A	7.3 B	7.0 A
	SE (<i>n</i>)	1.2 (25)	1.6 (18)	0.5 (19)	0.5 (15)	1.9 (6)	2.7 (3)
1985							
Oct	\bar{x}	12.1 A ^{**c}	7.2 A	2.6 A*	1.2 A	16.8 A*	11.5 A
	SE (<i>n</i>)	1.1 (28)	1.2 (25)	0.5 (21)	0.5 (19)	1.6 (8)	1.9 (6)
Nov	\bar{x}	14.2 A	12.1 B	2.8 A*	1.2 A	11.6 AB	12.8 A
	SE (<i>n</i>)	1.3 (20)	1.3 (24)	0.6 (15)	0.5 (20)	2.1 (5)	1.9 (6)
Dec	\bar{x}	10.5 A ^{**}	4.1 A	1.8 A	0.1 A	9.5 B	7.9 A
	SE (<i>n</i>)	1.4 (17)	1.2 (18)	0.6 (14)	0.7 (10)	2.3 (4)	1.6 (8)

^a Mean number of growing retrices in adults, mean number of juvenile retrices in juveniles.

^b Monthly (column) means within years not sharing the same letter were significantly different ($P \leq 0.05$), pairwise contrasts.

^c Significant difference between locations (columns) within months (rows), * = $P \leq 0.05$, ** = $P \leq 0.01$, pairwise contrasts.

= 5.21, $P = 0.030$, $r^2 = 0.157$) and non-breeding ($F_{1,16} = 6.72$, $P = 0.020$, $r^2 = 0.296$) males.

We attributed loss of protein by wing-molting males to breast muscle atrophy associated with diminished flight activity. Breast muscle wet mass declined in breeding (SNK, $P \leq 0.05$, $df = 64$) and non-breeding (SNK, $P \leq 0.05$, $df = 32$) males between hatching and wing molt. Atrophy of breast muscle after hatching was not offset by hypertrophy of leg muscles or other proteinaceous organs as occurred in breeding females. Breast muscle atrophy in breeding females coincided with diminished flight activity that began during nesting and continued through wing molt. Breeding females spent almost no time flying during nesting, and breast muscles had already declined (SNK, $P \leq 0.05$, $df = 60$) to levels observed during wing molt by the end of incubation. Although breast mass did not change (SNK, $P > 0.05$, $df = 60$), gizzard, intestine, and crus masses increased (SNK, $P > 0.05$, $df = 60$), contributing to increased protein levels in breeding females between hatching and wing molt (Table 4).

Hanson's (1962a) conclusion that wing molt is a physiologically stressful event can probably be attributed to lack of data from females collected at the end of incubation (Ankney 1979). Body masses that Hanson considered representative of incubating females averaged 3,287 g, a level similar to what we observed at the start of incubation. Additionally, Hanson (1962a) collected nesting birds within the breeding range of the Mississippi Valley Population (MVP) of *B. c. interior*. Wing-molting geese were obtained on Akimiski Island, a location now known to be part of the breeding range of the Southern James Bay (Tennessee Valley) Population of *B. c. interior* (Bellrose 1980). Nesting chronology is earlier on Akimiski Island than in more northern regions of the Hudson Bay Lowlands where most MVP geese breed (K. F. Abraham, Ontario Ministry of Natural Resources, personal communication). Therefore, Hanson's measures of body mass and composition of wing-molting females were not taken from the same population sampled in this study, or from the same population Hanson sampled during nesting.

FIGURE 1. Total molt intensities of adult and juvenile Canada Geese collected October–May 1984–1985 and 1985–1986 in southern Illinois, east-central Wisconsin, and northern Ontario (locations combined). Asterisks indicate differences ($P \leq 0.05$) between years within months. Sample sizes (1984–1985/1985–1986) are listed below each month.

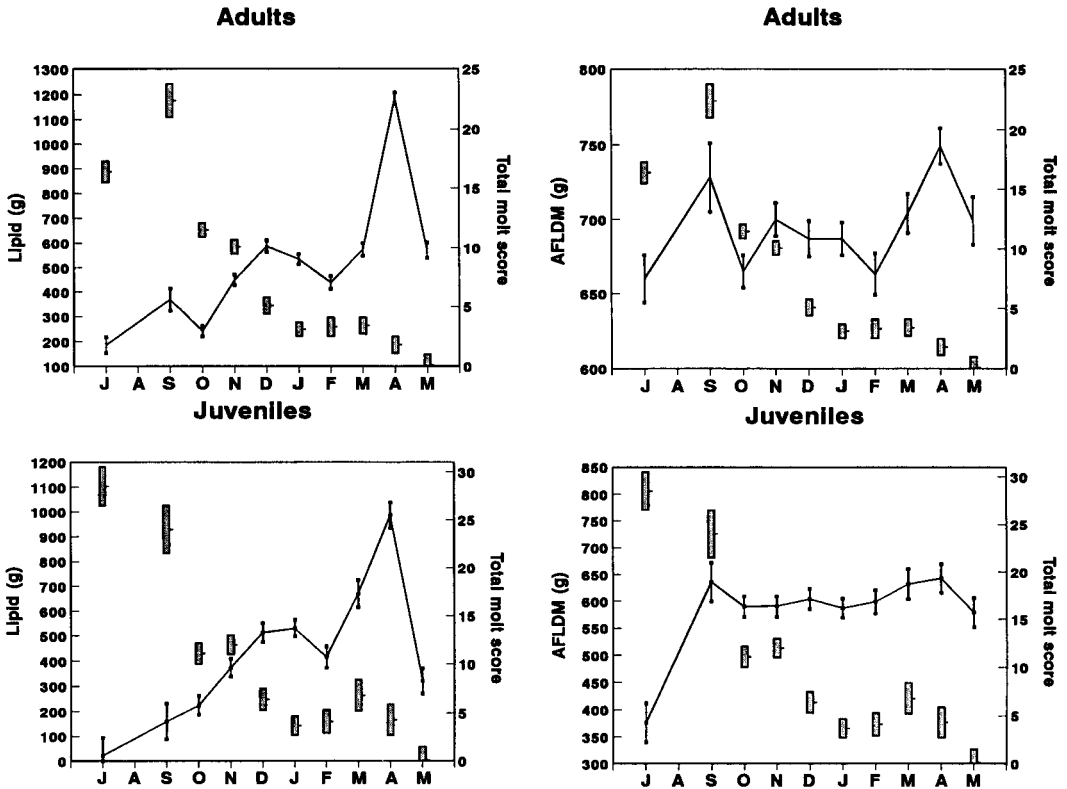


FIGURE 2. Mean total molt intensity scores in relation to lipid and ash-free lean dry masses (AFLDM) of adult and juvenile Canada Geese collected July 1984–February 1987 in southern Illinois, east-central Wisconsin, and northern Ontario (sexes, years, and locations combined). Solid line portrays seasonal trends in lipid or protein serves ($g \pm 1$ SE), shaded bars represent molt intensity scores (± 1 SE). Sample sizes are as they appear in Tables 1 and 2.

TABLE 4. Seasonal changes in lipid and protein reserves (g) of breeding male and female Canada geese collected June–August 1984–1985 and 1988–1990 in northern Ontario.

Sex	Reserve	Hatching	Wing-molt	Pre-fall ^a migration
Female				
Lipid	\bar{x}	10 A ^b	210 B	365 C
	SE (n)	2 (23)	16 (28)	104 (4)
Protein	\bar{x}	460 A	610 B	714 C
	SE (n)	10 (22)	14 (27)	56 (4)
Male				
Lipid	\bar{x}	80 A	237 B	426 C
	SE (n)	16 (33)	20 (30)	59 (3)
Protein	\bar{x}	760 A	773 A	778 A
	SE (n)	8 (33)	12 (30)	12 (3)

^a Data from 1985 only.

^b Differences among row means not sharing the same letter were significant ($P \leq 0.05$, Student-Newman-Keuls test).

TABLE 5. Seasonal changes in lipid and protein reserves (g) of non-breeding male and female Canada geese collected June–August 1984–1985 and 1988–1990 in northern Ontario.

Sex	Reserve	Hatching	Wing-molt	Pre-fall ^a migration
Female				
Lipid	\bar{x}	363 A ^b	150 B	426 A
	SE (n)	52 (11)	22 (20)	59 (3)
Protein	\bar{x}	636 A	595 A	778 A
	SE (n)	28 (11)	12 (20)	12 (3)
Male				
Lipid	\bar{x}	236 A	123 B	342 A
	SE (n)	36 (11)	18 (18)	52 (3)
Protein	\bar{x}	779 A	701 A	807 A
	SE (n)	21 (11)	13 (18)	24 (3)

^a Data from 1985 only.

^b Differences among row means not sharing the same letter were significant ($P \leq 0.05$, Student-Newman-Keuls test).

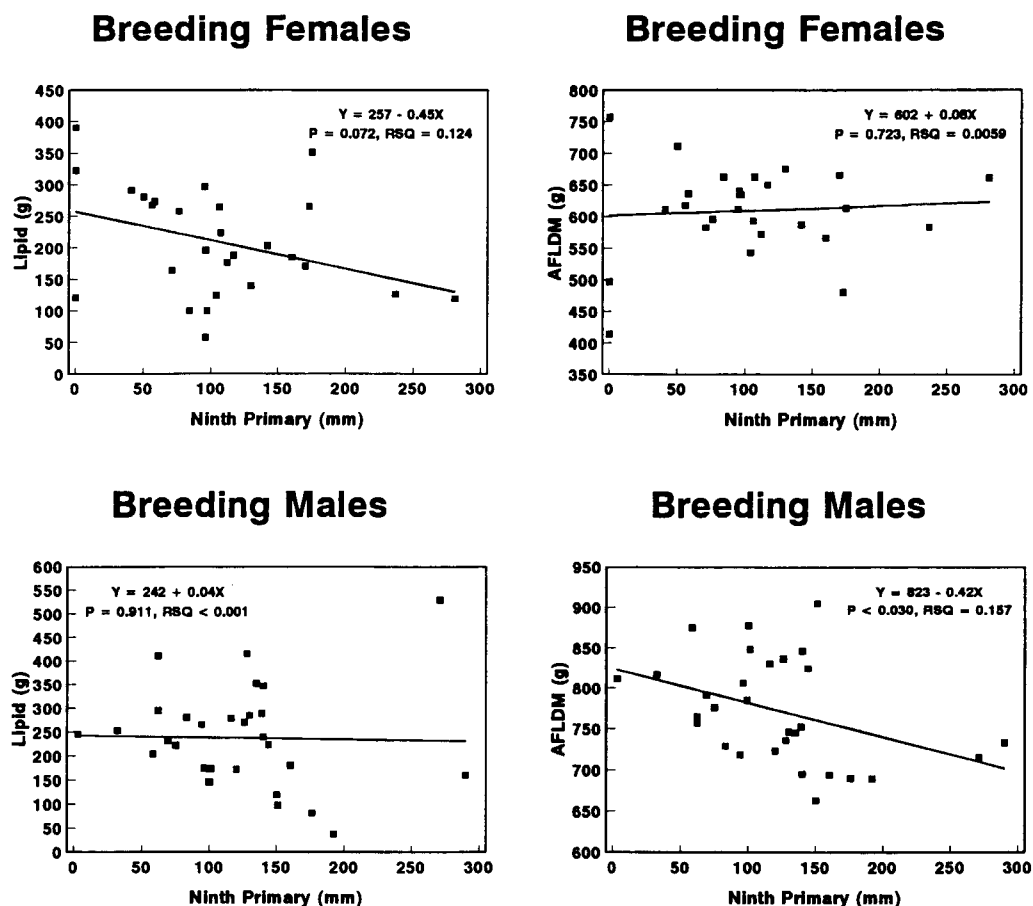


FIGURE 3. Relationships between nutrient reserve (lipid and protein) masses and ninth primary lengths of breeding male and female Canada Geese collected during the flightless period of the wing molt during July 1984–1985, and July 1988–1990 in northern Ontario.

Post-fall migration. Differences in molt intensity between years and locations were associated with variation in body composition. We conducted stepwise regression analyses to test whether annual and geographic differences in molt intensity were related to lipid and protein reserves. Stepwise regression models explained 44% of variation in molt intensity across months during October–December; 28% of variation in October, 52% in November, and 42% in December.

Lipid mass \times month (linear) was the strongest (partial $r^2 = 0.188$, $F_{1,243} = 57.6$, $P < 0.001$) variable retained in the regression model describing variation in molt intensity across months, years, and locations. Independent of the effects of all other variables retained in the model, lipid mass as a main effect had a weak positive as-

sociation (partial $r^2 = 0.040$, $F_{1,243} = 16.8$, $P < 0.001$) with total molt intensity. Larger lipid reserves were also associated with higher molt intensities in October (partial $r^2 = 0.189$, $F_{1,82} = 27.4$, $P < 0.001$), there was no relationship of lipid reserves with molt intensity in November ($P > 0.05$), and geese with larger lipid reserves had lower molt intensities in December (partial $r^2 = 0.135$, $F_{1,74} = 15.8$, $P < 0.001$). This pattern of association between lipid reserves and molt intensities indicated that geese with larger energy reserves after fall migration had progressed further in their prebasic molt, and molted more rapidly during fall than geese with smaller reserves. Lovvorn and Barzen (1988) similarly reported that molt intensity was highest in female Canvasbacks (*Aythya valisineria*) with largest

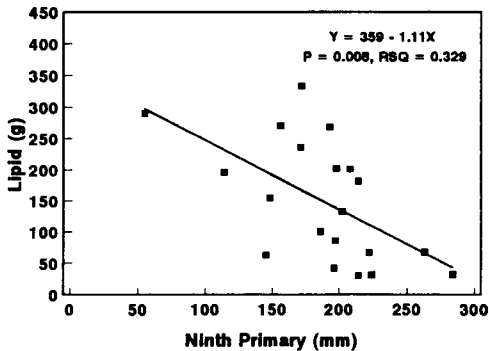
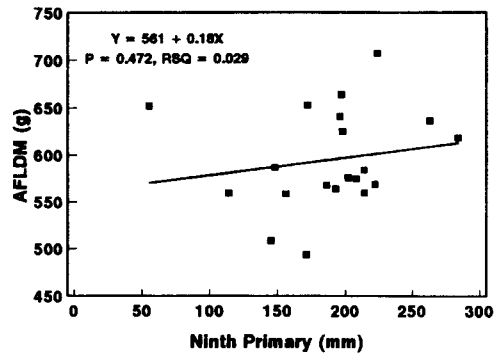
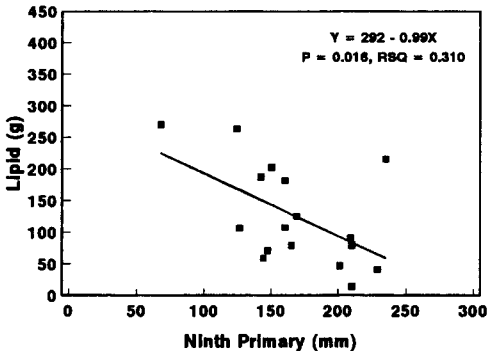
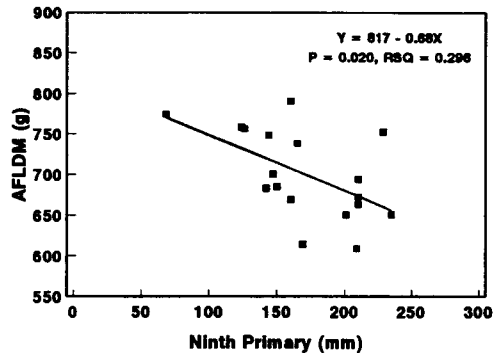
Non-breeding Females**Non-breeding Females****Non-breeding Males****Non-breeding Males**

FIGURE 4. Relationships between nutrient reserve (lipid and protein) masses and ninth primary lengths of non-breeding male and female Canada Geese collected during the flightless period of the wing molt during July 1984–1985, and July 1988–1990 in northern Ontario.

lipid and protein reserves during spring migration.

During October 1984 when geese arrived in Wisconsin and Illinois averaging 307 g lipid (SE = 20, $n = 37$), molt intensity was high, then declined through December at both locations (Table 3). During October 1985, lipid reserves averaged 194 g (SE = 13, $n = 46$) after fall migration and molt intensity remained high throughout fall in Illinois and peaked during November in Wisconsin. Thus, the later molt in 1985 was associated with smaller lipid reserves after fall migration compared to 1984.

Late migrants apparently molted more rapidly than early migrants during the later molt of fall 1985. Between October and December both years, late migrants consumed high energy and low pro-

tein diets in Wisconsin, accumulating 250–300 g more lipid than early migrants in southern Illinois that consumed diets with more protein but less energy (Gates 1989). Geese in Wisconsin were apparently able to acquire more productive energy that supported greater lipid deposition in both years, and a faster molt in 1985.

Stepwise regression analyses did not identify protein reserves as a significant main effect associated with total molt intensity. Interactions of protein with other variables were retained in stepwise regression models for all months combined, and within November and December, suggesting that protein reserves had an influence on molt intensity that varied with year, location, and/or month. Further analyses with simplified regression models failed to demonstrate that pro-

tein reserves were associated with molt intensity within locations, years, or months ($P > 0.178$).

Nutritional demands of molting in Canada Geese were apparently greatest during July–November. Although we lacked direct measurements, it appeared that relative amounts of productive energy allocated to molting vs. nutrient deposition varied inversely during late summer and fall. Molting appeared to receive greater energy allocation during July–October, while nutrient deposition was emphasized during October–December. This pattern of energy allocation allowed most of plumage replacement to occur before it was necessary to accumulate nutrient reserves before winter.

Catabolism of endogenous reserves did not appear to be an important source of energy or nutrients for molting geese during any season, including the flightless portion of wing-molt. Although energy requirements of molting birds can increase 5–50% over non-molting seasons (Payne 1972, Thompson and Boag 1976, Dolnik and Gavrilov 1979, King 1980, Walsberg 1983), individuals may increase food intake to meet elevated energy demands without mobilizing endogenous reserves. Protein metabolism is also accelerated in molting birds (Dolnik and Gavrilov 1979). Heitmeyer (1988a) estimated that during the peak of prebasic molt, female Mallards required a level of protein intake that exceeded their maintenance requirement by 75%. Studies of passerines indicate that protein and essential amino acid requirements can be met with diets of widely varying quality and without mobilizing endogenous protein (Newton 1968; Thompson and Boag 1976; Murphy and King 1984a, 1984b, 1984c).

CONCLUSIONS

Lipid mass was the only measurement of nutritional status that had any consistent association with seasonal patterns and intensities of molting. We believe that rate and intensity of molting was determined primarily by the amount of productive energy geese were able to allocate to feather growth, in addition to supplying nutrients for body growth (juveniles) or nutrient deposition (adults and juveniles).

We hypothesize that energy acquisition by geese prior to fall migration affected the progression of body molt during the ensuing fall and winter. Geese molted with greater intensity after fall mi-

gration in 1985, when they arrived in Wisconsin and southern Illinois with smaller lipid reserves compared to fall 1984. Less food energy may have been available for geese to allocate to molting and nutrient reserve deposition before fall migration in 1985, requiring that more of prebasic molt be completed during fall and winter 1985, than in 1984.

There was no evidence to conclude that wing or body molts were nutritionally stressful in Canada Geese. Although some nutrient reserves were catabolized by breeding and non-breeding geese during the flightless period, geese were still able to replenish nearly all of the lipid and protein reserves mobilized during the nesting season before fall migration. Hanson (1962a) considered wing molt to be most stressful in breeding females because of the additional demands of molting imposed on females already impoverished by egg-laying and incubation. Although breeding females needed to replace larger nutrient reserve masses after hatching, they attained levels of body condition that were similar to breeding males before fall migration. Thus, nutrient reserve masses replenished by breeding females exceeded masses replaced by breeding males, as has been shown for other waterfowl, (Milne 1976, Ankney 1979, Raveling 1979).

We interpreted several aspects of the molt pattern of *B. c. interior* as adaptations that minimized nutritional conflicts with maintenance, growth, and productive processes, despite some overlap of prebasic molt with seasons of growth, migration, and nutrient deposition. Daily nutritional requirements of feather growth were minimized by a prolonged molt that may have spanned ≥ 8 months in some individuals. Adults nearly completed wing molt before entering the most intense phase of body molt. By concentrating energy and nutrients on growth of remiges first, the flightless period was probably shorter than if energy and nutrients were diverted to more intense molt of body feathers at this time. In contrast, many ducks complete prebasic body molt and initiate prealternate body molt during the flightless period (Young and Boag 1982, Dubowoy 1985, Wishart 1985, Austin and Fredrickson 1986).

The apparent strategy of *B. c. interior* was to complete nearly all of wing molt and most of body molt during late summer and early fall when weather and feeding conditions were most favorable (Caithamer 1989; Gates et al., in press).

Plumage not replaced before fall migration was molted with declining intensity during fall and winter as geese devoted larger proportions of their energy budgets to maintenance or nutrient deposition.

The simple single annual molt of adult Canada Geese probably permits greater flexibility in adjusting molt intensity and chronology to environmental conditions than is possible for ducks that molt twice annually. Molt in Canada Geese primarily serves the function of plumage renewal, while in ducks, prealternate molt is also prerequisite to successful pairing (Paulus 1984, Heitmeyer 1987). Canada Geese need only to complete prebasic molt before the end of spring migration, whereas ducks must complete nearly all of prealternate molt before pairing. Female ducks then undergo a partial prebasic molt before nesting (Heitmeyer 1987, Bluhm 1988). Thus, molt chronology in ducks is more likely influenced by the timing of other annual events. Body molt in ducks may occur in a sequence of annual events (Heitmeyer 1987), or sometimes may overlap other nutritionally demanding events (Lovvorn and Barzen 1988), because of time requirements that do not constrain single molting species such as Canada Geese.

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