MOLT IN THE ANNUAL CYCLE OF RING-NECKED DUCKS[1]

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Abstract. Birds have increased energy and nutrient requirements during molt. Estimation of these costs has proven difficult; consequently, the nutritional significance of molt relative to other annual cycle events remains unclear. Here we describe patterns of molt for Ring-necked Ducks (*Aythya collaris*) throughout their annual cycle. A method was developed for indexing molting costs of waterfowl based on intensity of molt and proportional mass of feathers in eight feather regions (ADJMOLT). This method was then applied to Ring-necked Ducks so that we might examine molting costs in relation to sex and age of birds, month, and annual cycle events. To assess nutritional stress (demands greater than available resources) associated with molt, we examined the relation between remige length and structural size of adults. Contour feather molt in the head and neck, sides and flank, upper breast and back, lower breast and belly, mid-rump and lower back, scapular, humeral, and rectral feather regions varied by sex and month for first-year and after-first-year (adults) Ring-necked Ducks. Mean molt scores (i.e., molt averaged over all feather regions) and ADJMOLT of adults also varied by sex and month. The pattern of change in ADJMOLT was trimodal in females and bimodal in males. ADJMOLT of both sexes was greatest during the period of remigial molt (August) and was also elevated during winter (December and January). ADJMOLT was reduced during spring (March) and fall (October) migrations. Whereas molt remained at low levels in males throughout the breeding season, females initiated prebasic molt after arrival on breeding areas and were molting intensively while acquiring energy and nutrients needed for reproduction. Thus it was apparent that although molting costs were mostly staggered with minimal overlap with other energy- and nutrient-demanding processes, timing of molt in the annual cycle of Ring-necked Ducks was also influenced by non-nutritional factors (e.g., date). Remige lengths were significantly (albeit weakly) related to structural size of both males and females. We therefore concluded that, although costs of molt were greatest while birds were molting remiges, there was no evidence that molting Ring-necked Ducks were nutritionally stressed.

Key words: Aythya collaris; Ring-necked Duck; Anatidae; molt; nutrition; annual cycle; stress.

INTRODUCTION

Molt has been studied extensively in waterfowl during some segments of the annual cycle, especially during the winter period (e.g., Paulus 1984, Heitmeyer 1985, Miller 1986, Hohman et al. 1992a, Smith and Sheeley 1993) and period of remigial molt (Hohman et al. 1992b and references therein, Hohman 1993a, Moorman et al. 1993). Annual cycles of molt have been described quantitatively for only a limited number of species (e.g., Canada Goose [*Branta canaden-*

sis interior], Gates et al. 1993; Greater Scaup [*Aythya marila*], Billard and Humphrey 1972; Canvasback [*A. valisineria*], Lovvorn and Barzen 1988; Common Merganser [*Mergus merganser*], Erskine 1971). Consequently, factors influencing the timing of molt in the annual cycles of waterfowl are poorly understood.

Nutritional constraints may have a large influence on molt phenology (Payne 1974, King 1980; but see Lovvorn and Barzen 1988, Earnst 1992). Energy and nutrient costs of molt are substantial and include nutrients required for synthesis of feather components, increased amino acid metabolism, changes in water and blood volumes, and altered thermoregulatory capabilities (King 1980). Feathers are composed mostly of proteins; protein contained in the plumage

may constitute up to one third of that contained in the carcass (see references in Murphy and King 1984a: 324). Because birds have relatively limited capabilities for storage of protein (Blem 1990), are seemingly inefficient at converting dietary protein into feathers (Murphy and King 1984b), and require specific amino acids to synthesize feather proteins that are concentrated in feathers relative to their availability in the diet (Hanson 1962), there is potential for nutritional stress during molt ("stress" defined by Lovvorn and Barzen [1988] as "a situation when demands of one event [physiological, behavioral, or otherwise] are great enough to interfere with desirable allocation of resources to other processes"). Scheduling molt so as to minimize overlap with other energy- and nutrient-demanding processes is a mechanism whereby birds might reduce potential nutritional stress and survival risks associated with molt. Here we describe patterns of molt for Ring-necked Ducks (*Aythya collaris*) throughout their annual cycle. We develop an index of molting costs for Ring-necked Ducks based on the relative mass of feathers in various tracts and examine costs of molt in relation to sex and age of birds, month, and annual cycle events. We also assess nutritional stress associated with molt in Ring-necked Ducks.

Estimation of molting costs in birds has proven difficult (Walsberg 1983); nonetheless, overlap of molt with other annual cycle events (i.e., nutrient storage, migration, courtship, ovarian follicle development) has led some investigators to conclude that waterfowl were not nutritionally stressed during molt (e.g., Lovvorn and Barzen 1988). This conclusion apparently was corroborated by studies showing no correlation between indexes of molt and endogenous protein reserve (e.g., Ankney 1979, 1984; Young and Boag 1982; Moorman et al. 1993; but see Austin and Fredrickson 1987, Gates et al. 1993, Hohman 1993a). However, inaccurate indexing of molting costs and/or failure to take into account the extent of molt completion (i.e., cumulative nutrient investment) are important shortcomings in many of these analyses. Further, the degree to which individuals adjust molting patterns (e.g., sequence and intensity of molt, rates of feather growth, and quantity and quality of replaced feathers) to changing food availability, nutrient reserve levels, and non-nutritional constraints has not been considered, although variation in wa-

terfowl molting patterns is known to occur (Bailey 1981, Heitmeyer 1985, Miller 1986). Thus, whereas dynamics of body mass and composition during molt are well documented, relations between nutritional investments in molt and subsequent survival and performance of other annual cycle events remain unknown.

Wing length is commonly used as an index of structural size in waterfowl (e.g., Owen and Cook 1977) and other groups of birds (e.g., Murphy 1986); however, relations between wing length and other structural measures may vary in waterfowl because wing length is determined in part by remige length which may be affected by nutrition during the period of remigial growth (Pehrsson 1987). Changes in the body masses of migratory waterfowl through the annual cycle are extensive. For example, the extent of annual body mass fluctuation in Ring-necked Ducks was 19% for adult males and 27% for adult females (Hohman et al. 1988). The ability of birds to accommodate changes in body mass without reduction of flight capabilities ("condition capacity," Pehrsson 1987: 329) presumably is compromised in birds with shortened remiges. Moreover, if survival and reproductive performance of waterfowl are influenced by relative body mass (e.g., Haramis et al. 1986, Hepp et al. 1986), then reduced condition capacity could result in decreased survival and impaired reproductive performance (Pehrsson 1987).

To assess nutritional stress associated with molt in Ring-necked Ducks, we examined the relation between remige length and structural size of adults. As is the case for most other waterfowl species studied to date (e.g., Ankney and Alisauskas 1991, Hohman 1993b), body size is significantly related to mass of Ring-necked Ducks (Hohman and Weller 1994). That is, after adjusting for other factors such as sex, age, and date, large birds tend to weigh more than small birds. It follows therefore that within a particular size class of individuals there should be an optimal remige length to accommodate seasonal changes in body mass (i.e., significant positive correlation between remige length and body size). However, if birds were nutritionally challenged during remigial molt, then we predicted remige length would be influenced by nutrition rather than size and the association between remige length and size would be weakened. We further hypothesized that, because of greater time available to

males to complete molt, the correlation between remige length and size should be stronger in males than in females.

STUDY AREAS AND METHODS

Birds were collected throughout the annual cycle by shooting at the following sites and dates: *Breeding*—northwestern Minnesota, April–July 1978–1980 (see Hohman [1984] for site description); *Postbreeding*—southwestern Manitoba near Lake Winnipegosis, August to September 1983–1984 (Bailey 1983); *Spring and Fall Migration*—Navigation Pools on the Upper Mississippi River from LaCrosse, Wisconsin, to Keokuk, Iowa, October 1986 and 1987 or March 1989 (Jackson et al. 1981); and *Wintering*—southern Florida, November to February 1979–1980 (Hohman and Weller 1994). We measured bill length from the commissural point to tip of nail (± 0.1 mm), maximum bill width distal to nares (± 0.1 mm), keel length (± 0.1 mm), tarsal bone length (± 0.1 mm), and body length from the tip of the bill to the base of the middle rectrix (± 0.5 cm), with the bird on its back. Birds were categorized as first-year (immature) or after-first-year (adults) based on plumage (Hohman and Cypher 1986) or cloacal characteristics (Hochbaum 1942). We plucked and saved the fifth primary (P5) and fifth secondary (S5) remiges. Carcasses were wrapped in absorbent paper toweling and frozen in sealed plastic bags.

In the laboratory, we measured P5 and S5 lengths (± 0.5 mm) from the inferior umbilicus to the tip of the vane (feather flattened and rachis straightened). Skin was excised from thawed carcasses. Ovaries from females collected in northwestern Minnesota from April to July were removed, inspected for postovulatory follicles, and weighed (± 0.01 g). We assigned females and their mates to the following reproductive categories, based in part on Krapu (1974): *Arrival*—females with ovary mass ≤ 3 g and no postovulatory follicles; *Rapid follicle growth*—preovulatory females with ovary mass > 3 g and ovulating females; *Incubation*—incubating hens collected off nests or hens with brood patches; and *Brood-rearing*—hens attending ducklings.

Percentage of molting feathers was scored in eight feather regions (head and neck [HEAD], sides and flank [FLANK], upper breast and back [BREAST], lower breast and belly [BELLY], mid-

rump and lower back [BACK], scapular [SCAPS], humeral [WING], and rectral [TAIL]) by using procedures of Billard and Humphrey (1972). Following Billard and Humphrey (1972), feather regions were divided into 1 to 12 subdivisions. We examined everted skins for evidence of molt (follicles of developing feathers) and assigned molt scores to subdivisions based on the proportion of feathers that were being replaced (molt scores: 0 = none, 1 = 1–25%, 2 = 26–49%, 3 = ≥50%). Molt of contour and down feathers was scored separately. Regional molt scores were determined by summing molt scores for contour feathers and dividing by the number of subdivisions in each region. Molt score by region was averaged over all contour feather regions to calculate overall mean molt score (MEANMOLT). Overall down molt (DOWN) was the average molt score for down in all regions where it occurred (i.e., FLANK, BREAST, BELLY, and BACK).

To determine the relative proportion of feather mass in individual feather regions, we plucked contour feathers by region and down from 16 nonmolting Ring-necked Ducks (six adult and one immature male; four adult and five immature females). These birds were collected in late winter and were wearing complete alternate plumage. Contour feathers from individual regions and down were washed separately in detergent and petroleum ether, and then dried to constant mass (± 0.01). We then multiplied proportional feather mass (i.e., lean dry feather mass per region/lean dry plumage mass) by the mean molt score in respective regions and summed over all regions to calculate mass-adjusted molt intensity (ADJMOLT), an index of molting costs (Hohman 1993a).

Multivariate analysis of variance (MANOVA) was used to test for effects of sex and month on mean molt scores for the eight contour feather regions and DOWN for adult and immature Ring-necked Ducks (PROC GLM, SAS Institute, Inc. 1987). We used analysis of variance (ANOVA) with type III sums of squares (PROC GLM, SAS Institute, Inc. 1987) to test for effects of sex and month on MEANMOLT and ADJMOLT of adults and immatures. We also used ANOVA with type III sums of squares to test effects of sex, age, date, and reproductive category (status) on MEANMOLT and ADJMOLT of breeding Ring-necked Ducks. We used regression analysis

TABLE 1. Results of analysis of variance (Type III sum of squares) of sex and month effects on feather molt of adult ($n = 293$) and immature ($n = 162$) Ring-necked Ducks throughout the annual cycle.

Feather region[a]	Adults								Immatures							
	Sex df = 1		Month df = 11		Sex·month df = 10		R^{2b}		Sex df = 1		Month df = 10		Sex·month df = 9		R^{2b}
	F	P	F	P	F	P			F	P	F	P	F	P	
HEAD	2.24	0.135	16.13	<0.001	10.13	<0.001	0.605		5.59	0.019	10.64	<0.001	5.24	<0.001	0.520
FLANK	1.58	0.210	12.42	<0.001	7.80	<0.001	0.478		5.20	0.024	10.10	<0.001	5.86	<0.001	0.540
BREAST	3.89	0.049	13.98	<0.001	7.13	<0.001	0.586		3.34	0.069	5.57	<0.001	4.59	<0.001	0.427
BELLY	5.16	0.023	17.95	<0.001	6.05	<0.001	0.595		2.15	0.144	5.55	<0.001	5.37	<0.001	0.442
BACK	1.24	0.266	27.51	<0.001	7.81	<0.001	0.754		4.79	0.030	5.11	<0.001	2.52	0.010	0.390
SCAPS	3.12	0.078	16.81	<0.001	8.48	<0.001	0.578		5.69	0.018	11.58	<0.001	6.08	<0.001	0.556
WING	1.11	0.292	39.28	<0.001	1.18	0.302	0.785		5.12	0.025	2.41	0.011	1.87	0.061	0.322
TAIL	4.15	0.042	13.31	<0.001	4.59	<0.001	0.578		9.60	0.002	4.17	<0.001	1.86	0.062	0.342
DOWN	12.24	0.001	6.20	<0.001	5.06	<0.001	0.425		7.85	0.006	4.02	<0.001	3.26	<0.001	0.408
MEANMOLT[c]	4.20	0.041	27.75	<0.001	11.44	<0.001	0.725		9.32	0.002	9.97	<0.001	6.33	<0.001	0.554
ADJMOLT[d]	2.13	0.146	35.12	<0.001	10.94	<0.001	0.774		5.71	0.018	9.01	<0.001	6.46	<0.001	0.540

[a] Feather regions (head and neck [HEAD], sides and flank [FLANK], upper breast and back [BREAST], lower breast and belly [BELLY], mid-rump and lower back [BACK], scapular [SCAPS], humeral [WING], and rectral [TAIL] follow Billard and Humphrey (1972).
[b] Explained variance for full model.
[c] Mean molt scores by region averaged over all contour feather regions.
[d] Index of molting costs based on intensity of molt and proportional mass of feathers in eight contour feather regions. Proportional feather masses for HEAD, FLANK, BREAST, BELLY, BACK, SCAPS, WING, TAIL, and DOWN were 0.044–0.077, 0.084–0.091, 0.083–0.115, 0.246–0.280, 0.053–0.076, 0.060–0.072, 0.258–0.269, 0.016–0.019, and 0.048–0.111, respectively.

TABLE 2. Analysis of variance of sex, age, reproductive category, and date effects on molt of breeding Ring-necked Ducks.

		MEANMOLT[a]			ADJMOLT[b]		
Source	df	Sum of squares[c]	F	P	Sum of squares	F	P
Model[d]	25	66.57	12.71	<0.001	45.76	10.07	<0.001
Error	102	21.36			18.53		
Corrected total	127	87.94			64.29		
Date[e]	1	0.30	1.44	0.232	0.06	0.34	0.563
Sex	1	1.34	6.40	0.013	0.99	5.46	0.021
Date·sex	1	0.92	4.41	0.038	0.71	3.95	0.049
Age	1	0.51	2.46	0.119	0.31	1.73	0.191
Date·age	1	0.41	1.98	0.162	0.25	1.39	0.240
Sex·age	1	0.17	0.83	0.364	0.19	1.09	0.298
Date·sex·age	1	0.14	0.71	0.403	0.16	0.91	0.342
Status[f]	3	2.60	4.15	0.008	1.22	2.25	0.087
Date·status	3	2.83	4.51	0.005	1.33	2.46	0.067
Sex·status	2	0.59	1.42	0.247	0.26	0.72	0.488
Date·sex·status	2	0.71	1.72	0.184	0.31	0.88	0.417
Age·status	2	0.87	2.10	0.128	0.91	2.51	0.086
Date·age·status	2	0.93	2.23	0.113	1.01	2.80	0.065
Sex·age·status	1	0.02	0.12	0.734	0.04	0.25	0.619
Date·sex·age·status	1	0.00	0.04	0.838	0.02	0.13	0.714

[a] Mean molt score by region averaged over all contour feather regions.
[b] Index of molting costs based on intensity of molt and proportional mass of feathers in eight contour feather regions.
[c] Type III Sums of Squares (SAS Inst., Inc. 1987).
[d] Explained variance for full model: MEANMOLT, $R^2 = 0.76$; ADJMOLT, $R^2 = 0.71$.
[e] Julian date.
[f] Reproductive categories (status): 1 = arrival; 2 = rapid ovarian follicle growth; 3 = incubation; and 4 = brood-rearing.

to examine relations between remige lengths and structural size of adults. First, we subjected the correlation matrix of five structural measurements (tarsus, keel, bill, and body lengths, and bill width) to principal components analysis (PROC PRINCOMP, SAS for calculations). To more accurately characterize size of Ring-necked Ducks, we included birds live-trapped in Minnesota or Manitoba from April to September, 1978–1984 (combined $n = 554$). The first principal component accounted for 62% of the variance in the original measures, described positive covariation among all measures, and had loadings ranging from 0.38 to 0.49. We used scores along the first principal component as a measure of body size (SIZE, Ankney and Alisauskas 1991) in above regression analyses. SIZE was also used as a covariate in analyses examining sex and age effects on lean dry plumage mass of Ring-necked Ducks (PROC GLM, SAS Institute, Inc. 1987). Significance level was set a priori at $\alpha = 0.05$.

RESULTS

PATTERNS OF MOLT

Molting patterns of adult and immature Ring-necked Ducks varied by sex and month (MAN-OVA $F > 1.78$, $P < 0.001$). In adults, MEAN-MOLT, molt of contour feathers in all regions except WING, and DOWN molt varied by sex and month (Table 1). Patterns of molt in males and females were similar through most of the year but differed in spring (April and May) when females replaced feathers in all tracts except WING (Fig. 1). In winter (December–January), molt was confined to HEAD, FLANK, SCAPS, and BREAST in males but was somewhat more generalized in females. Molt in both sexes was most intense and generalized in August when adults replaced remiges. Down molt occurred from April to August. MEANMOLT of breeding ducks was not influenced by age but varied by date and status and by date and sex (Table 2).

In immatures, MEANMOLT, contour feather molt in all feather regions except WING and TAIL, and DOWN molt varied by sex and month (Table 1). As in adults, sexual differences in molting patterns of immatures were most evident in April and May (Fig. 2). Immatures collected in August following their first breeding season had not yet begun wing molt and had low molt scores compared to adults. (Note that immatures having molted remiges would have been categorized as adults.)
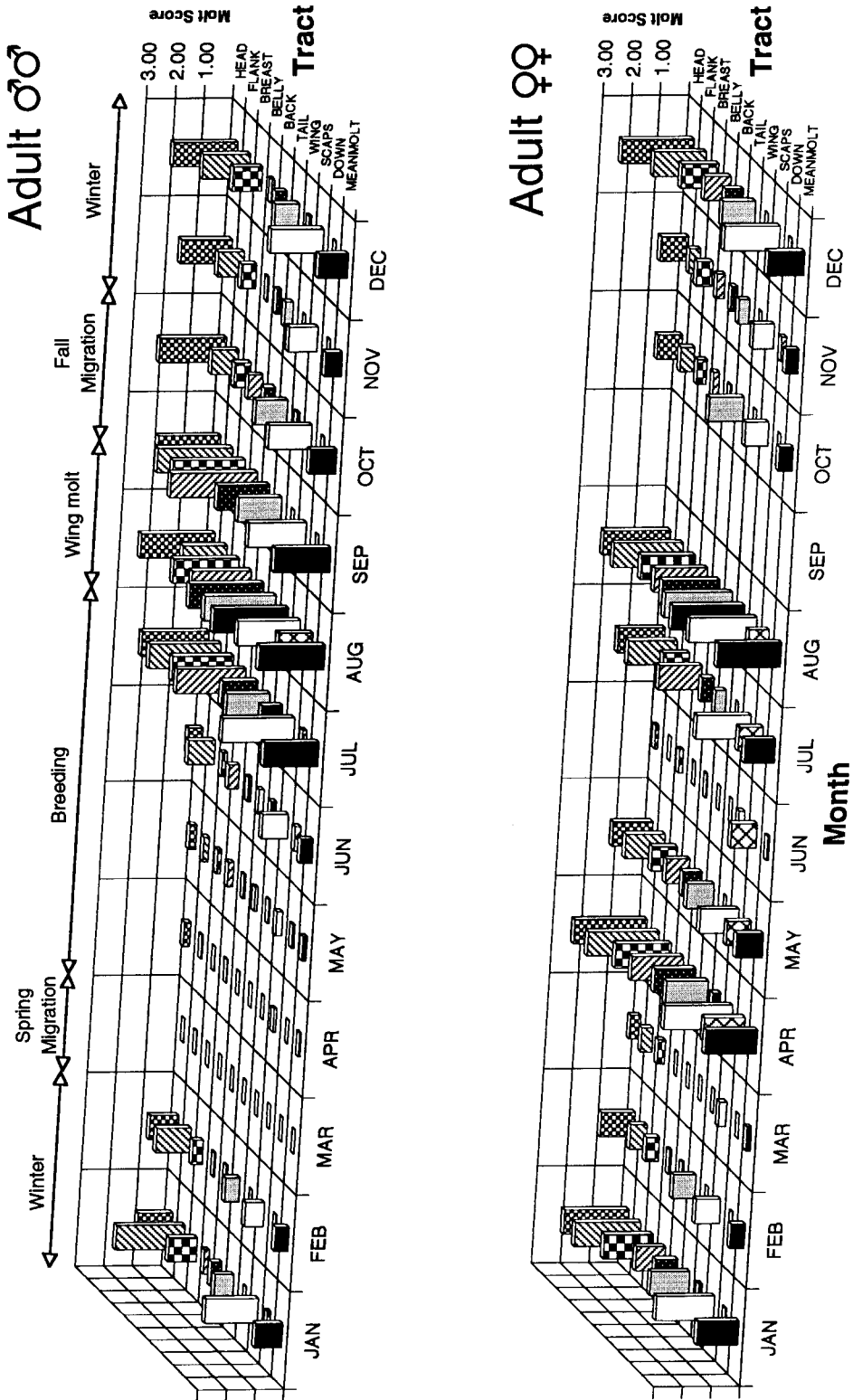
FIGURE 1.   Molt in the annual cycle of adult Ring-necked Ducks.
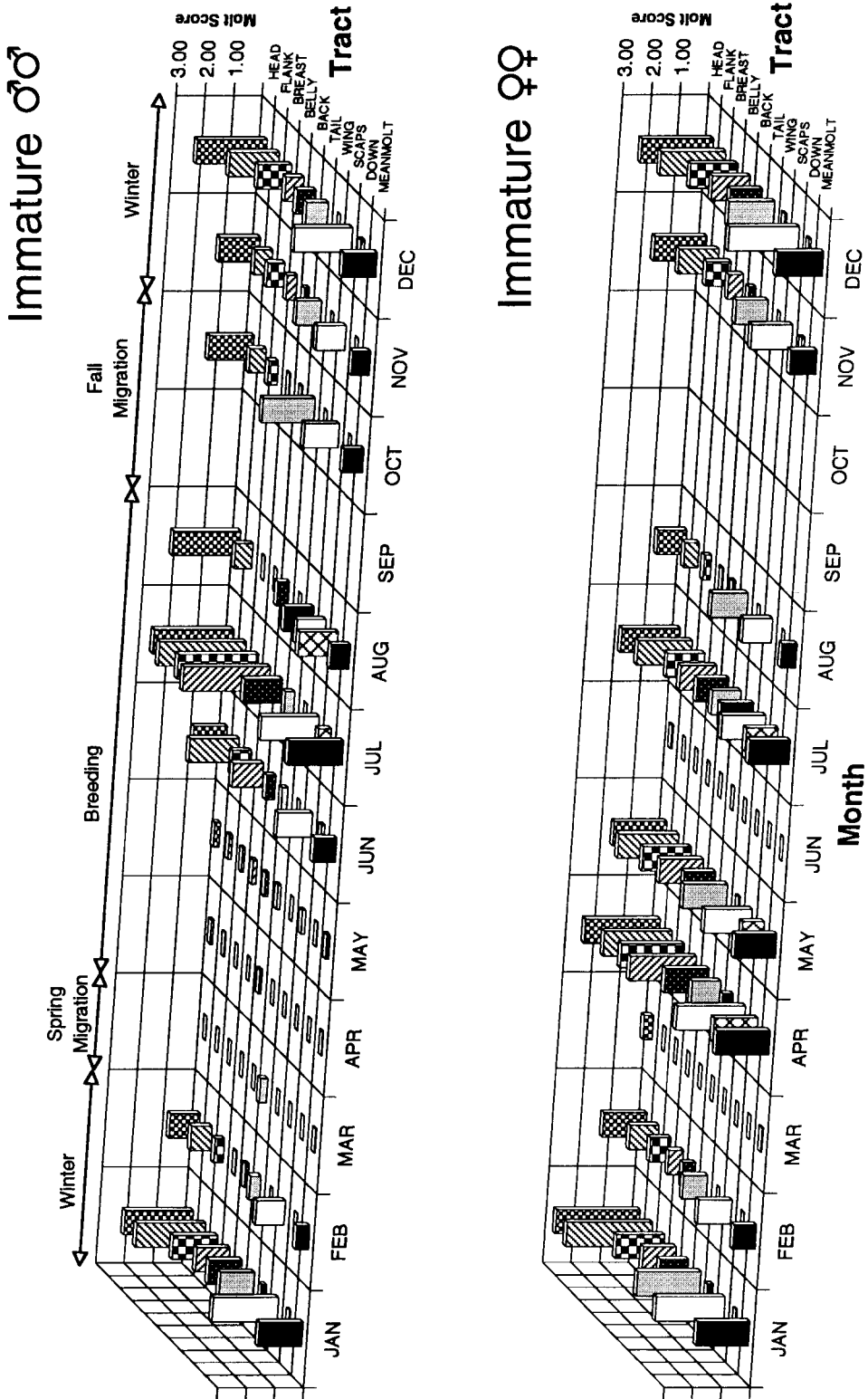
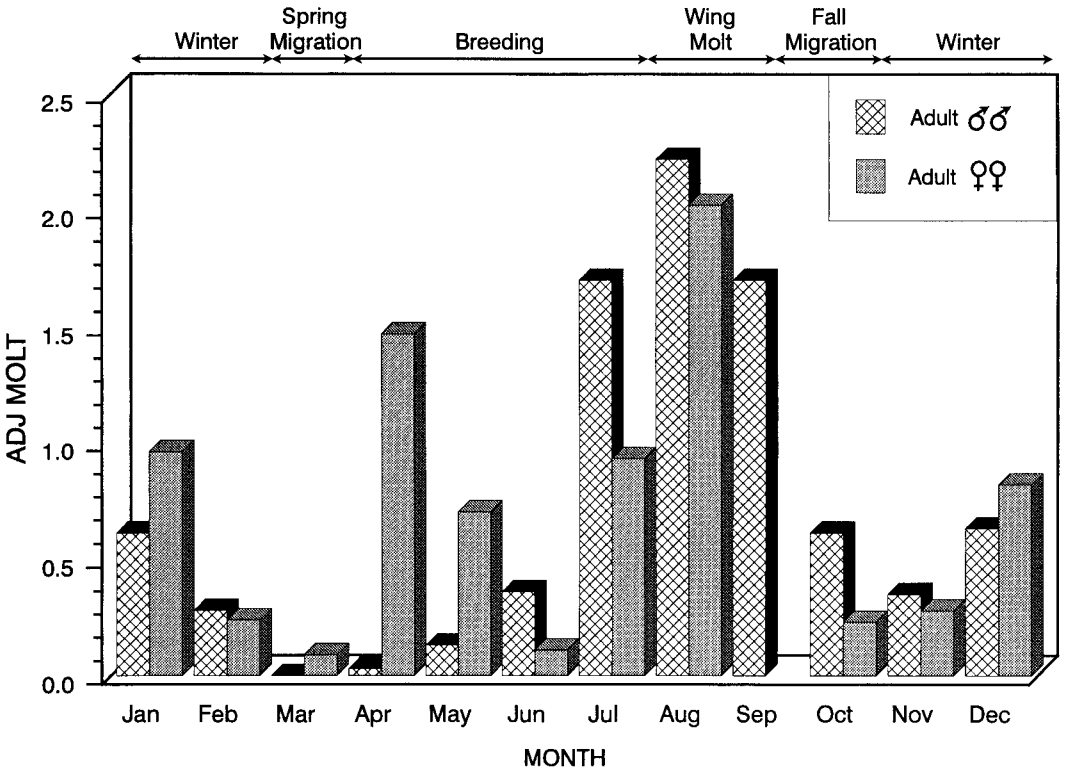FIGURE 2. Molt in the annual cycle of immature Ring-necked Ducks.

FIGURE 3.   Relative molting costs (ADJMOLT) of adult male and female Ring-necked Ducks throughout the annual cycle.

COSTS OF MOLT

Size-adjusted plumage mass was not affected by sex or sex*age interaction (F = 1.78–2.61; df = 1, 11; P > 0.135) but differed between adults and immatures (F = 9.66; df = 1, 11; P = 0.010). Consequently, ADJMOLT of adults and immatures before prebasic II (first definitive) molt were analyzed separately.

ADJMOLT of adults and immatures varied by sex and month (Table 1). In adults, the pattern of change in ADJMOLT was trimodal in females and bimodal in males (Fig. 3). ADJMOLT of males and females was greatest during the period of remigial molt (August) and also was elevated during winter and (December and January). ADJMOLT was reduced during spring (March) and fall (October) migrations. Neither age nor status affected ADJMOLT of breeding ducks but ADJMOLT changed differently in males and females during the breeding season (Table 2). In males, ADJMOLT remained at low levels throughout the breeding season. ADJMOLT was also reduced in females from mid-May to early

July but was elevated in breeding hens at other times (Fig. 3).

REMIGE LENGTH VERSES BODY SIZE

P5 and S5 lengths were significantly related to SIZE of adult males and females; however, models generally explained ≤ 5 percent of variation in SIZE (R^2 = 0.027–0.051, df = 81 [females] or 161 [males], P ≤ 0.012).

DISCUSSION

MOLTING PATTERNS

Molting patterns significantly differed for male and female Ring-necked Ducks but were similar in at least three respects: (1) peak molt intensity occurred following the breeding season while remiges were being replaced; (2) molt intensity was reduced during spring (March) and fall (October) migration periods; and (3) molt intensity was elevated during mid-winter. The principal difference between molting patterns of males and females occurred during the breeding season between arrival and onset of incubation when molt

intensity was elevated in females but not in males. We did not determine plumage aspect for all birds used in this study but ducks collected in late winter and used above to calculate plumage mass and spring migrants (March) for which plumage aspect was determined were in complete alternate plumage, so we assumed that molt in spring corresponded to prebasic molt and molt in winter represented prealternate molt. If this was indeed the case, then onset of prebasic molt in female Ring-necked Ducks was late relative to other species. Most female ducks initiate prebasic molt while on wintering areas. Female Mallards (*Anas platyrhynchos*) initiate prebasic molt as early as November and most probably complete molt before spring migration (Heitmeyer 1987); however, most Northern Pintail (*A. acuta*; Smith and Sheeley 1993 but see Miller 1986), Gadwall (*A. strepera*; Paulus 1984), American Wigeon (*A. americana*; Wishart 1985), Greater Scaup (*Aythya marila*; Billard and Humphrey 1972), and Canvasback (*A. valisineria*; Lovvorn and Barzen 1988) hens delay prebasic molt until late winter. Prebasic molt may continue in these species through spring migration into early stages of reproduction (reviewed by Hohman et al. 1992b).

Onset of prebasic molt may be related to pair status in Mallards (Heitmeyer 1987) but relations between female molt chronology and timing of pair formation are less evident in other species. For example, American Wigeon, Gadwall, and Northern Pintail generally form pairbonds in early to mid-winter (Rohwer and Anderson 1988) but, as indicated above, prebasic molt does not occur in these species until late winter. Moreover, although prebasic molt was generally more intense among paired than unpaired individuals, pairbond formation was not a prerequisite for start of prebasic molt in female Canvasbacks (Lovvorn and Barzen 1988), as suggested for Mallards (Heitmeyer 1985). Timing of pair formation in North American diving ducks (Aythyini) is late relative to that of most dabbling ducks (Anatini, Weller 1965). Ring-necked Ducks form pair-bonds during spring migration in March, most hens having obtained mates before arrival on nesting areas in April (Hohman 1986). Collections of spring-migrating ducks included paired individuals but none of these hens had initiated prebasic molt. Thus it was apparent that Ring-necked Ducks postponed prebasic molt until after spring migration and pair formation.

Adult and immature Ring-necked Ducks exhibited similar patterns of molt from fall migration through reproduction. This was so, in spite of the fact that Ring-necked Ducks undergo at least four molts (prejuvenal, prebasic I, prealternate I, and prebasic II) in their first year versus two molts/year thereafter (Palmer 1976). Adult males complete prealternate molt before immatures in some species (e.g., Mallard [Combs 1987], American Wigeon [Wishart 1983], Gadwall [Paulus 1984], and Northern Pintail in California [Miller 1986]). Likewise, basic plumage is acquired by adult female Mallards in advance of immatures (Heitmeyer 1987); however, as was the case in this study, age had no effect on molting patterns of Northern Pintails in Texas (Smith and Sheeley 1993), Canvasbacks (Lovvorn and Barzen 1988), or Greater Scaup (Billard and Humphrey 1972).

TEMPORAL DISTRIBUTIONS OF MOLTING COSTS

Size-adjusted mass of the definitive alternate plumages of male and female Ring-necked Ducks were equivalent. Thus, if males and females invested similarly in basic and alternate plumages and produced feathers at the same efficiencies, then costs of molt incurred by sexes during the plumage cycle likely were similar. Whereas costs of molt on an annual basis may have been similar, the temporal distribution of costs was different for males and females, especially during the reproductive period. Males deferred molting costs until after the breeding season. They abandoned their mates during incubation and migrated away from nesting areas to isolated sites where they underwent complete (prebasic) and partial (prealternate) molts before start of fall migration. Females, however, incurred costs of prebasic molt beginning soon after arrival on nesting areas. They ceased molting in June but resumed body molt in July while attending ducklings. Wing molt, completion of prebasic body molt, and initiation of prealternate molt occurred after young had fledged. This pattern of molt is typical of most ducks nesting in temperate regions of North America and is indicative of sexual differences in reproductive strategies and time and energy commitments to reproduction (Hohman et al. 1992b). That is, female ducks generally invest greater time and energy in reproduction than males (e.g., they incubate and rear young without assistance from their mates).

Initiation of prebasic molt during the reproductive period while mates are in attendance may be necessary for females, especially those that renest or successfully fledge young, to reduce subsequent molting costs and time required to complete molt before fall migration. Also, basic plumage is duller than alternate plumage and may serve to camouflage hens at nest sites (cf., Heitmeyer 1987).

The relative importance of nutritional vs. non-nutritional constraints in shaping annual molting patterns of Ring-necked Ducks is unclear; however, constraints seemed to act uniformly on all birds, as suggested by similarities in distribution of molting costs among sex-age classes. Reduced molt in migrating birds, breeding males, and incubating females might be interpreted as support for hypotheses ("staggered or sequential costs hypotheses," Lovvorn and Barzen 1988) that annual molt patterns evolved to minimize overlap in nutrient-demanding annual cycle events. As was the case for female Canvasbacks (Lovvorn and Barzen 1988), however, prebasic molt in female Ring-necked Ducks overlapped with nutrient acquisition for reproduction. The significance of this overlap was probably greater in Ring-necked Ducks than in Canvasbacks because prebasic molt in female Ring-necked Ducks was evident in all tracts whereas molt in female Canvasbacks was confined mostly to down and capital tracts, regions contributing only minor amounts to total plumage mass. Furthermore, analysis examining effects of sex, age, date, and reproductive status on ADJMOLT suggested molting costs were unrelated to status but were significantly influenced by sex and date. Nutrient demands obviously vary among stages of reproduction (e.g., period of rapid ovarian follicle growth vs. incubation), so we interpret this result to indicate that molting costs of breeding females were influenced by date rather than nutrient demands (as reflected by reproductive status). This leads us to conclude that annual molt patterns of Ring-necked Ducks probably are influenced by both nutritional and non-nutritional constraints.

NUTRITIONAL STRESS ASSOCIATED WITH MOLT

Remigial lengths were significantly (albeit weakly) related to SIZE of both males and females. We interpret these results to indicate that nutrition was not the primary determinant of defin-

itive remigial length. We therefore conclude that, although costs of molt were greatest while birds were molting remiges, there was no evidence that molting Ring-necked Ducks were nutritionally stressed.

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