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RELATIVE COSTS OF PREBASIC AND PREALTERNATE MOLTS FOR MALE BLUE-WINGED TEAL¹

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Abstract. We compared masses of definitive basic and alternate plumages of male Blue-winged Teal (*Anas discors*) to evaluate the hypothesis that nutritional investments in basic and alternate plumages are related to the duration that plumages are worn and to assess the relative costs of prebasic and prealternate molts. Because these plumages are worn by males for approximately equal durations, we predicted that masses of the basic and alternate body plumages would be similar. To assess nutritional stress (demands greater than available resources) associated with molt, we examined the relation between remigial length and structural size and compared predicted and observed plum-

age masses of Blue-winged Teal and other ducks. If birds were nutritionally challenged during remigial molt, then we predicted remigial length would be influenced by nutrition rather than size, and remigial length and size would be unrelated. Alternate body plumage of male Blue-winged Teal weighed about 10% more than the basic body plumage; however, masses of both plumages were less than that predicted on the basis of lean body mass. We argue that deviations between observed and predicted plumage masses were related to factors other than nutrition. Further, remigial lengths were significantly, albeit weakly, related to structural size. We therefore concluded that, although the potential for molt-induced stress may be greatest in small-bodied waterfowl species, there was no clear evidence that molting male Blue-winged Teal were nutritionally stressed.

Key words: *Anas discors*, *Blue-winged Teal*, *Anatidae*, *molt*, *nutrition*, *plumage*, *stress*.

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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 (> 90% dry mass) and collectively constitute greater than 25% of the protein content of the carcass (Murphy and King 1984b, 1991, and references therein). Because birds have relatively limited capabilities for storing protein (Blem 1990), are inefficient at converting dietary protein into feathers (Murphy and King 1984a), and require specific amino acids for feather synthesis that are concentrated in feathers relative to their availability in the diet (Hanson 1962), there is potential for nutrient demands of molt to exceed availability. The extent to which energy and nutrient demands of molt interfere with optimal allocation of resources to other processes ("nutritional stress," Lovvorn and Barzen 1988) is unclear (Murphy and King 1991). Mechanisms whereby molting birds reduce potential mismatches between nutrient need and availability include selective feeding (Murphy and King 1987, 1989), storage of energy and nutrient reserves in advance of molt (Murphy and King 1985, Brown 1986, Moorman et al. 1993), modified activity budgets (Bailey 1981, Paulus 1984), selection of favorable micro- or macrohabitats to reduce thermoregulatory costs (Hohman et al. 1992a), adjustments in molting patterns (i.e., number, quality, or growth rates of developing feathers) (Miller 1986, Smith and Sheeley 1993), scheduling molt to minimize overlap with other energy- and nutrient-demanding processes (Payne 1974, King 1980), or some combination of the above.

Ducks, geese, and swans (family Anatidae) exhibit a variety of molting patterns (Palmer 1976). In general, remiges are molted simultaneously once per plumage cycle, whereas molt of body feathers is much more variable. Whistling ducks, swans, and geese (subfamily Anserinae) have one body molt (prebasic) per plumage cycle and wear basic plumage throughout the year (terminology follows Humphrey and Parkes 1959). Other family members ("ducks," subfamily Anatinae) generally are smaller-bodied than Anserinae and have two or more body molts per plumage cycle. Basic plumage is replaced by alternate plumage in the prealternate molt. Except for remiges, this molt is complete (Palmer 1976). In male ducks, alternate plumage generally is brighter in appearance than the basic plumage and is worn from the time of pair formation until the cessation of breeding efforts. Quality of alternate plumage or extent of prealternate molt completion is positively associated with male participation in courtship and with pairing success (Wishart 1983, Amat 1990, Hohman and Ankney 1994). Because of species differences in pairing chronology, timing of prealternate molt completion in males and durations that the basic versus alternate plumage are worn vary among species (Hohman et al. 1992a).

The relative nutritional costs of prebasic and prealternate molts are unknown. In anatids, both wing and body feathers are replaced during prebasic molt, so feather mass replaced during prebasic molt may exceed that replaced during prealternate molt. Although

it was widely assumed that costs of replacing basic and alternate body feathers were the same for ducks, Wielicki (1986) determined that the basic body plumage of male Mallards (*Anas platyrhynchos*) weighed significantly less (40% less) than alternate body plumage. Nutritional investment in basic versus alternate plumage may be related to the duration that plumages are worn (Hohman et al. 1992a). That is, if nutritional investment in plumage is related to the duration that a plumage is worn, then it follows that male Mallards, which wear basic plumage for only a short duration, should invest less in basic than in alternate plumage.

We initiated this study to evaluate the hypothesis that nutritional investments in basic and alternate plumages are related to the duration that plumages are worn and to assess the relative nutritional costs of prebasic and prealternate molts for male Blue-winged Teal (*Anas discors*). We used lean dry mass of plumage as an index of molting costs, assuming that other costs associated with molt would be similar for prebasic and prealternate molts. Specifically, we were interested in comparing the masses of basic and alternate body plumage for male Blue-winged Teal. Because these plumages are worn by males for approximately equal durations, we predicted that masses of basic and alternate body plumage would be similar.

To assess nutritional stress associated with molt in Blue-winged Teal, we examined the relation between remigial length and structural size of adult males (Hohman and Crawford 1995), and compared predicted and observed plumage masses of Blue-winged Teal and other ducks. In general, structural size is significantly related to body mass of waterfowl (e.g., Ankney and Alisauskas 1991, Hohman 1993a). That is, after adjusting for other factors such as sex, age, and date, large birds tend to weigh more than small birds. We therefore assumed that within a particular size class of individuals there should be an optimal remigial length to accommodate seasonal changes in body mass (i.e., significant positive correlation between remigial length and body size). However, if birds were nutritionally challenged during remigial molt, then we predicted length of remiges would be influenced by nutrition rather than size, and remigial length and size would be unrelated.

METHODS

Migrating male Blue-winged Teal were collected by shotgun at Rockefeller State Wildlife Refuge in southwestern Louisiana, 21–27 March and 16–21 September 1990 and 1991 (see Paulus 1982 for site description). Male Blue-winged Teal acquire basic plumage in June–July and alternate plumage in December–January (Palmer 1976), so our collections of spring and fall migrants were made 2–3 months after molt completion. In the field, we measured (± 0.1 mm except where noted) bill length from the commissural point to tip of nail, maximum bill width distal to nares, tarsal bone length, keel length, body length from the tip of the bill to the base of the middle rectrix with the bird held on its back (± 0.5 cm), and length of the middle toe (± 1 mm). Synsacrum length and head length and width were measured in the laboratory. We plucked the fifth primary and fifth secondary remiges, and as-

sociated greater upper coverts. The above selected remiges also were obtained from birds killed by hunters in southwestern Louisiana in November–December 1990 and 1991 ($n = 138$ adult and 107 immature males). We subsequently measured length (± 0.5 mm) and dry mass (± 0.0001 g) of each feather, and secondary covert width (± 0.5 mm, Dane and Johnson 1975).

In the laboratory, skin was excised from the carcass. Molt intensity 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 = $\geq 50\%$). 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. Skins were examined externally to estimate percentages of definitive plumage in the HEAD, FLANK, BREAST, BACK, BELLY, and SCAPS regions. Estimates for the six feather regions were averaged to calculate overall percentage of definitive plumage.

To estimate mass of definitive plumage, we plucked contour feathers from the WING and all other feather regions (hereafter "BODY"). WING and BODY contour feathers were washed separately in detergent and petroleum ether, and then dried to constant mass (± 0.01 g).

Ages (adult [after-hatching-year] or immature [hatching-year]) of fall-shot males could be readily determined by using cloacal (Gower 1939) or rectral characteristics (Pirmie 1935), but these techniques were unreliable for age-classification of males collected in spring (Hochbaum 1942). Consequently, we used canonical discriminant analysis (CDA) with the nine remigial measurements to estimate parameters providing maximum separation between known-aged (i.e., fall-shot) adults and immatures (PROC CANDISC, SAS Institute 1989). In doing so, we assumed that age-related differences in size and mass of remiges (adults > immatures) evident in other ducks (e.g., Mallards, Gatti 1983; Canvasbacks *Aythya valisineria*, Serie et al. 1982; and Ring-necked Ducks *A. collaris*, Hohman and Cypher 1986) also occur in Blue-winged Teal. CDA of male Blue-winged Teal remigial measurements correctly classified 82% of immatures and 88% of adults ($F_{9,278} = 28.5$, $P < 0.001$; Hohman et al. 1995). We then applied this model to remigial measurements of spring-shot (i.e., unknown-age) males to separate adults and immatures.

Multivariate analysis of variance (MANOVA) with type III sums of squares was used to test for effects of definitive plumage type and year on masses of WING and BODY feathers of adult male Blue-winged Teal

(PROC GLM, SAS Institute 1989). Spring-shot males age-classified as immatures by CDA, and adults molting $\geq 5\%$ of contour feathers or wearing < 95% definitive plumage were excluded from analysis. We used regression analysis to examine relations between remigial lengths and structural size. First, we subjected the correlation matrix of nine structural measurements (tarsus, keel, bill, head, middle toe, synsacrum, and body lengths, and bill and head widths) to principal components analysis (PROC PRINCOMP, SAS Institute 1989). The first principal component accounted for 48% of the variance in the original measures, described positive covariation among all measures, and had loadings ranging from 0.26 to 0.40. We used scores along the first principal component as a measure of body size (SIZE, Ankney and Alisauskas 1991) and hence as a covariate in the above analysis. Significance level was set at $\alpha = 0.05$.

RESULTS

Our sample of Blue-winged Teal included 44 males in basic and 100 males in alternate plumages, of which 41 and 72, respectively, were classified as adults. In the subsequent analysis of plumage mass, we used 33 adults in basic plumage ($n = 15$ in 1990 and 18 in 1991) and 59 adults in alternate plumage ($n = 24$ in 1990 and 35 in 1991) that were determined to be non-molting and wearing > 95% definitive plumage.

Plumage mass of male Blue-winged Teal was unrelated to year or interaction of year and plumage type (MANOVA $F_{2,86} < 1.5$, $P_s > 0.24$), but plumage mass was affected by plumage type and structural size (MANOVA $F_{2,86} > 21.1$, $P_s < 0.001$). Year and season had no effect on size-adjusted mass of WING feathers (Table 1). Size-adjusted mass of BODY plumage also was unrelated to year but differed ($P < 0.001$) between alternate and basic plumages (Table 1). Alternate BODY plumage of male Blue-winged Teal weighed about 10% more than the basic BODY plumage (mean \pm SE = 14.79 \pm 0.11 g vs. 13.29 \pm 0.15 g).

Remigial lengths were significantly related to SIZE of adult males; however, models generally explained < 6% of variation in SIZE ($R^2 < 0.06$, $df = 111$, $P < 0.01$).

DISCUSSION

Our prediction that masses of basic and alternate body plumage of male Blue-winged Teal would be equal was not supported by the above analysis. Nonetheless, our finding that masses of basic and alternate body plumage of male Blue-winged Teal differed by only 10% versus 40% for male Mallards (Wielicki 1986) was clearly in the direction of the prediction. We assumed in our analysis that chemical composition and the number of feathers were the same for both plumages, and that plumages were worn for equal durations. We have no evidence that composition differed between plumages, that molts were not complete, or that plumage durations were unequal, but we acknowledge that failure of any of these assumptions would have invalidated the prediction. Likewise, we were unable to determine if variation in plumage mass was caused by generational differences in size, shape, or structure of all body feathers or if basic and alternate plumage masses were apportioned differently among feather

TABLE 1. General linear models used to describe differences in masses of definitive basic and alternate plumages of male Blue-winged Teal.

Source	df	Body ^a			Wing ^b		
		Sum of squares ^c	F	P	Sum of squares	F	P
Model ^d	4	95.6	32.7	<0.001	2.2	4.0	0.005
Error	87	63.5			12.1		
Corrected total	91	159.1			14.3		
Size ^e	1	29.4	40.4	<0.001	1.8	13.6	<0.001
Year	1	1.4	1.9	0.17	0.0	0.2	0.65
Plumage	1	45.5	62.3	<0.001	0.3	2.2	0.14
Year-plumage	1	0.8	1.2	0.276	0.3	2.4	0.13

^a Body = mass of feathers from all body regions except humeral tract (Billard and Humphrey 1972).

^b Wing = mass of humeral feathers.

^c Type III Sums of Squares (SAS Institute 1989).

^d Explained variance for full model: Body, $R^2 = 0.60$; Wing, $R^2 = 0.15$.

^e Size = scores along the first principal component: a linear combination of nine structural measurements based on their correlation matrix.

tracts. However, aspect and probably function differed between plumages. For example, if pairing success of male Blue-winged Teal was influenced by plumage quality and performance of displays as in other ducks (Wishart 1983, Amat 1990, Hohman and Ankney 1994), then we suspect that nutritional investments in some feather regions, especially those such as SCAPS featured prominently in male courtship displays (McKinney 1970), may have differed between basic and alternate plumages.

Although energy and nutritional costs of molt are difficult to estimate (Walsberg 1983), it is evident that relative costs of molt as indexed by plumage mass vary among anatids (Hohman et al. 1992a) and that, within species, costs may differ between plumages (Wielicki 1986, this study). It is further evident that these costs are not trivial. Plumage mass is related to body size of birds and, across species and habitats, averages about 6.3% of ingesta-free body mass (Turcek 1966). Proportional mass of plumage generally is greater in small- than in large-bodied birds (Turcek 1966), but that generalization apparently does not hold for ducks. For example, male Blue-winged Teal weigh less than male Mallards, but relative to their body mass they have similar basic plumage mass (4.9–5.6% vs. 4.5–5.3%, respectively) and less alternate plumage mass (5.3–6.1% vs. 6.2–7.2%, respectively; Table 2). Likewise for diving ducks (Aythyini), Ring-necked Ducks are lighter but have proportionately less alternate plumage mass than Canvasbacks (4.2–4.7% vs. 4.6–5.6%, respectively; Table 2).

Observed plumage masses of male Blue-winged Teal were substantially less than predicted plumage mass. Indeed, we estimate that observed mass of basic plumage was minimally 15% and alternate plumage was $\geq 9\%$ below plumage mass predicted on the basis of lean body mass of male Blue-winged Teal (Table 2). Basic plumage mass of male Mallards also was below predicted plumage mass, but observed alternate plumage mass was 14% greater than predicted mass. Whereas reduced plumage masses might be interpreted as evidence of nutritional constraints in molting waterfowl, it has been shown that, relative to their body size or mass, plumage masses of birds associated with aquatic habitats generally are lighter than those of

birds inhabiting forests or grasslands (Turcek 1966). Turcek (1966) suggested that habitat-related differences in plumage mass reflected the ineffectiveness of plumage as an insulator in water versus air (Turcek 1966). Reduced plumage masses in diving ducks compared to dabbling ducks (i.e., birds totally versus partially dependent on aquatic habitats) seem to support Turcek's (1966) interpretation and argue against the notion that deviations between observed and predicted plumage masses were related to the nutrition of birds during molt.

Nutrition is known to influence size of remiges in waterfowl and other waterbirds (Visser 1976, Owen and Montgomery 1978, Pehrsson 1987). Birds that are nutritionally stressed during remigial molt apparently develop smaller feathers than those with adequate nutrition (Pehrsson 1987, Virtiska 1995). Seasonal fluctuations in body masses of waterfowl are extensive (Hohman et al. 1988). The ability of birds to accommodate changes in body mass without reduction of flight capability is presumably compromised in birds with shortened remiges, potentially resulting in decreased survival and impaired reproductive performance (Pehrsson 1987).

Blue-winged Teal exhibit an unusually high degree of variability in their remigial measurements (Dane 1968, Hohman et al. 1995). Variability in remigial sizes of Blue-winged Teal and closely related Cinnamon Teal (*A. cyanoptera*) was attributed to nutrition during molt (Hohman et al. 1995). In the present study, remigial lengths were significantly, albeit weakly, related to SIZE of male Blue-winged Teal. We interpret these results to indicate that nutrition was not the primary determinant of definitive remigial length. We therefore conclude that, although the potential for molt-induced stress may be greatest in small-bodied waterfowl such as teal (Hohman 1993a), there was no clear evidence that molting male Blue-winged Teal were nutritionally stressed. Similar results were obtained for male and female Ring-necked Ducks (Hohman and Crawford 1995). These studies lend support to Ankney's (1979) assertion that molt does not cause nutritional stress in waterfowl.

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TABLE 2. Body and plumage masses (g) of some adult male ducks.

Tribe Species	Ingesta-free body mass ^a		Plumage mass			
			Predicted ^b	Observed ^c		Wing
	Intact	Lean		Basic	Alternate	
Anatini						
Blue-winged Teal	397	342	23.0–26.5	13.3 ± 1.1	14.8 ± 1.0	6.2 ± 0.4
(n)	(113)	(113)		(33)	(59)	(92)
Cinnamon Teal	362	334	22.5–24.3	—	15.0 ± 1.7	5.5 ± 0.5
(n)	(50)	(50)			(5)	(5)
Mallard	1,246	1,068	67.8–78.5	34.3 ± 3.6	54.7 ± 3.6	22.3 ± 1.1
(n)	(262)	(262)		(3)	(13)	(13)
Aythiini						
Ring-necked Duck	730	645	42.0–47.2	—	22.3 ± 2.1	8.2 ± 0.3
(n)	(184)	(67)			(6)	(6)
Canvasback	1,297	1,068	67.8–81.6	—	45.3 ± 4.2	14.4 ± 0.5
(n)	(113)	(113)			(5)	(5)
Oxyurini						
Ruddy Duck	598	509	33.5–39.1	—	20.5 ± 0.8	4.4 ± 0.1
(n)	(14)	(14)			(2)	(2)

^a Data sources: Blue-winged Teal (W. L. Hohman, unpubl. data), Cinnamon Teal (Hohman and Ankney 1994), Mallard (Whyte et al. 1986: Table 1), Ring-necked Duck (Hohman 1986), Canvasback (Hohman 1993b), Ruddy Duck (Hohman et al. 1992b).

^b Plumage mass = 0.09 × (body mass)^{0.95}; Turcek (1966). Range in predicted plumage mass estimated from intact and lean body masses.

^c Mean ± SD. Data sources: Blue-winged Teal (this study), Cinnamon Teal (W. L. Hohman, unpubl. data), Mallard (Wielicki 1986), Ring-necked Duck (Hohman and Crawford 1995), Canvasback (W. L. Hohman, unpubl. data), Ruddy Duck (Hohman 1993a).

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