

Effect of Winter-diet Restriction on Prebasic Molt in Female Wood Ducks

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Abstract: During winters 1990–1992, we manipulated food availability 5%–20% less than that of *ad libitum* feeding for captive groups of wild-strain North American wood ducks (*Aix sponsa*) to test effects of increasing levels of food restriction on prebasic molt of females. Birds fed *ad libitum* and 5%–15% restricted diets exhibited a protracted molt (>90 days) of low intensity. Most females fed a 20%-restricted diet did not initiate molt until resumption of *ad libitum* food availability. We hypothesize that a 20% restriction exceeds a threshold in food availability and possibly body condition needed by captive female wood ducks to meet nutritional demands of maintenance and prebasic molt. A lower threshold may exist for free-living wood ducks, implying the importance of adequate food availability and quality during winter to minimize negative effects on within- and cross-seasonal life-cycle functions. We encourage continued conservation of bottomland hardwood forests in southeastern United States because of their intrinsic values to sustaining populations of wood ducks in North America.

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Regeneration of plumage is a nutrient-demanding process in the life-cycle of birds (Payne 1972, King 1974). To provide an example from the family Anatidae (ducks, geese, and swans), Heitmeyer (1988) reported that daily protein costs of prebasic molt in female mallards (*Anas platyrhynchos*) ranked only second to those of egg laying. Waterfowl obtain most nutrients for molt from daily food intake (Ankney 1979, Heitmeyer 1987, Smith and Sheeley 1993). When poor habitat conditions (e.g., drought; Miller 1986, Reinecke et al. 1988) constrained opportunities for food intake, free-ranging northern pintails (*A. acuta*) and mallards delayed molt (Miller 1986, Heitmeyer 1987). Also, simulated poor feeding conditions in captivity during winter for wild-strain mallards and North American wood ducks (wood ducks here-

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after) impaired prebasic molt, survival, pair formation, and several reproductive components (Richardson and Kaminski 1992, Barras 1993, Dubovsky and Kaminski 1994, Vrtiska 1995, Demarest et al. 1997). Birds unable to reduce or avert nutritional constraints from decreased food or nutrient availability may suspend or delay molt, reduce rate or intensity of molt, and/or catabolize body reserves to reduce cost of maintenance (King and Murphy 1985).

The influences of food quality and a single level of diet restriction during winter on prebasic molt and body-mass dynamics in female mallards have been examined (Richardson 1989, Richardson and Kaminski 1992). However, use of incrementally increased levels of winter diet restriction to identify a possible threshold level of food deprivation that may delay or suppress prebasic molt in female ducks has not been attempted to our knowledge. Wood ducks are an appropriate species for this research. Adult females molt body contour feathers twice annually (Bellrose and Holm 1994), attaining a basic plumage during winter or early phases of breeding and an alternate plumage between late summer and autumn (Kirby and Fredrickson 1990). Moreover, wood ducks are ecologically and economically important ducks in North America (Fredrickson et al. 1990, Bellrose and Holm 1994). Thus, we conducted an experiment with captive, wild-strain wood ducks to determine if increasing levels of food restrictions (i.e., 5%–20% less than *ad libitum* feeding) during winter would impair prebasic molt in females. This type of manipulative dietary experiment could not be conducted with free-ranging wood ducks in natural habitats; hence, we used captive individuals to simulate the effect of an increasing restricted range of food availability on female prebasic molt during winter. Information from this study may improve our understanding of within- and cross-seasonal relationships between food availability and avian physiological processes (e.g., molt), as well as provide implications for conservation of forested wetlands—the primary habitat used year around by wood ducks.

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Methods

We conducted experiments in an outdoor aviary located 2 km southeast of Mississippi State University (MSU) in east-central Mississippi (33°27'N, 88°46'W). Characteristics of the aviary were described by Richardson and Kaminski (1992). We divided the aviary into 4 equal-sized arenas (3x18x1m), using wooden-framed parti-

tions covered with 2-mm felt material as physical and visual barriers among groups of wood ducks in arenas (Demarest et al. 1997).

To establish an experimental flock of wood ducks, we collected fresh eggs of wild wood ducks from nest boxes during 1989–91 at Noxubee and Yazoo National Wildlife Refuges in east-central and west-central Mississippi, respectively. At MSU, we artificially incubated eggs and reared hatched wood ducks, following accepted husbandry techniques (Ward and Batt 1973) and a research protocol approved by the MSU Institutional Animal Care and Use Committee (Study No. 91-065).

In late November 1990 and 1991 in preparation for our winter experiments, we randomly selected 120 wood ducks (60 males and 60 females) of 2 age classes (juvenile [5–7 months of age] and adult [17–19 months]). This was the maximum number of ducks that could be maintained in our aviary according to required space per bird, as dictated by our animal welfare protocol. During winters 1990–91 and 1991–92, we randomly assigned and placed 30 wood ducks of the following age-sex combinations in each of the 4 arenas: 7 adult and 8 juvenile males and 7 adult and 8 juvenile females. We maintained juveniles and adults together to mimic natural aggregations of age classes of wild wood ducks (Bellrose and Holm 1994). We clipped all dextral remiges of ducks to render them flightless and uniquely marked each duck with a colored plastic culmen marker and an aluminum leg band.

Before experimentation, we provided all birds *ad libitum* access to fresh water from 2 troughs (0.3 x 0.45 x 2.44 m) and a high-protein commercial ration (Richardson and Kaminski 1992). We provided food under 3 feeding shelters per arena to cover it from rain. We assumed that grit was adequately available from the gravel floor of the aviary (Demarest et al. 1997).

We assigned the following diet treatments randomly and without replacement to the 4 arenas for the winter 1990–91 experiment (1) *ad libitum* (control), (2) 5% diet restriction, (3) 10% restriction, and (4) 15% restriction. Wood ducks fed restricted diets received 5%, 10%, or 15% less food daily than the amount (g) consumed the previous day by the control group (Demarest et al. 1997). We imposed diet treatments from 21 December 1990 through 21 March 1991, after which ducks were returned to an *ad libitum* diet.

We maintained females and males together to simulate natural gregariousness of wood ducks during winter (Bellrose and Holm 1994), conduct a concurrent experiment on pair formation (Demarest et al. 1997), and because sociability has been shown to influence normal timing of molt in ducks (e.g., Leafloor and Ankney 1991). Because of needs for social interaction among our wood ducks, we imposed diet treatments on groups of birds instead of spatially isolated individuals. However, we treated individuals as experimental units for statistical analysis, because molt is an individual physiological process influenced by social cues from conspecifics in groups, and our experiment was conducted simultaneously with Demarest et al.'s (1997) study. We recognize that this approach did not employ true replication, but we contend that this constrained experimental approach was adequate to test for relative differences in molt responses among diet treatments, given the experimental and natural biological needs for social interactions among wood ducks in our studies.

We followed the same experimental protocol in winter 1991–92, except we used 10%, 15%, and 20% levels of diet restriction and a control group (*ad libitum* feeding) as treatments. Limitations on aviary space and lack of significant differences in frequency of occurrence of prebasic molt among winter 1990–91 diet treatments (see results) led us to abandon the 5%-restriction level in favor of the 20% level. We commenced diet treatments on 23 December 1991 and terminated them on 23 March 1992.

Following Richardson and Kaminski (1992), we clipped the tips of feathers in the flank ($N = 10$), scapular ($N = 10$), and tail ($N = 5$) regions on each female during the week preceding diet treatment to provide a marked sample of feathers for monitoring occurrence and timing of molt each winter. We initiated weekly evaluations of molt on 21 December 1990 and ended the last day of diet treatment on 21 March 1991. In winter 1991–92, we began weekly molt evaluations on 23 December 1991 and continued until 17 April 1992, approximately 4 weeks after termination of diet restriction and resumption of *ad libitum* feeding. We extended evaluation of molt in 1992 to examine molt responses of females to resumption of *ad libitum* diets.

We defined date of molt initiation within a plumage region as the median Julian date of the weekly interval between successive examinations of a duck when ≥ 2 of its clipped feathers were found absent from flank, scapular, and tail regions (Richardson and Kaminski 1992), or when sheathed feathers appeared in unclipped regions (belly, breast, crown, and mantle). We used loss of ≥ 2 feathers as a criterion for molt initiation to minimize bias from potential incidental loss of feathers (Richardson and Kaminski 1992).

Although we began experiments with 15 females per diet treatment, differential mortality (Demarest et al. 1997) and occurrence of prebasic molt (Barras 1993) by female wood ducks among diet treatments reduced sample size among diet treatments. Therefore, we set $\alpha = 0.1$ before analyses and used nonparametric statistical methods, because data on timing of molt were not normally distributed or exhibited unequal variances among diet-treatment groups. We did not test the possible effect of female age (juvenile or adult) on response variables, because including age as an experimental effect would have further reduced sample size and power. We used a Chi-square test of independence to test the null hypothesis of no difference in frequency of occurrence of prebasic molt in ≥ 1 plumage regions among diet treatments (SAS 1985). We used the Kruskal-Wallis procedure to test the null hypothesis that median initiation dates of prebasic molt within plumage regions did not differ among diet groups (SAS 1985). We used nonparametric multiple comparisons to test for differences in all pair-wise contrasts of median initiation dates of molt after an overall difference ($P \leq 0.1$) was detected using the Kruskal-Wallis test (Daniel 1990).

Table 1. Median initiation dates and 90% confidence intervals (CI) for prebasic molt within plumage regions of captive, wild-strain female wood ducks fed *ad libitum* (control) or restricted amounts of a high-protein ration, winter 1990–91.

Plumage region	Diet treatment			
	Control	5%	10%	15%
Flank				
Median	11 Feb A ^a	18 Mar B	11 Mar B	14 Jan A
90%CI	31 Dec–11 Mar	5 Mar–18 Mar	5 Mar–18 Mar	24 Dec–3 Mar
N ^b	7	3	4	8
Scapular				
Median	18 Feb A	14 Jan A	18 Jan A	31 Dec A
90%CI	14 Jan–18 Mar	31 Dec–18 Mar	14 Jan–5 Mar	24 Dec–11 Mar
N	4	9	4	3
Tail^c				
Median	21 Jan	d		
90%CI	24 Dec–28 Jan			
N	3	1	1	2

a. Medians within rows with different letters differ ($P \leq 0.10$, Kruskal-Wallis test).

b. N = number of female wood ducks.

c. Small sample sizes precluded statistical analysis.

d. Blanks denote that medians and CI's were not reported because $N \leq 2$.

Results

Winter 1990–91

All 60 females survived the period of diet treatment (21 December 1990–21 March 1991). Sixty-two percent of these females initiated prebasic molt in flank, scapular, and or tail regions during this period. There was a trend for more frequent occurrence of prebasic molt in ≥ 1 plumage regions of females in control and 5%-restricted groups (73%, 22/30) than in 10%- and 15%-restricted groups (50%, 15/30); however, occurrence of molt was independent of diet treatment ($\chi^2_3 = 4.724$, $P = 0.193$). Females in the 5%- and 10%-restricted groups initiated prebasic molt in the flank region 5 and 4 weeks later, respectively, than control females ($\chi^2_3 = 7.942$, $P = 0.047$; Table 1). However, females in the 15%-restricted group initiated molt in the flank region in mid-January 1991, earlier than all other groups (Table 1). Median dates of molt initiation in the scapular region did not differ among diet groups ($\chi^2_3 = 2.865$, $P = 0.413$; Table 1).

Winter 1991–92

Fifty-four (90%) of 60 females survived the period of diet treatment (23 December 1991–23 March 1992). Of 6 deaths, 4 were adults and 2 were juveniles (i.e., 1 female each in the 10%- and 15%-restricted diets, 4 females in the 20%-restricted diet). Seventy percent of the 60 females initiated molt in ≥ 1 plumage regions during the

period of diet treatments. All control and 10%-restricted females initiated molt during this period. Within a month after resumption of *ad libitum* feeding, 3 of 13 surviving females previously on the 15%-restricted diet and 4 of 8 females on the 20%-restricted diet initiated molt for the first time. When molt evaluation terminated on 17 April 1992, 91% (49/54) of surviving females had initiated molt.

Median initiation dates of prebasic molt differed among control and diet-restricted groups only in belly ($\chi^2_3 = 7.805$, $P = 0.05$) and breast ($\chi^2_3 = 7.348$, $P = 0.06$) regions (Table 2). Molt initiation dates in the belly region did not differ among groups of birds on restricted diets or between control and 15%-restricted groups, although females in the 15%-restricted group molted 1.5 weeks later than the control group. Females fed 10%- and 20%-restricted diets molted belly plumage 2.5 and 4.5 weeks later, respectively, than control-group females. Females in the 15%-restricted group molted breast plumage later than the control and 10%-restricted groups, but not later than the 20%-restricted group. We found no evidence of differential timing of molt in flank and scapular regions among diet-treatment groups (Table 2).

The proportion of female wood ducks that exhibited prebasic molt varied among plumage regions and diet groups in winter 1991–92. Female wood ducks were never observed molting in >4 plumage regions simultaneously during any weekly examination. Additionally, occurrence of molt in multiple regions (2–4)

Table 2. Median initiation dates and 90% confident intervals (CI) for prebasic molt within plumage regions of captive, wild-strain female wood ducks fed *ad libitum* (control) or restricted amounts of a high-protein ration, winter 1991–92.

Plumage region	Diet treatment	N ^a	Median	90%CI
Belly	Control	10	26 Feb A ^b	31 Jan–14 Mar
	10%	11	14 Mar B	29 Feb–07 Apr
	15%	8	7 Mar AB	22 Feb–22 Mar
	20%	8	31 Mar B	31 Jan–07 Apr
Breast	Control	11	22 Feb A	31 Jan–29 Feb
	10%	11	14 Feb A	3 Jan–29 Feb
	15%	9	7 Mar B	22 Feb–31 Mar
	20%	4	4 Mar AB	3 Jan–07 Apr
Flank	Control	5	14 Feb A	24 Jan–22 Mar
	10%	13	31 Jan A	18 Jan–07 Mar
	15%	6	4 Mar A	22 Feb–14 Apr
	20%	5	22 Mar A	3 Jan–07 Apr
Scapular	Control	5	29 Feb A	24 Jan–07 Apr
	10%	5	31 Jan A	3 Jan–14 Apr
	15%	4	26 Feb A	14 Feb–07 Mar
	20%	2	22 Feb A	3 Jan–14 Apr
Crown/ Mantle ^c	Control	2	14 Mar	7 Mar–22 Mar
	10%	4	31 Mar	22 Feb–14 Apr
	15%	3	22 Mar	7 Mar–14 Apr
	20%	3	7 Apr	7 Apr–14 Apr

a. Number of female wood ducks.

b. Medians within plumage regions with different letters differ ($P \leq 0.10$, Kruskal-Wallis test).

c. Small sample size precluded statistical analysis in crown and mantle regions.

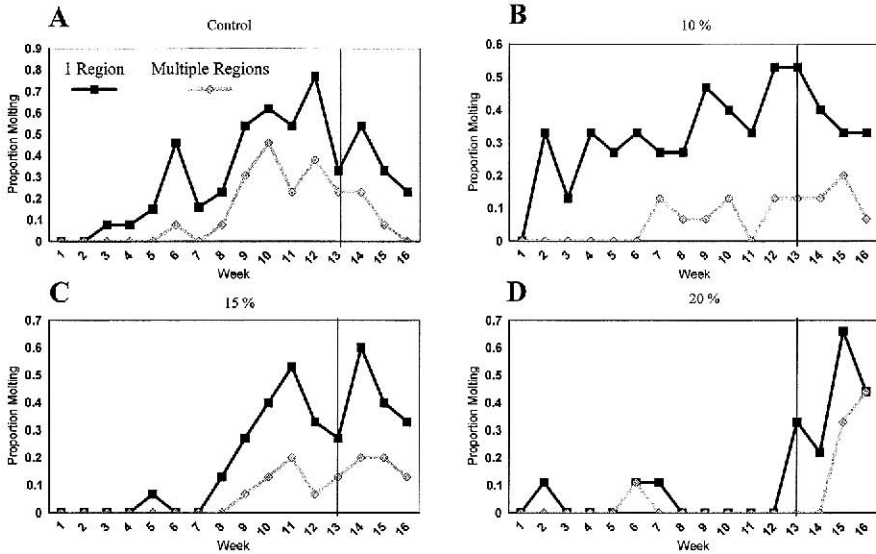


Figure 1. Proportion of captive female wood ducks ($N = 15/\text{group}$) fed either (A) a high-protein ration *ad libitum* (control group), (B) a 10%-restricted diet, (C) a 15%-restricted diet, or (D) a 20%-restricted diet that molted in 1 and multiple regions during winter 1991–92. Vertical line denotes inspection date 1 week following resumption of *ad libitum* diets in all treatment groups.

never exceeded 50% of the ducks (Fig. 1 A–D). Molt in multiple regions never exceeded 20% in any diet-restricted group during the treatment period. Molt in multiple regions was greatest in mid-late March 1992 (weeks 10–12) in the control, 10%-, and 15%-restricted groups. However, only 4 females in the 20%-restricted group initiated molt during diet restriction; 2 of these died before termination of food restriction. The 2 survivors had suspended molting by 18 February 1992, but began molting again after *ad libitum* feeding resumed on 23 March 1992 (Fig. 1 D).

Discussion

Effects of increasing levels of diet restriction during winter 1990–91 on occurrence and timing of prebasic molt in female wood ducks were counter to our predictions. Our results suggest that female wood ducks could initiate prebasic molt in flank and scapular regions in spite of food restrictions up to 15% *ad libitum* feeding. Additionally, females exposed to greatest diet restriction (15%) in winter 1990–91 molted flank and scapular plumage earliest. Thus, diet restriction up to 15% may not have been sufficient to preclude or delay captive female wood ducks from initiating

prebasic molt under the environmental conditions in our aviary during winter 1990–91.

Delayed molt in the breast and belly regions of females in the 15%- and 20%-restricted groups during winter 1991–92 may reflect a compensatory response to decreased availability of food or specific nutrients (*sensu* King and Murphy 1985), but we cannot distinguish between these alternative or their combined effects. At 20%-restriction, nutritional requirements of molt may not have been met due to limited food or nutrient availability, which also may have suppressed wood ducks' ability to molt in multiple plumage regions at this level of food restriction. Additionally, catabolism of body tissues was most apparent in the 20%-restricted group, as evidenced by lowest mean body masses and emaciation in these birds (Demarest et al. 1997). Although winter food restriction of >15%–20% inhibited prebasic molt in our captive female wood ducks, free-ranging females may be impacted by lower levels of food deprivation due to greater energetic costs of free living (Demarest et al. 1997).

The effect of decreasing food availability on occurrence and timing of prebasic molt during winter 1991–92 was further evidenced by initiation or resumption of molting by most 20%-restricted females after restoration of *ad libitum* feeding. Our captive wood ducks responded to changes in food availability similarly to wild northern pintails (Miller 1986) and mallards (Heitmeyer 1987) and captive mallards (Richardson and Kaminski 1992) by delaying or interrupting molt until food availability and possibly body condition improved.

Food deprivation during winter between 15%–20% of *ad libitum* may represent a threshold level at which nutrient availability and possibly diminished physiological condition may impair survival and productive functions, such as prebasic molt and reproduction in captive wood ducks. In a concurrent experiment, involving the same wood ducks, Demarest et al. (1997) found that body mass and pair formation of females decreased progressively with increasing levels of winter diet restriction, and that lowest mean body mass and frequency of pairing in females were recorded in the 20%-restricted group. Demarest et al. (1997) also suggested that a threshold level for mortality existed between 15%–20% diet restriction. Moreover, Vrtiska (1995) worked in the same aviary and under similar experimental conditions as us; he found that captive female wood ducks exhibited decreased reproductive performance (e.g., frequency of nesting, egg production and fertility, delayed reneating) in response to winter diet restrictions of 15% and 20%. Thus, we propose that winter food restriction of 15%–20% may decrease performance of current and cross-seasonal life-cycle functions of captive wood ducks. Similar cross-seasonal ramifications have been proposed for wild mallards (e.g., Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987).

Possible formation of dominance hierarchies among individuals within restricted diet groups could nullify treatment effects for dominant individuals and exacerbate food restriction for subordinate individuals. If dominance hierarchies did form within restricted diet groups, then one might predict that variances of mean body masses of wood ducks may differ among these groups. Demarest et al. (1997:826–827) reported weekly mean body masses and standard errors for the same

wood ducks used in our study. We compared the variances of mean body masses for females among diet groups, but found no evidence of heterogeneous variances within any weeks of the study (F_{\max} statistics < 1.11 , $P > 0.25$, $N = 9-15$). This result is consistent with our hypothesis that ducks within diet restriction groups all received the same diet treatment, and dominance among individuals of a diet group was not differentially affecting their body mass and condition.

Wood ducks are specialists of forested wetlands and therefore exhibit less foraging and habitat plasticity than mallards, for example, which also exploit forested wetlands during fall and winter (Heitmeyer 1985, Heitmeyer and Fredrickson 1990, Kaminski et al. 1993). Additionally, wood ducks use flooded live forests more than expected in all seasons, based on estimated availability of these and other habitat types (Heitmeyer and Fredrickson 1990). In naturally and artificially flooded red oak (*Quercus* spp.) bottomlands throughout the southeastern United States, wood ducks forage on acorns, other seeds, and aquatic invertebrates in fall and winter (Bellrose and Holm 1994, Barras et al. 1996, Wehrle et al. 1995). We and Demarest et al. (1997) demonstrated that reductions in winter food availability $> 15\%$ – 20% *ad libitum* can impede prebasic molt, survival, and reproductive activities of captive wood ducks. Similar consequences may exist for free-ranging wood ducks but likely at lower levels of food reduction because of greater energetic costs of free living. Indeed, bottomland hardwood forests in the Southeast provide critical foraging habitat for wood ducks during winter, as these birds physiologically prepare for spring migration and reproduction.

Although restoration of bottomland hardwood forests is underway extensively on public and private lands in the Southeast (Schoenholtz et al. 2001), area of freshwater forested wetlands continues to decline in the United States (Dahl 2000). Moreover, these forests have sustained the greatest overall loss in area of all wetland types in the United States since the 1950s (Dahl 2000). Because hardwood bottomlands provide critical food resources for wood ducks during several seasons of the year, we encourage continued maintenance, restoration, and proper management (e.g., silviculture, flooding [Reinecke et al. 1989, Kaminski et al. 1993, Gray and Kaminski 2002]) of these forests in the southeastern United States to help sustain wood ducks in the Mississippi and Atlantic Flyways. As restoration and management of bottomland hardwood forests continue in the Southeast (Schoenholtz et al. 2001), researchers should evaluate relationships between the status of these forests and wood duck populations. Also, there is a need to obtain precise estimates of foraging carrying capacity of bottomland hardwood forests (based on availability of red oak acorns) for wood ducks and other waterfowl using lowland forests (Loesch et al. 1994).

Because of constraints on sample size and a primary interest in the effect of food restriction on prebasic molt in female wood ducks, we did not test the effect of age-class (juvenile vs. adult) on molt. Future researchers may be interested in testing effects of age and restricted availability of total food and specific nutrients (e.g., energy, protein, sulfur amino acids) at different levels on prebasic and remigial molts of wood ducks and other waterfowl (e.g., Vrtiska 1995, Giuliano et al. 1996). Additionally, future researchers may use non-invasive, total-body electrical conductivity analysis

(Castro et al. 1990) to relate different physiological and behavioral processes (e.g., dominance) to body condition and thereby quantify a threshold level of body condition for molting and other productive functions (e.g., Dailey and Callahan 2000).

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