

NUTRIENT-RESERVE DYNAMICS OF BREEDING MALE WOOD DUCKS¹

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Abstract. Studies of reproductive bioenergetics in Anatidae have focused primarily on females, but reproductive effort of males is significant and of critical importance to the breeding success of their mates. We studied dynamics of nutrient reserves of breeding male Wood Ducks (*Aix sponsa*) in Alabama and Georgia to examine whether males used endogenous lipid and protein to help meet energy demands of reproduction. We also investigated variation in prebasic molt and testis mass of males in relation to breeding status. Carcass mass of males was greatest in February and declined during the laying and incubation periods of their mates. Reductions in carcass mass were due largely to changes in stored lipids, but carcass protein also declined. Lipids declined 123 g (79%) from February to late incubation; most of this loss (106 g; 86%) occurred from February to laying. The absolute amount and proportion of stored lipids used by breeding males were similar to that of breeding females (Drobney 1982). Protein declined from January (162 g) to late incubation (139 g) and remained low in late summer. Prebasic molt of males began while their mates were nesting, but timing and intensity of molt varied greatly among males. Molt score of males accompanying laying and incubating females was not correlated with testis mass. Testis mass peaked during laying and remained high through late incubation before declining in late summer.

Key words: *Aix sponsa*; Anatidae; male reproductive effort; molt; nutrient reserves; testis mass; Wood Duck.

INTRODUCTION

Studies of reproductive bioenergetics in waterfowl (Anatidae) have focused in large part on breeding females. Interest in females generally has been in response to evaluating whether clutch size and, hence reproductive performance, is limited by the size of lipid and protein reserves (review in Alisauskas and Ankney 1992). The role of nutrient reserves in limiting clutch size in waterfowl has been a controversial topic (Ankney et al. 1991, Arnold and Rohwer 1991), and one that will not be resolved easily with current methodologies.

Much less attention has been given to investigating the bioenergetics of breeding male waterfowl (Ankney and Afton 1988, Afton and Ankney 1991). However, the reproductive effort of males is significant and of critical importance to the breeding success of their mates (Anderson 1984). In swans and true geese (Anserini), for example, pairs engage in frequent social displays after arriving at breeding areas that reinforce pair bonds, and males aggressively establish breeding

territories and defend mates from conspecifics (Akesson and Raveling 1982, Anderson and Titman 1992). These activities can be energetically costly; male Cackling Geese (*Branta canadensis minima*) deplete almost all lipid reserves before their mates begin incubation (Raveling 1979). Male Anserini also defend nests from predators and conspecifics, and help females care for broods, which improves offspring survival (e.g., Schneider and Lamprecht 1990).

In North American ducks (Anatinae), males do not help females incubate eggs and usually leave their mates before eggs hatch; therefore, brood care by males is rare (McKinney 1986, Afton and Paulus 1992). However, male ducks invest large amounts of time and energy establishing and maintaining new pair bonds each year (Anderson 1984). These pair-bond expenditures are significant, and males in poor physical condition engage in courtship and pair later than males in good physical condition (Wishart 1983, Hepp 1986). Male ducks also play an important role in mate guarding during the breeding season. Mate guarding helps males protect their genetic investment (i.e., inhibits cuckoldry) and provides an undisturbed feeding area for females

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TABLE 1. Range of dates that male Wood Ducks were collected during each stage of the breeding period.

Breeding stage	Collection date
January	29 January–1 February
February	26–27 February
Laying	20 March–16 April
Late laying	1 May and 8 June
Early incubation	11 April–2 June
Late incubation	10 April–13 June
June	6–28 June
July	1–31 July
August	1–30 August

(Anderson and Titman 1992). Efficient foraging is important for breeding females because they produce relatively large clutches of energy-rich eggs. In some species (e.g., Northern Shoveler, *Anas clypeata*; Blue-winged Teal, *A. discors*, and Bufflehead, *Bucephala albeola*), males establish and defend fixed territories (Afton 1979, Stewart and Titman 1980, Gauthier 1987); while in other species (e.g., Green-winged Teal, *Anas crecca carolinensis*, and Canvasback, *Aythya valisineria*), males defend a mobile space around the female (Anderson and Titman 1992). As the breeding season progresses from arrival at breeding areas to establishing nests and laying eggs, breeding males spend more time alert, less time feeding, and more aggressively defend their mates from conspecifics (Dwyer 1975, Afton 1979, Stewart and Titman 1980, Anderson 1984). Hence, males may experience a negative energy balance during the breeding season (Afton and Ankney 1991, but see Ankney and Afton 1988).

Male Wood Ducks (*Aix sponsa*) often remain paired with females throughout incubation and defend a mobile space around their mate, which helps foraging females satisfy the high nutritional demands of reproduction (Bellrose and Holm 1994). Females depend entirely on exogenous sources of protein to satisfy the protein requirements of clutch production (Drobney and Fredrickson 1979; Drobney 1980, 1982). Male reproductive effort, therefore, undoubtedly is important to the breeding success of females; acquisition and use of nutrient reserves by males may help them meet their reproductive commitment. In this paper, we examine nutrient reserve dynamics of male Wood Ducks at a southern breeding site. We also investigate variation in prebasic molt and testis mass in relation to breeding status of males.

STUDY AREA AND METHODS

The study was conducted at Eufaula National Wildlife Refuge (4,520 ha), located on the border of Alabama and Georgia (32°N, 85°W) and centered on Lake W. F. George, an impoundment of the Chattahoochee River. Aquatic habitats make up 3,145 ha of the refuge and include open water, beaver swamps, three managed waterfowl impoundments, and mudflats associated with the river. Approximately 200 nest boxes are available for Wood Ducks in the managed impoundments and beaver swamps.

After-hatching-year (AHY) male Wood Ducks were collected in June–August 1990 ($n = 11$) with bait traps and in January–August 1991 ($n = 51$) with bait traps and shotguns. Early in the breeding season, Wood Ducks are gregarious and can be found in small groups of paired birds (Fredrickson 1990). Most of the January males were collected from small (< 5), mixed-sex groups; one male was collected in a bait trap. February males were collected either from small groups ($n = 2$) or as they accompanied a female ($n = 3$). In March–June 1991, some males were collected while they escorted females to nest boxes and were categorized according to the female's breeding status: laying, early-incubation (\leq day 10), or late-incubation ($>$ day 10). Approximate day of incubation was determined by candling eggs (Hanson 1954). Males not associated with females returning to nest boxes were classified by month of collection. In a two-year study of Wood Ducks at Eufaula NWR, Moorman and Baldassarre (1988) reported that nest initiations peaked during 28 February to 6 March in 1985 and 1986. Peak nesting during this study occurred in the second week of March (D. Hipes, unpubl. data). Collection of our birds on 26–27 February (see Table 1), therefore, coincided with a period when many females were in rapid follicular growth (RFG). We suggest that February is analogous to the RFG period of Drobney's (1982) study of breeding females.

Fresh body mass of males was measured with a Pesola scale (nearest 5 g), and wings and feet were separated from the body to facilitate removal of the skin. An incision was made from the cloaca to the neck along the midventral line; the skin was removed, placed in a plastic bag and frozen until analysis of the molt. Left testes were removed and blotted dry before measuring length, width, and mass (0.01 g). Birds were placed in

double plastic bags, and frozen until analysis of body composition.

Carcass analysis. Mass of thawed birds (hereafter called carcass mass) was determined following removal of contents of the gastro-intestinal tract. We recorded lengths (0.01 mm) of the keel, tarsometatarsus, and bill; wing length also was measured (1.0 mm) from the proximal end of the metacarpal to the end of the longest primary. Flight muscles (pectoralis, supracoracoideus, coracobrachialis), leg muscles (all muscles attached to the femur, tibiotarsus, and fibula), and gizzard (contents emptied) were removed, cleaned of adherent fat, and weighed (0.01 g). The entire carcass, including skin and feathers, was homogenized in a Hobart meat grinder. A sample of the homogenate (approximately 200 g) was removed and dried at 90°C to a constant mass. The dry sample was homogenized further in a coffee grinder, and a subsample (6–9 g) of the dry homogenate was used in proximate analysis of carcass composition. Lipids were extracted from subsamples with petroleum ether in a modified Soxhlet apparatus (Dobush et al. 1985). The proportion of lipid in the dry subsample was used to estimate lipid content of the dry carcass (FAT). Lean dry samples were ashed overnight (>12 hr) at 550°C in a Muffle furnace to determine ash content (ASH). Ash-free lean dry mass was used to estimate total body protein (PROTEIN). Analysis of carcass composition followed methods of Alisauskas and Ankney (1985).

Blood parasites. Certain parasitic hematozoa (e.g., *Haemoproteus nettionis*, *Leucocytozoon simondi*) of Wood Ducks differ in their north-south distribution and may be used as biological tags to distinguish northern birds from individuals originating at more southern latitudes (Thul et al. 1980, Thul and O'Brien 1990). *H. nettionis* is found in Wood Ducks at latitudes $\geq 37^\circ\text{N}$ (from Virginia through Maine and eastern Canada); the southern boundary of *L. simondi* occurs at 42–43°N in upstate New York and northern Massachusetts (Thul et al. 1980). Wood Ducks originating from northern and southern breeding sites certainly were present at Eufaula NWR in January, and possibly in February. We thought it important to identify and exclude any northern males from our January and February samples if possible, because nutrient levels may have varied depending on whether males were resident or migratory. Blood smears were prepared for each male; slides were fixed in 100% methanol,

stained with Giemsa, and scanned at low power (40 \times) for presence of *H. nettionis*, and *L. simondi* (see Thul et al. 1980). No infections were detected; therefore, we assumed all individuals collected in January and February originated from southern latitudes.

Molt. The underside of skins was examined to determine molt intensity. We used a modification of the scoring system of Billard and Humphrey (1972) to help quantify molt intensity. The skin was divided into eight feather regions (neck, breast, belly, leg, side, flank, scapular, and back; Hipes 1993). Each region was examined for developing follicles and scored as follows: 0—no feather replacement, 1—light feather replacement, 2—moderate feather replacement, 3—heavy feather replacement. Scores were summed across feather regions to provide a total molt score for each bird (maximum score = 24). We noted only whether feathers were being replaced, and did not differentiate between the prebasic and prealternate molts. Some birds collected in late summer may have initiated prealternate molt (Bellrose and Holm 1994). Therefore, we limit discussions to timing and intensity of early prebasic molt (i.e., males associated with laying and incubating females).

Statistical analysis. To account for possible variation in carcass composition due to structural size, a principle components analysis (PCA; PROC PRINCOMP, SAS Institute 1989) was completed using the four structural measurements (lengths of keel, tarsometatarsus, bill and wing). The first principal component (PC₁) accounted for 43% of the variation. Eigenvectors for the first principal component ranged from 0.44 to 0.61, indicating positive correlation between the four measurements. This covariation was interpreted as variation in body size, thus PC₁ scores were used as indices of body size. Fresh body mass and body components were regressed on PC₁ values. Fresh body mass, carcass mass, leg mass, gizzard mass, FAT, and ASH were not related ($P > 0.05$) to structural size (PC₁). PC₁ accounted for 7% of the variation ($P = 0.03$) in PROTEIN, and 11% of the variation ($P = 0.01$) in breast mass. Residuals from regressions of PROTEIN and breast mass were used in further analyses to correct for body size. One-way analyses of variance followed by *a posteriori* Tukey-Kramer multiple comparison tests were used to compare differences in body composition, testis mass and molt score by stage of the

TABLE 2. Mean (\pm SE) carcass composition (grams), testis mass, and molt score of male Wood Ducks.

Component	January	February	Laying	Early incubation	Late incubation	June	July	August	$F_{3,34}$ ^a
<i>n</i>	7	5	8	9	7	9	6	11	
Body mass	704.3 \pm 17.0 AB	750.0 \pm 8.4 A	636.9 \pm 16.2 BCD	620.0 \pm 14.5 CD	584.3 \pm 17.5 D	657.8 \pm 13.4 BC	612.5 \pm 14.1 CD	607.7 \pm 15.8 CD	10.0**
Carcass mass	655.6 \pm 16.3 AB	694.4 \pm 10.1 A	584.0 \pm 24.6 BC	556.7 \pm 12.7 C	526.6 \pm 17.2 C	599.7 \pm 12.3 BC	564.1 \pm 17.9 C	538.5 \pm 12.7 C	9.8**
Fat	88.0 \pm 12.9 B	155.4 \pm 6.9 A	49.2 \pm 10.9 BC	37.3 \pm 7.6 C	32.5 \pm 8.8 C	72.0 \pm 10.4 BC	66.6 \pm 17.3 BC	43.2 \pm 7.9 BC	11.2**
Protein	161.6 \pm 2.9 A	156.6 \pm 2.5 AB	151.6 \pm 5.1 ABC	145.8 \pm 3.0 BC	139.1 \pm 3.4 C	145.9 \pm 1.9 BC	139.7 \pm 3.4 C	143.7 \pm 2.2 BC	4.9*
Ash	20.1 \pm 0.6 A	19.7 \pm 0.3 A	19.9 \pm 0.6 A	19.9 \pm 0.6 A	17.8 \pm 0.7 A	19.1 \pm 0.7 A	18.0 \pm 0.8 A	17.3 \pm 0.4 A	3.5*
Breast ^b	75.0 \pm 1.0 A	70.7 \pm 1.4 AB	68.1 \pm 1.8 ABC	64.7 \pm 1.7 BC	60.7 \pm 2.5 BC	65.0 \pm 1.8 BC	61.9 \pm 3.1 BC	59.8 \pm 1.5 C	6.6**
Leg ^b	26.7 \pm 1.1 AB	25.8 \pm 0.9 ABC	27.6 \pm 0.3 A	24.6 \pm 1.0 ABC	21.9 \pm 0.6 C	23.2 \pm 1.1 BC	22.0 \pm 1.1 C	23.7 \pm 0.7 ABC	5.3**
Gizzard	23.3 \pm 0.8 A	20.1 \pm 0.4 A	20.4 \pm 1.3 A	21.1 \pm 1.1 A	20.8 \pm 1.2 A	21.6 \pm 1.2 A	21.5 \pm 2.2 A	24.2 \pm 1.7 A	1.1NS
Left testis	0.13 \pm 0.02 B	0.46 \pm 0.04 B	1.19 \pm 0.20 A	1.08 \pm 0.14 A	1.11 \pm 0.24 A	0.34 \pm 0.14 B	0.04 \pm 0.01 B	0.05 \pm 0.003 B	14.0**
Molt score	0 C	0 C	4.3 \pm 2.8 C	5.9 \pm 2.3 BC	7.3 \pm 3.1 BC	15.0 \pm 1.9 AB	18.0 \pm 1.2 A	19.1 \pm 1.3 A	14.4**

** $P < 0.005$; * $P < 0.0001$. Row means with different letters are significantly different ($P < 0.05$).

^b Breast mass and leg mass represent wet masses and are one-half of the total.

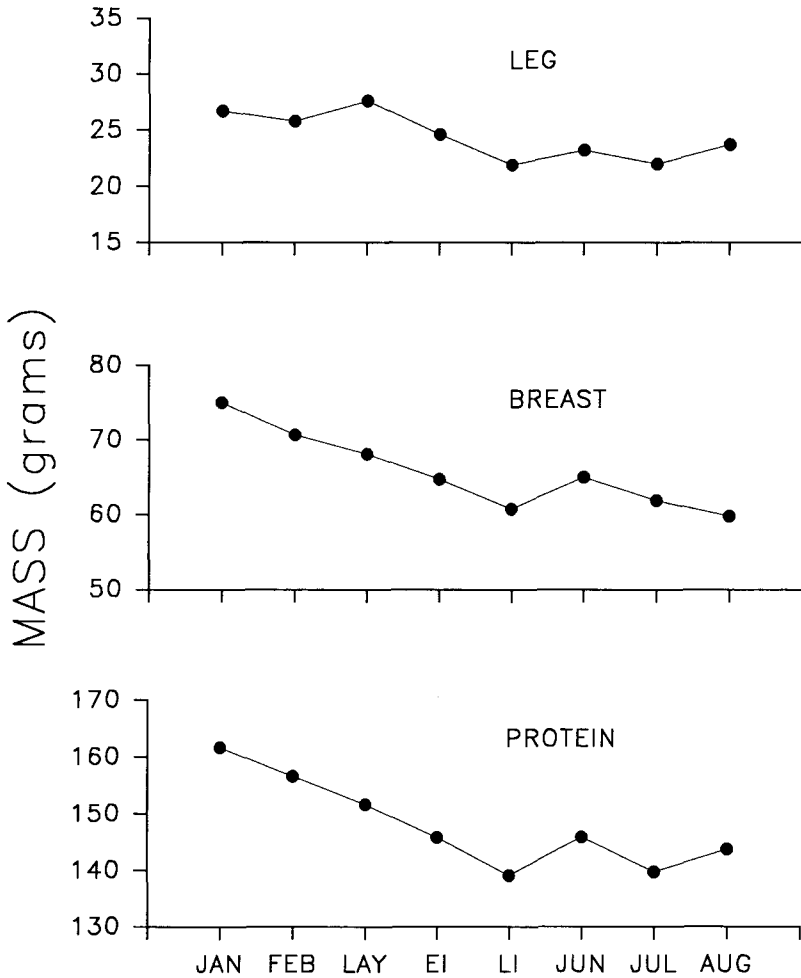


FIGURE 1. Masses of PROTEIN (ash-free lean dry), breast muscle and leg muscle of male Wood Ducks by stage of reproduction. Breast and leg are wet masses that represent half of the total mass. JAN = January; FEB = February; LAY = egg laying; EI = early incubation (\leq day 10); LI = late incubation ($>$ day 10); JUN = June; JUL = July; AUG = August.

breeding period. For unplanned pairwise comparisons with unequal sample sizes, the Tukey-Kramer test is recommended because it controls the experimentwise error rate (type I error) while providing maximum power (Day and Quinn 1989:452).

RESULTS

We collected 62 male Wood Ducks from January–August; range of collection dates for each period is presented in Table 1. Two of eight laying females abandoned nests after their mate was collected; the remaining females finished their clutches. On the day that males were collected,

these six females had completed an average of 62% (range = 33–100%) of the final clutch size.

Two males were collected with laying females on 1 May and 8 June (Table 1). The average initiation date of first nests at the study site in 1985 and 1986 was 10 April and 26 March, respectively (Moorman and Baldassarre 1988), so these females probably were nesting for a second time. Deleting “late-laying” males had no effect on the outcome of statistical analyses of carcass components. Mean values of components were higher when late-laying males were excluded, because they were relatively light. However, results of multiple comparison tests did not change;

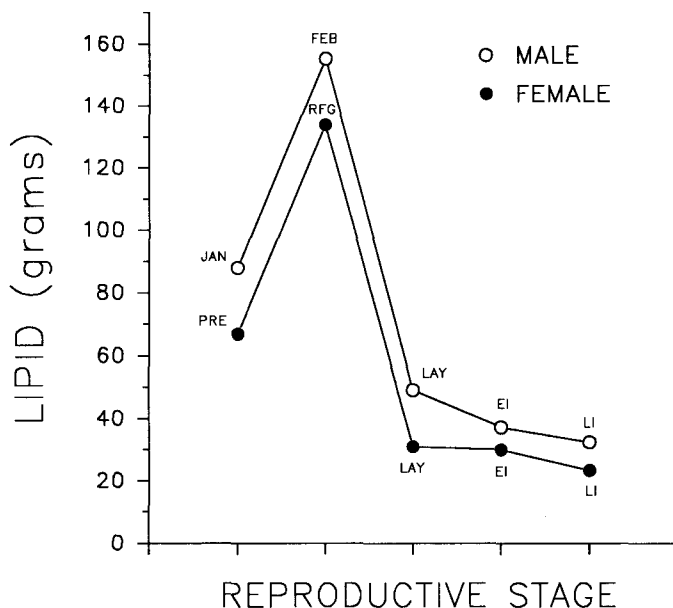


FIGURE 2. Comparison of lipid reserves of male and female Wood Ducks by stage of reproduction. Female data are from Drobney (1982). Female: PRE = prebreeding, largest ovum ≤ 7 mm; RFG = rapid follicular growth, largest ovum > 7 mm; LAY = final stages of laying; EI = early incubation, brood patch present, all follicles ruptured or regressing and ovary ≥ 1 g; LI = late incubation, well-developed brood patch and ovaries < 1 g. Male: JAN = January; FEB = February; LAY = male's mate was laying eggs; EI = early incubation (\leq day 10); LI = late incubation ($>$ day 10).

therefore, we included late-laying males in the overall analyses.

After testing for yearly differences, data were combined across years for June, July and August. Fresh body mass and carcass mass varied with stage of the breeding period (Table 2), peaking in February (750 and 694 g, respectively) and reaching lowest levels during late incubation (584 and 527 g, respectively). From February to late incubation, carcass mass declined approximately 24% (167 g); most (110 g or 67%) of this loss occurred from February to laying (Table 2).

PROTEIN levels were greatest early in the season (Table 2). Changes in breast mass and leg mass paralleled those of PROTEIN (Fig. 1), but gizzard mass remained constant (Table 2). Stage of the breeding period explained a significant amount of variation in ASH, but Tukey's multiple comparison test yielded no period differences (Table 2).

FAT declined an average of 123 g (79%) from peak lipid levels in February to late incubation (Table 2). Most (106 g or 86%) of this loss occurred from February to laying; males regained some lipids in late summer.

Prebasic molt of males was not evident in January and February but began while their mates

were nesting (Table 2). The first molting male was collected on 11 April accompanying an early-incubating female. With the exception of two males that were accompanying late-laying females in May and June, males with laying females were not molting. However, molt proceeded rapidly, and 69% (11 of 16) of males with incubating females had initiated prebasic molt. Intensity of molt during incubation was variable, ranging from no molt ($n = 5$) to light molt (range = 1-4; $n = 5$) and heavy molt (range = 12-19; $n = 7$). Variation in molt intensity was not related ($P > 0.05$) to stage of incubation (Table 2). There was no correlation (Spearman's rho: $r_s = -0.32$; $n = 24$; $P = 0.12$) between molt score and testes mass of males paired with laying and incubating females.

Testis mass was relatively low in January and February, peaked during laying, remained high throughout incubation, and declined in late summer (Table 2).

DISCUSSION

Carcass composition. Use of endogenous nutrients by female anatids during reproduction has been widely discussed (reviewed by Alisauskas and Ankney 1992). Much of the focus has been

TABLE 3. Average decline of lipid reserves of male Anatidae during the breeding season.

Species	Average decline in lipid reserves (%)	Period of lipid decline ^a	P ^b	Reference
<i>Branta bernicla</i>	32	Prelaying-postlaying	*	Ankney 1984
<i>B. canadensis minima</i>	86	Prelaying-postlaying	*	Raveling 1979
<i>Aix sponsa</i>	68	February-laying	*	This study
<i>Anas acuta</i>	46	RFG-laying	*	Mann and Sedinger 1993
<i>A. clypeata</i>	19	Prelaying-laying	ns	Ankney and Afton 1988
<i>Aythya affinis</i>	70	Pre-RFG-RFG	*	Afton and Ankney 1991
<i>A. collaris</i>	47	Arrival-laying	*	Hohman 1986
<i>A. valisineria</i>	15	RFG-laying	ns	Barzen and Serie 1990

^a Reproductive periods are those of the male's mate; terminology is that of authors. Arrival = return to breeding areas, ovary weight of females <3 g; pre-RFG = dry weight of largest ovarian follicle <0.2 g; RFG = rapid follicular growth: ovary masses >3 g and diameter of largest follicle \geq 6 mm or dry weight of largest follicle \geq 0.2 g; prelaying = females with no postovulatory follicles; laying = females in process of laying; postlaying = last egg of clutch had been laid.

^b * $P < 0.05$; ns $P > 0.05$. Significance levels are from tests examining variation in lipid levels between reproductive periods and are from the original reference with the exception of *Aythya collaris*. Here we used a t-test to test the equality of two means with unequal variances (Sokal and Rohlf 1981, pp. 411-412).

on clutch development. For example, female Wood Ducks acquire large lipid reserves before laying and on average lose 77% (103 g) of stored lipids from the period of RFG to the end of laying (Drobney 1982). These endogenous lipids supply about 88% of the energy and nutrient requirements of egg production (Drobney 1980); egg protein is obtained from a diet of protein-rich invertebrates (Drobney and Fredrickson 1979, Drobney 1982).

Our results indicate that male Wood Ducks also rely heavily on lipid reserves to fuel their reproductive effort. The pattern is remarkably similar to that of females (Fig. 2), with the greatest use of stored lipids occurring prior to incubation. This is an important period of time when breeding pairs generally engage in courtship and establish exclusive areas that they defend from predators and conspecifics (McKinney 1986). It also is an important period when female ducks gather nutrients for clutch development. During this time male ducks spend less time feeding and are more vigilant, aggressively guarding mates from conspecifics (Dwyer 1974, 1975; Seymour and Titman 1978; Afton 1979; Stewart and Titman 1980). Male Wood Ducks, for example, spend much less time feeding than their mates (34% vs. 73%); most (44%) time is spent in alert behavior (Drobney and Fredrickson 1979). Behavioral changes by males allow females more time to feed without interruption and also help to guarantee paternity (Anderson and Titman 1992).

Other species of male Anatidae also use lipid reserves during reproduction (Table 3). Male geese rely heavily on nutrient reserves. They ar-

rive at breeding areas before most foods are available and use lipids acquired during migration to fuel reproductive activity (Raveling 1979, Ankney 1984). Male ducks generally have food available to them upon arrival at breeding areas; however, several species (Ring-necked Duck, *Aythya collaris*, Hohman 1986; Lesser Scaup, *A. affinis*, Afton and Ankney 1991; and Northern Pintail, *Anas acuta*, Mann and Sedinger 1993) use stored lipids before females begin incubation. Loss of lipid reserves by male Lesser Scaup coincided with decreased feeding and increased time spent alert and mate guarding (Afton and Ankney 1991). Breeding male Canvasbacks also may rely on lipid reserves, but results are somewhat uncertain because of small sample size (Barzen and Serie 1990).

Breeding male Northern Shovelers do not rely on nutrient reserves during the prelaying and laying periods (Ankney and Afton 1988), despite aggressively defending territories (McKinney 1973). A diet consisting primarily of animal matter (Ankney and Afton 1988) makes the relatively stable lipid reserves of males all the more interesting. Increased time spent feeding by males while laying females are on nests may allow males to maintain stored nutrients (Ankney and Afton 1988).

Male Wood Ducks also experienced reductions in carcass protein. Inclusion of feathers with carcasses confuses interpretation of PROTEIN variation because feathers are mostly protein. Any differences in PROTEIN may be caused partly by changes in feather mass and not by changes in actual protein reserves. However, changes in breast mass, the body's major protein

depot, paralleled variation in PROTEIN (Fig. 1), suggesting that there was a steady loss of protein reserves from January and February to late incubation. The Ring-necked Duck is the only other species of duck in which males have been reported to use protein reserves during the breeding period (prelaying-laying; Hohman 1986).

Male Anatidae obviously play an important role in reproduction, and use nutrient reserves, much like females do, to help meet the time and energy constraints of reproduction. Magnitude of lipid reserves used by breeding males of some species is similar to that expended by their female counterparts. This certainly is true of male Wood Ducks who use some protein reserves as well.

Molt. Prebasic molt of male Wood Ducks in central Illinois begins in late May, and the proportion of males in basic plumage increases linearly through July (Bellrose and Holm 1994). We collected the first molting male in early April. Prebasic molt generally was initiated when males still were paired to breeding females, but timing and intensity of molt were highly variable. Male American Wigeon (*Anas americana*) also begin prebasic molt as their mates initiate incubation (Wishart 1985), and prebasic molt of male Northern Shovelers often begins while they are paired to females (DuBowy 1985).

In some avian species, a decline in testicular activity has been correlated consistently with onset of molt in males (Pitelka 1958, Payne 1972, Wingfield and Farner 1978). However, some male Mallards (*A. platyrhynchos*) have fully functional testes in the early part of prebasic molt (Johnson 1961). We found no relationship between testis mass and molt score in males accompanying laying and incubating females. Our results suggest that onset of prebasic molt in male Wood Ducks is not controlled simply by a decline in gonadal function.

PROTEIN did not change during late summer when intensity of molt was greatest. Similar results have been reported for other waterfowl species (reviewed by Ankney 1984, Heitmeyer 1988), indicating that amino acid requirements for molt are met by diet rather than catabolism of body protein.

Testes. Testis mass of Wood Ducks was low in January and February, peaked during laying, and remained high through late incubation. In other species of ducks, testes decline in incubation. Testis mass of Northern Pintails breeding

in Alaska, for example, is greatest during pre-RFG, RFG, and laying but declines rapidly during incubation (Mann and Sedinger 1993). Testosterone levels and testis mass of Mallards also are greatest when mates are laying eggs but decrease rapidly soon after incubation begins (Donham 1979). Interspecific variation may be related to differences in reproductive behavior. Male Wood Ducks remain with their mate through most of incubation, but Mallard and Northern Pintail males leave females in early incubation (Bellrose 1980). Longer attendance by male Wood Ducks does not increase nest success of their mate (Hipes and Hepp 1993), but may increase their chances of mating with females again in the event of a nest failure, or of a second nesting attempt. The breeding season is lengthy for Wood Ducks at southern latitudes, and renests and second nests are common (Kennamer and Hepp 1987, Moorman and Baldassarre 1988). Increasing the duration of pair bonds while maintaining testes in a functional state makes good sense for a monogamous species with a prolonged breeding period.

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