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BODY WEIGHT AND COMPOSITION CHANGES AND ADAPTATIONS FOR BREEDING IN WOOD DUCKS

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ABSTRACT.—The weight and carcass composition of Wood Ducks (*Aix sponsa*) collected in southeast Missouri were analyzed during fall and at specific stages of the reproductive cycle. Males lost 4% of their body weight between fall and spring. Decreases in the weights of digestive organs were primarily responsible for the change. The body weights of hens increased 14% between fall courtship (618 g) and the maximum attained during laying (706 g). Nearly all of the weight gain of females occurred on the breeding grounds and was the result of fat deposition and increases in the weights of the reproductive organs. Body weights of hens decreased 164 g during laying and incubation. Utilization of stored fat for egg production accounted for most of this weight loss. The lack of significant changes in the ash-free lean dry mass of the carcass as well as a change in food habits indicated that the protein requirements for the clutch are obtained by foraging for invertebrates during laying. Weight losses during incubation were small, indicating that hens are able to meet nearly all incubation energy requirements by foraging during inattentive periods. Female Wood Ducks satisfy their nutrient and energy requirements during the reproductive cycle by foraging and the use of endogenous reserves. Adaptations that maximize the use of stored lipids for egg production and facilitate the conservation of endogenous protein and the acquisition of dietary protein enable hens to produce and incubate large clutches of relatively large eggs without significant changes in body protein.

Studies of weight changes in breeding ducks (Weller 1957, Folk et al. 1966, Harris 1970, Korschgen 1977, Landers et al. 1977) have shown that the body weights of females increase prior to clutch initiation and then decline rapidly during laying and incubation. These weight changes have been attributed primarily to the growth and subsequent involution of the ovary and oviduct and fat deposition and mobilization. Changes in the weights of digestive organs and atrophy or mobilization of muscle tissue have also been implicated, but to a lesser degree.

Although previous investigators have identified the variables that influence changes in body weight, these variables (especially changes in carcass composition) have not been well measured at specific stages throughout the reproductive cycle for ducks. Information of this kind is nevertheless needed to meaningfully interpret weight data collected in the field and to better understand adaptations for breeding and the impact of reproductive efforts on the physiological condition of hens.

The results reported here represent a portion of the data collected during a three-year study of the feeding ecology, nutrition, and reproductive bioenergetics of Wood Ducks (*Aix sponsa*; Drobney 1977). The purpose of this paper is to quantify the variables responsible for changes in body weight during the reproductive cycle and to relate changes in carcass composition to the breeding biology of Wood Ducks.

STUDY AREA AND METHODS

Body and organ weights were obtained from 159 Wood Ducks (84 females and 75 males) collected during 1975–1977 on the Duck Creek Wildlife Management Area in southeastern Missouri. All birds except for six hens that were removed from nest boxes, were obtained by shooting in flooded timber foraging areas during morning (06:00–11:00) and afternoon (15:00–19:00) collection periods. Carcass analyses were performed only on the 1976–1977 sample consisting of 43 females and 38 males.

Following collection, birds were taken to the laboratory, weighed, and dissected. Fat attached to mesenteries and internal organs was removed and weighed, but not included in the carcass composition analyses. These fat deposits are referred to as visceral fat in this paper. Internal organs (contents removed) were weighed to the nearest 0.01 g (wet weight). Birds that were to be analyzed for carcass composition were plucked, sealed in plastic bags, and frozen.

Carcass composition was analyzed using methods described by Rogers and Odum (1964), Ricklefs (1967), and Brisbin (1968). Before processing, birds were removed from the freezer and thawed for approximately 30 min. The head and scaled portion of the legs distal to the tibia were used for other aspects of the study and were therefore removed before grinding. The eviscerated carcass was then ground in a Globe food grinder. Each bird was passed through the grinder at least six times and mixed thoroughly after each grinding.

A random sample of the homogenate, weighing 10% of the eviscerated carcass weight, was removed for analysis (Brisbin 1968). Each sample was first dried to a constant weight in a vacuum oven at 40°C (Rogers and Odum 1964). Water content was determined by subtracting the weight of the dry residue from the wet weight. Lipids were then extracted from the dry residue using a 2:1 mixture of chloroform and methanol. The dry extracted material was subsequently combusted in a muffle furnace at 500°C to determine ash content (Ricklefs 1967). Ash-free lean dry weight (AFLDW) was determined by subtracting the weight of the ash from the weight of the dry extracted material. The AFLDW contains a small amount of carbohydrate but was assumed to provide a reasonably good estimate of the protein content of the carcass. To evaluate this assumption, the carbohydrate content of a subsample of six birds was determined using proximate analysis. All chemical analyses were performed by the University of Missouri Agricultural Experiment Station Chemistry Laboratory using standard laboratory techniques (Horwitz 1975).

Female Wood Ducks were assigned to seven categories (FC—fall courtship, PB—prebreeding, FG—follicle growth, L—laying, TL—terminal laying, EI—early incubation, I—incubation) and males to two categories (R—reproductive, FC—fall courtship) using criteria described by Drobney (1980).

Statistical comparisons were made using a one-way analysis of variance (Sokal and Rohlf 1969). All hypotheses were tested at the 5% level of significance.

RESULTS AND DISCUSSION

BODY AND ORGAN WEIGHTS

Nearly all of the weight gain of Wood Duck hens occurred on the breeding grounds just prior to laying. Hens began the spring breeding period weighing slightly, but not significantly ($P > 0.05$) less than during fall courtship (Fig. 1). Their weight increased markedly during the period of follicle development (612 to 678 g) and reached a maximum during laying (706 g). Weights subsequently declined reaching the lowest point of the reproductive cycle during incubation (542 g). The preceding changes in the body weights of hens were significant

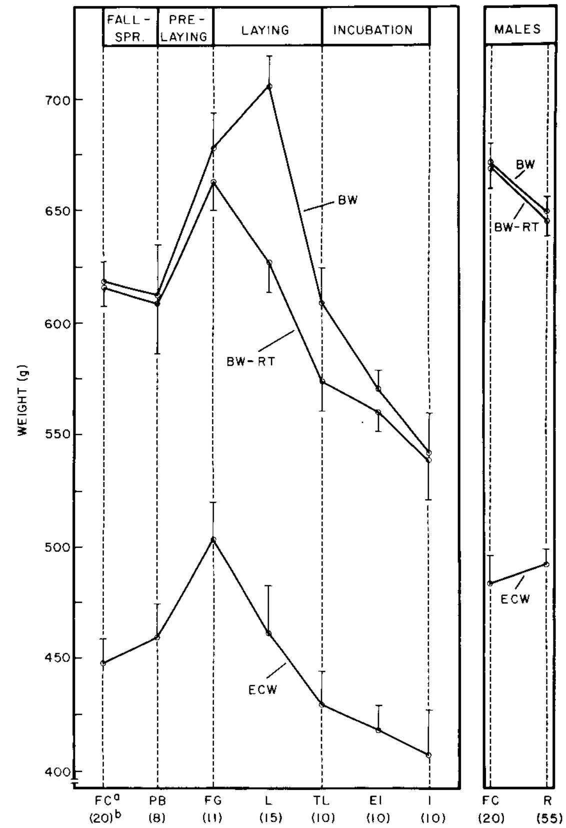

FIGURE 1. Changes in body weight (BW), body weight minus the weight of the reproductive tract (BW − RT) and eviscerated carcass weight (ECW) of males and females during the reproductive cycle. Values are presented as $\bar{x} \pm$ SE. [a]FC = fall courtship; PB = prebreeding; FG = follicle growth (rapid growth phase of ovarian development); L = laying; TL = terminal laying; EI = early incubation; I = incubation; R = reproductive males. [b]Sample size.

($P < 0.01$). The average body weight of males declined significantly ($P < 0.01$) by 23 g between fall and spring.

Comparison of changes in the body weight (BW) and body weight minus the reproductive tract curves (BW − RT) (Fig. 1) shows that a large proportion of the body weight change of hens was attributable to changes in the weight of the ovary and oviduct. With two exceptions, the shape of the BW − RT curve closely approximates that of the eviscerated carcass weight (ECW). The close correspondence between these curves indicates that the net effect of weight changes in the viscera had a relatively minor effect on changes in total body weight. The first exception occurred between fall and spring in both sexes. The BW − RT curve decreased from fall to spring while the ECW increased, indicating that the loss of internal organ weights was greater than the increase in carcass weight. This difference was

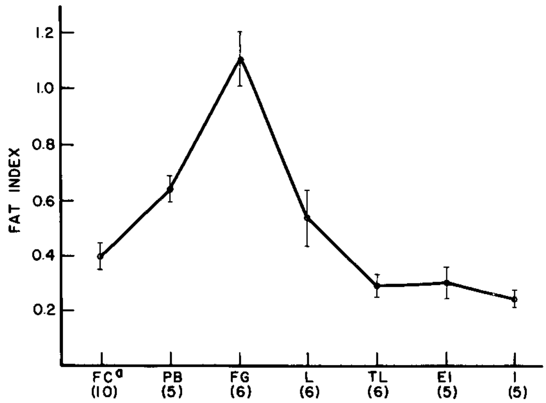

FIGURE 2. Changes in the mean fat index (g fat/g lean dry mass) ± SE of Wood Duck hens during the reproductive cycle. [a]FC = fall courtship; PB = prebreeding; FC = follicle growth (rapid growth phase of ovarian development); L = laying; TL = terminal laying; EI = early incubation; I = incubation.

the result of decreases in gizzard weights from fall to spring (Drobney 1977). The second exception occurred during laying and resulted from increased weights of the liver and lower digestive tract (Drobney 1977).

Although female waterfowl typically attain their heaviest weight prior to laying, the average weight of Wood Duck hens was maximum during laying. The peaks in the BW − RT (Fig. 1) and fat index (Fig. 2) during the follicle growth period show that the higher weight of hens in the laying category was not the result of better condition, but was caused by the increased weight of the reproductive organs. Many of the birds in the laying category had laid fewer than six eggs and therefore still contained fully developed ovaries. In addition, all but three had an egg in the oviduct when collected. Females in the follicle growth category, however, contained ovaries and oviducts in various stages of development and consequently their average weight was lower than that of laying hens. The weights of two females collected just prior to laying averaged 752 g, indicating that maximum weights are in fact reached before the laying cycle commences.

CARCASS COMPOSITION

The most important changes in metabolic reserves are reflected in the ECW curve (Fig. 1). The mean ECW of hens increased 56 g prior to laying and decreased 97 g during laying and incubation. Of the four components measured, significant changes were found only in the lipid and ash content of females.

Lipids. The fat contents of fall (46.2 g) and breeding (46.1 g) males were nearly identical and only slightly higher than in fall females (40.4 g) (Table 1). In the spring, the lipid weights of females exceeded those of males during all periods except at the end of laying and during incubation ($P < 0.05$).

Changes in the eviscerated carcass weight of hens during the reproductive cycle are largely attributable to the deposition and utilization of fat. The fat index increased significantly ($P < 0.001$) before laying, declined during laying ($P < 0.001$), but did not change significantly ($P > 0.05$) between the end of laying and incubation (Fig. 2).

Prebreeding females contained an average of 66.9 g of fat, reflecting a significant ($P < 0.02$) 66% increase in carcass fat deposits from fall to spring. Although visceral fat deposits were not included in the carcass composition analyses, samples from several birds as well as visual estimates indicated that little visceral fat was deposited during either of these periods. Visceral fat from four fall and four prebreeding hens averaged less than 3 g during each of the two periods.

The most intensive period of fat deposition by female Wood Ducks occurs just before laying. Hens that had entered the follicle devel-

TABLE 1. Carcass composition of male and female Wood Ducks during the reproductive cycle.

	AFLDM[a]	Ash	Water	Lipid
Reproductive status (n)	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE
Females				
Fall courtship (10)	88.8 ± 2.5	11.7 ± 0.6	304.2 ± 6.2	40.4 ± 5.2
Prebreeding (5)	91.8 ± 3.0	12.2 ± 0.3	288.1 ± 11.1	66.9 ± 4.8
Follicle growth (6)	84.1 ± 4.8	12.4 ± 0.7	299.6 ± 10.2	107.0 ± 10.3
Laying (6)	89.9 ± 2.8	14.8 ± 1.0	298.9 ± 9.1	57.2 ± 13.9
Terminal laying (6)	89.6 ± 2.7	15.0 ± 0.9	293.1 ± 8.0	30.9 ± 5.2
Early incubation (5)	86.9 ± 2.0	12.4 ± 1.4	289.2 ± 3.2	30.0 ± 8.1
Incubation (5)	85.5 ± 3.1	11.5 ± 0.6	286.8 ± 14.1	23.4 ± 3.8
Males				
Fall courtship (10)	96.6 ± 3.1	13.3 ± 0.7	324.0 ± 9.4	46.2 ± 4.6
Reproductive (28)	99.8 ± 1.8	14.4 ± 0.4	331.0 ± 4.8	46.1 ± 3.6

[a] Ash-free lean dry mass.

opment stage of the reproductive cycle contained an average of 107.0 g of carcass fat and 26.9 g of visceral fat. The 67-g increase in fat between prebreeding and follicle growth represents 50% of the average fat content of hens during follicle growth and more than 70% of the fat accumulated since fall courtship.

Mallard (*Anas platyrhynchos*) hens also accumulate large fat reserves before laying (Krapu 1981), but differ from Wood Ducks in both the timing of fat deposition and the relative magnitude of their fat reserves. In Mallards, most of the lipid reserves are acquired before they arrive on the breeding grounds and little, if any, fat deposition appears to occur during follicle growth. The estimated prelaying fat reserves of Wood Duck hens were nearly twice as large, comprising 20% of the body weight as compared to 11% in Mallards.

Fat deposits were rapidly depleted during laying. Females that had completed a clutch had expended nearly all visceral fat and 71% (76 g) of their carcass fat. Visceral fat deposits were used more rapidly than carcass fat during laying. Comparisons between the number of ruptured follicles and changes in visceral fat indicated that these deposits were depleted (less than 0.5 g remaining) by the time the fifth egg was laid.

The decrease in body lipids between terminal laying and incubating females was small (7.5 g) and not significant ($P > 0.05$). Because the incubating category (I) represents an average of all birds from day six until the end of incubation, this change does not reflect the total decrease in body lipids. Three hens that were known to be at the end of incubation (determined from nest box records of banded birds) contained an average of 14.0 g of fat. On the basis of the average remaining lipid reserves of these three birds, hens would expend approximately 16.9 g of fat during incubation. This weight change, distributed over a 30-day incubation period would represent an expenditure of only 0.56 g of fat per day. In comparison to the utilization of nearly 300 g of fat by incubating Common Eiders (*Somateria mollissima dresseri*; Korschgen 1977), the amount expended by Wood Ducks is relatively low.

Ash. The ash content of the carcasses of males did not change significantly ($P > 0.05$) between fall courtship and breeding (Table 1). The 21% increase in the ash content of hens from prebreeding to laying ($P < 0.04$) and the significant decline after laying ($P < 0.006$) probably reflect changes in medullary bone. Medullary bone serves as a storage area for calcium and functions to supplement dietary calcium during periods of egg formation (Sturkie 1976). The lack of significant changes ($P > 0.05$) in ash between laying and terminal laying females indicates that dietary sources of minerals are sufficient to satisfy most requirements for egg shell formation.

Ash-free lean dry mass and water. The mean water and ash-free lean dry mass (AFLDM) content of females declined slightly from laying through incubation (Table 1); however, statistical analyses indicated no significant changes ($P > 0.05$) in these components. The AFLDM was least variable, differing by only 7.7 g between the highest and lowest means recorded.

In birds, the AFLDM is assumed to be mostly protein (Ricklefs 1974), but probably also contains a small amount of carbohydrate. To assess the extent to which carbohydrates might bias AFLDM as an estimator of carcass protein, proximate analyses were conducted on a subsample of six birds. The results of these analyses showed that carbohydrates comprised a rather small percentage ($\bar{x} = 1.2\%$ range 0.4–1.8%) of the eviscerated carcass weight; therefore, AFLDM should provide a reasonably good estimate of carcass protein. On the basis of these results, the lack of significant changes in the AFLDM of hens throughout the reproductive cycle indicates that Wood Duck hens use little carcass protein to produce and incubate their eggs. Similar findings have been reported for Mallards (Krapu 1981).

Although the mean water and AFLDM content of breeding males were greater than fall males by 6.2 g and 1.1 g respectively, these differences were not significant ($P > 0.05$). Of all weights and measurements taken, males consistently exceeded females only in the total AFLDM and water content of the carcass. The higher weights of these components in males is most likely the result of sexual dimorphism in body size. However, on the basis of total body weight, this dimorphism is obscured during some stages of the reproductive cycle because of the weight of fat and reproductive organs in hens.

ADAPTATIONS FOR BREEDING

Wood Ducks and many other waterfowl rely on dynamic wetland ecosystems that vary in abundance and quality from year to year for reproduction. Because of periodic fluctuations in the suitability of wetlands for breeding, it would be advantageous for these species to be able to produce large clutches so that high productivity can be achieved during years when conditions are favorable.

For waterfowl, the production of large clutches and precocial young is energetically expensive and concentrates reproductive requirements during laying and incubation (King 1973, Ricklefs 1974). Current evidence indicates that waterfowl meet reproductive requirements in different ways and two general patterns are evident. Common Eiders (Korschgen 1977) and Arctic-nesting geese (Ryder 1970, MacInnes et al. 1974, Ankney 1977, Raveling 1979) feed little during laying and incubation and therefore rely almost exclusively on endogenous sources of nutrients and energy to produce and incubate their eggs. Wood Ducks (Drobney 1980) and Mallards (Krapu 1981) by contrast, meet their reproductive requirements by foraging and by using endogenous metabolic reserves. Hens of both Mallards (Krapu 1981) and Wood Ducks store large quantities of fat before laying and subsequently expend a large proportion of their fat reserves during laying. My earlier evaluation of the bioenergetics of reproduction in Wood Ducks (Drobney 1980) showed that the lipids expended by hens during reproduction were sufficient to meet nearly all lipid and energy requirements for a 12-egg clutch at a production efficiency of 77%. Therefore, the principal remaining requirement for the clutch (other than minerals) would be a source of protein.

Studies of other species of birds (Jones and Ward 1976, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979), indicate that some labile protein can be obtained from the gizzard and/or body musculature to meet protein requirements for eggs. In Wood Ducks, the average combined weights of the gizzard and intestine decreased by only 1.2 g between follicle growth and the end of laying (Drobney 1977). During this same period, the AFLDM (assumed to be mostly protein) actually increased by 5.5 g, however, the difference was not significant ($P > 0.05$). On the basis of the preceding evidence, I must conclude that Wood Ducks satisfy protein requirements primarily by foraging rather than from endogenous sources. The shift to a diet predominated by invertebrates during laying (Drobney and Fredrickson 1979) further supports this conclusion.

Nest attentiveness almost certainly reduces the time available for foraging during incubation. This contention is supported by a decrease in the weight of digestive organs during incubation that apparently results from reduced food intake (Drobney 1977). However, the small and nonsignificant decreases in the average fat and AFLDM content of the carcasses of incubating females indicate that hens are able to spend enough time feeding to satisfy nearly all nutritional requirements during the 28–30 days of incubation. The resumption of a diet predominated by readily available, energy-rich plant foods during incubation (Drobney 1980) probably assists hens to meet their nutritional needs despite reduced foraging time.

Adaptations that: 1) conserve endogenous protein; 2) facilitate the intake of dietary protein; and 3) maximize the use of stored lipids for egg production, enable Wood Ducks to achieve high productivity and minimize stress associated with reproductive effort. The ability to satisfy requirements for incubation energy by foraging allows hens to expend stored fat reserves for egg production rather than as an energy source during incubation. Use of stored fat during laying in turn enables hens to concentrate foraging efforts on invertebrate foods to obtain enough protein for egg synthesis and thereby conserves endogenous protein.

A review of the results of several nesting studies (Bellrose 1976:189) shows that Wood Ducks commonly renest once and, at times, twice. More remarkably, however, some Wood Duck hens produce and rear two broods in a single season and are the only North American waterfowl species known to do so. Studies in southeastern Missouri (Hansen 1971) and Arkansas (Brown 1972) show a higher incidence of second broods than in Massachusetts (Grice and Rogers 1965), suggesting that this phenomenon is related to the length of the nesting season.

I think that the propensity of Wood Duck hens to renest and their ability to produce second broods might also be in part related to the kinds and amounts of endogenous materials expended in the production of earlier clutches. The degree to which endogenous reserves are depleted would influence the amount of time required to regain prelaying condition. Therefore, the renesting interval would be affected by the type and quantity of endogenous reserves expended as well as the sources and availability of substrates needed for their replacement.

Body protein would seem to be more time-consuming to replace than fat because of the requirement for a dietary source of essential amino acids. Chemical analyses of the major foods consumed by Wood Ducks (Drobney 1977) showed that plant foods are low in protein and deficient in many essential amino acids. Animal foods contain a higher percentage of protein and a better balance of essential amino acids, but owing to their small size and high water content, large numbers of invertebrates are needed. Because Wood Ducks do not seriously deplete endogenous protein during laying and incubation, the major requirement for regaining prebreeding condition is to replenish fat reserves.

Lipids can by synthesized from a number of different substrates (protein, carbohydrates, and fat). Windrowed plant seeds provide particularly good sources of lipid substrates (Drobney 1977) that are easily obtained and readily consumed by Wood Ducks (Drobney and Fredrickson 1979). Furthermore, the rapid increases in the fat content of hens before laying indicate that lipids can be replenished in a relatively brief period.

Additional research is needed to determine specific relationships between the rate of replenishment of endogenous reserves, size of clutches in renests, and renesting intervals.

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