EFFECT OF DIET ON VISCERAL MORPHOLOGY OF BREEDING WOOD DUCKS[1]

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ABSTRACT.—Changes in Wood Duck (*Aix sponsa*) digestive organs reflect adaptations to accommodate changes in diet quality, metabolism, and food intake. The size of the gizzard, intestine, ceca, and liver of males decreased between fall and spring and correlated with a reduction in the fiber content of the diet. The mean size of the intestine, liver, and ceca of hens increased in response to high dietary fiber in fall and hyperphagia during laying. Decreases in the size of digestive organs in hens were associated with reduced feeding during incubation and decreased dietary fiber between fall courtship and prebreeding. *Received 1 April 1983, accepted 8 July 1983.*

CHANGES in the intestinal morphology of gallinaceous birds have been studied extensively (Leopold 1953, Breitenbach and Meyer 1959, Breitenbach et al. 1963, Anderson 1972, Moss 1972, Pendergast and Boag 1973), but these changes in waterfowl have received less attention. Data that are available for waterfowl indicate that changes in the size of digestive organs can be induced by diet changes in penned birds (Miller 1975) and also occur under free-living conditions in both breeding (Korschgen 1976, Ankney 1977) and wintering (Paulus 1982) birds.

The size of digestive organs in American Eiders (*Somateria mollissima dresseri*) (Korschgen 1976) and Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney 1977) declines substantially during laying and incubation. Both species reduce feeding activity during these stages of the reproductive cycle, and, therefore, decreases in the size of their digestive organs have been attributed to reduced food intake and/or to the mobilization of protein for reproduction.

In contrast, Wood Duck (*Aix sponsa*) hens feed throughout laying and incubation and exhibit marked changes in diet during the reproductive cycle (Drobney and Fredrickson 1979). Therefore, an evaluation of the dynamics of gut morphology in this species provides an opportunity to assess the significance of the changes observed in the size of the digestive organs of Wood Ducks in relation to food habits, diet quality, and reproductive state.

METHODS

Organ weights and measurements were obtained from Wood Ducks collected on the Duck Creek Wildlife Management Area in southeastern Missouri during a feeding ecology study (Drobney 1977). A total of 159 birds (84 females and 75 males) was collected during 1975–1977, but measurements of all organs were not taken from all birds during the first year of the study; therefore, sample sizes differ between organs.

Weight and measurement data were recorded in the laboratory within 6 h following collection. After digestive-tract contents, adhering mesenteries, and fat were removed, organs were towel-dried and weighed. The intestine included all portions of the digestive tract posterior to the gizzard and anterior to the cloaca. The esophagus consisted of the upper digestive tract anterior to the gizzard. Cecal length was measured as the combined length of both ceca.

Data were analyzed by reproductive state rather than date of collection, because hens were not synchronous in the timing of events in the reproductive cycle, and because changes in food habits were influenced by reproductive state. For analysis, female

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TABLE 1. Mean weights (g) and measurements (cm) of Wood Duck digestive organs during the reproductive cycle.

	Females[a]							Males[a]	
	FC	PB	FG	L	TL	EI	I	FC	B
Esophagus (g)	6.5	7.5	7.2	7.3	7.2	7.4	6.7	6.5	6.8
SE[b]	±0.4	±0.6	±0.5	±0.4	±0.3	±0.2	±0.4	±0.2	±0.2
n[c]	(10)	(5)	(6)	(6)	(6)	(5)	(5)	(20)	(43)
Gizzard (g)	32.2	23.4	21.4	19.5	17.7	19.3	17.7	35.3	20.8
SE	±0.8	±1.5	±1.1	±0.9	±0.8	±1.2	±0.6	±1.5	±0.7
n	(20)	(8)	(11)	(15)	(10)	(10)	(10)	(20)	(55)
Intestine (g)	21.0	14.6	15.9	21.5	18.4	17.6	14.3	18.4	13.8
SE	±1.9	±1.8	±1.3	±1.1	±1.0	±1.7	±1.5	±0.8	±0.5
n	(10)	(5)	(6)	(6)	(6)	(5)	(5)	(10)	(28)
Ceca (cm)	199	182	178	233	181	194	183	207	186
SE	±4.0	±9.0	±8.0	±8.0	±7.0	±8.0	±7.0	±6.0	±4.0
n	(20)	(7)	(8)	(13)	(9)	(10)	(10)	(20)	(50)
Liver (g)	11.6	10.4	14.7	22.2	16.2	15.2	12.9	12.4	10.8
SE	±0.5	±0.7	±1.2	±0.4	±1.1	±1.7	±0.7	±0.7	±0.3
n	(10)	(5)	(6)	(6)	(6)	(5)	(5)	(10)	(28)

[a] FC = fall courtship, PB = prebreeding, FG = follicle growth, L = laying, TL = terminal laying, EI = early incubation, I = incubation, B = breeding males.
[b] SE = standard error.
[c] *n* = sample size.

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 (B—breeding, FC—fall courtship) by means of criteria described by Drobney (1980). Statistical analyses were made using Mann-Whitney *U*-tests (Siegel 1956). All hypotheses were tested at the 5% level of significance.

RESULTS AND DISCUSSION

Liver weights.—Average liver weights of hens increased more than 50% between prebreeding and laying (Table 1). The weight of the liver declined following laying, reaching 12.9 g in incubating females. Both of these weight changes were significant (Table 2).

Liver weights of females exceeded those of males during all periods except fall courtship and prebreeding. Liver weights of males during fall courtship were slightly (2.5 g) but significantly heavier than those of breeding males.

Previous studies of Ring-necked Pheasants (*Phasianus colchicus*) (Breitenbach and Meyer 1959, Anderson 1972), Spruce Grouse (*Dendragapus canadensis*) (Pendergast and Boag 1973), American Eiders (Korschgen 1976), and Snow Geese (Ankney 1977) have shown that the liver weights of females increase just before or during laying, following a pattern similar to that of Wood Ducks.

Liver-weight changes are induced by several variables. Because of the central role of the liver in intermediary metabolism, the weight of the liver changes in relation to the level of food intake and metabolism (Ankney 1977). Estrogen also influences liver weight by promoting fat and protein accumulation (Common et al. 1948: 265).

Weight fluctuations of Wood Duck livers corresponded to changes in food intake, metabolism, and estrogen levels. Time-budget analysis showed that breeding Wood Duck hens spent more than twice as much time feeding as males (Drobney and Fredrickson 1979). Liver-weight increases were also associated with periods of intense fat deposition during follicle growth and fat utilization during laying (Drobney 1980, 1982) and occurred during the time of increased estrogen secretion.

Intestine weights.—With the exception of the fall courtship period, the pattern of weight changes in the intestines of hens resembled that of the liver (Table 1). Mean intestine weights peaked during fall courtship (21 g) and laying (21.5 g) and were lowest in prebreeding (14.6 g) and incubating females (14.3 g). Significant decreases occurred from fall (FC) to spring (PB)

TABLE 2. Results of statistical analyses of weights and measurements at selected stages during the reproductive cycle of Wood Ducks. Mann-Whitney *U*-tests were used in the analysis.

	Females[a]					Males[a]
Component	FC vs. PB	PB vs. L	FG vs. TL	TL vs. I	L vs. I	FC vs. B
Esophagus weight	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
Gizzard weight	$P < 0.001$	$P < 0.025$	$P < 0.01$	$P > 0.05$	$P > 0.05$	$P < 0.001$
Intestine weight	$P < 0.025$	$P < 0.007$	$P > 0.05$	$P < 0.04$	$P < 0.009$	$P < 0.001$
Liver weight	$P < 0.05$	$P < 0.002$	$P > 0.05$	$P < 0.034$	$P < 0.002$	$P < 0.02$
Ceca length	$P < 0.05$	$P < 0.001$	$P > 0.05$	$P > 0.05$	$P < 0.001$	$P < 0.001$

[a] See Table 1 for definition of symbols.

and during incubation (Table 2). Intestine weights of fall males (18.4 g) were significantly greater than those of breeding males (13.8 g).

Previous studies have shown that the size of the intestine is influenced by changes in the amount of feeding (Ankney 1977) and the fiber content of the diet (Miller 1975). The net effect in either case results from the amount of food presented to the intestine for digestion. In geese, reduced feeding during laying and incubation caused a decrease in organ size, but when feeding resumed, gut size increased (Ankney 1977). Reduced digestibility of food, resulting from high fiber diets, necessitates a compensatory increase in food consumption and digestive-organ size in order to use the food efficiently (Miller 1975: 172).

Changes in the intestine weight of Wood Ducks were associated with changes in food intake and diet quality. The decreased weight of the intestine between fall (FC) and spring (B-males, PB-females) in both sexes corresponded with a change from hard-seeded, high-fiber plant foods during fall to soft, low-fiber plant foods in the spring (Drobney and Fredrickson 1979). The seeds of watershield (*Brasenia schreberi*), smartweed (*Polygonum hydropiperoides*), and oaks (*Quercus* spp.) predominated in the fall diet, comprising 89% of the plant foods consumed by males and 84% consumed by females. More than half the plant foods consumed by both sexes during spring consisted of elm (*Ulmus* spp.) and maple (*Acer* spp.) seeds. Proximate analysis showed that the average fiber content of the major fall plant foods (31%) was more than twice as high as that of plant foods consumed in the spring (15%) (Drobney 1977).

The increased intestine weight of hens between prebreeding and laying occurred when the fiber content of the diet was lowest and therefore was not due to decreased diet quality. Invertebrates, which have a low fiber content (Landers et al. 1977), comprised 82% of the diet of laying hens (Fig. 1). Increased food intake stimulated by estrogen (Moore and Breitenbach 1966) is the best explanation for the peak intestine weight attained during laying. The facts that the fiber content of the diet of both sexes decreased during spring and that the increase in intestine weight was found only in hens support this hypothesis.

The decreased intestine weight during incubation probably resulted from reduced feeding activity. Although direct evidence of the amount of food consumed by incubating females is not available, nest attentiveness during incubation reduces the amount of time available for feeding and would thereby be likely to reduce food intake.

Ceca lengths.—Cecum length of hens was greatest during fall courtship and laying (Table 1). The timing of these changes resembled that of changes in the liver and intestine. The small decrease in length between the prebreeding and follicle growth periods was not significant ($P > 0.05$). Similarly, the increase in length during early incubation was not significantly different ($P > 0.05$) from the lengths during the periods preceding (terminal laying) or following (incubation) early incubation. Length did decrease significantly in both sexes from fall to spring (Table 2). The most dramatic change in cecal length was in laying hens, in which the ceca were 28% longer than those in prebreeding or incubating females and differed significantly from them.

The decreased length between fall and spring could be due to the lower fiber in spring diets. Interspecific differences in cecal length of gallinaceous birds have been attributed to differences in dietary fiber (Leopold 1953). Intraspe-

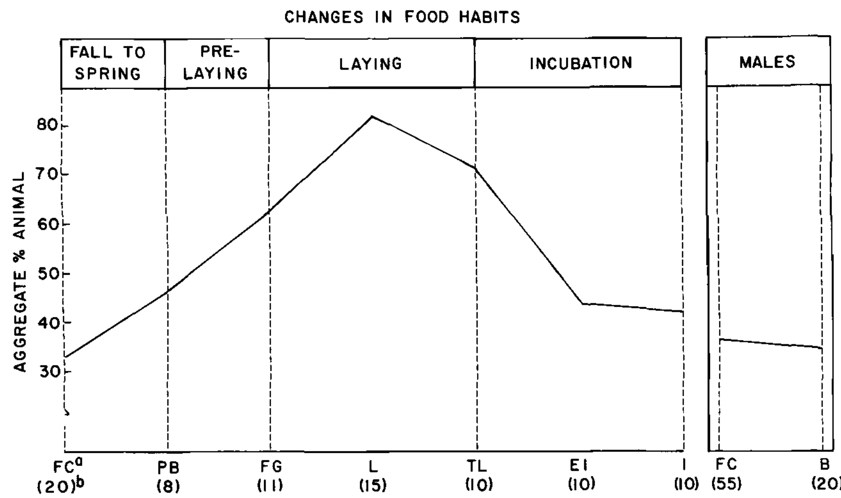

Fig. 1. Proportion of animal foods in the diets of males and females during the reproductive cycle. [a] See Table 1 for definition of symbols. [b] Sample size.

cific changes in cecal length have been induced in captive Mallards (*Anas platyrhynchos*) by dietary changes (Miller 1975) and have been associated with seasonal changes in the fiber content of the diet of gallinaceous birds in the wild (Pendergast and Boag 1973). Ceca lengths of birds on high-fiber diets generally increase to a greater extent than the small and large intestine. Therefore, it has been suggested that the ceca are more sensitive to dietary fiber and have a more specialized function in the digestion of poor foods than other organs (Moss 1972, Miller 1974: 63).

The significance of changes in cecal length is difficult to interpret because the function of the cecum in waterfowl is poorly understood. Possible functions in waterfowl include absorption of water and the soluble products of digestion, vitamin B_{12} synthesis, antigenic stimulation (Mattocks 1971), and the production and absorption of volatile fatty acids (Miller 1976). If the digestion of cellulose occurs at all, it is probably not the main function of the ceca in waterfowl (Mattocks 1971, Miller 1974).

Previous workers have been concerned primarily with the effects of dietary fiber on cecal length. Generally, they have concluded that high-fiber diets stimulate increased food consumption and cause an increase in the size of digestive organs (including the ceca) to accommodate and more effectively utilize these diets.

Diet quality, however, is apparently not the only factor influencing cecal length. On the basis of fiber content, the diets of laying Wood Ducks were of higher quality during laying than at any other time, and yet cecal lengths reached their maximum during this period. A similar pattern of changes in cecal length was noted for female pheasants (Anderson 1972); changes in the diet associated with the length change were not recorded, however.

Hormonally induced, seasonal hyperphagia seems to provide a more plausible explanation for the increased length during laying. Data from Wood Ducks suggest that the quantity of food ingested influences cecal length as much or more than food quality. Food quality would therefore affect cecum length indirectly through its influence on consumption. The lack of evidence for a functional relationship between the digestion of cellulose and the cecum in waterfowl supports this hypothesis, but further research is needed on cecal physiology.

Gizzard weights.—With the exception of the gizzard, organs associated with the utilization and processing of foods (liver, lower digestive tract, and ceca) reached their maximum size in laying females. Gizzard weights were greatest in the fall (32.2 g) and declined 45% through the laying period (17.7 g) (Table 1). Significant weight changes occurred from fall to spring and during laying (Table 2). Throughout incubation, gizzard weights remained nearly constant. Weight changes in the gizzards of males followed a similar trend. Maximum weights were attained in the fall (35.3 g) and declined significantly in breeding males (20.8 g).

Decreases in gizzard weight similar to those found in Wood Ducks have been reported for American Eiders (Korschgen 1976) and Lesser Snow Geese (Ankney 1977). Several hypotheses have been advanced to account for these changes. In Snow Geese, the food intake has been implicated. Gizzards of Snow Geese were largest when they arrived on the breeding grounds but declined during laying and incubation when little feeding occurred. Resumption of feeding in "failed-nesters" and "post-hatch" females resulted in an increase in gizzard weight, indicating that gizzard weight and feeding were correlated (Ankney 1977: 279). Increased availability of soft foods, such as insects, earthworms, and rain-softened seeds, were thought to be in part responsible for the decrease in gizzard weights of pheasants (Anderson 1972: 481). Eiders rarely feed during laying and incubation. Rapid decreases in gizzard weight during egg production were therefore interpreted as utilization of tissue protein rather than atrophy due to disuse (Korschgen 1976: 41).

In Wood Ducks, the change in gizzard weight reflected a dietary change. High-fiber plant foods with tough seed coats requiring considerable muscular activity by the gizzards for processing predominated the fall diets of males and females. Spring diets, by contrast, consisted primarily of invertebrates or soft, low-fiber seeds.

The preceding evidence indicates that the decrease in gizzard weight of Wood Ducks was the result of a dietary shift to soft, low-fiber foods during spring. This hypothesis is consistent with the results of a pen study of Mallards that showed a positive relationship between the fiber content of the diet and gizzard weight (Miller 1975).

Esophagus weights.—Only minor and nonsignificant changes ($P > 0.05$) in the weight of the esophagus occurred among the various stages of the reproductive cycle (Tables 1 and 2). The weight of this organ was similar between sexes during both spring and fall. The esophagus apparently accommodates changes in food intake primarily by distension and contraction rather than by changes in the amount of tissue. Because the esophagus functions principally as an organ of transport and storage, few changes would be expected.

Conclusions

The results of this and other studies indicate that changes in digestive organs are influenced by a number of variables and that the significance of these changes must be evaluated in relation to the biology of the species investigated.

Changes observed in Wood Ducks were primarily related to the quality and/or quantity of food ingested, although not all organs responded in the same way at a given stage in the reproductive cycle. For example, gizzard weight in both sexes was greatest in the fall, when high-fiber foods predominated in the diet. As the fiber content of the diet decreased during spring, gizzard weights also decreased, indicating that changes in this organ were related to dietary fiber. Changes in the lower digestive tract and cecum, on the other hand, were influenced by the quantity of food ingested. The size of these organs peaked during the fall courtship and laying periods in hens, whereas in males they were largest in the fall and decreased in size during spring. Increased food consumption necessitated by reduced digestibility of high-fiber foods presumably resulted in the greater size of these organs during the fall. Enlargement of the intestine and ceca of hens during laying was apparently caused by hyperphagia. The fact that the diet quality of both sexes increased during spring and that the size of these organs increased only in females lends support to this hypothesis.

Although future research under controlled conditions should be designed to determine the specific relationships between foods and digestive organ size, information concerning changes that occur under free-living conditions is needed so that laboratory experiments can be properly designed and meaningfully interpreted. To be of value to laboratory researchers, data on food habits, chemical composition of foods, feeding behavior, and stage in the annual cycle should be gathered concurrently with organ measurements of birds collected in the field.

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