Effects of dietary fiber and diet diversity on digestive organs of captive Mallards (*Anas platyrhynchos*)

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We studied the effects of dietary fiber, of plant versus animal diets, and of diet diversity on the digestive organ morphology of captive Mallards (*Anas platyrhynchos*). Four experimental diets were used: whole corn (low fiber, plant), trout chow (low fiber, primarily animal), rabbit chow (high fiber, plant), and a diverse diet consisting of each of the preceding diets fed daily in random order. Every 5 days for 25 days, we sampled birds from each diet group ($N = 6-8$) and weighed each bird and its abdominal fat, gizzard, ceca, small intestine, and liver, and then measured its ceca and small intestine length. Other than differences explained by their different body sizes, the sex of the birds had no effect on gut measurements. Changes in body weight and abdominal fat weight suggested that Mallards existed equally well on each of the four diets, presumably because changes in their digestive organs allowed them to have similar digestive efficiencies when eating different diets. Birds on the high fiber diet had the largest digestive organs, but birds on all diets showed changes in digestive organs. The diverse diet produced effects on digestive organ morphology similar to those of the two low-fibre diets. Except for a larger gizzard for macerating corn in birds on that diet, there was no difference in the digestive organs between birds eating animal foods and those eating low fiber plant foods. The maximum weight of gizzard, intestine, and ceca of birds on the high fiber diet was reached in 10 days. However, ceca and intestine lengths of these birds were still increasing after 25 days. This observation suggests that birds can continue to respond to a change in diet after limits to the mass of their digestive organs have been reached.

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Nous avons étudié les effets des fibres dans le régime alimentaire, des régimes végétariens et des régimes carnivores, de même que les effets d'un régime alimentaire varié sur la morphologie des organes de digestion chez le Canard malard (*Anas platyrhynchos*). Quatre régimes expérimentaux ont été éprouvés : maïs entier (teneur faible en fibres, régime végétarien), moulée à truite (teneur faible en fibres, régime surtout carnivore), moulée à lapins (teneur élevée en fibres, régime végétarien), régime varié constitué de chacun des régimes précédents donné chaque jour selon une séquence aléatoire. Des oiseaux de chaque groupe ($N = 6-8$) ont été échantillonnés tous les 5 jours pendant 25 jours; ces oiseaux ont été pesés et certaines mesures ont été effectuées : masse des graisses abdominales, du gésier, du foie, masse et longueur des caecums et du petit intestin. À part les différences associées aux différences de taille, les mesures du tube digestif ne sont pas influencées par le sexe des oiseaux. Les variations de la masse corporelle et de la masse des graisses abdominales indiquent que les canards se portent tout aussi bien à un régime qu'à un autre, probablement parce que les ajustements de leurs organes digestifs leur confèrent une efficacité digestive constante, quel que soit le régime. Les oiseaux soumis à un régime riche en fibres avaient les organes digestifs les plus gros, mais il s'est produit des changements dans les organes digestifs chez tous les oiseaux, quel qu'ait été le régime. Le régime varié a produit sur la morphologie des organes digestifs des effets semblables à ceux qu'ont entraîné les deux régimes à teneur faible en fibres. Les oiseaux nourris de maïs avaient le gésier plus gros, mais à part cette différence, les organes digestifs étaient semblables chez les oiseaux soumis à un régime carnivore et chez les oiseaux soumis à un régime végétarien à faible teneur en fibres. Chez les oiseaux soumis à la diète à haute teneur en fibres, le gésier, l'intestin et les caecums parvenaient à leur masse maximale en 10 jours. Cependant, la longueur de l'intestin et des caecums continuait encore d'augmenter après 25 jours chez ces oiseaux. Cela signifie sans doute que les oiseaux peuvent continuer à s'ajuster à un changement de régime, même après qu'aient été atteintes les limites de masse des organes digestifs.

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Introduction

Food habits, diet quality, quantity of food, and reproductive state are factors that influence size of digestive organs in birds, and changes in one or more of these factors can cause changes in the morphology of the digestive tract (size of gizzard, small intestine, and (or) ceca) (Leopold 1953; Breitenbach *et al.* 1963; Davis 1964; Moss 1972, 1974, 1983; Pendergast and Boag 1973; Miller 1975; Savory and Gentle 1976; Ankney 1977; Paulus 1982; Drobney 1984; Thomas 1984; Kehoe and Ankney 1985).

Experimental studies comparing effects of high and low fiber diets on gut morphology have shown that longer guts and larger gizzards enable birds that eat high fiber diets to increase their digestive efficiency (Miller 1975; Savory and Gentle 1976). Sturkie (1976) stated that herbivorous (relatively high fiber diet) and omnivorous (diverse diet) birds usually have longer small intestines than do carnivorous (low fiber and diversity) birds. Kehoe and Ankney (1985) found that among five species of diving ducks (*Aythya* spp.), omnivorous species had relatively longer guts than did herbivorous species and they suggested that dietary diversity may have a greater influence on gut length than does amount of dietary fiber. Drobney (1984) found that intestine length of female Wood Ducks (*Aix sponsa*) increased between prebreeding and laying, when their diet was lowest in fiber, with invertebrates comprising 82% of the diet; intestine length of males did not change. Drobney suggested that increased intestine length of females was caused

by increased food intake. Although fiber content of diets of both sexes decreased during breeding (Drobney 1984), only females showed a marked increase in diet diversity (Drobney and Fredrickson 1979). Davis (1964) found that gut length of both sexes of Rufous-sided Towhees (*Pipilo erythrophthalmus*) decreased from winter to summer as their diet changed from plant to animal material, but no data were presented about dietary diversity for the birds. Thus, the relative effects of the proportion of animal matter in the diet, of dietary fiber, and of diet diversity on gut morphology remain poorly understood.

Miller (1975) outlined a need to assess limits of gut adaptation, time required to achieve maximum adaptation, specific circumstances that require morphological and functional changes in the gut, and the specific physiological and physical mechanisms involved in such changes. Savory and Gentle (1976) experimented with Japanese Quail (*Coturnix coturnix japonica*) and found that maximum adjustment of digestive organs occurred within 3 to 4 weeks although significant changes occurred within 1 week. The quail adjusted to high fiber diets by eating more food, thus maintaining the same level of nutrient intake as when consuming low fiber diets, and by gut enlargement, which presumably increased digestive efficiency. Data in Miller (1974, cited in Miller 1975) suggested that waterfowl may adapt more quickly to diet changes than do quail. However, relationships between changes in diet and the limits of adaptation of the gut, on the one hand, and the time required to achieve maximum adaptation, on the other, remain unknown for waterfowl.

The liver is important in intermediary metabolism as it alters and stores nutrients after they are absorbed from the gut and releases them as needed (Hazelwood 1972). Weight of the liver changes in relation to quantity of food eaten (Ankney 1977) and to changes in metabolism (Raveling 1979; Drobney 1984). The liver may also be important in accommodating short-term undernutrition (Breitenbach et al. 1963). Although changes in liver size have been related to seasonal changes in diet, in breeding status, and in digestive efficiency, we are unaware of any research that has experimentally examined the relationship between changes in diet and changes in liver size.

Our objectives in this study were (*i*) to study relative effects of fiber and diversity on gut morphology, (*ii*) to compare sizes of digestive organs of birds on low fiber plant diets with those of birds on low fiber animal diets, (*iii*) to study the rate at which and extent to which guts adjust to changes in diet, and (*iv*) to examine the magnitude of changes in liver size of birds on different diet types. To meet these objectives we fed four diets that differed in fiber content, in diversity, and in animal versus plant protein content, to four groups of captive Mallards (*Anas platyrhynchos*).

Materials and methods

A flock of 164 young-of-the-year Mallards, one generation removed from the wild, which had been raised as part of another study at the Delta Waterfowl and Wetlands Research Station in Manitoba, Canada, was used in the experiment. All experimental birds hatched between 25 May and 7 June 1986. The experiment began 1 September 1986 and continued until 1 October 1986. Before the experiment, birds were free flying and were held outdoors in a common flight pen. For the purpose of the experiment, the wings of the birds were clipped and the birds were moved into a large building where they were divided into five groups; initial body weight was recorded for each bird. Birds were allowed 5 days to adjust to their new environment

TABLE 1. Composition (%) of experimental diets

Diet	Crude protein	Crude fat	Crude fibre	Ash	Nitrogen-free extract
Delta diet[a]	25.0	2.5	5.0	2.9	64.6
Corn	10.9	4.7	2.4	1.6	80.3
Trout chow	40.0	12.0	5.0	11.5	31.5
Rabbit chow	17.0	2.5	18.0	1.8	60.7
Diverse[b]	23.6	6.4	8.5	5.0	56.5

[a]Composed of 50% wheat grain and 50% duck starter.

[b]Equal to the mean of the values for corn, trout chow, and rabbit chow diets over a 3-day period; see Materials and methods.

before the experiment began.

All birds had been reared on the same diet, which was formulated for captive waterfowl at Delta (Table 1). A group of 20 birds (10 males, 10 females) (the initial group) was killed on the 1st day of the experiment (5 September). The remaining 144 Mallards were divided into four groups of 36 (18 males, 18 females). Each of these groups was fed an experimental diet: diet 1, corn (low fiber, plant); diet 2, diverse (the 25-day experiment allowed 24 feeding days as birds were not fed on the morning that they were killed; these 24 days were divided into eight 3-day blocks, during each of which birds in the diverse diet group were fed each diet once although the order of feeding was chosen randomly); diet 3, trout chow (low fiber, 60% animal : 40% plant); and diet 4, rabbit chow (high fiber, plant). Composition of the diets is presented in Table 1. All groups were fed *ad libitum* and given grit and a vitamin supplement.

A sample of birds from each diet group was killed every 5 days after the experiment began. Each sample had a 50:50 sex ratio. Eight birds from each diet group were killed on days 5, 10, and 15, and six birds from each diet group were killed on days 20 and 25.

Birds were killed and measured on the same day. Seven external measurements were taken: keel length ($\pm$ 0.1 mm), tarsus length ($\pm$ 0.1 mm), bill width ($\pm$ 0.1 mm), culmen length ($\pm$ 0.1 mm), head length ($\pm$ 0.1 mm), body length ($\pm$ 0.5 cm), and body weight ($\pm$ 1.0 g). Seven internal measurements were taken: intestine length ($\pm$ 0.5 cm), combined ceca length ($\pm$ 0.5 cm), empty intestine weight ($\pm$ 0.1 g), empty ceca weight ($\pm$ 0.1 g), liver weight ($\pm$ 0.1 g), empty gizzard weight ($\pm$ 0.1 g), and abdominal fat weight ($\pm$ 0.1 g). Ceca were removed at their point of attachment, laid end to end along a metre stick, and measured together. The small intestine was separated from the large intestine and gizzard and measured. The gizzard was separated from the proventriculus and opened, its contents were removed, and it was then washed, blotted with a paper towel, and weighed. The liver, including the gall bladder, was blotted with a paper towel and weighed. Ceca and small intestine weights were taken after their contents, mesentery, and fat were removed by drawing the organs under a dull blade. Abdominal fat was the fat found in the abdominal cavity, not associated with viscera.

Past studies have noted the importance of considering differences in body size when making comparisons of gut morphology (Thomas 1984; Kehoe and Ankney 1985). Those interspecific comparisons used analysis of covariance with body weight as a covariate. For intraspecific comparison of gut morphology, however, the first principal component score from an analysis of several structural size variables is a more suitable covariate because it is independent of the nutritional state of the bird (Alisauskas and Ankney 1987). Thus, we chose the first principal component score from an analysis of the correlation matrix of keel length, tarsus length, culmen length, head length, bill width, and body length. These variables were characterized by the eigenvector 0.39, 0.37, 0.42, 0.44, 0.37, 0.45. The gut morphology data were regressed (each variable separately) on the first principal component scores to adjust them to body size. The regressions of each variable on PC1 were all positive and significant ($P <$ 0.05) although PC1 explained only a little of the overall variation in

FIG. 1. Effect of diet on weight of abdominal fat and on body weight of Mallards; percent difference in body weight was calculated as (initial weight − final weight)/initial weight × 100. Initial weight of each bird was taken 5 days before day 0. Diets were 1, corn; 2, diverse; 3, trout chow; and 4, rabbit chow.

size of each variable (range of r^2 values: 0.03−0.12). The residuals for each bird, from each regression, were used to calculate a new value (y_i), corrected for body size, for each digestive organ measurement: $y_i = y_{obs} - [a + b(PC1)] + \bar{y}_{obs}$. Corrected values were used in three-factor analyses of variance (ANOVA) to examine effects of diet type, time after diet change, and sex on differences in each variable (Proc GLM, SAS 1982).

We assessed the effects of diet type, and of time after change in diet, on changes in body weight. To do this, we subtracted the weights of the birds on the date that they were killed from their initial weights on 1 September. We then plotted mean percent weight change of birds in each treatment over time (Fig. 1).

Results and discussion

Body and abdominal fat weights

On day 0, 5 days after the birds were placed in the experimental groups, but before they were given the experimental diets, they had lost, on average, 13% of their initial weight (Fig. 1). Birds on all diets subsequently regained body weight until day 15, but thereafter birds on the high fiber diet continued to gain weight whereas birds on the other diets did not. The heavier weight of birds on the high fiber diet was partially due to their heavier digestive organs (see below). Miller (1975) reported that his ducks, particularly those fed corn, lost weight throughout the 21-day experiment. However, as he only weighed birds at the beginning and end of the experiment, he could not determine the pattern of change during that period. Hill and Dansky (1954, cited in Fisher 1972) found that percent fiber (0, 10, 20, 30, 40%) did not affect body weight in chickens, and birds that ate high fiber diets were able to compensate adequately for reduced diet quality by increasing their consumption. From this result, we presume that our ducks on the high fiber diet ate considerably more food than did ducks eating the other three diets.

Diet had a strong effect ($P < 0.001$) on weight of abdominal fat (Fig. 1, Table 2) and the effect of time was nearly significant ($P < 0.07$). Although the birds on the low fiber diets were able to maintain or increase their abdominal fat stores, those on the high fiber and diverse diets were not. Similarly, there was a negative relationship between body fat and level of dietary fiber in the chickens studied by Hill and Dansky (1954, cited in Fisher 1972). We note, however, that all of the loss of fat in our ducks on the high fiber diet occurred during the first 5 days of the experiment. This result, in conjunction with the data about body weights, suggests that the large changes in digestive organs of these birds allowed them to compensate for their energy-poor diet.

Gut morphology

Sex of the birds had no effect ($P < 0.05$) on any of the gut measurements and, therefore, we discuss only the effects of diet and of time, and the interaction between these two factors. Diet type affected the size of all digestive organs (Table 2) and time after diet change had an effect on all variables except ceca and intestine lengths. There were, for all variables, significant ($P < 0.05$) interactions between the effects of diet and of time since diet change. These interactions preclude a detailed discussion of the main effects of diet and of time and so we describe the major trends, which are apparent in Fig. 2.

The high fiber diet clearly had the greatest effect on size of digestive organs (Fig. 2), a pattern similar to that found by Miller (1975). Contrary to the hypothesis of Kehoe and Ankney (1985), dietary diversity had far less effect on gut size than did fiber content. This may have been simply because our diverse diet did not adequately simulate the diverse diet of a free-ranging omnivore and thus did not produce a proximate response. Alternatively, some interspecific differences observed by Kehoe and Ankney (1985) may have been the result of long-term selection within the different species, i.e., an ultimate response for optimum digestive efficiency, given their respective "normal" diets. (Moss (1972) observed marked decreases in intestine and cecum length of captive Red Grouse (*Lagopus lagopus*) over several generations, and argued that these were genetic changes resulting from selection for optimal gut size.) For example, it may be that Lesser Scaup (*Aythya affinis*), which are omnivores, would have signifi-
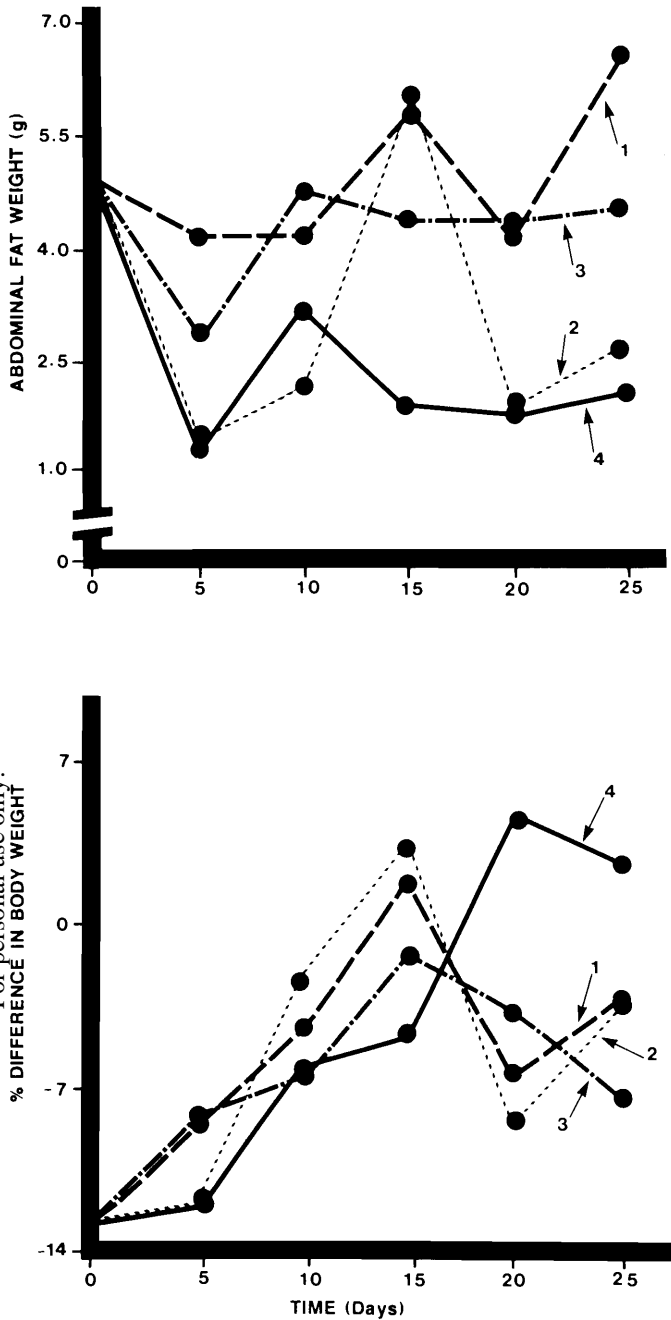
TABLE 2. Summaries of three-way analyses of variance for each of seven independent variables measured on Mallards fed four experimental diets

	Source of variation	P	r^2
Liver weight	Overall	0.0001	0.62
	Time	0.0004	0.07
	Diet	0.0001	0.11
	Time × diet	0.0001	0.38
Gizzard weight	Overall	0.0001	0.62
	Time	0.0024	0.05
	Diet	0.0001	0.32
	Time × diet	0.0015	0.11
Intestine weight	Overall	0.0001	0.83
	Time	0.0001	0.10
	Diet	0.0001	0.52
	Time × diet	0.0001	0.09
Ceca weight	Overall	0.0001	0.76
	Time	0.0001	0.36
	Diet	0.0001	0.59
	Time × diet	0.0198	0.05
Intestine length	Overall	0.0001	0.67
	Time	0.2422	0.02
	Diet	0.0001	0.44
	Time × diet	0.0001	0.16
Ceca length	Overall	0.0001	0.71
	Time	0.6860	0.01
	Diet	0.0001	0.53
	Time × diet	0.0001	0.17
Abdominal fat weight	Overall	0.0175	0.36
	Time	0.0655	0.05
	Diet	0.0003	0.11
	Time × diet	0.5368	0.06

NOTE: After correcting for body size (see Materials and methods), the effect of sex by itself or of sex interacting with diet and time was not significant, and thus is not shown. Variance explained (r^2) is based on the ratio of the orthogonal sums of squares to the total sums of squares.

cantly different gut morphology than, for instance, Canvasbacks (*Aythya valisineria*), which feed largely on soft tubers, even if both were fed the same diet. Regardless, our finding that diversity *per se* had little effect on gut size supports Drobney's (1984) conclusion that increased gut size of laying female Wood Ducks was likely due to increased volume of food. The limits of plasticity of digestive organs to dietary change within a species are unknown but we think it likely that some species show greater plasticity than do others. Variation in gut morphology within some species, collected in different locations and seasons and feeding on different diets, e.g., Gadwalls (*Anas strepera*) (Paulus 1982) and White-winged Scoters (*Melanitta fusca*) (Dobush 1986), was greater than that found in some interspecific comparisons, e.g., among five *Aythya* spp. (Kehoe and Ankney 1985).

Changes over time in digestive organs of birds on low fiber diets (corn, trout chow) were remarkably similar and, except for the gizzard, the organs were nearly identical in size by the end of the experiment. Differences in gizzard weights among these two groups likely reflect the greater amount of grinding required to macerate corn as opposed to trout chow. Miller (1975) reported similar results for Mallards on corn and turkey starter (also low fiber). We conclude that in Mallards, at least, size of the intestines, ceca, and liver is not useful for distinguishing birds feeding on animal foods from those feeding on low fiber plant foods.

The response of Mallard digestive organs to dietary change

was even more rapid than that detected by Miller (1975) and was as rapid as that found in quail (Savory and Gentle 1976). For example, weights of gizzard, intestine, and ceca of birds on the high fiber diet had peaked by day 10 (Fig. 2) and measurements of the other variables were also larger then. In virtually all diet by digestive organ comparisons, there were apparent increases in digestive organ size by day 5.

Although some authors (e.g., Miller 1975; Paulus 1982) have reported weights and lengths of intestines and ceca, others have reported only weights (e.g., Drobney 1984, for intestine) or lengths (e.g., Ankney 1977; Kehoe and Ankney 1985). Thomas (1984: p. 2259) thought that cecal length and small intestine length were inferior to weight as measures of organ size because the two variables weight and length were uncorrelated. Our results, the first that allow a comparison of lengths and weights of these organs across time and diets, indicate that the two measures do not give redundant information for birds on a high fiber diet. Both weight and length of intestine and ceca increased sharply during the first 10 days of the experiment (Fig. 2; $P < 0.05$, Student–Newman–Keuls (SNK) tests) and there was little change during the ensuing 5 days. However, during days 15–25, there were further large increases in intestine length (+12%; $P < 0.05$, SNK test) and ceca length (+20%; $P < 0.05$, SNK test) with no net change in the weights of these organs ($P < 0.05$, SNK test). Clearly, in Mallards, physiological adaptation to a high fibre diet entailed concurrent increases in biomass and length of intestine and ceca initially, but there was further "lengthening" of these organs subsequently. If such a phenomenon occurs in ptarmigan, it may explain why Thomas (1984) did not find a correlation between weights and lengths of their intestine and ceca. That, however, does not support his conclusion that gut length is inferior to weight as an index of diet. Unfortunately, we cannot assess when intestine and ceca length reached an asymptote as they apparently had not stopped increasing by 25 days (Fig. 2). Thus, although digestive organs of Mallards respond to a change of diet as rapidly as did those of quail (see above), they apparently did not reach maximum size in the 3–4 weeks reported for the quail (Savory and Gentle 1976).

Liver weight was dependent on diet and on time after change in diet (Table 2), but the interaction between diet and time explained the highest proportion of the variance in liver weight. This made it difficult to interpret the fluctuations in liver weight that occurred during the first 15 days. The relationship between diet and liver weight was obvious by days 20 and 25 as birds on the high fiber diet had much heavier livers. We noted that liver weights of birds on the other diets generally increased in response to the diet change, but then declined to their initial weight by day 25.

The liver has many functions, including glycogen and lipid storage, intermediary metabolism (e.g., lipogenesis), and the production of bile (Sturkie 1976). Enlarged livers of ducks eating the high fiber diet possibly resulted from greater increases in these liver functions than in ducks eating the other three diets. If increased lipogenesis caused the enlarged livers, then any lipid storage must have occurred in the liver rather than as distinct adipose tissue (recall that the high fiber group of ducks had little abdominal fat as did ducks eating a diverse diet, but livers of ducks eating a diverse diet did not differ from those of ducks eating corn or trout chow). We suspect that the liver's role as a storage organ was greatest in ducks eating a high fiber diet. Because we did not analyze livers, we do not know if this result was due to greater lipid and (or) greater
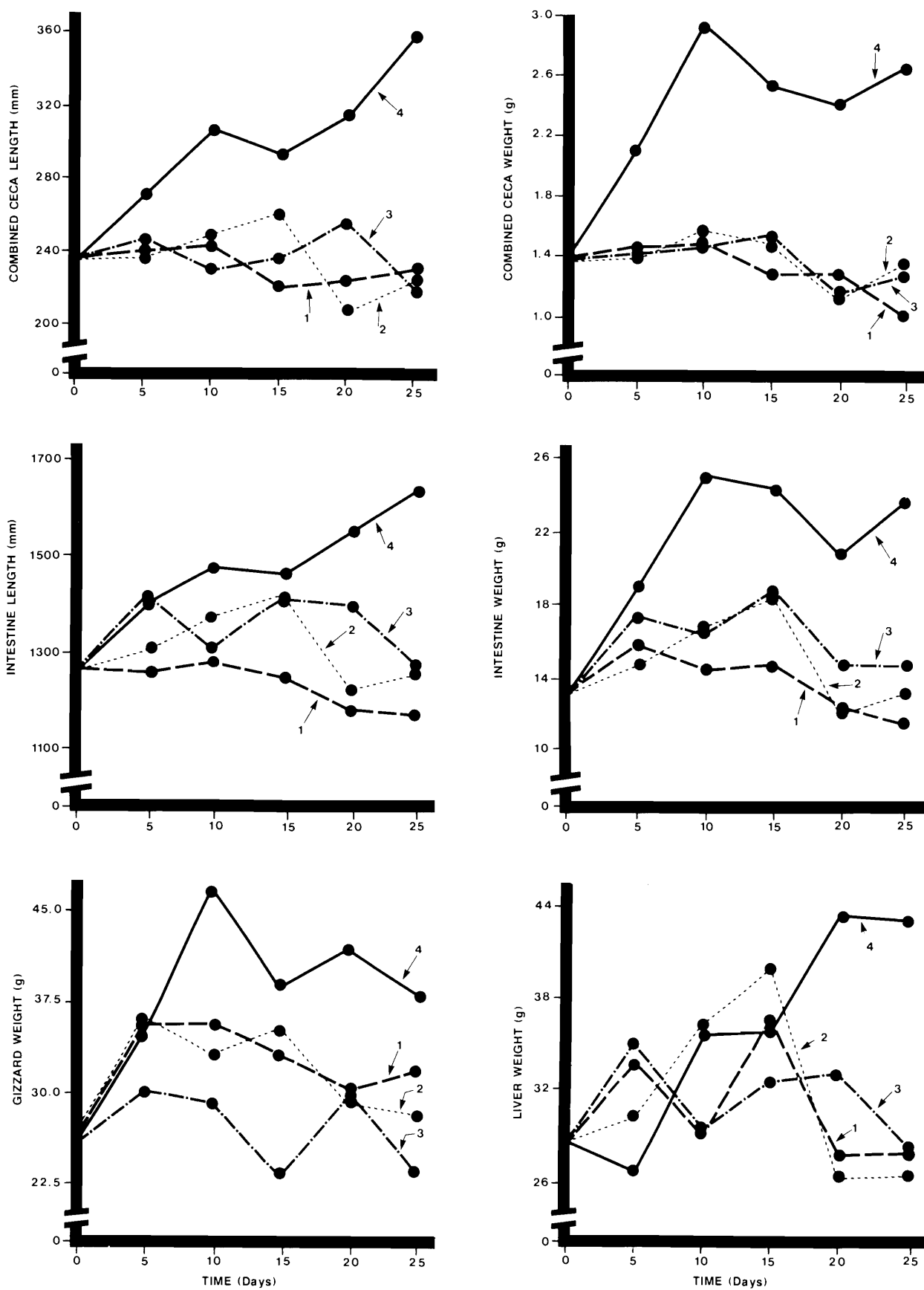
FIG. 2. Effect of diet on the digestive organs of Mallards. Diets were 1, corn; 2, diverse; 3, trout chow; and 4, rabbit chow.

glycogen storage. Alternatively, larger livers may reflect increased metabolic activity of birds on a low quality diet. However, the low rate of intake of digestible energy of such birds, combined with their greater maintenance costs, due to heavier body weights, may have required them to store energy in the liver. The livers of birds eating high fiber diets may also have been heavier because of increased production of bile. Bile contains amylase which is important for the digestion of starches (Sturkie 1976). Such a response may enhance the efficiency of digesting and absorbing such low quality food.

We think that maintenance costs of ducks eating a high fiber diet may have been particularly high, irrespective of their greater body weight, because of involuntary muscle activity of their gizzards. This activity must have been at a greater rate and of longer duration in the ducks on the high fiber diet, because of their higher food consumption (see above). Such muscle activity would require a more continuous and greater rate of energy supply than in birds that feed less, as well as less often. We are unaware of studies that have correlated energy expenditure and gizzard size, but suspect that the importance of this cost has generally been ignored or underestimated.

Conclusions

Our study provides further evidence about the remarkable plasticity of the digestive organs of birds. This plasticity is probably particularly important for migratory species, such as Mallards, or in species inhabiting highly variable environments, as it enables them to exploit a great range of foods. The Mallards in our experiment were able to exist as granivores (corn diet), herbivores (rabbit chow), and omnivores (trout chow, diverse diet). Such adaptability supports Miller's (1975) suggestion that it may be difficult to categorize the general diets of waterfowl species, as Leopold (1953) did for grouse, based on the size of their digestive organs. However, it remains unknown if there are general overall differences in the digestive organs of the various species that are related to their respective usual diets. For example, regardless of their diet shortly before they are analysed, herbivores such as Gadwalls may have longer guts and heavier gizzards, relative to body size, than do, for instance, granivores such as Northern Pintails (*Anas acuta*).

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