Variation in digestive organ size among five species of diving ducks (*Aythya* spp.)

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Ceca length, small intestine length, and gizzard weight were measured for individuals of five species of diving ducks collected at Long Point Bay, Lake Erie, and Mitchell's Bay, Lake St. Clair, Ontario, in the falls of 1982 and 1983. The five species were Lesser Scaup (*Aythya affinis*, $N = 84$), Ring-necked Duck (*Aythya collaris*, $N = 57$), Greater Scaup (*Aythya marila*, $N = 54$), Redhead (*Aythya americana*, $N = 58$), and Canvasback (*Aythya valisineria*, $N = 112$). The diets of these species reportedly differ in diversity as well as in amount of fibre, and interspecific differences in gut morphology, not explained by differences in body weight, were accounted for by general differences in diet. Canvasbacks, although the heaviest species, had the shortest ceca, short intestines and light gizzards, presumably because their diet contains the least fibre. Conversely, the relatively small-bodied scaup species had the longest small intestines, likely because of their diverse diets which include animal and plant material. Our results show that morphological differences in waterfowl guts reflect dietary differences at a particular time and location and also illustrate the importance of adjusting gut measurements to body weight before making interspecific comparisons.

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La longueur des caecums, du petit intestin et du gésier a été mesurée chez cinq espèces de canards plongeurs de la baie de Long Point, Lac Erié, et de la baie de Mitchell, Lac St-Clair, en Ontario, au cours des automnes de 1982 et de 1983: le Petit Morillon (*Aythya affinis*, $N = 84$), le Morillon à collier (*Aythya collaris*, $N = 57$), le Grand Morillon (*Aythya marila*, $N = 54$), le Morillon à tête rouge (*Aythya americana*, $N = 58$) et le Morillon à dos blanc (*Aythya valisineria*, $N = 112$). D'après les données de la littérature, les régimes alimentaires de ces espèces diffèrent par leur diversité et par la quantité de fibres qu'ils contiennent; de plus, les différences interspécifiques de morphologie du système digestif qui ne s'expliquent pas par des différences de masse totale sont considérées comme le résultat de différences dans l'alimentation. Les Morillons à dos blanc, quoique les oiseaux les plus lourds, ont les caecums les plus courts, l'intestin très court et le gésier léger, probablement parce que leur régime est celui qui contient le moins de fibres. Inversement, les espèces de morillons relativement plus petites ont les intestins les plus longs, probablement parce que leur régime alimentaire plus diversifié contient à la fois des matières animales et des matières végétales. Nos résultats indiquent que les différence morphologiques entre les systèmes digestifs des oiseaux aquatiques sont le reflet de différences dans l'alimentation en fonction du temps de l'année et de l'endroit et elles soulignent l'importance d'ajuster les mesures du système digestif à la masse totale avant de faire des comparaisons interspécifiques.

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Introduction

Several studies have indicated that the gross morphology of the digestive tract reflects the diets of birds (Drobney 1984; Leopold 1953; Moss 1972, 1974, 1983; Miller 1975; Paulus 1982; Pendergast and Boag 1973; Thomas 1984). Moss (1972) and Leopold (1953) suggested that the gut, especially the ceca, could be used as an index of food habits in Galliformes. Moss (1974) related gut lengths to winter diet and interspecific competition for food in Alaskan ptarmigan (*Lagopus* spp.). Miller (1974; cf. Miller 1975) found that the gut morphology of waterfowl (*Anas* spp.) was altered rapidly with changes in diet and suggested that this militated against concluding, as Moss (1972) did for Galliformes, that the gut was a useful index to waterfowl food habits. Miller (1975) also stated, however, that more data were needed on comparative gut lengths of wild waterfowl before such conclusions were completely dismissed.

Five species of migratory waterfowl of the genus *Aythya* are sympatric on the major fall staging areas of the Great Lakes; these are the Ring-necked Duck (*A. collaris*; hereafter called the ring-neck), the Lesser Scaup (*A. affinis*), the Greater Scaup (*A. marila*), the Redhead (*A. americana*), and the Canvasback (*A. valisineria*). These species are similar in gross morphology, macrohabitat use, and feeding mode (Bellrose 1976; Smith 1979). These similarities suggest ecological isolation by either foraging microsite or food type. Lack (1971) suggested that species of *Aythya* in Europe (*A. marila, A. ferina, A. nyroca, A. fuligula*) are segregated by food type.

Smith (1979) studied ecological isolation between *Aythya* spp. at Long Point Bay, Ontario, by comparing food types, food availability, foraging areas, and gut and bill morphology. He found that ring-necks foraged in a habitat different from that used by the other species, that Canvasbacks and Redheads used a different part of the Bay than the two scaup, and that the Canvasback, Redhead, and the two scaup had different diets. He also found some relationship between diet and bill and gut morphologies, consistent with Moss' (1972) findings for the Galliformes, but his samples were small, which probably obscured important interspecific differences. Smith (1979) also did not adjust his measurements of gut morphology to account for differences in body weight. Thomas (1984) showed that gut size was positively correlated with body weight in tetraonids. Thus, only after adjusting for body weight can a distinction be made between those morphological differences which are due to diet and those which are due to body weight.

Our objectives in this study were (*i*) to more fully describe differences in gut morphology among the five *Aythya* spp. from two Great Lakes staging areas to increase information on comparative gut sizes in waterfowl and (*ii*) to determine to what extent such differences can be explained by interspecific differences in body weight. To meet these objectives we obtained a much larger sample of birds than that used by Smith (1979).

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TABLE 1. Body weights and gut measurements (±SE, *n* in parentheses) for the five species of *Aythya*

Species	Body weight (g)	Ceca length (cm)	Intestine length (cm)	Gizzard weight (g)
Lesser Scaup	731±9.6*a* (84)	27.1±0.4*ab* (77)	172.1±2.0*a* (78)	31.9±0.8*a* (75)
Ring-necked Duck	749±11.4*a* (57)	25.5±0.6*a* (55)	118.0±2.5*b* (54)	38.4±1.1*b* (55)
Greater Scaup	908±14.8*b* (54)	29.2±0.6*b* (54)	169.6±2.6*a* (54)	42.8±1.8*b* (53)
Redhead	997±14.5*c* (58)	32.6±0.6*c* (54)	149.5±1.7*c* (54)	65.7±1.7*c* (52)
Canvasback	1206±11.9*d* (112)	28.1±0.3*b* (108)	139.6±1.1*d* (107)	41.6±0.8*b* (108)
F value	301.6	24.83	127.8	104.4
F probability	0.0001	0.0001	0.0001	0.0001

NOTE: Values in a column followed by the same letter are not significantly different (Sheffe's multiple-range test; $p < 0.05$).

TABLE 2. Mean values (*n* in parentheses) for gut measurements for each of the five species adjusted to body weight by ANCOVA

Species	Ceca length (cm)	Small intestine length (cm)	Gizzard (g)
Lesser Scaup	26.6*ad* (77)	166.9*a* (78)	33.6*a* (75)
Ring-necked Duck	26.7*abd* (55)	120.5*b* (54)	42.4*bd* (55)
Greater Scaup	29.6*ac* (54)	170.9*a* (54)	42.9*b* (53)
Redhead	30.3*bc* (58)	139.9*b* (54)	58.7*c* (52)
Canvasback	24.9*d* (108)	124.7*b* (107)	33.9*ad* (108)

NOTE: Values in a column followed by the same letter are not significantly different (Sheffe's multiple-range test; $p < 0.05$).

Materials and methods

Data were collected during the falls of 1982 and 1983 at Long Point Bay, Lake Erie, and in 1983 at Mitchell's Bay, Lake St. Clair, Ontario. We visited the Ontario Ministry of Natural Resources, Long Point Waterfowl Management Unit check station, where weights, age, and sex of *Aythya* were recorded as birds were brought in by hunters. The gizzard, small intestine, and ceca (hereafter collectively called guts) of each bird were removed, sealed in a plastic bag with an identifying label, and frozen. The large intestine was not included in our analyses. We also contacted several commercial duck cleaners at Mitchell's Bay and Long Point who agreed to record the weight of each *Aythya* spp. brought to them and to freeze the guts and one wing from each bird.

Three gut measurements were taken: (*i*) intestine length (±0.5 cm), (*ii*) combined cecum length (±0.5 cm), and (*iii*) empty, towel-dried gizzard weight. Ceca were removed at their point of attachment, laid end to end along a metre stick, and measured as one unit; the small intestine was separated from the large intestine and gizzard and measured separately. The gizzard was separated from the proventriculus, opened, its contents were removed, and then it was washed, dried with a paper towel, and weighed.

Our major goal was to quantify interspecific differences in gut morphology and, thus, birds from different age-classes and sex classes, collection sites, and dates were pooled for each species. One-way analysis of variance (ANOVA) and Sheffe's tests were performed on gut measurements to test for interspecific differences in unadjusted means. We then used analyses of covariance (ANCOVA) with body weight as the covariate or independent variable, gut measurement as the dependent variable, and species as groups. By using ANCOVA we also accounted for any intraspecific variation in body weight as a result of age and (or) sex.

Results

We obtained data from 84 Lesser Scaup, 57-ring-necks, 54 Greater Scaup, 58 Redheads, and 112 Canvasbacks.

There were interspecific differences ($p < 0.05$) in all gut measurements (Table 1). Even before correcting for differences in body weight with ANCOVA, it was clear that some differences in gut morphology were not explained by interspecific differences in body weight. For example, the heaviest species, the Canvasback, had the second shortest intestine, the shortest ceca, and an intermediate gizzard weight. The Redheads, with a body weight only 75% of that of Canvasbacks, had gizzards almost twice as heavy as those of Canvasbacks.

In each ANCOVA there were no interspecific differences ($p > 0.05$) in the slopes relating gut size to body weight and in each case the common slope was greater than zero ($p < 0.01$). After ANCOVA, interspecific differences still existed (Table 2). These differences were those which could not be explained by differences in body weight. For example, in Table 1, the species could be put into four discrete groups based on differences in intestine length, but after adjusting for differences in body weight only two groups could be recognized, those species with long intestines, the scaup, and those with short intestines, the Canvasback, Redhead, and ring-neck (Table 2).

ANOVA showed that the five species formed three relatively distinct groups on the basis of ceca length (Table 1), but most of these differences were explained by differences in body weight (Table 2).

Before we adjusted gizzard weight to body weight, there were three distinct groups, those species with small, medium, and large gizzards (Table 1). When gizzard weight was adjusted for body weight, however, only Redheads had a gizzard that was distinctly different from those of other species (Table 2).

Discussion

Although we did not analyse the diets of our specimens, differences in gut morphology not explained by body weight differences are likely related to dietary differences (Drobney 1984; Leopold 1953; Miller 1975; Moss 1972, 1974; Pendergast and Boag 1973; Smith 1979; Paulus 1982). The diets of these five *Aythya* species differ with season and

TABLE 3. Relative gut size, predicted dietary fibre and (or) dietary diversity based on relative gut size, and observed diets (Smith 1979) of five species of *Aythya*

	Relative gut size [a]				
Species	Ceca length	Intestine length	Gizzard weight	Predicted dietary fibre and (or) diversity	Observed diet (Smith 1979)
Lesser Scaup	Medium	Long	Light	Diverse[b]	Invertebrates, 53%; seeds, 47%; N=5
Ring-necked Duck	Medium	Short	Medium	Intermediate fibre[b,c]	Seeds, 66%; leafy vegetation, 35%; N=2
Greater Scaup	Long	Long	Medium	Diverse and (or)[b] high fibre[c]	Invertebrates, 34%; tubers, 10%; leafy vegetation, 54%; N=2
Redhead	Long	Short	Heavy	High fibre[b,c]	Leafy vegetation, 70%; other vegetation, 28%; N=11
Canvasback	Short	Short	Light	Low fibre[b,c]	Tubers, 96%; N=11

[a] Scaled to body weight by ANCOVA.
[b] From Moss (1974).
[c] From Miller (1975).

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location (Bellrose 1976). Consequently, most data about the food habits of these birds, compiled in other areas, may not apply to birds staging on the Great Lakes during the fall.

Smith (1979) presented data on the fall diets of these species at Long Point Bay and, although his sample sizes were small, e.g., N = 2 for ring-necks and Greater Scaup, they are the only available data on *Aythya* spp. relevant to our study. Below we predict the diets that the *Aythya* spp. should have had, based on their gut measurements and on how other authors have related gut morphologies and diets of birds, and compare these predictions to Smith's (1979) observations (see Table 3).

The function of the ceca in waterfowl is poorly understood (Drobney 1984). It has been shown, however, that cecal lengths of birds increase with the amount of fibre in the diet (Leopold 1953; Miller 1975; Moss 1974). Gizzard weight in congeneric species has also been positively correlated with dietary fibre (Miller 1975; Moss 1974). If similar relationships between ceca, gizzard size, and the amount of dietary fibre occur in the *Aythya*, then the Redhead should have the highest fibre diet and the Canvasback should have the lowest fibre diet, with the other species being intermediate. Smith (1979) found that the Redhead fed mainly on leafy aquatic vegetation (high fibre diet), that the Canvasback fed chiefly on tubers (low fibre diet), that the two scaup were omnivores (intermediate fibre diet), and that the ring-neck fed mainly on seeds and some leafy vegetation (intermediate fibre diet). Therefore, predictions from our data on ceca and gizzard morphology are consistent with the data on food habits obtained by Smith (1979) (Table 3).

Moss (1974) suggested that a species should have the shortest possible gut for a given diet to reduce metabolic costs of maintenance. Moss (1974) found that ptarmigan (*Lagopus* spp.) with the most diverse diets had the longest intestines and suggested that this enabled them to digest whatever foods were available at a given time. On this basis we predicted that of the five *Aythya* species, the Greater and Lesser Scaup would have the most diverse diets. This predictions is supported by Smith's (1979) data which showed that the two scaup were omnivores and ate molluscs, seeds, and leafy vegetation, but that the other *Aythya* had more specialized, herbaceous diets. Greater Scaup, as well as having long small intestines, have long ceca (Table 3). This suggests that they should have a relatively high fibre diet and when compared with the other species, the leafy vegetation component of their diet is second only to that of Redheads. Thus, the Greater Scaup's diverse and high fibre diet (Smith 1979) is reflected in its gut morphology. Leopold (1953) found that among herbivorous Galliformes, seed eaters had shorter guts than browsers and he suggested that this was because seeds were more easily digested than green vegetation. Moss (1983) stated that a high intake of fibrous foods results in a long gut length in tetraonids. Redheads are browsers and eat leafy vegetation, ring-necks are seed eaters, and Canvasbacks eat tubers (also easily digested; Smith 1979); Redheads have a proportionately longer gut than do Canvasbacks or ring-necks. Our data for the gut morphologies of the *Aythya* spp. are consistent with the observation on the relationship between intestine length and diet for Galliformes (Moss 1974, 1983; Leopold 1953).

In conclusion, we found that interspecific differences in gut morphology do exist between the five *Aythya* spp. staging on the Great Lakes during fall migration. Some interspecific differences in gut morphology were explained by differences in total body weight, demonstrating the importance of correcting for body weight differences before relating interspecific differences in morphology directly to dietary differences. Interspecific differences in gut morphology which are not accounted for by interspecific weight differences can be explained by differences in diet. Given what is known about the diets of the *Aythya* spp. at Long Point (Smith 1979), the variation that we found in gut morphology of *Aythya* spp. is comparable to observations made on the gut morphologies of other bird species with known diets (Leopold 1953; Moss 1972, 1974, 1983; Pendergast and Boag 1973; Miller 1975; Paulus 1982). Further, a comparison of data from the scaup with those from Redheads suggests that dietary diversity may be more important than dietary fibre in determining gut length.

The concerns of Miller (1975) regarding the usefulness of waterfowl guts as an index of food habits are unjustified. Although waterfowl digestive organs show a rapid response to changing diets, when a large random sample of the population is taken, morphological differences in guts do reflect dietary differences at a particular time and location.

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