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Adaptive Interplay Between Feeding Ecology and Features of the Digestive Tract in Birds

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SYNOPSIS

Different foods require different digestive processing. This simple fact has led to a wide adaptive variety in digestive systems. This chapter considers the relationship between the size of three digestive organs (stomach, intestine, and liver) and food intake, diet type (e.g. degree of softness/hardness in the case of carnivores and fiber-content in the case of herbivores), and seasonal factors. Our arguments are based on comparisons of diet-organ size associations within ecologically and phylogenetically uniform groups and on analyses of organ size changes within species and individuals. The phenotypic flexibility of the digestive organs is considerable; changes of 10–100% in organ size in response to changing conditions are found in a wide range of bird groups. Experimental work has shown changes in gizzard size of 50–100% in just 5–7 days. Ease of breakdown of food (a function of the strength of protective hard parts or the amount of fibrous ingredients) and total food intake determine the size of the stomach (and more specifically, its muscular part, the gizzard). Food intake also influences the size of the small intestine and the liver. Among waders (Suborder Charadrii), taxa consuming and crushing hard-shelled mollusks also have a heavier intestine (but not liver) than taxa eating softer foods. Much work remains to be done investigating the fine-tuning of capacities among the different digestive organs, the precise trade-offs involved in organ size changes, and the genetic basis of organ size and flexibility.

INTRODUCTION

While the structural characteristics of birds and mammals are essentially fixed in size once maturity has been reached, internal organs can vary substantially in size and mass throughout the annual cycle (Jehl, 1997; Piersma and Drent, 2003; Piersma and Lindström, 1997). Many species experience changes in habitat, diet, energy demand or climate during the year, all of which may influence digestive morphology. Digestive organs can be large and metabolically highly active and therefore energetically expensive. Thus there will be energetic and mass-related costs associated with having a large digestive system. A large gut may provide the ability to use foods of low quality that are difficult to handle mechanically or chemically. The size of the digestive tract should therefore reflect the balance between the costs of maintaining the system, and the benefits of having organs of that size. Because the internal and external demands for individuals or populations may vary over time, internal flexibility rather than constancy may be the norm in many bird species. Here the following questions are asked: (1) How widespread are digestive organ changes in different bird groups? (2) Are these (endogenously controlled) anticipatory changes related to upcoming needs, or responses to variation in external conditions? (3) What are the roles of diet in determining the size of the digestive organs?

We base our analyses on two main approaches, comparisons among higher taxa, and comparisons within species and individuals. We focus on the role of ecological factors, especially diet, in determining organ size. Our analyses involve three main sources of data: (1) changes in organ size in various taxa (especially galliformes and waterfowl) published over the past 30 years; (2) body composition and organ masses of waders (or shorebirds, Order Charadriiformes) dissected at the Royal Netherlands Institute for Sea Research (T. Piersma and P.F. Battley, unpubl. data); and (3) recent noninvasive studies that illustrate the reversible morphological flexibility of the digestive tract within individuals.

The digestive system of birds can be divided into several main components (Table 8.1). In any one taxon, each of these digestive organs will have morphological characteristics that functionally reflect the evolutionary history and contemporary ecology of the taxon (Stevens and Hume, 1995). We do not deal here with these morphological features per se, but instead take them as given and examine overall size patterns, under the assumption that size (or mass) indicates functional capacity. The relationship between size and function is complex and must also involve adjustments at lower levels of organ structure (tissue structures, cell metabolism; see Chapter 7 by Starck, this volume). Increasing costs associated with organ size will cause the net benefit of increasing organ size to be a decreasing benefit function rather than a linear function. Nevertheless, at the level of organization studied

Table 8.1 Subdivision of the major components of the digestive system in birds (from Klasing, 1998)

Organ	Alternative name /components	Primary functions
Oesophagus + crop		Food storage, movement of food toward proventriculus
Proventriculus	Glandular stomach	Gastric secretion
Gizzard	Muscular stomach	Crushing or grinding food, mixing food with gastric secretions
Small intestine	Duodenum, jejunum, ileum	Enzymatic digestion, absorption of digestive end products
Ceca		Microbial fermentation, water and nitrogen absorption, immunosurveillance
Rectum	Colon, large intestine	Electrolyte, water and nutrient absorption
Cloaca		Storage and excretion of urine and faeces
Liver		Metabolism of absorbed nutrients, production of bile acids and bile salts
Pancreas		Secretion of digestive enzymes

here (entire organ mass) we assume that organ size roughly equates to organ function.

The alimentary tract (primarily the gizzard, small intestine or gut to the rectum) and the liver to a lesser extent have been widely studied in birds and other animals. Accordingly, our review is restricted to those three organs. Lack of data rather than lack of interest precluded making equivalent studies of other organs involved more in intermediary metabolism.

CONSTRAINTS ON SIZE OF DIGESTIVE ORGANS

Before assessing variation in organ size, it is worth considering some general factors that may set upper bounds to the size of the digestive system in birds.

Space

It is obvious that there is a physical limit to the volume available for organs within the abdominal cavity of a bird. Fat deposits in the abdomen may further reduce the available space for the digestive tract. For example, migratory shorebirds deposit a thick layer of fat around the outer side of the gizzard, covering the intestines and rectum, and pressing up against the posterior end of the skeleton. In great knots (*Calidris tenuirostris*) about to depart on migration from Australia, fat in the abdominal cavity (95% of which was in discrete deposits) made up 38% of the total abdominal tissue mass (P.F. Battley, unpubl. data). At such times the profile of the abdomen

changes, with fat birds showing a “bulge” behind the legs (Owen, 1981; Wiersma and Piersma, 1995). Conflicts for space between fuel stores and organs may limit the maximum size of the digestive organs.

Mass

Internal organ mass may directly affect flying performance of the birds. The morphology and physiology of most birds favors minimal body mass. Because the costs of flight increase with body mass (Kvist et al. 2001) and maneuverability may be impaired at heavier masses (e.g. Kullberg et al. 1996; Metcalfe and Ure, 1995), minimizing digestive organ mass may be an important consideration. In a comparative study of raptors, Hilton et al. (1999) showed that “pursuing” species (that require fast and maneuverable flight) had shorter guts than “searching” species, presumably reflecting the pursuers’ need to minimize mass. The shorter retention time of these species would reduce the period of time they had food in their guts, also keeping body mass low, though at a cost of lowered digestive efficiency. Sedingler (1997) showed that grouse have ceca 4–5 times longer than waterfowl feeding on the same diet, and suggested that the small ceca in waterfowl reflect a balance between the costs of flight for waterfowl and the benefits of the ceca for nutrient balance.

Minimizing mass during flight has been proposed as the explanation for why some shorebirds seem to reduce the mass of their digestive organs shortly before departure on migratory flights (Piersma, 1998; Piersma et al. 1999b; Piersma et al. 1993). In these cases, reducing the size of the digestive organs would also increase the space available for fat deposition.

Energy Turnover

Even in animals at rest, mass-specific maintenance costs of the intestine and liver are greater than those of muscle and adipose tissue (Blaxter, 1989; see chapter 2 by Hume, this volume; Krebs, 1950; Scott and Evans, 1992). Reductions in metabolically active tissues therefore dramatically reduce basal energy requirements (Battley et al. 2001a; Konarzewski and Diamond, 1995).

CHANGING ORGAN SIZES IN GALLIFORMES, PASSERINES, WADERS, AND WATERFOWL

Organ size and mass changes are widespread and substantial in wild and captive birds. Figure 8.1 summarizes, from published literature, the magnitude of changes in three major gastrointestinal components, the gizzard, gut or small intestine, and liver. Data are separated into four taxonomic groups: galliformes (primarily grouse and quail), passerines, waders (shorebirds), and waterfowl. Changes in organ mass of 20–80% were common across a wide range of species; length changes of the intestine were lower, generally 10–20%.

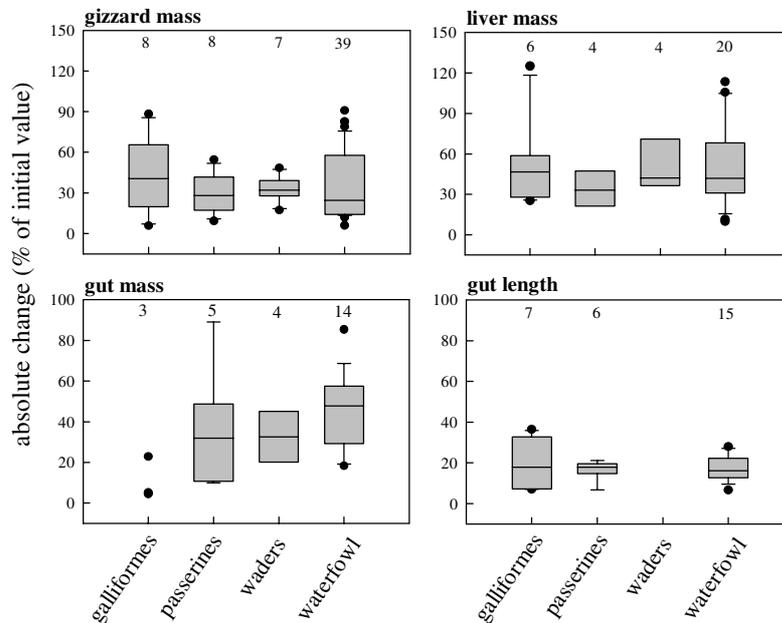


Fig. 8.1. Absolute change (either increase or decrease) in digestive organs of birds. Data represent maximum percent changes recorded in studies for age- or sex-classes of birds, due to factors including diet type or quality, migration, breeding, and food intake. Measurements from wild and captive birds are included. The gut category represents data for both the entire gut (including ceca and rectum) and the small intestine only. Sample sizes for each taxonomic group are given above the box or points. Boxes represent the 25–75 percentiles (divided by the median), whiskers represent the 10th and 90th percentiles, and outliers are shown as dots. For groups with only a few values, individual data points are plotted.

Interspecific Comparisons

Surprisingly few interspecific comparisons of digestive organ size in birds have been made (Table 8.2) and the comprehensiveness of the comparisons varied greatly (sample sizes varied from 3 to 154 species). Substantial variation in organ size between species was attributed to differences in diet even though a direct link was not always established. A dietary explanation was suggested when variation in organ mass could not be fully accounted for by differences in body mass. Differences in gizzard and intestine mass were attributed to diet. For the gizzard, hardness of the diet is implicated, while for the intestine ease of energy assimilation of the diet is suggested (DuBow, 1985; Richardson and Wooller, 1986).

Intraspecific Comparisons

Numerous studies have compared organ sizes in groups of birds collected during different periods of the year, or under different ecological or energetic conditions. For galliformes, the literature includes a good mixture

Table 10.2. Interspecific comparisons of digestive organ size and dietary factors in wild birds

Organ	Taxonomic group	No. of spp.	Genera	Factor	Measure	Response	Reason	Explanation	Source
Gizzard	Galliformes	10	<i>Bonasa, Dendragapus, Lagopus, Tetrao</i>	Species	Length	Varied	Diet	Spruce grouse feeding on pine and spruce needles had especially large gizzards.	1
	Psittaciformes	6	<i>Barnadius, Glossopsitta, Neophema, Melopsittacus, Platycercus, Trichoglossus</i>	Diet	Length	Varied	Diet	Nectar-feeding lorikeets had smaller gizzards than nonnectarivorous parrots.	2
	Passeriformes	20	<i>Acanthiza, Anthochaera, Colluricincla, Eopsaltria, Lichmera, Malurus, Meliphaga, Pachycephala, Pardalotus, Phylidonyris, Sericornis, Smicromis, Zosterops</i>	Diet	Mass	Varied	Diet	Nectarivores had smaller gizzards than insectivores of similar size, apart from two species of nectarivores that include larger insects in their diets.	3
	Charadriiformes	19	<i>Arenaria, Calidris, Charadrius, Haematopus, Limosa, Numenius, Tringa</i>	Species	Mass	Varied	Diet	Species feeding on hard prey had gizzards much heavier than the (allometric) average.	4
	Anseriformes	18	<i>Anas, Aythya, Branta, Bucephala, Clangula, Lophodytes, Mergus, Somateria</i>	Species	Mass	Varied	Diet	Comparison of feeding guilds – carnivore, omnivore, and herbivore. Differences in organ mass between species over and above differences due to body mass.	5
	Anseriformes	5	<i>Aythya</i> spp.	Species	Mass	Varied	Diet?	Differences between some species remained after body mass was accounted for.	6

contd.

Table 10.2 *cont'd.*

Organ	Taxonomic group	No. of spp.	Genera	Factor	Measure	Response	Reason	Explanation	Source
	Anseriformes	5	<i>Clangula, Histrionicus, Melanitta, Somateria</i>	Species	Mass	Varied	Diet	Scaled against body mass, largest gizzards in species with high proportions of hard prey.	7
Gizzard + intestine									
	Passeriformes	34	34 genera of New World passerines	Diet	Structure	Varied	Diet	Insectivores, frugivores and granivores separable on gizzard and intestine morphology.	8
Intestine									
	Galliformes	20	<i>Alectoris, Bonasa, Callipepla, Diet Canachites, Centrocerus, Colinus, Cyrtonyx, Dendragapus, Lagopus, Lophortyx, Meleagris, Oreortyx, Pedioecetes, Perdix, Phasianus, Tetrao, Tympanuchus</i>	Diet	Length	Varied	Diet	Grouse ("browsers") have longer intestines for their mass than seed-eating galliformes.	9
	Galliformes	3	<i>Lagopus</i>	Diet	Length	Varied	Diet	Length of intestine reflects diet of the three species – willow ptarmigan has shortest intestine, eats willow twigs and buds. Rock and white-tailed ptarmigan consume more birch, or have a more varied diet, and have longer intestines.	10

cont'd.

Table 10.2 *cont'd.*

Organ	Taxonomic Group	No. of spp.	Genera	Factor	Measure	Response	Reason	Explanation	Source
	Passeriformes	20	<i>Acanthorhynchus</i> , <i>Acanthiza</i> , <i>Anthochaera</i> , <i>Colluricincla</i> , <i>Eopsaltria</i> , <i>Lichmera</i> , <i>Malurus</i> , <i>Meliphaga</i> , <i>Pachycephala</i> , <i>Pardalotus</i> , <i>Phylidonyris</i> , <i>Sericornis</i> , <i>Sminthopsis</i> , <i>Zosterops</i>	Diet	Mass	Varied	Diet	Insectivores had longer intestines for their mass than nectarivores, reflecting the more easily assimilated food (nectar).	3
	Anseriformes	5	<i>Aythya</i> spp.	Species	Mass	Varied	Diet?	Differences among some species remained after body mass was accounted for.	6
	Anseriformes	5	<i>Clangula</i> , <i>Histrionicus</i> , <i>Melanitta</i> , <i>Somateria</i>	Species	Mass	Varied	Diet?	Scaled against body mass, longest in common eider and shortest in harlequin duck and black scoter.	7
Liver	Anseriformes	5	<i>Clangula</i> , <i>Histrionicus</i> , <i>Melanitta</i> , <i>Somateria</i>	Species	Mass	None	None	Scaled against body mass, no difference among species.	7

¹Moss (1983); ²Richardson and Woller (1990); ³Richardson and Woller (1986); ⁴Piersma et al. (1993); ⁵Barnes and Thomas (1987); ⁶Keohoe and Ankeny (1985); ⁷Gouldie and Ryan (1991); ⁸Ricklefs (1996); ⁹Leopold (1953); ¹⁰Moss (1974).

of comparisons between categories of wild birds and captive experiments. Studies of passerines have tested for organ changes due to diet, season, breeding, migration, fasting and energy turnover. Field studies of waders have focused on changes associated with migratory preparation and long-distance flight; captive studies have investigated the influence of diet hardness on gizzard size.

In the following summaries, organ changes in response to changing factors (e.g. season, diet quality) are identified, and the proposed reasons are given. Because different organs may respond differently to the same factor, data are summarized by organ rather than by study. As the biological questions addressed in these studies tend to be similar within bird groups, we review the intraspecific literature in four taxonomic groups: the galliformes, passerines, waders, and waterfowl.

By far the largest body of information has been compiled for waterfowl, for which seasonal changes in organ size have been studied in many taxa. These studies are sometimes difficult to interpret because more than one environmental or biological change occurred during the period. Nevertheless, combining results from these four groups gives a good overview of the nature of organ changes across diverse taxa (Table 8.3).

Gizzard

Food or energy intake was the most common factor affecting gizzard size in the studies surveyed. Changes in intake resulted from changing food quality, increased energy demand during migratory fueling or experimental work level, and changes in feeding activity during breeding. Any factor that causes a change in volume of food being processed will apparently result in a change in gizzard size.

The primary role of the gizzard is to mechanically grind or crush food. It is not surprising that the nature of the diet also influenced gizzard size in all four bird groups. The common dietary correlate with changes in gizzard size was fiber content of the food. Captive experiments demonstrated that birds on high-fiber diets have larger gizzards than those on low-fiber diets (Kehoe et al., 1988; Miller, 1975; Savory and Gentle, 1976; Starck, 1999), but a shift to a high-fiber diet is also generally associated with an increase in food intake to compensate for the lower digestive efficiency of a high-fiber diet (Liukkonen-Anttila et al., 1999; Miller, 1975; Savory and Gentle, 1976). Studies of wild birds demonstrated that fiber alone cannot explain some of the changes observed in gizzard size. In female mallards (*Anas platyrhynchos*), gizzards were generally large when fiber was high, but there was also an increase before migration, even though fiber was low at that time (Heitmeyer, 1998). In spur-winged geese (*Plectropterus gambiensis*), gizzards increased dramatically during molt when the geese eat water plants high in fiber (Halse, 1985). This increase was only partly directly due to increased fiber (gizzards increased proportionately more than other digestive organs), as gizzard mass

returned to original levels or lower after molt when dietary fiber content was higher (but intake presumably lower).

The hardness of the prey also directly affected gizzard size, at least in red knots (*Calidris canutus*) that crush shellfish whole in their gizzards (e.g. captive birds fed on soft prey had much smaller gizzards than wild, shellfish-eating counterparts: Piersma et al., 1993) and in canvasbacks (*Aythya affinis*) feeding on hard pondweed seeds during molt (Thompson and Drobney, 1994). Experiments with captive quail (*Coturnix coturnix*) demonstrated that changes in grinding requirements (through varying amounts of nondigestible fiber in the diet) led to dramatic, reversible changes in gizzard size that were considered to result primarily from diet composition rather than food intake (Starck, 1999). In passerines, an increase in the proportion of plant food in the diet also resulted in increased gizzard mass (Ankney and Scott, 1988; Spitzer, 1972) but whether the supposed lower digestibility of plant food affected gizzards via changes in intake or grinding requirements was not clear.

In waders, staging red knots that fly several thousand kilometers typically build up the size of the digestive tract (including the gizzard) as they fuel up (Piersma, 2002; Piersma et al. 1999b). In contrast, in a short-hop migrant, the western sandpiper (*Calidris mauri*), gizzard enlargement was found only during migration periods and not during fueling in the tropics that preceded it, suggesting that the increases were in response to feeding en route during migration rather than fueling beforehand (Guglielmo and Willians, 2003). Whether this reflects a general pattern in short-hop migrants (that need to be able to refuel rapidly during short stopovers) in contrast to long-haul migrants, is not known.

Decreases in gizzard mass were also recorded for nondietary reasons. In waders, a decrease in gizzard size just prior to migration has been documented in red knots and bar-tailed godwits (*Limosa lapponica*), and been interpreted as a strategic loss to minimize body mass for long migratory flights (Piersma, 1998; Piersma et al., 1999b; Piersma et al., 1993). During long-distance flight and fasting in captivity, digestive organs of great knots decreased in lean mass, reflecting unavoidable protein turnover and disuse atrophy (Battley et al., 2001b; Battley et al., 2000). Equivalent patterns were found in migratory passerines, with even more rapid changes than in the knots (Biebach, 1998; Hume and Biebach, 1996; Karasov and Pinshow, 1998). Passerines after long flights also had smaller gizzards than birds after shorter flights (Schwilch et al., 2002). Such decreases in gizzard mass can affect the immediate fueling capacity on arrival (Hume and Biebach, 1996; Karasov and Pinshow, 2000; Klaassen and Biebach, 1994). In waterfowl, factors associated with breeding were identified (egg formation: Mann and Sedinger, 1993) or implicated (postbreeding increase: Austin and Fredrickson, 1987) in gizzard reductions. A rapid decrease in gizzard size during breeding in female common eiders (*Somateria mollissima*), when birds feed very little if

at all, could reflect protein demand rather than “functional” atrophy (Korschgen, 1977).

Intestine

As with the gizzard, general diet type was associated with differences in intestine size (Table 8.3), particularly between galliform populations that fed on foods of differing digestibilities. Scottish red grouse (*Lagopus lagopus scoticus*) feeding on heather (*Calluna vulgaris*), high in fiber and tannins, had the longest guts of any population studied, while rock and white-tailed ptarmigan (*Lagopus mutus* and *Lagopus leucurus*) populations feeding on willow (*Salix*, which is highly digestible) had unusually short intestines (Moss, 1983). Likewise, black grouse (*Tetrao tetrix*) in Scotland feeding on heather had longer guts than Russian birds feeding on birch (*Betula*) catkins and twigs. Because high fiber results in low digestibility, lengthening of the intestine with high fiber levels allows for more food to be processed (higher intake) more efficiently. Moss (1989) showed that increasing the proportion of heather in the diet of captive red grouse resulted in increased food intake and intestine length. Concomitantly the heather in the diet was digested increasingly well (from a partial digestibility of 9.4% to the average for wild birds of 46%). He suggested that at high fiber levels, bulk limits food intake and the intestine (and perhaps more importantly the ceca) enlarges to improve digestion. For capercaillie (*Tetrao urogallus*), Russian birds had longer intestines than Scottish birds, despite similar diets, suggesting that the colder and shorter days in Russia resulted in higher food intake (Moss, 1983).

Although diet quality/fiber content and food intake interact strongly, other studies demonstrate that the intestine per se can respond to intake rather than fiber. Indeed, the factor most frequently identified behind changes in intestine length or mass was food intake. Rufous-collared sparrows (*Zonotrichia capensis*) had longer intestines in winter due to increased digesta volume (Novoa et al., 1996). Yet at the same time the diet shifted from seeds to high-energy insects, a change that was expected to lead to intestinal shortening. In waterfowl, changes in intestine mass were mostly ascribed to changes in intake, though increased intestine masses in birds on a low-quality or low-lipid diet probably reflected a need for increased digestive efficiency rather than changed food intake (Ankney and Afton, 1988; Thompson and Drobney, 1994). Food intake may also have been responsible for the increased intestinal size attributed to fiber (high-fiber diet mallards recorded by Kehoe et al., 1988).

In migrant passerines and waders, the intestine may show hypertrophy during fueling. Like the gizzard, the intestine responds to periods without food intake, whether during long-distance flight or during a sedentary experimental fasting period, with mass loss. For red knots, there is evidence of strategic mass reductions in the intestine before long-distance flights (Piersma et al., 1999b, also see below).

Table 8.3. Changes in three major components of the avian digestive system. Reasons given for any changes in the mass (or length for some intestinal studies) of the organ are summarized by taxonomic group. Numbers refer to the number of times that a change in organ size was attributed to that cause. Numbers in parentheses represent possible causes. Number of studies is the number reviewed for each organ/group. Because some studies comprised multiple comparisons or findings, the total number of causes documented may be higher than the number of studies.

Organ	Diet			Metabolism			Diges- tive effi- ciency	No expla- nation	No No. of studies	Sources	
	Intake Fibre	Qua- lity	Hard- ness	Fat	Protein	Strat- tegic mass loss					Flight
Gizzard											
<i>Galliformes</i>	3		3							4	1-4
<i>Passeriformes</i>	4	1				2	2		1	10	5-14
<i>Choradriiformes</i>	3		2			3	1			9	15-19
<i>Anseriformes</i>	7	2 (1)	1		1		1 (1)	3	3	29	20-45
Intestine											
<i>Galliformes</i>	1 (2)	1							1	11	4, 46-52
<i>Passeriformes</i>	5 (1)	(1)					1	2		11	5-7, 10-13, 53-55
<i>Choradriiformes</i>	4					2	1	1		6	15-19, 56
<i>Anseriformes</i>	6 (2)	1	2 (1)				1 (1)	1	3	18	21, 22, 25-31, 34-37, 43, 44

contd.

Table 8.3 cont'd...

Organ	Intake Fibre Qua- lity		Diet		Metabolism			No. Sources of explanatory studies
	Fibre	Quality	Hard- ness	Type	Fat	Protein	Strat- tegic mass loss	
<i>Galliformes</i>	(1)	1	1	(1)				1
<i>Passeriformes</i>	1	1			1		2	42, 4, 46, 57
<i>Charadriiformes</i>	4				3	1	1	67, 11, 12, 54
<i>Anseriformes</i>	4 (1)				4 (3)	(1)	(2)	715-19, 56, 58

Liver

¹Liukkonen-Anttila et al. (1999); ²Moss (1989); ³Savory and Gentle (1976); ⁴Starck (1999); ⁵Al-Dabbagh et al. (1987); ⁶Ankney and Scott (1988); ⁷Biebach (1998); ⁸Brugger (1991); ⁹Dykstra and Karasov (1992); ¹⁰Geluso and Hayes (1999); ¹¹Hume and Biebach (1996); ¹²Schwilch et al. (2002); ¹³Spitzer (1972); ¹⁴Walsberg and Thompson (1990); ¹⁵Battley et al. (2001b); ¹⁶Battley et al. (2000); ¹⁷Guglielmo and Williams (2003); ¹⁸Landys-Ciannelli et al. (2003); ¹⁹Piersma et al. (1999b); ²⁰Ankney (1977); ²¹Ankney and Afion (1988); ²²Austin and Fredrickson (1987); ²³Drobney (1984); ²⁴DuBowy (1985); ²⁵Gauthier et al. (1992a); ²⁶Gauthier et al. (1992b); ²⁷Gauthier et al. (1992a); ²⁸Halse (1985); ²⁹Halse (1985); ³⁰Heitmeyer (1998); ³¹Hobaugh (1985); ³²Keohoe et al. (1988); ³³Klaassen (1999); ³⁴Korschgen (1977); ³⁵Mainguy and Thomas (1985); ³⁶Mann and Sedinger (1993); ³⁷Miller (1975); ³⁸Miller (1986); ³⁹Moorman et al. (1992); ⁴⁰Paulus (1982); ⁴¹Reinecke et al. (1982); ⁴²Smith and Sheeley (1993); ⁴³Thompson and Drobney (1994); ⁴⁴Tome (1984); ⁴⁵Whyte and Bolen (1985); ⁴⁶Fenna and Boag (1974); ⁴⁷Leopold (1953); ⁴⁸Millán et al. (2001); ⁴⁹Moss (1974); ⁵⁰Moss (1983); ⁵¹Pulliaainen (1976); ⁵²Starck and Kloss (1995); ⁵³Davis (1961); ⁵⁴Karasov and Pinshow (1998); ⁵⁵Novoa et al. (1996); ⁵⁶Piersma (2002); ⁵⁷Mortensen et al. (1983); ⁵⁸Piersma and Gill (1998).

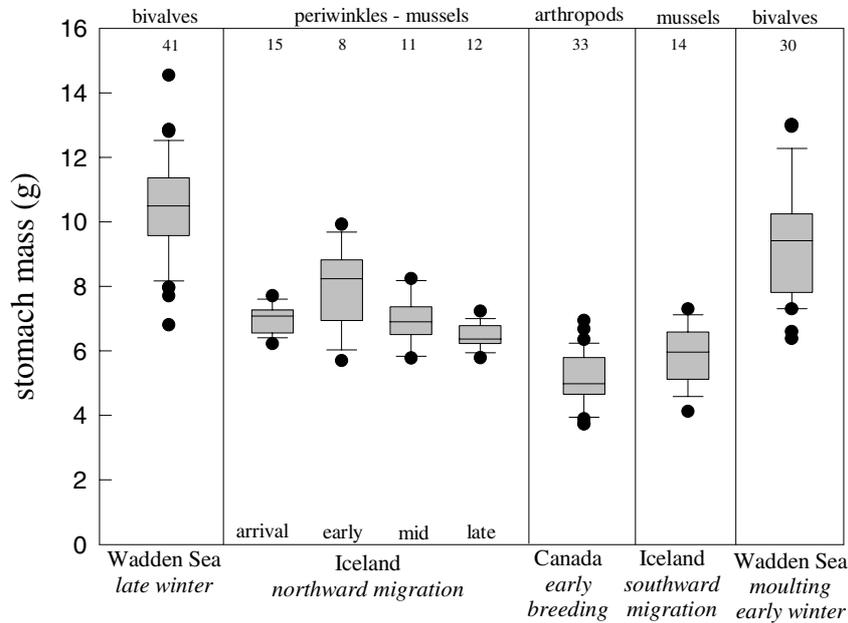


Fig. 8.2. Changes in the stomach mass of red knots of the subspecies *islandica* through the annual cycle, with indications of diet type and general activity. Data for the Wadden Sea are from T. Piersma (unpublished), for Iceland from Piersma et al. (1999b) and for Arctic Canada (northern Ellesmere Island) from R.I.G. Morrison, N.C. Davidson & T. Piersma (unpubl. data). Sample sizes are given above each box.

Liver

Although livers show as much capacity for change as the gizzard and the intestine (Fig. 8.1), liver size changes have attracted less attention. As with gizzard and intestine masses, increases in liver mass were associated with increased energy intake, while decreases were associated with flight and fasting (Table 8.3). In red knots and other very long-distance migrant waders, there is evidence that livers show strategic mass reductions before take-off (Piersma, 1998; Piersma and Gill, 1998; Piersma et al., 1999b).

In addition, livers may undergo considerable temporary mass increases before and during the egg-laying period (Ankney and Afton, 1988; Drobney, 1984). It has been suggested that these variations correlated with changes in the intensity of lipid storage and protein metabolism (Ankney and Scott, 1988; Mortensen et al., 1983), mechanisms that would also explain changes in liver size during simultaneous molt in waterfowl (Austin and Fredrickson, 1987).

In summary, the gizzard generally changes size with changes in fiber content (energy dilution of the diet), diet hardness (texture; this can also be a factor in fiber content), and flight considerations. The small intestine generally changes size with fiber content and/or substantial changes in food

intake. The liver changes size with dietary dilution, food intake, and flight mass considerations (and undoubtedly also diet secondary chemistry, though this was not reviewed here). Thus, knowing the generality of these changes, we should be able to predict how changes in organ size will occur in birds in new situations.

FLEXIBILITY OF THE DIGESTIVE TRACT: DIET-RELATED VARIATIONS WITHIN RED KNOTS

Correlations between digestive organ size changes and food type and intake illustrate the variety of functional interactions that can be found in birds. It is probable that the same range of interactions occur within species or even individuals through an annual cycle. We examine this possibility on the basis of the variable masses of the stomach (i.e. gizzard plus proventriculus, which is small in most waders: Piersma et al., 1993) of the red knot. This molluskivore species has a relatively large stomach (see Table 8.2 and below) and spends most of the year in seashore habitats, but breeds much farther north on high arctic tundra where it eats spiders and arthropods rather than bivalves and gastropods (Piersma et al., 2003). Red knots enable us to examine the effects of diet type, food requirement, and long-distance flight on digestive organ size within a species.

The red knots that breed in northern Greenland and northeast Canadian Arctic and spend the nonbreeding season in northwestern Europe (subspecies *islandica*), show a twofold variation in stomach mass over the course of a year (Fig. 8.2). In late winter on the nonbreeding grounds, the stomach has an average mass of more than 10 g, while on the tundra breeding grounds the stomach weighs only about 5 g. These data provide a basis for evaluating the roles of diet type, food intake and possible weight savings during long-distance flights. The stark difference in stomach size during breeding and overwintering cannot be a result of differences in energy turnover, as the overall energy expenditure of *islandica* knots on the tundra breeding grounds and the coasts of Europe in midwinter is remarkably similar (Piersma, 2002; Wiersma and Piersma, 1994). The difference in stomach mass must instead reflect the contrast in diet type between the two periods; the spider and arthropod diet on the tundra requires only half the stomach mass of the hard-shelled mollusk diet in late winter. Increases in stomach mass of red knots between early and late winter in the Wadden Sea are probably due to increases in energy expenditure (Wiersma and Piersma, 1994) and therefore higher food intake on the molluskan diet.

We have experimentally confirmed that stomach size does affect intake rate in knots eating hard-shelled prey. It is possible to manipulate the stomach size of captive knots by feeding them soft food pellets rather than their natural hard-shelled prey (Dietz et al., 1999a; Piersma et al., 1993). The gizzard of

long-term captive birds is roughly a quarter to half the mass of wild birds'. By using ultrasonography to non-invasively estimate stomach size and mass (Dietz et al., 1999a; Dietz et al., 1999b; Starck et al., 2001), the relationship between stomach size and intake rate could be studied. In an experimental situation, hungry red knots with reduced stomachs had significantly lower intake rates than birds with large stomachs (van Gils et al., 2003). In fact, the maximal sustained intake rate of hard-shelled prey (including time spent in digestive pauses) was directly proportional to stomach size. In contrast, when feeding on soft bivalve flesh (shells removed) there was no difference in intake rate between the groups.

Changes in stomach mass of *islandica* knots during their stopover in Iceland (Fig. 8.2; Piersma et al. 1999b) illustrate the loss of stomach mass before and/or during a 2,500 km flight from the southern North Sea basin to Iceland (note low stomach masses at arrival) and the build-up of stomach mass during the fueling phase when food intake is necessarily high. The subsequent decline in stomach mass as birds approach departure condition for another 2,000–3,000 km flight from Iceland to the tundra breeding grounds may be an endogenously controlled mass reduction before flight or an adaptive preparation to the impending diet change on the breeding grounds (Piersma et al. 1999a). A diet shift during staging from periwinkles to mussels supplemented with chironomid larvae (Alerstam et al. 1992) could either reflect or induce such a change. The stomach mass of red knots staging in Iceland during southward migration is low and may still reflect adjustments to a diet of soft foods on the tundra. Small stomachs are likewise found in red knots of the *canutus* subspecies arriving in the Dutch Wadden Sea from the Siberian tundra (A. Dekinga et al. unpubl. data).

During their spring stopover in Delaware Bay, red knots of the *rufa* subspecies totally rely on the small eggs of horseshoe crabs (*Limulus polyphemus*) which are abundant on some beaches (Tsipoura and Burger, 1999). Horseshoe crab eggs require a grinding rather than a crushing action of the stomach, and small stones are found in the stomachs of red knots from Delaware Bay, presumably to assist with grinding. Patterns of change in stomach mass are remarkably similar in Iceland and Delaware Bay despite considerable differences in prey type and processing style (Piersma et al. 1999a). An initial increase in size at both sites is followed by a decrease in mass. Stomach masses peak at about 8 g when refueling rates are highest. The time course of changes in stomach mass has been confirmed by experimental studies on red knots that demonstrate halvings and doublings of stomach mass over 5–7 days if the diet shifts are drastic (Dekinga et al. 2001).

Recent field studies have confirmed the tight relationships between diet and stomach mass (estimated from ultrasonography) of radio-tagged red knots in the Wadden Sea (Piersma et al., 1999a). In August 1997 estimated stomach mass correlated with the extent to which the flocks in which

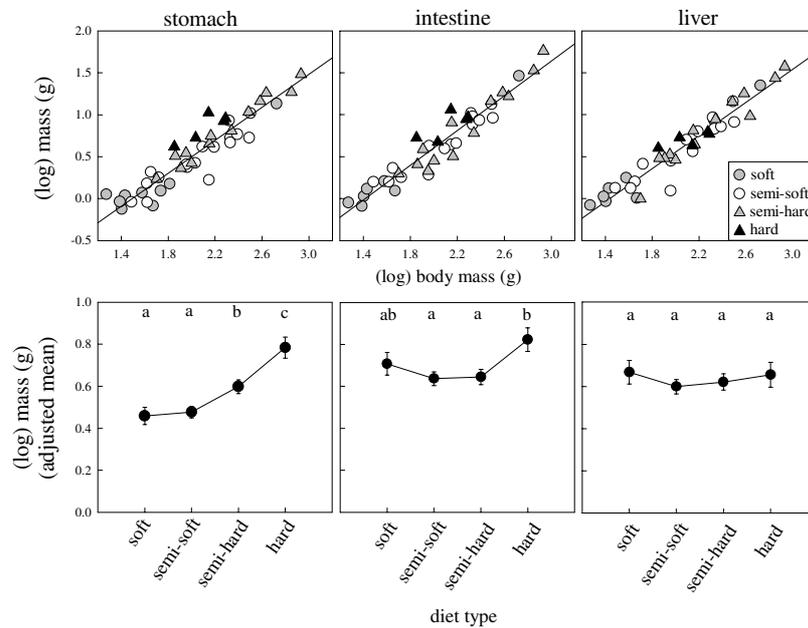


Fig. 8.3. Allometry of the fresh masses of stomach, intestine (the entire but emptied intestinal tract) and liver in 41 species of wader from four different families, assigned to four different diet “hardness” categories. The lower three panels show the (log) mean organ masses adjusted for differences in (log) body mass for the four diet categories. Diet categories sharing the same letter do not differ statistically. Covariance analyses were carried out in SYSTAT 10, and, incidentally, found no evidence for organ mass differences at the family level.

radio-tagged birds were found fed on cockles (*Cerastoderma edule*) rather than other bivalve prey that are easier to swallow and to crack. No other phenotypic characteristic of the radio-tagged individuals (sex, age, bill length, wing length, tarsus length, body mass) correlated with these differences in diet. Similarly, in August-September 1998 red knots fed at two sites, one dominated by rather soft, small shorecrabs (*Carcinus maenas*), and another where cockles were abundant. Radio-tagged individuals recorded feeding only at the shorecrab site had significantly smaller stomachs than individuals found only at the cockle site. Individuals feeding at both sites had intermediate stomach sizes (Piersma et al., 1999a).

FEEDING ECOLOGY AND DIGESTIVE TRACT: COMPARISONS AMONG WADERS

Our work on red knots has demonstrated that this species, depending on ecological context, can have stomachs that are either very small (in captive birds feeding on soft food pellets and in breeding birds on the tundra) or very

large (in wintering birds needing lots of hard-shelled mollusks to maintain a favorable energy balance). It would be very hard to pick a stomach mass 'typical' of red knots for comparative analyses (cf. Harvey and Pagel, 1991) and, given the above summaries of studies on other birds (Fig. 8.1), this is likely to be true for most birds with seasonally variable diets. For a comparative analysis of organ size characteristics in such an ecologically and phylogenetically homogeneous group as the waders it seems much more relevant to categorize the diet of the birds than to worry about phylogenetic relationships. We therefore performed an allometric comparative analysis (Ricklefs and Starck, 1996) of the size of stomach, intestine, and liver in 41 wader species belonging to four Charadriiform families: oystercatchers Haematopodidae, avocets Recurvirostridae, plovers Charadriidae, and sandpipers and allies Scolopacidae.

The diet of each species was categorized on the basis of stomach and intestinal content and on data from the literature (Table 8.4). For species with large body size differences between the sexes (ruff *Philomachus pugnax*, Eurasian curlew *Numenius arquata*, and bar-tailed godwit *Limosa lapponica*), males and females were handled as separate entities, bringing the effective sample size to 44 taxa. We then assigned scores to the diets, ranging from 1–4; these are 1 = only soft prey items such as polychaete worms, or extracted shell flesh as in oystercatchers, 2 = a mix of soft prey and soft-cased arthropods, 3 = mainly arthropods, and 4 = predominantly hard-shelled molluscan prey). We tested the prediction from this review and earlier studies (Piersma et al. 1999a; Piersma et al. 1993) that the stomach mass increases with diet hardness. In view of the interspecific correlation between stomach and intestine size shown from a smaller database (Piersma et al. 1999a), we predicted that a harder diet should also lead to a larger intestine.

For stomach mass, increasing diet hardness clearly led to a heavier stomach (Fig. 8.3) while no differences were found between the two soft prey categories (1 and 2). As with red knot stomachs from the tundra and coastal wintering areas (Fig. 8.2), the stomach mass (adjusted for body mass) for wader species eating hard-shelled prey was more than double that of species eating soft prey. The intestine of molluskivore species (category 4) was larger than that of taxa of intermediate diet categories (2 and 3) but not of species with the softest diet. For species that ingest mollusks whole, crush the prey in their stomach, and evacuate the crushed shells via the intestinal tract, heavier intestines may reflect the need to withstand the wear and tear of hard and sharp fragments during passage. As expected, there were no differences in the relative size of the liver between the different diet categories.

Table 8.4. Source details and diets of shorebirds used in analyses of digestive organ size in relation to body mass and diet. Species are ordered taxonomically. Specimens from Canada are breeding birds from Churchill, Manitoba (R.E. Ricklefs, unpub. data). All other specimens were analyzed at the Royal Netherlands Institute of Sea Research. Diet code is a categorical scale from soft (1) to hard (4).

Family	Common Name	Scientific Name	n	Localities	Predominant Diet	Code
Haematopodidae	Eurasian oystercatcher	<i>Haematopus ostralegus</i>	4	Netherlands	bivalve flesh, polychaetes	1
	recurvirostridae	<i>Recurvirostra avosetta</i>	3	Netherlands, Germany	small worms + crustaceans	2
Charadriidae	northern lapwing	<i>Vanellus vanellus</i>	1	Netherlands	earthworms, terrestrial insects	2
	Eurasian golden-plover	<i>Pluvialis apricaria</i>	107	Netherlands	earthworms, terrestrial insects	2
	American golden-plover	<i>Pluvialis dominica</i>	4	Canada	terrestrial insects	3
	grey plover	<i>Pluvialis squatarola</i>	7	Guinea-Bissau, Mauritania, Netherlands	polychaetes, mollusks	2
	ringed plover	<i>Charadrius hiaticula</i>	6	Mauritania, Morocco, Wadden Sea	polychaetes	1
semipalmated plover		<i>Charadrius semipalmatus</i>	5	Canada	polychaetes, gastropods	2
	Kentish plover	<i>Charadrius alexandrinus</i>	2	Morocco,	crustaceans, polychaetes and mollusks Mauritania	2
greater sand-plover		<i>Charadrius leschenaultii</i>	4	NW Australia	crustaceans including crabs, mollusks	3
Oriental plover		<i>Charadrius veredus</i>	2	NW Australia	terrestrial insects (mainly beetles), snails and seeds	3
Scolopacidae	jack snipe	<i>Lymnocyrtus minimus</i>	1	Netherlands	annelids, adult and larval insects	1
	great snipe	<i>Gallinago media</i>	4	Norway	earthworms, gastropods, adult and larval insects	2

contd.

Table 8.4 *contd.*

Family	Common Name	Scientific Name	n	Localities	Predominant Diet	Code
	common snipe	<i>Gallinago gallinago</i>	1	Europe	larval (+adult) insects, earthworms, small crustaceans	2
	short-billed dowitcher	<i>Limnodromus griseus</i>	3	Canada	larval, pupal and adult insects	2
	black-tailed godwit	<i>Limosa limosa</i>	3	Netherlands	adult and larval insects	2
	Hudsonian godwit	<i>Limosa haemastica</i>	3	Canada	larval insects	2
	bar-tailed godwit	<i>Limosa lapponica</i>	44	Netherlands	polychaetes, bivalves, crustaceans, Tipulid larvae, earthworms	3
	little curlew	<i>Numenius minutus</i>	3	NW Australia	insects, spiders, vegetable matter	3
	whimbrel	<i>Numenius phaeopus</i>	6	Mauritania, Netherlands, Canada	crabs, terrestrial arthropods, earthworms	3
	Eurasian curlew	<i>Numenius arquata</i>	5	Netherlands	mollusks, crabs, polychaetes, earthworms	3
	redshank	<i>Tringa totanus</i>	4	Wadden Sea, Mauritania	crustaceans	2
	lesser yellowlegs	<i>Tringa flavipes</i>	4	Canada	larval and adult insects	3
	terek sandpiper	<i>Tringa terek</i>	2	NW Australia	crabs	3
	ruddy turnstone	<i>Arenaria interpres</i>	6	Morocco, Mauritania	crustaceans, annelids, mollusks	2
	surfbird	<i>Aphriza virgata</i>	5	Alaska	barnacles, bivalves, periwinkles and limpets	4
	great knot	<i>Calidris tenuirostris</i>	56	NW Australia	bivalves, gastropods, crustaceans, annelids, sea cucumbers	4
	red knot	<i>Calidris canutus</i>	40	Netherlands, Germany	bivalves, gastropods, some crustaceans	4

contd.

Table 8.4 contd.

Family	Common Name	Scientific Name	n	Localities	Predominant Diet	Code
	sanderling	<i>Calidris alba</i>	7	Morocco, Netherlands, Brazil	small crustacea	2
	semipalmated sandpiper	<i>Calidris pusilla</i>	1	Brazil	polychaetes	1
	red-necked stint	<i>Calidris ruficollis</i>	157	SE Australia	small worms and mollusks	1
	little stint	<i>Calidris minuta</i>	17	Guinea-Bissau, Mauritania, Morocco	small worms	1
	least sandpiper	<i>Calidris minutilla</i>	3	Canada	crustaceans, insects, worms	2
	white-rumped sandpiper	<i>Calidris fuscicollis</i>	6	Brazil	worms	1
	sharp-tailed sandpiper	<i>Calidris acuminata</i>	1	NW Australia	insects, crustaceans, worms	2
	curlew sandpiper	<i>Calidris ferruginea</i>	2	Mauritania	worms	1
	purple sandpiper	<i>Calidris maritima</i>	26	Scotland, Norway	gastropods, bivalves	4
	rock sandpiper	<i>Calidris ptilocnemis</i>	20	Alaska	gastropods, bivalves	4
	dunlin	<i>Calidris alpina</i>	98	Guinea-Bissau, Mauritania, Morocco, Wadden Sea, Canada	worms, small crustaceans and mollusks	2
	stilt sandpiper	<i>Micropalama himantopus</i>	4	Canada	adult and larval insects, snails, seeds	3
	ruff	<i>Philomachus pugnax</i>	58	Netherlands	pupal and adult terrestrial insects, worms	3
	reeve	<i>Philomachus pugnax</i>	19	Netherlands	insects, worms	2
	red-necked phalarope	<i>Phalaropus lobatus</i>	5	Canada	insects, small invertebrates	2

Adaptive interplay

GENERAL DISCUSSION

The three digestive organs reviewed here are all equally flexible in size in the wild and in captivity. While the reasons behind the size changes overlap, interpretation of size changes of the gizzard (digestive preparations), the intestine (digestion and absorption), and the liver (various metabolic processes related to digestion) becomes more uncertain the further one “climbs the digestive chain”. This may reflect the diversity of physiological functions of each of the organs (i.e. low in gizzard, high in liver), on the basis of which we would expect size variations in gizzards to be most easily accounted for by characteristics of diet and food intake characteristics. However, it may also reflect our ignorance about these functions, and the relationships between functional capacities and size, of the most complicated and understudied organ, the liver (e.g. Whittow, 2000). Expanding the view to the entire digestive system (Table 8.1), do we expect strong correlation between size and capacity of these organs, which vary in complexity and range of function? In other words, is there consistent coadjustment between different parts of the digestive tract (Weibel, 2000)? Such studies would call for a much better understanding of the specific functions of different digestive organs, especially the intestine, the liver and accessory organs such as the pancreas and the ceca.

Detailed studies on organ function are also required to assess the other side of the equation, i.e. the costs associated with having organs of a certain size. Organs are clearly not maintained at maximal size and capacity throughout the year, but must reflect the costs and benefits in different ecological contexts. For example, what are the yields relative to the costs (in energetic terms) of temporary reductions in organ size and capacity before and during migration flights with different lengths and risk factors (Piersma, 1998; Weber and Hedenström, 2001)? This calls for studies of the trade-offs in functional morphology, leading to the field “behavioral ecology” of organ systems (Piersma and Lindström, 1997).

Piersma et al. (1993) provided a heuristic scheme for understanding the influences of exogenous and endogenous factors on gizzard mass (Fig. 8.4). In general, some components of this model were supported in the next ten years. The model suggests that the mass of the gizzard is influenced by direct (endurance) training and by atrophy through disuse if the ingested volume of food decreases and/or food gets softer or less fibrous, and additionally by factors such as protein reallocation. There is strong evidence for exogenous effects but the presence of a direct influence of an endogenous circannual oscillator on gizzard mass remains to be demonstrated (note that Dietz et al. 1999b, failed to find such an effect in red knots). Likewise, the extent to which proteins stored in the gizzard may be strategically shifted to other organs during the final phase of a migratory stopover, remains to be properly documented as well.

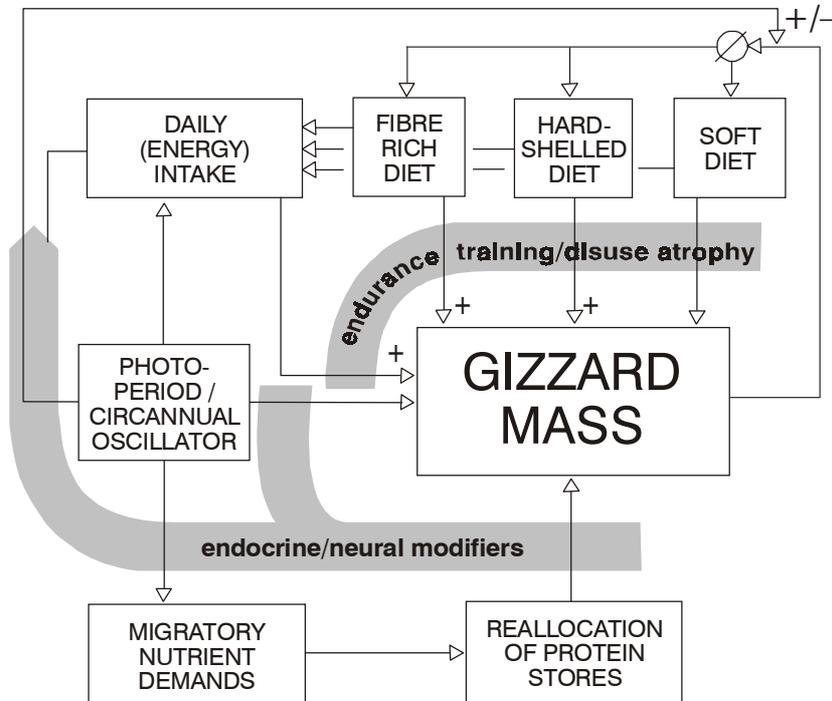


Fig. 8.4. Scheme outlining the causal feedback loops between gizzard mass, diet type and other external or internal modifiers. The valve in the upper right corner of the scheme indicates that there may be a minimum gizzard mass that determines whether or not hard-shelled or fibrous rich food can actually be ingested. Unmodified from Piersma et al. (1993).

Levels of adaptive modification other than the size and capacity of the digestive organs exist (Pérez-Barbería et al., 2001). For example, gizzard linings may become more keratinized and the thickness of the intestinal mucosa may increase as prey become harder and their fragments sharper. We know that some waders replace their entire gizzard linings periodically (Meeuws et al., 1985) but the functional context and consequences for feeding are not yet clear. In addition to structural modifications, there may be chemical adaptations required to feed on parts of plants, including fruits, that are not readily digestible and may carry obnoxious chemical compounds (also see Levey and Martínez del Rio, 2001).

An important area not explored in this chapter is whether there are genetic limits to the enormous phenotypic flexibility shown by digestive organs. How much additive genetic variation is there in organ size and/or flexibility for natural (or artificial) selection to work on? As an example, in a study of differences in growth, energetics, organ size and capacity in junglefowl (*Gallus gallus*) and their highly selected relatives, domestic broiler chickens (Jackson and Diamond, 1996), it was shown that selection for big bodies, rapid growth,

and long and heavy intestines has also led to small brains and light bones. This implies (1) that there is genetic variation for selection to work on and (2) that trade-offs exist not just within, but between different organ systems in the body. Complete understanding of variation in organ dimensions will eventually require studies of these trade-offs.

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