

S37.2: Digestive strategies of avian herbivores

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Body size puts limits on the quality of foods that can be eaten by herbivores and influences the processes by which the food is digested. Recent work on avian herbivores demonstrates that selective retention of digesta and nutrient uptake rates may help minimise these allometric constraints. Like other foregut fermenting vertebrates, the Hoatzin selectively retains particulate digesta and passes the liquid fraction much more quickly. The opposite pattern, selective retention of fluid digesta, is typical of some avian cecum fermenters such as galliformes although other hindgut fermenting birds such as the Emu *Dromaius novaehollandiae*, Canada Goose *Branta canadensis*, and Snow Goose *Anser caerulescens* show no selective retention of digesta at the whole-animal scale. For geese, however, the lack of whole-animal differences in passage rate of fluid or particulate fractions of the digesta may be the result of an interaction between selective retention of fluid digesta in the hindgut and increased mechanical processing of particulate digesta in the foregut (i.e. gizzard). Patterns of specific uptake rates in the goose support the hypothesis that birds feeding on relatively bulky diets maintain high rates of ileal uptake and thereby increase their integrated uptake capacity (IUC) without the costs associated with increasing gut mass. The cecal contribution to IUC for glucose and amino acids was higher for geese (24% and 6-19%) compared to chickens (2% and 4%), but modest compared to those for grouse (49% and 25%) and is consistent with the hypothesis that galliformes rely more on caecal fermentation and absorption of the products than do geese. Relatively high rates of aminopeptidase-N activity in the goose caeca (accounting for 24% of total hydrolytic capacity) along with high nutrient uptake capacity supports the hypothesis that the avian caeca plays an important role in protein digestion and absorption.

INTRODUCTION

Herbivore diet selection is influenced by available food nutrients, the relative ability to extract nutrients from the food, and anti-nutrient features such as indigestible bulk and toxins. Body size is thought to put limits on the quality of foods that can be eaten by herbivores and to influence the processes by which the food is digested. But current ideas about how body size influences diet breadth, mode of digestion, and ability to tolerate possibly antinutritive plant secondary metabolites are either mainly theoretical, based on a limited number of studies, or are based on ruminant physiology that may not apply to hindgut fermenters.

Avian herbivores are particularly interesting in terms of the proposed allometric constraints because they have relatively high metabolic rates and are generally smaller in size compared to mammalian herbivores. The relative rarity of avian herbivores suggests these allometric constraints are difficult to circumvent. Only 3% of existing bird species eat leaves and most birds that eat leaves are poor flyers (e.g. grouse, quail, ptarmigan (all in the Order Galliformes), and the Hoatzin *Opisthocomus hoazin*). True geese (Order Anseriformes, Family Anatidae, Tribe Anserini) are exceptional herbivorous birds in that they are strong flyers that range in adult body size from the diminutive Ross' *Anser rossii* and Red-breasted Goose *Branta ruficollis* (ca. 1000 g) to the 'Giant' subspecies of Canada Goose *Branta canadensis maxima* (ca. 7000 g).

In this review, I will primarily discuss recent work on the digestive strategies of certain species of true geese in relation to other avian herbivores, specifically, and to vertebrate herbivores, generally. I use the term 'digestive strategy' as shorthand for the interplay between energy and nutrients in ingested food, the nutritional requirements of the forager, and features of digestive

physiology (retention time, extraction efficiency, gut morphometrics, hydrolysis rates of digestive enzymes, nutrient uptake rates) that influence the supply of usable energy and nutrients to the forager. Excellent recent reviews are available that outline how adjustments in digestive physiology influence the supply of energy and nutrients in primarily insectivorous, frugivorous, and nectarivorous birds (Martinez del Rio *et al.* 1994, Karasov 1996, Karasov & Hume 1997). Here I will focus on what we know about selected aspects of the digestive strategies of herbivorous birds.

I begin with a brief introduction to the theory derived from studies of mostly ruminants that relates body size and fibre digestion. I then discuss how recent work on small hindgut-fermenting herbivores demonstrates that selective retention of more digestible fractions of the diet and perhaps increased specific nutrient uptake rates and hydrolysis rates of digestive enzymes can ease or eliminate these allometric constraints. Most of the review focuses on whether these mechanisms for reducing the proposed allometric constraints are important for small avian herbivores.

Body size, metabolism, and fiber digestion

One feature of diet quality is fibre, which is typically considered the most important factor determining intake and digestibility in herbivores. In general, as body size of herbivores declines so does the fibre level of the selected diet and the proportion of energy requirements satisfied by energy yield from fermentation (Illius & Gordan 1993). This empirically and theoretically-based pattern of decline in reliance on fibre with decreasing body size in vertebrate herbivores is believed to occur because of unequal allometries of energy requirements and gut capacity (Demment & VanSoest 1985).

If metabolic rate determines the energetic requirement and gut size determines the capacity to process food into nutrients, then smaller herbivores generally and avian herbivores especially must process food rapidly to satisfy their higher mass-specific metabolic rates. Reliance on fermentation is also predicted to become increasingly difficult with decreasing body mass because fast passage rates and smaller absolute size of fermentation chamber reduce the efficiency of fermentative use of fibrous material.

More recently, however, the applicability of these allometric relationships for explaining digestive strategies of smaller herbivores has been questioned (Foley & Cork 1992, Cork 1994). Two of these criticisms are particularly pertinent for understanding digestive strategies of avian herbivores. First, the digestive strategies of smaller mammalian herbivores may not maximise fermentation of fibre by maximising retention time as assumed for ruminants (Parra 1978, Demment & Van Soest 1985). Instead, smaller mammalian herbivores may increase intake and passage rates and reduce fibre digestibility when eating higher fibre diets so that energy or nutrient gain is maximised. Apparently, higher intake increases energy yield from digestion of cell contents and not cell wall which compensates for increased endogenous losses caused by higher fibre intake (Cork 1994). The prediction is that small herbivores eating higher fibre diets will increase their intake (within limits), and that fibre digestion should decrease with increased intake (also see Illius & Gordan 1992, Justice & Smith 1992, Illius & Gordan 1993).

This potentially important adjustment in intake and digestibility in response to changes in dietary fibre has rarely been adequately tested in avian herbivores (Savory & Gentle 1976a,b; Karasov 1990). Daily food intake of Japanese Quail (*Coturnix japonica*) increased with dietary fibre, as predicted; however, contrary to the predictions, digestibility (total dry matter and just the fibre fraction) did not change with increased dietary fibre (Savory & Gentle 1976a,b). More such tests need to be conducted before we can evaluate whether avian herbivores maximise energy or nutrient gain by increasing their intake and passage rates and by reducing their fibre digestibility when eating diets with higher fibre.

A second reason why the proposed allometric relationships derived from work on larger mammalian herbivores may not hold for smaller mammalian or avian herbivores is that gut capacity as estimated by maximum volume or mass of the fermentation chamber may provide a relatively poor estimate of the capacity to process food into nutrients. There are at least two good reasons why gut capacity may provide a poor estimate of the capacity to process food into nutrients. First, small herbivores can effectively reduce the predicted allometric constraints by selectively increasing retention of the more digestible fibre while

maintaining relatively fast passage rates. The prediction is that large particle-size, refractory portions of ingested fibre will have shorter retention times than smaller particle-size, soluble portions of ingested fibre which are more rapidly digestible. Second, higher reaction rates (e.g. hydrolysis rates of digestive enzymes and nutrient absorption rates) can increase the capacity to process food into nutrients independent of gut size. The prediction is that reaction rates are relatively high especially in regions of the gut of particular importance for breakdown and absorption of plant fibre. In the remainder of this review, I will evaluate these two predictions and the general hypothesis that both selective retention of digesta and increased reaction rates reduce the proposed allometric constraints for avian herbivores.

Selective retention of digesta in avian herbivores

Relative rates of passage of fluid versus particulate fractions of digesta provide important insights into digestive strategy. In foregut fermenting ruminants and macropods, and in many mammalian colon fermenters, particulate digesta is typically retained longer than the fluid digesta (Stevens & Hume 1995). The opposite pattern, selective retention of fluid digesta, is typical of small mammalian cecum fermenters such as rabbits and the Koala (Type C caecum fermenters in Stevens & Hume 1995), although many mammalian cecum fermenters show little or no selective digesta retention (Robbins 1993, Stevens & Hume 1995).

All avian herbivores so far described except the Hoatzin are hindgut fermenters and so are expected to retain smaller particle size, fluid fractions of digesta as long or longer than particulate fractions. Galliformes such as ptarmigan selectively retain fluid digesta in the caeca and rely on caecal fermentation of fibre (Gasaway *et al.* 1975). As a result, the fluid fraction of digesta has a longer total mean retention time than the particulate fraction in ptarmigan ([Table 1](#)). In contrast, the Emu (Herd & Dawson 1984) shows no selective digesta retention ([Table 1](#)) perhaps because the Emu is a large bird that relies primarily on fermentation of fibre in the colon. The Hoatzin like other foregut fermenting vertebrates selectively retains particles in the foregut and passes the liquid fraction much more quickly (Grajal & Parra 1995) ([Table 1](#)).

The few studies of selective retention of digesta in geese demonstrate that, like in galliformes, the caeca contains only small particles and there is likely retrograde movement of urinary by-products into the caeca (Clemens *et al.* 1975, Bjornhag & Sperber 1977). These studies as well as our own recent work on particle size distribution of digesta in the goose gut suggest that there is selective retention of small particle size, fluid digesta in the caeca. However, unlike in galliformes, total mean retention time of the fluid fraction of digesta in geese was similar or shorter than the particulate fraction ([Table 1](#)). If both geese and galliformes have similar selective retention mechanisms in the hindgut, perhaps differences in how food is processed in the foregut can explain why the fluid fraction of digesta had a longer total mean retention time than the particulate fraction in galliformes but not in geese.

Foregut processing of food in geese and galliformes involves storage in the proventriculus and crop, respectively, and then grinding of the food in the gizzard. The gizzard of geese is much larger than in galliformes for a bird of similar size (Hallsworth & Coates 1962, but see Sedinger 1997) which suggests more extensive foregut processing of food in geese. Clemens *et al.* (1975) showed that larger particles are retained for further degradation in the gizzard of geese until particle size is reduced. A pattern of selective retention of larger particles in the foregut of geese until food particles are reduced in size would be analogous to the particle-size reduction process in the ruminant fore stomach (van Soest 1982). If larger particles were selectively retained in the foregut as long as smaller particles were selectively retained in the hindgut, then total mean retention time of both fractions of digesta would be similar. Testing of this hypothesis requires more detailed studies of passage rates of particular fractions of ingested fibre in the foregut and hindgut of geese.

Hydrolysis rates of digestive enzymes

If hydrolysis rates of digestive enzymes or nutrient uptake rates per unit volume or mass of the small intestine or caeca are elevated in small herbivores then gut size may provide a poor estimate of the capacity to process food into nutrients. Increasing

