Gastrointestinal physiology and nutrition in wild birds

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ANATOMY OF GASTROINTESTINAL TRACT

The avian digestive system clearly demonstrates evolutionary adaptations which reduce body mass to improve efficiency of flying. Teeth and heavy jaw muscles and bones seen in mammals and reptiles have been replaced by much lighter beak, jaw bones and jaw muscles. Because birds to not chew their food, the oesophagus is large in diameter to accomodate large items. The heavy muscular stomach (gizzard) takes over the function of teeth in mechanical digestion of ingesta. The main mass of birds, the breast muscles and viscera are 'suspended' under the wings for flying efficiency.

The tongue and beak are used for food manipulation and exhibit many interesting adaptations in birds (McLelland, 1979). There is no soft palate in most birds and the hard palate connects with the nasal cavities via a median slit.

Salivary glands are poorly developed in species that ingest aquatic food and well developed in those eating dry food. The glands of some species (e.g. house sparrow (*Passer domesticus*)) contain appreciable amounts of amylase (*EC* 3.2.1.1), but those of domestic chickens and turkeys do not. Feeding stimulates salivary secretion. Birds have taste buds and their location and density varies between species (Duke, 1986).

Birds have relatively long necks because their beak must serve the function of hands or paws in food gathering, preening, etc. Their oesophagus is, therefore, also relatively long. It has numerous mucous glands to help lubricate the passage of food. The crop is an enlargement of the oesophagus and it serves to store food for subsequent passage to the stomach. (This is analogous to the cardia in the mammalian stomach.) The size and shape of crops vary between species. Pigeons have two large lateral pouches, gallinaceous birds have a single pouch, hawks have a spindle-shaped enlargement of the oesophagus and owls have no crop (Fig. 1).

The glandular stomach (proventriculus) also varies in size between species, being relatively small in graminivores, but often quite large and distensible in carnivores that ingest large food items and in ostriches which use it for water storage (Degen *et al.* 1994). In most species, however, food passes rapidly through the glandular stomach and is held in the muscular stomach wherein the actions of the gastric secretions (pepsin (*EC* 3.4.23.1), HCl, and mucus) occur. The muscular stomach is complex in most species (Fig. 1) and consists of two pairs of opposing muscles called the 'thin' and 'thick' muscle pairs (1–3 mm and 6–9 mm thick respectively) which consist entirely of smooth muscle. A more simple muscular stomach is found in birds of prey and heron-like species (Duke, 1986).

There are variations in this general anatomical scheme for the stomach, most notable being a third chamber below the muscular stomach called the pyloric stomach found in many aquatic species. It contains feathers and bones usually and is believed to act as a filter to prevent bones from entering the intestines.

The avian small intestine is histologically divided into only the duodenum and ileum (Fig. 1). It tends to be longer in herbivores and graminivores than in carnivores, presumably because plant tissues are more difficult to digest than animal tissues. The small
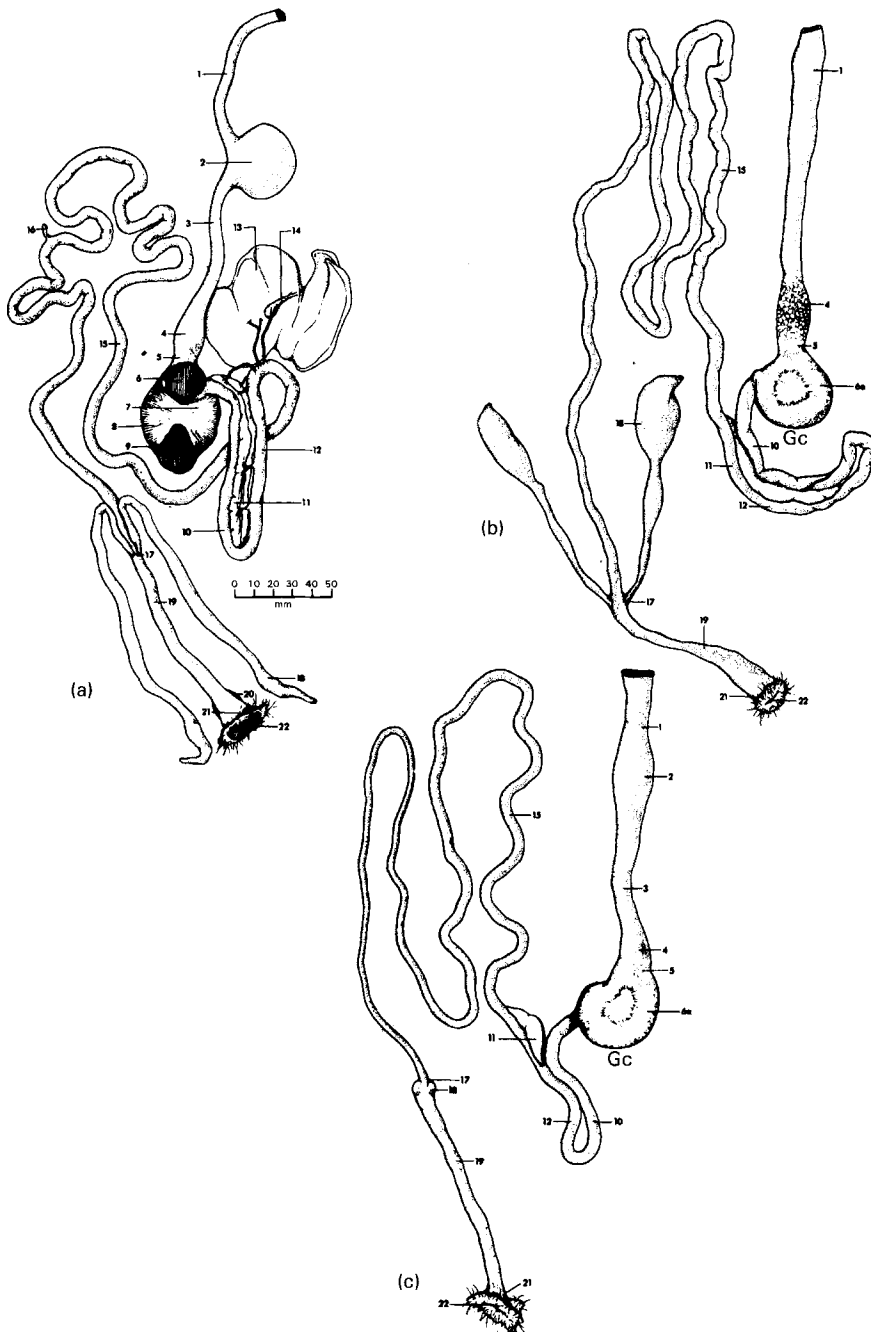
Fig. 1. Gastrointestinal tracts of: (a), domestic turkey; (b), great-horned owl (*Bubo virginianus*); and (c), red-tailed hawk (*Buteo jamaicensis*). Included are: (1) precrop oesophagus, (2) crop, (3) post-crop oesophagus, (4) glandular stomach, (5) isthmus, (6) thin craniodorsal muscle, (6a) muscular stomach of raptors, (7) thick cranioventral muscle, (8) thick caudodorsal muscle, (9) thin caudoventral muscle, (6–9) muscular stomach, (10) proximal duodenum, (11) pancreas, (12) distal duodenum, (13) liver, (14) gall bladder, (15) ileum, (16) Meckel's diverticulum, (17) ileo-caeco-colic junction, (18) caecum, (19) rectum, (20) bursa of Fabricious, (21) cloaca, (22) vent, (Gc) greater curvature. (From Duke, 1985.)

intestine is the principal site of chemical digestion, using enzymes of both intestinal and pancreatic origin. It is also the principal site of nutrient absorption (Duke, 1986).

About half all avian species have caeca; they are absent, however, in hawks, parrots and song birds. These are blind pouches originating at the juncture of the small and large intestines. Several functions have been ascribed to the caeca, but the most important appear to be participation in water balance, recycling of nitrogenous waste to create amino acids and fermentation of fibre. In view of these functions, it is difficult to deduce what evolutionary pressure led to their presence in owls but not in hawks. They do seem to be important in water conservation in great-horned owls (*Bubo virginianus*; Duke *et al.* 1981).

The rectum is relatively short in most species and it is primarily involved in water absorption from the indigesta and from urine which is passed orally from the ureters (terminating in the cloaca) and in elimination of the indigesta.

GASTROINTESTINAL TRACT MOTILITY

Avian gastrointestinal contractile activity, i.e. motility, in those species with the thin and thick muscles is unique relative to mammals. The thin and thick muscles contract alternately; first the thin muscle pair contracts to push ingesta into the centre of the muscular stomach, then the thick muscle pair contracts to grind the ingesta. Grit aids in this grinding. This action is analogous to the cheeks and jaws of mammals. Gastric motility in those avian species lacking the thin and thick muscles is similar to that of mammals with a simple stomach, i.e. a contraction starts at the pylorus and proceeds around the greater curvature to mix the gastric contents (Duke, 1989).

Small intestinal reflux

Small intestinal motility is similar to that in mammals, except for the occurrence of small intestinal refluxes. This is a contractile pattern that is totally unique to birds and involves a periodic reverse peristalsis which moves virtually all the contents of the upper ileum and duodenum back into the muscular stomach. The latter organ is simultaneously relaxed to permit entry of the duodenal contents. These refluxes have been observed via image intensification radiology in all species thus far examined, but they occur at different frequencies between species. Leach's storm petrel (*Oceanodroma leuchorhoa*) chicks eating very-high-fat diets had approximately eight refluxes per h postprandially (Duke *et al.* 1989). Raptors (i.e. birds of prey) had one to two per h (Duke *et al.* 1976) on a diet of mice. Turkeys on standard poultry rations typically had two to three refluxes per h (Dziuk & Duke, 1972; Duke *et al.* 1975*b*). Only one small intestinal reflux was observed in cedar waxwings (*Bombycilla cedorum*) during approximately 25 h of observation (Levey & Duke, 1992). Similarly, only one was seen in ostriches (*Struthio camelus*) during 12 h of observation (Degen *et al.* 1994). These observations led me to wonder what stimulated the evolutionary development of small intestinal refluxes in birds.

Since birds have high metabolic rates, they must find, digest and metabolize more nutrients per d to maintain normal activity, reproduction, etc. when compared with other vertebrates. One way to achieve this increased digestive capacity would be to increase the size of the gastrointestinal tract, a disadvantage to a flying animal because of added weight. A second way would be to increase foraging time. Increased effort in foraging, however, exposes birds to increased potential for predation. To reduce exposure to the latter risk and also to reduce the volume of the gastrointestinal tract required to digest larger quantities of food, the use of the same part of the gastrointestinal tract more than once in the digestion of

one meal would be an evolutionarily-wise response. A high nutrient density (such as in prepared rations for poultry) or a high-fat diet (as eaten by petrels) would be more difficult to digest than more simple diets and be more likely to lead to evolutionary development of small intestinal reflux activity, i.e. the greater the small intestinal reflux frequency, the greater would be the digestibility.

CARBOHYDRATE DIGESTION

The digestive strategies for handling the three classes of nutrients varies. More is known about carbohydrate digestion and more carbohydrate sources (leaves, seeds, fruits, etc.) have been tested than high-fat or protein foods.

Fibre

Many species eat mainly carbohydrate diets, but they employ different digestive strategies. Even within similar species with similar diets, different strategies can be seen. If we compare ratites, ostriches have relatively large caeca and a very long colon, both involved in fermentation of plant fibre. They are also coprophagic. Through this combination of strategies they achieve approximately 40–60 % digestibility of their diet of grasses, leaves and occasional insects or lizards (Swart *et al.* 1993; Angel, 1994). Emus (*Dromaius novaehollandiae*) have relatively much shorter caeca and colon, but, they have a very long small intestine. Their mainly carbohydrate diet of tender shoots, seeds, fruits and insects is nutrient rich and readily digestible in the small intestine (Dawson & Herd, 1983).

The hoatzin (*Opisthocomus hoazin*) is folivorous but uses foregut fermentation (Grajal, 1995). The crop is enlarged and the oesophagus is elongated; together they account for 77 % of the total gut capacity. Both organs are quite muscular and both maceration and fermentation occur therein. Approximately 60–80 % digestibility is achieved from a very poor, coarse diet. Gallinaceous birds such as chickens, turkeys and ring-necked pheasants (*Phasianus colchicus*) tend to eat more seeds and less foliage than ratites or the hoatzin, and they achive 60–70 % digestibility. Hindgut fermentation in these species can add an extra 4–11 % in diet digestibility (Duke, 1986).

Poultry are generally not considered to be able to 'digest' fibre. However, if they are pre-conditioned to a high-fibre diet before digestibility is tested, their digestibilities improve. Domestic turkeys fed on either 28 or 161 g oat hulls/kg in isoenergetic diets labelled with ^{14}C-labelled cellulose were only able to digest 2·3 % of it (as determined by collecting [14]CO_2 in exhaled air) when fed on the diet containing 28 g cellulose/kg for 6 weeks, but digested 10·4 % of the cellulose (on average) after eating the diet containing 161 g cellulose/kg (Duke *et al.* 1984).

Nectar

Another carbohydrate source used mainly by hummingbirds and passerines is nectar. In feeding trials, hummingbirds were found to prefer sucrose over glucose, fructose or a mixture of glucose and fructose. While all three sugars are highly assimilated by hummingbirds (greater than 97 %), glucose was assimilated more slowly (birds rested longer between feeding bouts), thus making a glucose diet less efficient (Martinez Del Rio, 1990*a*). Hummingbirds have very high rates of intestinal sucrose hydrolysis and glucose transport (Martinez Del Rio, 1990*a*). A comparison of intestinal sucrase (*EC* 3.2.1.48) and maltase (*EC* 3.2.1.20) activities between three species of hummingbirds and nine species of

fruit-eating passerines that had significant intestinal sucrase activity indicated that intestinal sucrase was between two times and 118 times higher in hummingbirds (Martinez Del Rio, 1990*b*). Thus, these birds are highly adapted to specific carbohydrate diets. Martinez Del Rio (1990*a*) found that the nectar secreted by flowers preferred by hummingbirds is rich in sucrose, whereas, nectar secreted by flowers preferred by passerines contains a mixture of glucose and fructose.

Fruits

A third diet high in carbohydrates and eaten by many species is fruits. Most fruit-eating birds consume sizable quantities daily, absorb the sugars and defaecate the pulp, gaining little nutrient value from it. Cedar waxwings (*Bombycilla cedorum*) eating artificial fruits (sphere-shaped, red-dyed agar with 150 g glucose/kg and a plastic bead as a 'seed') were observed radiographically (Levey & Duke, 1992). Typically two or three 'fruits' were eaten at once and passed into the gizzard within 3 min (on dissection, this species does not appear to have a crop, but the seeds were held in the upper oesophagus). The pulp and seeds were separated within seconds by contractions of the muscular stomach and the pulp was emptied into the intestine within about 8 min. The seeds remained in the musclar stomach for about 30 min; however, once they were passed from the stomach they moved through the small intestine in less than 10 min. Pulp appeared to be 'pushed' through the intestine by the seeds. Both pulp and seeds remained in the rectum for several minutes. This presumably allowed absorption of nutrients not absorbed in the small intenstine before defaecation of the pulp. Active absorption of D-glucose was found to be high in the rectum (Levey & Duke, 1992). In previous studies it was found that glucose absorption averaged 92 % on this diet (Karasov & Levey, 1990), thus processing and absorption are very efficient. Absorption of a large proportion of ingested sugars is typical of most frugivores (e.g. Karasov & Levey, 1990).

Digestion is complicated by seasonal changes in diet in some birds. American robins (*Turdus migratorius*) switch from eating fruits in the autumn to insects in the spring (Levey & Karasov, 1992). This switch is accompanied by changes in digestive enzyme secretions from the intestinal epithelium and appears to be seasonally induced (probably by photoperiod) rather than in response to diet. In some cases, seasonal dietary changes involve changes in volume eaten due to the bulk of the new diet (Walsberg & Thompson, 1990) or due to eating more in response to a lower environmental temperature (Dykstra & Karasov, 1992). So, gut structure, size and function may all change seasonally.

Chitin

One last type of carbohydrate eaten by many birds is chitin, one of the most abundant biopolymers on earth. In feeding trials with six species of seabirds, sooty albatross (*Phoebetria fusca*), white-chinned petrels (*Procellaria aequinotialis*), Leach's storm petrels, rockhopper penguins (*Eudyptes chrysocome*), gentoo penguins (*Pygoscelis papua*) and king penguins (*Aptenodytes patagonicus*) digestibilities of 35-84 % were observed (average 50·6 %; Jackson *et al.* 1992).

PROTEIN DIGESTION

Since chitin provides the exoskeleton of all arthropods, birds eating chitin are also very likely to be eating protein from the muscles, internal organs, etc. of the arthropods. Protein

is essential for growth and development in all young birds and for maintenance and replacement in adult birds. Thus, all birds are capable of digesting some protein; however, protein makes up most of the diet in carnivorous birds.

Birds eating high-protein diets generally have less complicated digestive systems than those eating complex carbohydrates (Fig. 1). The muscular stomach of raptors and fish-eating birds (e.g. herons and penguins; McLelland, 1979; Duke, 1985) is simple, without the thin and thick pairs of muscles (described previously). Although hawks have a poorly developed crop, it does function in food storage postprandially. Owls have no crop so swallowed food passes immediately into the glandular stomach.

Gastric digestion

Four phases of gastric digestion can be observed in great-horned owls: (1) filling of the stomach characterized by high amplitude and moderately-high-frequency contractions (1–1·5 per min); (2) chemical digestion which is a long (4–8 h) period of very-low-amplitude, low-frequency contractions (0–1 per min); (3) fluid evacuation which occurs over a 1–2 h period during which contractile activity slowly increases to about 1·5 contractions per min; (4) pellet egestion which involves very-high-amplitude and high-frequency contractions (2 per min) for 4–10 min followed by pellet egestion during which vigorous oesophageal anti-peristalsis moves the pellet from the stomach to the mouth in about 8–12 s (Kostuch & Duke, 1975; Duke et al. 1976).

During gastric digestion, the pH of gastric contents averaged 1·6 (range 1·3–1·8) in samples taken orally from five species of falconiforms and 2·35 (range 2·2–2·5) in samples from two species of owls (Duke et al. 1975a). The pellets of falconiforms contain virtually no bones from their prey, while those from owls contain nearly all the bones of their prey. Using mouse bones cleaned from mouse carcasses by dermested beetles, it was found that a solution of HCl at pH 1·6 at 40° entirely dissolved the bones overnight. Gastric proteolytic activity was found to be similar between the two orders of raptors. Food metabolizability averaged approximately 60 % in great-horned owls eating a mouse diet.

Pellet egestion

The single most unique gastrointestinal event occurring in raptors and many other avian carnivores is pellet egestion. Pellets are formed in the stomach from the undigested remains of hair (falconiforms) or hair and bones (owls). This oral egestion avoids having to digest bones and hair and pass them through the entire gastrointestinal tract. The physiological mechanism of pellet egestion differs from vomition in mammals with simple stomachs and from regurgitation of the cud in ruminants. Implanted strain-gauge transducers or bipolar electrodes on the oesophagus, muscular stomach and on the abdominal muscles indicated that at about 12 min before egestion, vigorous gastric contractions formed the pellet and pushed it into the lower oesophagus. Only one gastric contraction precedes vomition and regurgitation of the cud. The pellet was moved orally by oesophageal anti-peristalsis, which occurs during cud regurgitation, but not in vomiting. This orally-directed movement of the pellet required 8–10 s to move the pellet to the mouth. No abdominal muscle contractions occurred in owls as they do during vomiting (Duke et al. 1976).

Small intestinal refluxes and colonic anti-peristalsis (Dzuik, 1971; Duke, 1985) have been observed in raptors, the former presumably increases digestion and the latter enhances water balance.

In owls, meal-to-pellet intervals vary between species and with meal size. Meal-to-pellet interval is shorter for smaller owls and for relatively smaller meals in all species. In contrast, the falconiforms tend to egest pellets at dawn unless meals are eaten late on the previous day. Great-horned owls and most other owls may hunt during both daylight and darkness, whereas falconiforms hunt strictly during daylight. Thus, egesting at dawn would be advantageous because by emptying the stomach early in the day, a new meal may be ingested as soon as it can be captured. If the first meal is small, one or more additional meals may be eaten before darkness.

FAT DIGESTION

Most animals which eat meat are incidently eating fat; similarly frugivores consume many fruits which contain lipid. Many avian species periodically seek high-fat diets in order to increase their levels of body fat in preparation for migration or in anticipation of food scarcity. However, some birds eat very-high-fat diets routinely; the best examples are seabirds. Seabirds are uniquely able to assimilate wax esters at efficiencies greater than 90 % (Jackson & Place, 1990); efficiencies in mammals are less than 50 %. Marine foods available to seabirds have a high lipid content as an energy store, for buoyancy or for insulation in marine mammals (eaten as carrion). This high efficiency is accomplished by: (1) a comparatively very high intestinal bile salt concentration to aid lipid digestion; and (2) regular small intestinal refluxes which repeatedly expose ingesta to pancreatic and duodenal lipases and bile (Duke *et al.* 1989). Radiographic studies which disclosed the high frequency of refluxes (about eight per h) also allowed observation of how the high-fat meal was processed in the gastrointestinal tract of Leach's storm petrel chicks. Ingesta accumulated in the glandular stomach and eventually separated into two phases, a lipid phase floating on an aqueous phase. The latter phase, presumably containing amino acids (from digested protein) and small amounts of lipid, regularly emptied from the stomach into the duodenum.

Three terrestrial species are efficient also at digesting lipids and they consume high-lipid diets. The lesser honey guide (*Indicator minor*) which consumes wax esters in honeycomb, and yellow-rumped warblers (*Dendroica coronata*) and tree swallows (*Tachycineta bicolor*) which eat fruits with a waxy coating (Place & Stiles, 1992).

Virtually all organic matter on earth (and some inorganic ions) serves as food for some species of animal. By fitting into a myriad of niches, birds have taken advantage of this organic matter to meet their energy and protein needs. The feeding and digestive mechanisms they use are just part of what makes them interesting to man.

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