Anatomy and Physiology of the Avian Gastrointestinal Tract

Stacey Gelis BVSC MACVSc

Coolum Veterinary Surgery/Australian Wildlife Hospital, 43 Coolum Yandina Road, Coolum Beach QLD. 4573

The avian gastrointestinal tract is composed of a beak, mouth, oesophagus, crop proventriculus, ventriculus or gizzard, intestine, caeca, rectum and cloaca. Evolution, natural selection and adaptation have resulted in varying degrees of development of each of these structures, particularly in relation to flight. Birds have evolved a lightweight beak and a centrally located muscular ventriculus to replace the heavy bones, muscles and teeth of reptiles and mammals. The GI tract is comparatively shorter in length and the digestive process is more rapid to facilitate the higher metabolic rate required for flight.

The Upper GI Tract

The **beak** (or bill) is the avian equivalent of teeth and lips. It allows the grasping and processing of food, as well as playing a role in behaviour (for example; biting, preening).

The beak is made up of the maxilla and premaxilla and is covered by the horny layer known as the rhamphotheca. In the upper bill, it is called the rhinotheca and covers the premaxilla and partly covers the maxilla. It is composed of hard keratin in most species, except in waterfowl where only the tip is hard. The horny layer covering the lower beak is called the gnathotheca. Rhamphothecal growth is continuous in response to wear and tear. Beak shape is thus largely influenced by diet.

The parrot family has the most developed and powerful beak of all the commonly kept species. The rhinotheca is wide with a curved tip; the gnathotheca has a blunt chisel-shaped prominence that pushes against the ridge protruding from the underside of the rhinotheca. Functionally, psittacine birds have an advantage in that the mandible and maxilla can be moved independently due to their possession of a prokinetic maxilla. This allows prehension of larger food items, increased dexterity in positioning food items within the beak, and greater shock absorption when cracking seeds and nuts.

Raptors also possess a hooked beak but lack a prokinetic maxilla.

Most passerines, however, have more conical bills which are less keratinised.

Many beaks possess sensitive nerve endings especially in species which probe for food such as waders and diving ducks.

Birds possess an **oropharynx** instead of a distinct mouth and pharynx. The palate occupies the roof of the rostral oropharynx (birds lack a soft palate). It contains two ridges which aid in removal of the husk in seed-eating birds such as budgies and cockatiels, canaries and finches.

The **choana**, a longitudinal slit in the hard palate, connects the oral and nasal cavities. It forms a wide “V” shape in psittacine birds with caudally pointing papillae. By contrast, in falcons it forms a narrow “V” with few papillae and in pigeons it is narrow and lacks papillae. At the caudal edge of the choana is the infundibular cleft- the caudal opening of the left and right pharyngotympanic tubes (Eustachian tubes or *Rami infundibuli*) from the middle ear.

The **tongue** arises from the floor of the oropharynx. The hyoid apparatus and associated musculature and articulating bones are responsible for tongue movement. Its role is to collect, manipulate and assist in swallowing of food. The psittacine tongue contains additional striated muscle anteriorly which increases its flexibility. It is short, smooth and muscular. This combination facilitates the extraction of seeds and nuts from their husks or outer casings. Lories and lorikeets differ in having relatively long tongues which contain fine papillae at their tips. These can be everted during feeding on flowers which allows nectar to flow into the mouth by capillary action and pollens to be harvested.

Raptors tend to have a rasp-like tongue with a roughened tip and many small, caudally-pointing papillae at their base.

Ducks have a scoop-like end to the tongue which contains two rows of overlapping bristles on the lateral edges which work with the beak lamellae to filter particles.

The beak, tongue and oral cavity contain many touch receptors making the mouth an important sensory area. However, taste receptors are not particularly well developed in birds (300-350 in chickens and parrots vs 9000 in humans). These are mostly found on the posterior tongue and on the palate near the salivary glands.

The laryngeal mound lies just behind the tongue and contains the tracheal opening or **glottis**. The glottis lies directly under the caudal choana, or just caudally in raptors. There are rows of caudally directed papillae on the laryngeal mound which assist the movement of food towards the oesophagus during swallowing. Birds do not have an epiglottis.

Salivary glands vary in number, distribution and composition between species. Granivorous species (incl most commonly kept species) have many glands in the roof, cheeks and floor of the oropharynx. The saliva they produce help to lubricate the dry foodstuffs that are ingested. Birds of prey have less developed salivary glands and fish-eating (piscivorous) birds have poorly developed glands or none at all. The content of the saliva produced also varies between species. House sparrow saliva contains significant amounts of amylase whereas that of chickens and turkeys contains little amylase.

Mandibular glands are well developed in some species for specific functions. For example swifts produce a mucilaginous substance which helps to bind their mud nests. Woodpeckers have a sticky salivary coating on their tongues for capturing insects whilst probing in wood cracks and holes.

The **oesophagus** is a distensible tube allowing the movement of food from the oropharynx to the proventriculus. It is thin walled and divided into a cervical and thoracic region. Longitudinal folds increase the oesophagus's distensibilty and hence these folds are most developed in species which swallow large prey items (for example owls) or which store large amounts of food (for example gulls). By contrast psittacine birds show little oesophageal fold development.

Mucus-secreting glands are present in the oesophageal mucosa of most avian species, particularly in the thoracic oesophagus. They are actually absent from the budgerigar cervical oesophagus.

The oesophageal wall consists of a mucosa, submucosa, a muscular tunic and a serosa. A circular layer of smooth muscle predominates. Food prepulsion results from the peristalsis of inner circular and outer longitudinal muscles in an aborad direction.

The **crop** (ingluvies) is a dilatation of the cervical oesophagus which acts as a food storage structure. It lies mostly on the right side of the neck, but may also lie to the left and rest on the furcula when full. Species variation is considerable. Parrots have well developed crops with a prominent right pouch and small left pouch located at the caudal cervical oesophagus. Pigeon crops are even more developed having both right and left lateral pouches well developed. These pouches produce "crop milk"- a mainly protein and fatty-acid-containing holocrine secretion produced in response to prolactin in pigeons of both sexes when raising young. Interestingly it contains no calcium nor any carbohydrate. Striated muscle sheets attach to the crop adventitia to support the large crop. A functional sphincter exists where the crop joins the thoracic oesophagus and helps to form and regulate food boluses being transported to the proventriculus. Birds, however, lack the true upper and lower oesophageal sphincter found in mammals.

The simplest crop is a spindle-shaped enlargement of the cervical oesophagus as seen in ducks and owls.

Many granivorous birds, for example finches lack a true crop but possess a very expandable oesophageal pouch that can store food items. Other birds such as penguins, gulls and ostriches lack a crop but have a very distensible oesophagus. The Australian Bustard also has a well developed oesophageal sac.

Crops are rudimentary or absent in gulls, penguins and insectivorous birds.

As a storage organ the crop allows for the relatively risky activity of food foraging to occur rapidly. The bird can then digest the food items in a safer location at a more leisurely rate. It also allows for a continued energy supply overnight following pre-roosting feeding.

In addition it acts to soften ingested food, especially if water is swallowed, and by contributing mucus to the saliva. Digestion may also occur as a result of microbes in the crop or enzymes within the food. Glucose uptake by the crop mucosa is possible but is of minimal significance. In chicks, the crop is particularly well developed to store food fed by the parents. The food is premoistened and softened in the crop and oesophagus of parents of altricial chicks before being regurgitated. The crop also plays an important immunological function in pigeons feeding squabs.

Food Movement in the Upper GI Tract

In the domestic chicken, food is moved caudally by the tongue whilst the choana reflexively closes (oral phase).

In the pharyngeal phase, food is propelled into the oesophagus. This is achieved by closing the glottis, the hyoid apparatus becomes concave, the tongue moves backward whilst the oesophagus is brought forward. The head is raised and the tongue and infundibular mound push the food by moving rostrocaudally.

In the oesophageal phase, peristaltic waves move the food towards the stomach. These waves are controlled by the extrinsic, not the enteric nervous system. In fasted birds, the crop can be bypassed by the contraction of a longitudinal muscle layer which closes the crop opening. This muscle relaxes once the ventriculus is partly filled. Typically, food bypasses the crop for the first few hours after dawn in fasted turkeys, but fills during late afternoon feeds.
Spontaneous electrical contractions originating from the oesophageal muscles do occur. Their function is unclear, but they may help to clear the oesophagus of food particles.

The Lower GI Tract

The avian stomach consists of two distinct structures: the **proventriculus** (glandular stomach,) and the **ventriculus** (gizzard or muscular stomach). These structures vary in shape and size across avian taxa largely as a result of diet. Most birds kept in captivity are granivorous, omnivorous or insectivorous. Their food items are relatively hard. The proventriculus is thin walled and glandular. The ventriculus is thick-walled, muscular and powerful and the intermediate zone connects the two. By contrast, carnivorous and piscivorous birds which eat relatively soft food items have very distensible stomachs which may be difficult to differentiate grossly.

The proventriculus is the avian equivalent of the mammalian glandular stomach. It is lined with a mucous membrane whose epithelium contains two main gland types. The tubular glands secrete mucus whereas the gastric glands secrete hydrochloric acid and pepsin which provide an acidic environment for digestion. Examples of gastric pH levels include: fasted chicken – ph2.6; pigeon- ph2.1. Nectarivorous parrots have gland- free spaces between the longitudinal rows of glands. This may be an adaptation to pollen digestion by allowing increased distension of the glandular stomach. Both these gland types make up the majority of the thickness of the proventricular wall. The proventriculus of carnivorous and piscivorous birds usually contains longitudinal ridges.

The proventricular musculature is composed of the innermost circular layer and the outermost longitudinal layer. The outermost longitudinal layer is poorly developed or absent in psittacine birds, waterfowl and some passerines. In these birds the myenteric plexus is located immediately under the serosa rather than between the two muscle layers.

The intermediate zone (or isthmus) between the two stomachs is aglandular and lacks folds. In parrots and pigeons it closes tightly during ventricular contractions to separate the ventriculus from the proventriculus.

The **ventriculus** has evolved to mechanically break down food and so is best developed in species that need to grind their food down for example granivores and insectivores (exoskeleton digestion). It is also a site of further chemical breakdown of food by hydrochloric acid and pepsin produced in the proventriculus.

The ventriculus is lined by a cuticle known as the koilin, which protects the underlying mucosa from chemical digestion as well as acting as a grinding surface. It is a matrix composed of a combination of proteinaceous rod-like projections produced by the tubular glands and desquamated epithelial cells. It forms a hardened composite which exhibits raised ridges and distinct longitudinal and transverse grooves which aid in mechanical digestion. It is thickest in species with well developed, muscular stomachs. It is continuously replaced in many species but may occasionally be sloughed in falcons. Green, brown or yellow discolouration of the koilin lining is due to bile staining due to ventricular reflux from the small intestine and is a normal finding.

The ventriculus contains two pairs of opposing muscles. The cranioventral and caudodorsal thick muscles provide the powerful grinding contractions seen in the gizzard. The craniodorsal and caudoventral thin muscles line the caudal and cranial sac of the gizzard. This asymmetric muscle contraction arrangement provides the gizzard's mixing and grinding actions.

A small pyloric fold separates the ventriculus from the small intestine. This regulates food passage into the small intestine by slowing large particle movement. In nectarivorous species such as lorikeets and honeyeaters, the proventricular and pyloric openings of the ventriculus lie in a median plane. This is thought to facilitate rapid movement of ingesta.

Ventricular size can alter as a result of diet change. In some species it is softer and lighter in summer when fruits are eaten but hardens and thickens in winter when dry seeds form the bulk of the diet.

There has been much written about the role of grit in digestion. Insoluble grit may assist food maceration in the gizzard and is especially useful in species which do not dehusk their seed for example pigeons, chickens, quail. It is controversial whether this grit ingestion is deliberate or incidental whilst feeding on food or soils containing mineral or trace elements. Grit tends to be absent from the stomachs of nectarivorous birds, which tend to have poorly developed ventriculi.

Gastric Movement

In general, food entering the proventriculus is coated with hydrochloric acid and pepsin but undergoes little enzymatic digestion. Digestion is controlled by the hormones gastrin, secretin, cholecystokinin and pancreatic polypeptides and by the vagus nerve. The food is quickly propelled by circular smooth muscle contraction into the ventriculus where most of the mechanical digestion occurs. This involves the coordinated contraction of ventricular muscles and the abrasive qualities of insoluble grit. In parrots (and turkeys) the ventricular muscles contract in a clockwise direction around the ventriculus. First the paired thin muscles contract and the isthmus closes, separating the ventriculus from the proventriculus. At maximum contraction, the pylorus opens allowing the passage of digesta into the duodenum. The thin muscles then relax as the thick muscles contract, the pylorus closes and duodenal peristalsis commences. At the same time the isthmus may open allowing retroprepulsion of food back into the proventriculus to allow further digestion by pepsin and hydrochloric acid. This allows additional time for the breakup of large lipid globules and proteins. Lipid in particular is retained in the anterior region of the tract and digested more slowly than are proteins or carbohydrates. This cycle of contractions is a smooth and continuous process and gives the appearance that the ventriculus is flipping. The myenteric plexus controls the coordination of these contractions. It is under intrinsic control by a pacemaker situated in the isthmus but is also reliant to some extent on external neural input such as the vagus nerve.

Raptors possess a more simplified stomach which in addition to its normal digestive function has to produce pellets- the indigestible fur, feathers, bones etc from their prey. Neck extension and head pumping assist the peristaltic propulsion of food into the proventriculus. Over the next hour the stomach fills with digestive juices. Vigorous, frequent, contractile waves occur clockwise from the isthmus to the pylorus. This is followed by a 7 to 9 hour period of chemical digestion where forceful proventricular contractions occur at low frequency, after which digestion is complete. Next, a short phase of paired contractions removes any further liquid from the pellet. Pellet compaction occurs over the next 5-6 hours after which it is expelled orally by retroperistalsis. This process is known as **egestion**. It involves increasing frequency and amplitude of ventricular contractions which in Great Horned Owls (*Bubo* virginianus) begin approximately 12 minutes prior to egestion. This compacts the pellet & moves it into the lower oesophagus. Approximately 8 to 10 seconds prior to egestion, the pellet is propelled orally by oesophageal retroperistalsis. This process is unlike vomiting or regurgitation in mammals as neither abdominal nor duodenal muscles are involved. The exact timing of pellet ejection varies with the species.

The Intestines

The avian small intestine is the main site for enzymatic digestion and nutrient absorption. It shows less differentiation between avian taxa than do the previous, more proximal parts of the gastrointestinal tract.

The duodenum emerges from the ventricular pylorus and forms a loop which encompasses the pancreas. The **pancreas** is trilobed in most species with the third or splenic lobe not being attached to the other two lobes in most species. In the budgerigar and pigeon, each lobe is drained by a separate duct. In pigeons, all 3 empty into the distal duodenum whereas in budgies, 2 empty into the distal duodenum adjacent to the bile duct whilst the third empties into the opposite side of the duodenum.

The exocrine pancreas is similar to mammals in producing amylase, lipase, trypsin, chymotrypsin, carbopeptidases A,B and C, deoxyribonucleases, ribonucleases and elastases and also the intestinal pH buffer bicarbonate.

Pancreatic amylase breaks down starch to glucose which is absorbed in the small intestine.

Pancreatic lipase hydrolyses triacylglycerides into monoglycerides, diglycerides, fatty acids and glycerols. When mixed with bile acids and fat-soluble vitamins these form micelles which are then absorbed.

The intestinal wall mucosa also produces amylase, sucrase, maltase, enterokinase, lipases and peptidases. These enzymes are produced as a result of duodenal distension, vagal stimulation and the presence of cholecystokinin , secretin and vasoactive intestinal peptide. Birds appear to lack lactases and so should not be fed foods containing significant amounts of lactose.
In general, the jejunum is thought to begin just distal to where the ascending duodenal loop begins to turn back on itself, where the jejunal branches of the mesenteric artery begin. The ileum is thought to begin at the vitelline (Meckel's) diverticulum and end at the recto-caecal junction. There is much interspecies variation of the jejunum and ileum.

Nectarivorous and insectivorous birds have shorter intestinal tracts than granivorous and herbivorous species. This is due to the higher digestibility of the former birds' diets.
The intestinal epithelium contains villi, microvilli and crypts. There are no lacteals (lymphatic projections into the villi) in the avian small intestine. Instead, absorption of nutrients is reliant upon the increased surface area of capillaries in the lamina propria of the villi. Increased capillary flow allows efficient transport of nutrients to the portal blood system. Goblet cells produce a thick mucus layer which protects the intestinal epithelium from digestive juices and physical abrasion.

The inner circular and outer longitudinal muscle layers allow mixing and propulsion of the digesta through the intestinal tract.

The avian duodenum has the ability to propel food distally as well as in a retrograde direction via peristaltic contractions. Retroperistalsis of food back into the ventriculus allows for further maceration and digestion and occurs up to once a minute in parrots fed a moderate-fat diet, or every 20 minutes in the turkey. These waves are forceful and visibly distinct from the normograde peristaltic waves. Frequency of retroperistalsis increases with increases in dietary fat levels.

The **liver's** bile ducts empty into the distal duodenum. It produces bile acids and salts which emulsify fats, allowing lipases to digest the lipids. Bile acids and salts, cholesterol and phospholipids are secreted into bile canaliculi which drain into the bile duct. Gall bladders are absent in most psittacine birds and pigeons, but are present in raptors and waterfowl.

The **caeca** are most developed in chickens, turkeys, ostriches, ducks, owls and many herbivorous birds, and in particular in the grouse where their combined length may exceed that of the remainder of the intestinal tract. The caeca and are important in microbial fermentation of vegetable matter (cellulose) in some species and in water balance.

They arise at the ileocolic junction and in the chicken accompany the ileum cranially, to which they are attached by ileocaecal folds, before doubling back so that their blind ends lie near the cloaca. The proximal segment has well developed villi and heavy muscle coat (the caecal sphincter) and contains an accumulation of lymphoid tissue, the caecal tonsils. The thin-walled middle section has longitudinal folds with small villi and appears green due to its content. The distal caecum contains both longitudinal and transverse folds with small villi and the blind ends appear thick-walled and bulbous.

The ostrich has a particularly well developed caecum. It contains a fold which spirals approximately 30 times transforming the lumen into a long spiral cavity. The fold contains a mucosa, muscularis mucosa and submucosa and a muscular core proximally. Distally it is expanded to form a frill which greatly increases its surface area. The fold plays an important role in the absorption of volatile fatty acids and other products which result from the caecal microbial fermentation of cellulose and hemicellulose.

Caeca are at best vestigial nodules located at the ileo-caecal junction in small, insectivorous passerines and are absent or rudimentary in parrots, most raptors, penguins, hummingbirds, swifts, woodpeckers and toucans. In the domestic pigeon they are entirely lymphoid in structure and are called the caecal tonsils. They are singular in herons and grebes but secretary birds have double-paired caeca. There has been no correlation found between diet and caecal development.

The caeca are filled as a result of the ileal peristaltic waves meeting the rectal antiperistaltic waves. The caecal “sphincter” allows only fluid and very small particles to enter the caeca and hence the caecum is an important site for water resorption.

The caecum is also responsible for improving the amount of energy that can be obtained from food, the digestibility of fibre and helps prevent the loss of amino acids from the gut.

The **rectum** or **colon** is located between the ileo-caecal junction and the cloacal coprodaeum. It is very short (except in the ostrich) and is structurally similar to the small intestine except it has smaller villi which are richer in lymphoid follicles.

The avian rectum exhibits marked retroperistalsis. Thus urine from the urodaeum and coprodaeum enters the colon and caecum where further water resorption can occur.

In parrots, the rectum enters the coprodaeum from the left side at a 60-90 degree angle, whereas it enters from the right side of the coprodaeum in pigeons.

The Cloaca

The cloaca is where digestive, urinary and reproductive end products are deposited. It is a wide, three-chambered structure. The rectum enters into the first chamber, the **coprodaeum.** This is the largest chamber in psittacine birds. It has a flat, vascular mucosa consisting of columnar epithelium. It is separated from the urodaeum, the second chamber, by a circular ridge of tissue, the coprodaeal fold. This fold can act as a sphincter and completely close off the coprodaeum from the rest of the cloaca. This helps prevent contamination of eggs or semen during egg laying or ejaculation.

The **urodaeum** is the smallest cloacal chamber in parrots, pigeons and falcons. It receives the ureters, oviduct (females) and ductus deferens (males). The ureters enter either side of the dorsal midline. In females, the oviduct has a rosette-like opening on the left dorsolateral urodaeal wall. It is harder to see in immature birds and may be covered by a membranous tissue which is broken once an egg is laid.

In males the ductus deferens enter on raised papillae located on the left and right dorsolateral walls of the urodaeum.

The urodaeal mucosa is smoother and less vascular than that of the coprodaeum.
The urodaeum can push urates and urine retrograde into the coprodaeum and rectum to facilitate further absorption of water and solutes. This retroperistalsis explains why urates and faeces can appear to be intertwined when passed.

The uroproctodaeal fold separates the urodaeum from the proctodaeum and is more developed dorsally rather than ventrally.

The **proctodaeum** is the final cloacal chamber and the most frequent location of papillomas in psittacine birds. It also gives rise to the Bursa of Fabricius on the dorsal midline, just caudal to the uroproctodaeal fold. The bursa is most developed in juveniles where its lymphoid tissue produces B-lymphocytes. As a bird matures the lymphoid tissue involutes (usually between 2-6 months of age) but the bursa's opening and chamber often remain visible during endoscopy.
The pudendal artery and vein provide most of the cloacal blood supply. The pudendal nerve follows the ureters to the dorsal cloacal wall where the cloacal ganglia are found. These are important during surgery.

The **vent** is a transverse opening in the ventrocaudal aspect of the body wall and marks the final landmark of the gastrointestinal tract through which body wastes and reproductive structures are passed. It is characterised by dorsal and ventral lips and a voluntary muscle sphincter which provides some control over defaecation. Physiologically, this is exemplified by incubating hens which pass large droppings during nest changeover; psittacine birds can often be trained to defaecate on command.

Cloacal sucking has been noted in breeding female and juvenile psittacine birds. This involves the bringing in of material from the outside into the cloaca under negative pressure. In breeding females this is thought to help sperm transport and hence fertilization in species where males lack a phallus. In chicks, it is thought to help stimulate the immune system by exposing the bursa's B cells to external antigens (and, unfortunately pathogens).

Regulation of Food Intake

Birds are able to regulate both their energy and protein intake.

This regulation occurs both within and outside the central nervous system (CNS).

Within the CNS, the avian hypothalamus is a major site of food intake regulation, with the medial area responsible for satiety whilst the lateral hypothalamus is responsible for hunger.

However there are at least 5 neural pathways involved in food intake regulation which all affect the autonomic nervous system. It appears that decreased sympathetic nervous system activity results in obesity.

Neorochemical control of food intake is complex. Serotonin, cholecystokinin and bombesin all decrease appetite whilst adrenaline, neuropeptides Y and YY, avian pancreatic polypeptide, beta-endorphin and [Met]-enkephalin, endogenous opioids and even nitrous oxide within the CNS all increase food intake. Some of these also work outside the CNS to affect appetite. Brain concentrations of glucose appear to have no effect on appetite.

Food intake regulation outside the CNS involves the gastrointestinal tract and the liver. Osmoreceptors within the duodenum when triggered by high glucose or other hyperosmotic solutions may decrease food intake by slowing gastrointestinal motility.

The liver is an important site for food intake regulation in birds. High intrahepatic levels of glucose, lysine or lipids can all decrease food intake, but the results vary with species and strains.

The crop appears to play little role in regulating food intake.

References

Klasing KC. 1999. Avian Gastrointestinal Anatomy and Physiology. *Semin Avian Exotic Pet Med* **8**:42-50

Denbow DM. 2000. Gastrointestinal Anatomy and Physiology. *In* Whittow GC (ed): Sturkie's Avian Physiology. Academic Press, San Diego, CA. pp 299-325

Taylor M. 2000. Anatomy and physiology of the gastrointestinal tract for the avian practitioner. *In* Birds 2000. Post Grad Foundation in Vet Sci, Uni of Sydney, Aus. Proc **334**:107-113

Taylor M and Murray MJ. 2002. The psittacine cloaca: A clinical review. *Proc Assoc Avian Vet*, Monterey, CA. pp 265-269.

Gelis S. 2006. Evaluating and Treating the Gastrointestinal System. *In* Harrison GJ, Lightfoot TL (eds): Clinical Avian Medicine. Spix Publishing Inc, Palm Beach, Florida, pp 411-440.

Gartrell BD. 2000. The nutritional, morphologic and physiologic bases of nectarivory in Australian birds. *J Avian Med Surg* **14**: 85-94

Bezuidenhout AJ. 1993. The Spiral Fold of the Caecum of the Ostrich. *J Anat* **183** (Pt 3): 587-592