A GUT FEELING

feeding & digestion in birds

ALBERT FRONEMAN

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The sight of a wriggling fish disappearing down a cormorant's throat has an air of utter finality about it, the culmination of an age-old struggle in which the predator's ability to locate and subdue its victim is pitted against the prey's capacity to avoid detection and evade capture. However, this is also the beginning of another complex and, at least for the bird, equally important process. Before the cormorant can use its recently ingested meal as fuel for its metabolic engine or to power activity, growth and reproduction, the fish needs to be broken down and the nutrients locked away in its tissues have to be made available to the trillions of individual cells that comprise the bird.

A bird's gut, or digestive tract, is a sophisticated disassembly line that strips food down to its component molecules by sequentially fragmenting it into smaller particles. The first step is the mechanical breakdown of whole food items that enter the gut via the mouth. Because birds lack teeth and the ability to chew, they rely on a muscular stomach (the gizzard) to physically break down large items. From here, partially digested food enters the small intestine, where a series of enzymes cleave food particles by means of chemical reactions. Enzymes are highly specific in terms of the chemical bonds they target and dozens of different enzymes are required to completely digest a meal.

Once enzymatic digestion is complete, the carbohydrates, fats, proteins and other nutrients that once comprised the food item are available for absorption into the bloodstream, either directly across the gut wall or, in the case of fats, indirectly via the lymphatic system. The bloodstream then transports these nutrients ▶

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to the bird's cells for storage or to be used for fuelling metabolism, maintaining existing tissues or synthesising new ones. The processes of digestion and absorption are very similar in mammals and birds, but the transport of nutrients to cells differs in some fundamental ways, particularly during exercise (see box, page 50).

The major anatomical difference between the digestive system of a bird and that of a mammal is the presence in birds of a gizzard and, in some species, a crop. A crop is a muscular pouch below the throat, formed by an enlarged section of the oesophagus, that functions as a storage container for food. Crops are particularly important in birds such as vultures, which feed relatively infrequently but gorge themselves when food is available. The crop allows them to take advantage of short periods of abundance and then control the rate at which the food enters the lower sections of the digestive system for processing.

Given the complexity of the digestive process and the hundreds of chemical reactions involved, avian digestion occurs surprisingly quickly. Biologists measure the rapidity of digestion by giving food marked with a brightly coloured but indigestible dye, typically food colorant, to captive birds. The dye subsequently appears in the birds' faeces, thereby providing a precise measure of the time required for food to pass through the entire gut, a measurement often referred to as the passage rate. Small birds typically process food much faster than large birds: the average passage rate is approximately 45 minutes in a waxbill-sized bird, just less than two hours in a pigeon-sized bird, and around six hours in an ostrich. However, the time required for digestion also depends on the type of food. Hard-shelled seeds, for instance, take far longer to break down than soft fruit pulp, with the result that the passage rates of seed-eaters tend to be longer than those of frugivores.

The demands placed on the digestive system vary dramatically between different types of food, with some diets being straightforward to process but others posing significant physiological challenges. Often, a food item consists of a combination of easily digestible and indigestible components. A Black-shouldered Kite's digestive system, for example, can easily process the proteins and fats in a mouse but cannot break down the hair and bone. Diurnal raptors, owls and some other birds, including swifts, form pellets consisting of hair, bone and other similarly indigestible material, with the pellets cast in the gizzard and then regurgitated. In this way these problematic materials are kept out of the birds' intestines.

Some of the most intriguing aspects of avian digestion concern birds that feed on fruit. Many plants have evolutionarily co-opted birds to act as seed dispersers by producing seeds contained within edible fruits. These fruits attract frugivorous birds, which consume them and disperse the seeds by defecating or regurgitating them, often some distance from the parent plant. This seemingly amicable evolutionary arrangement, however, conceals levels of deceit and manipulation worthy of a Shakespearean tragedy. Plants produce a veritable laboratory of chemicals in their fruits, which affect birds' digestive systems in remarkable and, in some instances, devious ways.

Birds will generally only feed on fruits if the latter are reasonably nutritious, or at least taste as though they are. Plants that produce low-quality fruits containing few nutrients can be at a distinct disadvantage in terms of seed dispersal if they are in the vicinity of other species that produce nutritious, high-quality fruits. Some plants seem to have circumvented this problem by producing fruits that have almost no nutritional value, but contain small amounts of chemicals that taste many times sweeter than the sugars that birds typically obtain from fruits. An example is the West African miracle fruit *Synsepalum dulcificum*, whose berries contain a protein that is a thousand times sweeter than glucose. By making low-quality, nutritionally worthless fruits taste like high-quality, carbohydrate-rich items, these molecules and the plants that produce them are thought to deceive birds into feeding on fruits from which they gain negligible benefit. Some of these compounds are used by humans as artificial sweeteners, where they similarly deceive our tastebuds by making low-calorie food items taste as though they are full of sugars.

Another way in which plants manipulate the guts of avian frugivores concerns chemicals that influence passage rates. From the plants' perspective, one of the pitfalls of relying on birds to disperse seeds is that the latter can be damaged by digestive enzymes if retained in the birds' guts for too long. Some plants reduce the time their seeds spend in birds' digestive tracts by including in their fruits chemicals that function as avian laxatives. There is evidence, for instance, that the fruits of *Witheringa solanacea*, a shrub that occurs in Costa Rica's cloud forests, contain laxative chemicals that speed up passage rates in avian frugivores such as the Black-faced Solitaire. By accelerating the movement of seeds through frugivores' guts, these chemicals improve the chances that seeds emerging from the bird are undamaged and can still germinate. Other plants, such as members of the genus *Solanum*, do the opposite and produce chemicals that constipate birds, ensuring that hard-shelled seeds are softened. ▷

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PETER STEYN

Above *Pellets regurgitated by raptors and some other birds consist of indigestible materials, most notably bone and fur.*

Top *A Black-shouldered Kite's gizzard will separate the digestible and indigestible components of its mouse meal.*

Opposite, above *The crop of this Cape Vulture is swollen with stored food, which will gradually be released for digestion.*

Opposite, below *The digestion of hard-shelled seeds by Bronze Mannikins and other seed-eaters typically takes longer than the digestion of softer items, such as fruit pulp.*

Previous spread *A fruit of the red-leaved fig begins its journey through the digestive tract of an African Green-Pigeon, where its nutrients will be processed and supplied to the bird's tissues.*

DAVID SHACKELFORD

Above *The Hoatzin feeds predominantly on leaves and its crop acts as a cellulose-digesting fermentation vat, similar to the stomach of a ruminant mammal.*

Below *The evolutionary relationship between plants and frugivorous birds is complex, and the gut of this Brown-headed Parrot may be biochemically manipulated by the plants on which it feeds.*

OBESE AVIAN ATHLETES

During intense exercise, mammals rely on carbohydrates stored within muscle cells – this is the phenomenon that underlies the benefits endurance athletes gain by 'carbo-loading'. Once the muscle carbohydrate stores are exhausted, fatigue sets in and further exercise is possible only at much lower intensities.

In birds, however, fat molecules are continuously transported from reserves to the muscle cells. Thus, instead of becoming fatigued once muscle cells run out of stored carbohydrates, birds simply convert large stores of fat into fuel while in flight – this is the secret behind the non-stop, ultra long-distance flights undertaken by some migrants. A better understanding of avian fat metabolism could have huge implications for human exercise and obesity research. To quote the authors of a recent study, birds 'repeatedly become morbidly obese, exercise at levels that far surpass elite athletes, and then cure themselves'.

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Differences in digestive physiology between various animal groups have also been targeted in the evolutionary relationship between plants and frugivores. Several chemicals that make mammals violently ill, or even kill them, do not affect birds in the least. The chemical atropine, for instance, causes blurred vision, dizziness, nausea and rapid heart rate in humans, yet is present in heavy concentrations in some fruits that birds feed on without unpleasant consequences. The molecule capsaicin, which is responsible for the fiery taste of chillies and peppers, is repellent to many mammals, but birds feed on these fruits with impunity. In southern Africa, the berries of the invasive Persian lilac *Melia azedarach* are consumed by avian frugivores like the Grey Go-away-bird, despite being toxic to humans and other mammals. Equally, the fruits of the deadly nightshade plant, infamous as a poison in Roman and medieval times, are devoured by birds without any apparent ill-effects. Many frugivorous birds have very large livers, which are thought to be important in their capacity to deal with toxic compounds. The phenomenon of geophagy, in which birds eat clay soils, is also thought to play a role in the detoxification of chemicals contained in fruit. Geophagy is best known from the Amazonian clay licks frequented by vividly coloured flocks of parrots, but it also occurs in African species, including mousebirds, Grey Go-away-birds and African Green-Pigeons.

Whereas frugivores often need to deal with a potpourri of chemical compounds in their diets, nectar-feeding birds such as sunbirds and hummingbirds face completely different digestive challenges. Nectar is biochemically simple and consists almost entirely of dissolved sugars. The problem is that nectar is often very dilute and birds need to consume vast quantities to obtain enough nutrients to sustain themselves (see *Africa – Birds & Birding* 11(1): 11). To meet their nutritional requirements, nectarivorous birds routinely drink several times their own body mass in nectar each day, with the record currently held by captive White-bellied Sunbirds, which have been observed drinking up to eight and a half times their body mass daily. Avian nectarivores cope with this prodigious water intake by producing a great deal of extremely dilute urine. Sunbirds have a poorly understood physiological mechanism in which all of the sugar in ingested nectar is absorbed from the intestine into the bloodstream, but most of the water passes straight through the bird's gut.

At the opposite end of the food-processing spectrum are herbivorous birds that feed on leaves and other plant material. The problem is that most of the nutrients are 'locked up' as cellulose, which is indigestible by the vast majority of animals since they lack the necessary enzyme. Herbivorous mammals, most notably ruminants such as cattle, rely on microbes in their guts to ferment and digest cellulose, breaking it down into simpler compounds that are then available to the animal. One of the most spectacular avian digestive adaptations occurs in the Hoatzin, a taxonomically enigmatic bird that frequents South America's lowland rainforests. More than 80 per cent of the Hoatzin's diet consists of leaves. To cope with this specialised food type, the bird possesses a massively enlarged crop that functions as a microbial fermentation vat, like the rumen of cattle and other ruminant mammals. The Hoatzin's highly specialised gut provides one of the most remarkable examples of convergent evolution, a phenomenon in which unrelated groups of animals independently develop similar solutions to a common environmental challenge.

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A diet of dilute nectar poses a significant physiological challenge, since birds such as this White-bellied Sunbird must ingest vast quantities in order to obtain sufficient nutrients.

ALBIE VENTER

Although most birds feed predominantly on one food type, many species regularly switch diets. This is often a response to the sudden appearance of an abundant resource, such as a termite emergence, when many frugivores and granivores take advantage of the fat-loaded alates. Such adaptability is also important for long-distance migrants. During migration, many normally insectivorous species switch to feeding on berries and fruits, carbohydrate-rich food items that require less digestive processing and contain nutrients that are easier to mobilise.

Recent research has shown that migratory birds' guts are remarkably flexible in terms of their physiology and that diet switching is associated with fundamental changes in gut function. For instance, when North American Pine Warblers are fed a protein-rich diet, they optimise their guts for protein digestion by producing more of the enzymes that break down protein molecules. When the same birds are given a sugar-rich diet, the production of protein-digesting enzymes slows and their guts generate more carbohydrate-digesting enzymes. Such digestive flexibility allows the warblers to handle a wide range of diets and extract enough energy to fuel their migratory flights using whatever food items are available. □

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