about birds...

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THE SWEET LIFE OF NECTIVORES

The Purple-crowned Lorikeet *Glossopsitta porphyrocephala* is a highly nectivorous species of parrot, seen here feeding on *Eucalypt* blossoms

INTRODUCTION

Nectivory—a diet mainly comprising nectar—has evolved independently in a number of major bird lineages occupying different geographic regions. Examples include the 325–340 hummingbird species (family Trochilidae) mainly from the New World neotropics and passerines including the 132 sunbird species (Nectariniidae) from Africa, southern Asia and Malaysia, the honeycreepers (Drepanididae) from Hawaii (reduced to 18 species owing to recent extinctions), Australasia's 182 honeyeater species (Meliphagidae), and South Africa's two sunbirds (Promeropidae).

Within parrots (order Psittaciformes), the 53 lories and lorikeets (Loriinae) of Australasia are specialised nectivores, possessing a suite of adaptations absent in other parrots to enable efficient use of nectar and pollen. The Swift Parrot *Lathamus discolor*, Hanging Parrots (*Loriculus*), and *Brotogeris* parakeets also convergently evolved nectivory. Various other bird species also include nectar in their diet to varying degrees.

The amount of nectar in the diet depends on the species. Hummingbirds are the most specialised nectivores, with nectar comprising typically 90% of the diet (excluding nesting females). In honeyeaters, nectar accounts for about 60% (depending on availability) of the diet, with the remainder comprising insects, fruit, manna (a sugary exudate *Eucalyptus* secrete from sites damaged by phytophagous insects), honeydew (sugar secretions of nymphal aphids, coccids, and psyllid insects) or lerp (waxy, sugary material secreted as a protective scale by psyllid insects). Flowers (nectar and pollen) often form 87% of the diet of Rainbow Lorikeets *Trichoglossus moluccanus* (seasonally ranging from 68–100%), with fruits and leaf buds making up the balance.

Accessing Nectar

A bird extracts nectar by inserting its bill into the flower, extending the tongue into the nectar chamber where nectar is collected on the tongue by capillarity, then retracting the tongue. Hence, nectivores feed by 'licking' nectar—they do not 'suck' (nectivores' fast licking speeds, and elastic tongues, which bear central troughs, actually make sucking impossible). Hummingbirds average 13.8 licks per second, but can extend to 17 licks per second. Sugar concentration, nectar volume, and corolla length and orientation also influence how fast nectar is extracted. More concentrated nectars are more viscous, reducing the rate of nectar harvesting, whereas high nectar volumes mean the tongue takes up more nectar, increasing nectar extraction rates.

Hummingbird approaching red, long-tubed corollas of flowers to feed on the nectar contained at the base while hovering in flight

Two Western Australian species, the Western Wattlebird *Anthochaera lunulata* and Red Wattlebird *Anthochaera carunculata* contesting to feed on the same Banksia bloom

Brown Honeyeater *Lichmera indistincta* feeding on Kangaroo Paw at Wireless Hill south of Perth—note the pollen being deposited on the back of the bird's neck

A DIET OF NECTAR

Nectar is a dilute solution produced by plants to attract pollinators. Sugars comprise almost 100% of its dry weight. Nectar provides large volumes of easily digestible energy for birds evolved to harvest it. Nectar has advantages over other foods, like insects, that must be captured and often possess tough chitinous exoskeletons and defensive structures or chemicals, or seeds enclosed in tough casings.

However, nectar contains very low levels of amino acids (a nitrogen source required for protein synthesis) and is also poor in vitamins and trace minerals required for a bird's maintenance, growth and reproduction.

Nectivores require very little nitrogen. For example, both honeyeaters and hummingbirds have protein requirements of only ~1.5%, compared with ~8% for granivorous birds.

However, amino acids are still necessary. Minimal levels in nectar (<2%) mean most nectivores supplement their diet with alternative nitrogen sources. Pollen is a plant's male gametes, brushed off onto pollinators to achieve cross-pollination as they feed between flowers, but can also be used as food. Pollen protoplasm (pollen grain content) contains highly digestible protein with copious amounts of diverse amino acids, and can be harvested with nectar. Active pollen harvesting has been observed especially in Rainbow Lorikeets, Purple-crowned Lorikeets *Glossopsitta porphyrocephala* and Swift Parrots.

Unlike lorikeets, a honeyeater's digestive tract cannot extract the contents of pollen grains, hence they obtain negligible nourishment from pollen (any pollen ingestion likely occurs incidentally).

Insects are the main protein source for most nectivores (especially large honeyeaters). Insects are predated mainly during bird reproduction, especially to meet growing chicks' higher protein requirements. However, many insects cannot be digested by many nectivores which lack gizzards capable of shattering insects' tough exoskeletons.

Nectivore Gut Structure

Mechanical digestion of food occurs in the gizzard. Corresponding to their liquid diet, the gizzard of nectivores is comparatively smaller and less muscular, and in *Glossopsitta* lorikeets, the gizzard is barely recognisable. Longer guts increase the retention time of food so that hard-to-digest food can be broken down. With their highly digestible diet, nectivores are characterised by short intestines. With a soft, liquid diet, nectivores have reduced the glands within the oesophagus, lying below the crop, which produce mucous to help hard foodstuffs glide through the glandular stomach (proventriculus) and prevent hard items causing damage to the gut.

A High-sugar Diet

Nectivores are major sweet-tooths (or sweet beaks)! Consuming prodigious amounts of sugar corresponds to high glucose levels that would be deemed severely hyperglycaemic for humans. In hummingbirds, fasted blood glucose is 300mg/dl, increasing to 740mg/dl following feeding. Not only do specialised nectivorous birds thrive on this high-sugar diet, they recover most of the glucose filtered by the kidneys rather than losing it in urine. Hence, despite being naturally hyperglycaemic, they do not become diabetic and are free from developing polyuria (glycosuria), polydipsia and polyphagia most animals suffer when ingesting excessive sugar.

Specialised nectivores have guts physiologically adapted to process high sucrose levels. They have high levels of sucrase (the enzyme responsible for hydrolysing sucrose) in their intestines, resulting in almost 100% digestion efficiency. In contrast, specialised insectivorous birds (namely species in the superfamily Muscicapoidea, eg thrushes), lack sucrose and hence are sucrose-intolerant. If they are fed sucrose, it accumulates undigested in the gut, leading to osmotic diarrhoea.

A Dilute Diet

For most land animals, the major challenge is to prevent desiccation and dehydration, and to conserve water. Nectar's high water content, low protein content, yet relatively high sugar concentration means nectivores are at the other end of the spectrum in regulating water and solutes.

Because nectar is relatively dilute, wild hummingbirds do not drink free-standing water, obtaining enough water solely from their diet. However, for other nectivores, additional water is vital. Because nectar is more concentrated than blood, when passing through the gut, the concentration gradient causes water to be drawn out of the blood into the gut and lost in the urine. To prevent dehydration, most nectivores must drink fresh water regularly. The hummingbird's ability to avoid osmotic dehydration is a result of their intestinal membranes being impermeable to glucose. Instead, special proteins regulate glucose uptake from the gut, without water being lost into the gut in the process.

Nectivores can ingest prodigious amounts of water. Broad-billed Hummingbirds *Cynanthus latirostris* ingest 4–6 times their body mass in water daily! In other terrestrial animals excessive water intake (polydipsia) would result in 'water intoxication', accompanied by solute imbalances in the blood, like hyponatraemia (low plasma sodium) and rupturing of red blood cells.

The need to ingest such large volumes of water just to obtain enough energy has fitted nectivores with a suite of physiological adaptations. The rate of water passing through the body is extremely high, contrasting starkly with most birds, in which water conservation is a priority. With such a high urine production, nectivores are 'chronically diuretic', and need to prevent sugars and minerals from being lost in the urine. Their kidneys are ideal for processing large volumes of water while absorbing most of the solutes in their diet before it is voided, consequently producing highly dilute urine. Solute recovery by nectivores could not be more efficient—in fact, White-bellied Sunbirds *Nectarinia talatala* excrete urine as dilute as tap-water! Unlike typical bird kidneys, with specialised nephrons for maximising the reabsorption of water to produce a highly concentrated urine, nectivores' kidneys are designed to process and filter large volumes of water while recovering important solutes otherwise lost in the urine. This trade-off means nectivores are vulnerable under dehydrating conditions because they cannot produce concentrated urine. Hence, providing shade and water for nectivorous birds in summer is recommended.

When provided only dilute nectar, nectivores increase their food intake to compensate for the reduced energy concentration. However, there is a limit. With extremely dilute nectar, hummingbirds cannot increase their intake above a certain volume, which means they can't maintain their energy balance. Sunbirds are better able to cope because they 'shunt' excess water directly through the gut, avoiding having it absorbed and processed by the kidneys.

So, although nectivores handle ingesting high volumes of dietary water, there are physiological constraints on feeding intake. Interestingly, when given a choice between nectar of high versus low concentrations of sugars, they choose more concentrated nectar, since they can obtain the same amount of energy in more concentrated nectar without having to ingest as much water.

ADAPTATIONS TO NECTARIVORY

Owing to a shared dietary niche, nectivorous lineages convergently evolved a suite of adaptions for exploiting nectar. Nevertheless, differences exist, reflecting independent evolution from different ancestral species in different geographical regions.

Terrific Tongues

Sunbird and hummingbird tongues are bifurcated at the tip. The pronged tips each have a groove, which in sunbirds join to form a single central trough, continuing to the back of the tongue. The tips act as dynamic liquid-trapping devices, rapidly changing shape when moving in and out of nectar, making the tongue extremely effective in liquid extraction.

Honeyeaters, sugarbirds and nectivorous parrots have brush-tipped tongues, suited to harvesting the types of flowers common in their habitats. In honeyeaters, the tongue tip divides into many parts, with each prong bearing many fine bristles. Bristle numbers range from approximately 20 for the Grey-bellied Honeyeater (or Plumed Longbill) *Toxorhamphus iliolophus* to 120 for the Red Wattlebird *Anthochaera carunculata*. Larger species with correspondingly longer tongues tend to have more bristles. The numerous prongs have grooves which converge along the length of the tongue to form a broad trough, extending back almost to the base. While various other nectar-feeding


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Collared Sunbird *Hedydipna collaris* female with its bill inside a tubular flower, licking nectar located at the flower's base

animals—including nectivorous parrots, nectivorous bats and the unique nectivorous marsupial, the Honey Possum *Tarsipes rostralis*—also have brush-tipped tongues, the structure differs from honeyeaters. Rather than the fairly long (5mm) bristles of honeyeaters, brush-tips of these other large nectivores comprise short (<1mm) papillae. It is also suggested that papillae aids in collecting pollen which, unlike for honeyeaters, is a major part of the diet. Nectivorous parrots have more extensible, muscular tongues than most parrots, and are unique among parrots in possessing a brush tip composed of clusters of thread-like papillae, increasing the tongue's surface area and producing a capillarity effect for nectar extraction.

Different tongue forms can be explained by differences in body size and flower structures, and reflect alternative solutions to provide highly efficient nectar-collecting structures. Despite differing tongue morphologies, hummingbirds, sunbirds and honeyeaters extract nectar at a similar range of rates (1–15μl/s). Larger honeyeaters, with their broader tongues, likely require a brush-tipped tongue for capillary collection to occur. It has been suggested the bristles function by collecting and channelling nectar by capillarity into the central trough of the tongue, or by collecting fluid between them (like paintbrush bristles). Honeyeaters' broader, brush-tipped tongues also cover a larger surface area. This enables honeyeaters to exploit nectar from Australian flowers—in which nectar typically is thinly spread over larger surfaces—and enables feeding on honeydew and lerps.

Flora which exploit hummingbirds or sunbirds as pollinators have tubular flowers with a distinct nectar chamber at the base. The long, thin tongues of hummingbirds and sunbirds are adapted to efficiently extract nectar from plants with this design.

Bills

Bills range from 7–42mm in hummingbirds, 11–47mm in honeyeaters, and 12–39mm in sunbirds. Despite these families differing in body size, most species have bills measuring approximately 20mm, but larger species have longer bills. Bill length and shape largely determine the range of corolla lengths that can be exploited, and many studies have shown a species' bill length and shape correlate with the type of flowers it pollinates. For example, the Magnificent Hummingbird *Eugenes fulgens* has a relatively straight 30–35mm bill and largely feeds on the long, straight *Centropogon talamancensis* flowers, whereas the Green Violetear Hummingbird *Colibri*

Note the papillae on the tongue of this Rainbow Lorikeet harvesting nectar from an Umbrella Tree

thalassinus with a short (21mm) decurved bill visits the shorter curved *Centropogon valerii* flowers. Generally, long flowers are visited by long-billed nectivores specialised to pollinate them, whereas shorter-billed species are restricted to short-tubed or open flowers (which tend to be visited by diverse pollinating taxa, including insects).

Because nectar is contained at the flower's base, if a bird's beak is too short, its tongue, once protruded, is ineffective at extracting nectar. There are however 'cheaters' among shorter-billed nectivores. 'Nectar robbers' (including the aptly named Cinnamon Flower-piercer *Diglossa baritula*) steal the nectar reward without pollinating the flower by piercing the nectar base.

While hummingbirds, honeyeaters and sunbirds all include species with bills decurved to varying degrees, honeyeaters have conical-shaped bills, and only hummingbirds include species with straight or even up-curved bills—likely tied to differing foraging styles. For honeyeaters and sunbirds that perch while probing flowers, a slightly decurved bill is most efficient for reaching and inserting the bill into flowers positioned slightly above or to the side of the bird, especially those at the end of branches which cannot support these birds' larger weight. In contrast, hummingbirds hover, so they can position themselves immediately opposite a flower's opening, making a straight bill most efficient for inserting into a flower's opening. This link between beak shape and foraging style is supported by how the White-tipped Sicklebill *Eutoxeres aquila*, a hummingbird with one of the most decurved bills, feeds on decurved Heliconia flowers by perching on bracts beside or below the flower, rather than hovering in front of them.

Being parrots, lorikeet bills were inherited from an ancestral species with the characteristic parrot hookbill, adapted for crushing seeds and tough fruits. Nevertheless, lorikeet bills are more slender and structurally weaker than granivorous parrots, reflecting reduced dependence on hard foodstuffs.

Foraging Patterns

Feeding on nectar involves not only extracting nectar from flowers—where bill and tongue shape are important—but also accessing and moving *between* flowers. Body mass, wing and leg shape influence how a species forages, and the speed and efficiency of moving between flowers. This determines what types of floral structures, positioning of flowers on a plant, and flower-patch distributions a species uses. When multiple nectivores occupy the same habitat, they partition otherwise similar resources (in time, space and type) and differ in body size, bill length and shape, and aggressiveness, allowing species to specialise on different flowers in order to reduce competition.

Hummingbirds are unique in having the capacity for sustained hovering flight and to remain hovering when feeding. Hovering is more energetically costly than perching but allows more rapid rates of flower visitation and hence faster rates of energy-gain. Different foraging strategies between hummingbirds and passerines relate to body size, since hovering is cost-effective only for small body sizes. Hovering versus perching may also relate to different habitat structures where different species occur. Vegetation where hummingbirds forage tends to offer few perches sufficiently close to flowers, and many hummingbird-pollinated flowers are exposed on the plant's periphery, with sparse surrounding foliage (that would otherwise restrict wing movements). In contrast, flowers visited by passerines tend to have less-exposed flowers, and are situated near robust surrounding vegetation and branches which provide perches for these larger-bodied nectivores.

Most nectivores dedicate 10–35% of daylight hours to foraging. However the largest nectivores, honeyeaters, devote up to 60% of the day to foraging. The smallest nectivores, hummingbirds, spend as little as 5% of the day foraging. This could explain why the female hummingbird, with less of her time spent foraging, is able to raise the offspring alone, whereas the parental care workload must be shared between parents (or be a group effort) in honeyeaters.

Utilising nectar has also led to behavioural adaptations. For dispersed flowers, birds must remember where and when the flower 'hot-spots' are located, as well as how long ago each flower was visited, so that they don't return to a particular flower patch before flowers have renewed their nectar. Studies have revealed hummingbirds have amazing temporal and spatial navigation and memory abilities for this purpose. abk