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The Sweet Life of Nectivores

Part 2—Bird and Plant Co-Evolution

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Bird-pollinated flowers often have red petals and long corollas to attract avian pollinators like this honeyeater

Nectar-feeding birds are involved in a mutualistic relationship with their food plants. During nectar extraction, pollen from anthers (the male flower part), brushes onto the bird's feathers, and when the bird travels to another flower to feed, pollen is transferred onto the stigma (female flower part), achieving fertilisation. Nectivore foraging therefore determines pollination success and many plants have evolved distinctive floral traits to entice nectivorous species that serve as plant pollinators.

However, the birds' sugar reward represents an energetic cost to plants. Research into food-choice preferences using artificial sugar solutions finds that nectivores prefer concentrated solutions (31–45% up to 60%) over dilute ones, yet sugar concentrations in bird-pollinated flowers are comparatively dilute—about 25% sugars. (Only 5% of flowers contain over 35% sugars.) Nectar amount and concentration must also reflect a balance between providing enough to entice favoured pollinators, but not so much as to satiate the pollinator so that it does not go on to feed on more flowers—meaning no cross-pollination. It is possible that, unlike in lab situations, the reduced concentration is also favoured by birds in the wild since it reduces viscosity, making nectar uptake more efficient, or because dilute nectar simultaneously provides a bird's water requirements. It might also discourage pollinators not preferred by these bird-pollinated flowers, namely insects.

But since insects with comparably low energy demands also pollinate plants and, ancestrally, all animal-pollinated flowers were insect-pollinated, why should plants evolve to attract birds, and consequently invest more energy to secrete higher volumes of sugar-rich nectar? The answer is that the 'cost' is worth it. Birds, being larger and more mobile than insects, are reliable long-distance pollinators, preventing inbreeding depression that occurs when pollen moves only between closely related flowers. In south-west Western Australia, many plants have evolved to be specifically pollinated by birds because plant species are largely confined to isolated, patchy populations. Bird pollination is especially common among large, long-lived plants with poor seed dispersal and patchy distributions. Birds' greater mobility also means they can migrate in response to patterns of flower availability, allowing a reliable pollination service for plants flowering seasonally, which cannot sustain local small insect pollinators. As birds are endotherms, they are also more reliable pollinators than ectothermic insects, because birds are consequently less sensitive to temperature, and remain active under conditions insects cannot. So, birds are more reliable, effective long-distance pollinators because of being endothermic and larger, but consequently have high metabolic rates and energy demands, requiring plants to secrete larger nectar volumes to attract them.

Traits for attracting avian pollinators include not only greater nectar rewards but also red or orange-coloured flowers that attract birds (see my article *The Secrets Behind Red Colouration* in ***Australian BirdKeeper***, vol. 28 no. 9). They also have reduced scent so as not to attract insects—because birds forage mainly by sight and have a relatively poorly developed sense of smell. Long floral tubes with thickened walls, preventing access to less-effective insects, are only accessible to birds.

Adopting a nectivorous diet led to evolutionary radiations in the species-rich hummingbirds, honeyeaters and lorikeets. It represented an evolutionary innovation, creating an ecological opportunity which resulted in species proliferation. Given their relatively recent split from other parrot lineages, Loriinae are unexpectedly species-rich. Owing to their more recent history of nectivory (approximately 15 million years), lories are more generalised nectivores. This contrasts with the high degree of specialisation of co-evolution between specific flowers and hummingbirds, with hummingbirds co-evolving with plants for at least 33 million years and potentially more than 50 million! This long co-evolutionary history has produced nearly 8000 bird-pollinated plant species in the Neotropics.

The degree of flower-bird specialisation is influenced by how long ago a bird lineage evolved nectivory. Also, highly specialised plant-pollinator interactions can only evolve when nectar-producing flowers are lasting and predictable in space and time. This may explain the tight co-evolution and specialisation of Neotropical hummingbirds to particular plants, whereas the variable flowering regime of Australia's flowering plants in space and time favoured lorikeets and honeyeaters to be generalist pollinators.

Body Size and Feeding Patterns

Larger nectivores require more energy, but have a greater capacity to store energy, travel distances, are better at defending resources, and lose less body heat than smaller nectivores. Hence, larger nectivores tend to be territorial and defend resource-rich, high-energy floral patches, or forage between widely dispersed but high-energy flower patches. Smaller nectivores, which require less absolute energy but have higher metabolic rates per unit mass and higher rates of heat loss, cover shorter distances per unit of time, and have limited energy reserves, feed frequently on lower-reward flowers dispersed at small distances.

Larger nectivores are able to monopolise patches of 'prime real estate' because larger species are more aggressive and are able to exclude smaller, subordinate birds from accessing dense nectar-rich flower patches for meeting their higher energy demands.

Differences in nectar availability throughout the day between plants characterising Australia versus the Neotropics may contribute to disjunct body sizes between the larger honeyeaters and smaller hummingbirds. In Australia, nectar shows a distinct diurnal pattern, with nectar availability often being 5–10 times greater at dawn, then declining throughout the day. Honeyeaters' larger body size and consequently greater capacity to fast enables them to ingest large volumes in the morning, storing the surplus to see them throughout the day and into the night.

Nectivores inhabiting the same habitat typically differ in body size as a result of natural selection favouring divergence to reduce competition. This is furthered by the co-evolution between particular birds to specialise in plants featuring different floral structures and energy rewards, with different plants in turn co-evolving with the nectivores that are adapting to pollinate them.

For example, hummingbird-pollinated flowers fall into two broad categories:

- Flowers with short corollas producing 1–2mg of sucrose/day, which provide just enough nectar to sustain small hummingbirds (and are visited almost exclusively by small hummingbirds eg *Chlorostilbon*) and
- Flowers producing 4–27mg of sucrose/day, which are pollinated almost exclusively by large species (eg *Anthracothorax*), with long corollas. This prevents smaller birds from harvesting their large nectar supplies and thereby supports the energy demands of the larger birds.

BODY SIZE

Nectivores—Sweet and Small

Body size has a pervasive influence on all aspects of an animal's biology. As most nectivores weigh 3–30g, nectivorous birds are among the smallest of all birds. While bigger birds require more energy overall, smaller birds require more energy per unit of body mass and need to feed more frequently. Evolving small body size was permissible on a nectar diet since the abundance of nectar allows birds to cope with these costs and fulfil this highly profitable niche.

Of the three major nectivore families, hummingbirds are the smallest (2–20g), sunbirds are slightly larger (5–22g), and honeyeaters are the largest (8–200g). No honeyeater weighs less than 8g, which is close to the upper limit of most hummingbirds. (The aptly named 18–24g Giant Hummingbird *Patagona gigas* is the exception.) The Bee Hummingbird *Mellisuga helenae*, weighing just 1.6g—not bigger than a large insect—is the smallest bird on Earth. Minimum size is likely set by the ability to ingest and store enough energy to meet a bird's high energy demands (relative to insect pollinators) for thermoregulation, fasting when not foraging, and reproduction, as well as competition with insect pollinators.

The largest nectivores are some honeyeaters (Yellow Wattlebirds *Anthochaera paradoxa* average 175g) and parrots. This upper limit is probably set by how much energy a plant will invest in producing copious amounts of nectar to sustain the demands of a large pollinator. Less-specialised nectivores attain greater sizes.

NECTIVORES IN CAPTIVITY

Nectivores have been kept in captivity since the 19th century. Because initially people fed them only sugar-water mixes which didn't cater for the birds' unique diet, hummingbirds only lived a few weeks. Fortunately, scientific studies into nectivore nutrition and physiology have enabled nectivores to be kept with increasing success.

Nevertheless, a review on nutritional requirements and diets for hummingbirds and sunbirds by Peaker (1990)[1] found many commercial mixtures were based on folklore, not science, and did not cater to nectivores' specific requirements.

Red Wattlebirds Anthochaera carunculata are one of the larger nectivores. The species' common name denotes the reddish fleshy wattle on the side of the neck

Yellow-bellied Sunbird Cinnyris jugularis male after feeding on Hibiscus flowers—note the decurved bill

Many parrots, such as this Red-capped Parrot Purpureicephalus spurius, although not entirely nectivorous, do consume pollen, nectar and livefood, such as lerps, in their wild diet

Honeyeaters, like this New Holland Honeyeater Phylidonyris novaehollandiae, perch on braches when feeding

Blue-faced Honeyeater Entomyzon cyanotis feeding on nectar using its narrow tongue, bearing long bristle-like filaments

A pair of White-naped Honeyeaters Melithreptus lunatus. Like most specialised nectivores, their slender beaks are adapted to probing inflorescences

They were defective due to a high fat content, low/absent Vitamin D_3, being deficient in certain minerals, and problematic regarding protein solubility. While providing protein in the form of live, small insects can cater to protein needs, different species are highly specific about the insects they consume, or will not readily consume insects at all. Formulated solutions, which include sufficient protein, can prove vital for successfully maintaining and breeding such species. Peaker concluded that a formulated complete liquid diet was the key to successful care and reproduction of most nectivores. He said the alternative form of protein, insects, was unreliable, impractical for most bird keepers and unsuitable for some species. Supplying pollen as a protein source can be successful. However, for species that do not normally ingest pollen, success can be limited given that their digestive tract may be ineffective at extracting protein from the tough pollen coats.

Supplying increased protein, as well as live insects, is advisable during breeding since many nectivores feed their chicks insects. Even though nectar is not fed to young, nectar concentration should be increased at this time, because this significantly influences how much care the parent(s) can invest in rearing the young. For a given species of a given body size, protein and energy requirements increase during moulting and cold weather and, for breeding females, will often double that required for maintenance.

Nectar contains three major carbohydrates in the wild—sucrose, fructose, and glucose—and studies have found hummingbirds prefer solutions containing all three. It is potentially concerning that many artificial diets are based on sucrose alone. Calcium is an important mineral for all animals—especially female birds during the breeding season. Since nectar is deficient in calcium, nectivores must obtain calcium from alternative sources. In the wild they ingest calcium-rich substrates, but in captivity powdered cuttlefish should be supplied. Fruit should be provided for nectivorous parrots. Parrots relish fresh fruits, which provide some amino acids, but importantly are also a rich source of vitamins and minerals. Offering branches with native inflorescences (eg *Banksia* and *Eucalyptus*) not only supplies nectar and pollen but is important for environmental and behavioural enrichment.

While nectivores prefer stronger sugar solutions, and more concentrated solutions provide more energy for a given volume, highly concentrated solutions can cause health problems. This is because highly concentrated nectar travelling down the intestine causes water to be pulled osmotically into the intestine, causing irreversible damage, and leading to dehydration and even death. Peaker recommends a sugar concentration of about 83g/L. However, under cold temperatures, increasing energy concentration is advisable. Concentrations above 150g/L should be avoided.

CONCLUSION

Evolution of nectivory resulted in radiations of diverse bird lineages on different continents. Nectivores' co-evolution with bird-pollinated flowers has produced a suite of morphological, behavioural and physiological adaptations for exploiting the abundant, energy-rich, dilute yet nitrogen-poor food source which nectar represents. These small, active birds are amazing illustrations of evolution.

BIBLIOGRAPHY

[1] Peaker, M 1990, 'Nutritional requirements and diets for hummingbirds and sunbirds', *International Zoo Yearbook*, vol. 29, no. 1, pp. 109–118.