Alimentary adaptations to nectarivory in swift parrots and musk lorikeets

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Introduction

Nectarivorous birds are those that rely predominantly on the products of flowering trees and shrubs to provide their energy (Simpson and Day 1984). Nectar is a sugar rich, liquid food source that provides abundant amounts of energy for birds able to harvest it (Keast 1968, House 1997, Vogel 1983). However, it contains very low levels of amino acids, vitamins and trace minerals (Vogel 1983, Lüttge 1976), all of which are necessary for avian maintenance, growth and reproduction (Brue 1994, Roudybush and Grau 1986). Therefore, birds classified as nectarivores need to forage for other food resources. Pollen, manna (a sugary exudate from damaged eucalypt leaves or woods), honeydew (the sugary excretion of nymphal stages of aphids, coccids and psyllids), lerp (a waxy material secreted by insects belonging to the family Psyllidae as a protective scale), insects, and fruits are alternative resources used by different species to supplement nectar and meet their nutritional requirements (Paton and Ford 1977, Oliver 1998, Paton 1980, Richardson and Wooller 1990).

This paper summarises some of our recent research on the alimentary anatomy of the swift parrot, *Lathamus discolor* and the musk lorikeet, *Glossopsitta concinna* and discusses how the birds have adapted to their specialised diets. The swift parrot is an endangered species that is believed to have evolved from granivorous ancestors in the southeastern eucalypt forests of Australia, filling a niche made available by the absence of lorikeets (Christidis et al. 1991). The musk lorikeet is an unrelated trichoglossid nectarivore that is thought to have arrived in these forests relatively recently, spreading south from New Guinea (Christidis et al. 1991). Trichoglossid lorikeets are considered to be highly specialised nectarivores (Güntert and Ziswiler 1972).

Alimentary adaptations

Tongue

In most nectarivorous birds, the tongue is modified to aid in the harvesting of nectar and, in some cases, pollen (Simpson and Day 1984, Ford and Paton 1985, Higgins 1999). The Australian lorikeets and the swift parrot have a specialised brush tip to their extensible and muscular tongue (Holyoak 1973, Smith 1975, Güntert and Ziswiler 1972). This consists of a cluster of thread-like papillae that increase the surface area of the tongue and may produce a capillary effect, which allows the rapid harvesting of nectar (Churchill and Christensen 1970). The brush tongue has also been implicated by observations of feeding behaviour in the harvesting of pollen (Hopper and Burbidge 1979, Gartrell et al. 2000).

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Crop

In most parrots, the crop serves as a reservoir for food prior to digestion. This allows the birds to harvest food at a faster rate than it can be digested (Ziswiler & Farner 1972, Duke 1986). In the swift parrot and musk lorikeet, the crop is relatively wider than in the green rosella; this may be an adaptation to allow the Swift Parrot to collect large volumes of nectar. Field observations show that many birds will harvest nectar and pollen until the crop is visibly distended; non-breeding birds will spend time preening while digestion takes place. Breeding males need to ferry large volumes of nectar to nest hollows during the incubating period to feed their mates. Preliminary observations of captive birds indicate that incubating females are fed every twenty minutes when food is readily available (Gartrell unpubl. obs.).

Proventriculus

The proventriculus is the glandular stomach of birds and the compound glands of its lamina propria are responsible for the production of hydrochloric acid and pepsin (Ziswiler and Farner 1972). In nectarivorous parrots, the proventriculus has compound glands arranged in longitudinal rows with the areas between free of glands to allow the distension of the stomach (Ziswiler and Farner 1972). In the swift parrot, the proventriculus is relatively longer than that of the green rosella and the arrangement of the glands in the lamina propria more closely resembles that of the musk lorikeet, although this observation is based upon only very few rosella and lorikeet specimens. Further studies are needed to determine if this apparent change in histological structure represents greater acid production capacity.

In birds, crop-emptying time appears to be set by the time taken for acidification of stomach contents; thus, a greater acid production capacity may result in faster crop emptying (Richardson and Wooller 1990). Crop emptying seems to limit the frequency of feeding bouts in hummingbirds (Diamond et al. 1986) and a similar mechanism may be possible in the swift parrot and lorikeets. Further, a greater degree of acidification may also aid in the digestion of pollen by opening pollen germination pores; experimental studies are needed to test this hypothesis.

Gizzard

The gizzard or ventriculus is considered to be the site of mechanical digestion and its size has been related to the presence of hard dietary items, such as seeds (Joseph 1986) and hard bodied insects (Richardson & Wooller 1986). Nectarivorous parrots have varying degrees of gizzard muscle reduction, with the most extreme being seen in the lorikeets of the genus *Glossopsitta* in which the gizzard is barely recognisable (Richardson and Wooller 1990, Gartrell et al. 2000, Güntert and Ziswiler 1972); **Table 1**. The proventricular and pyloric opening of the gizzard in lorikeets and honeyeaters both lie in the median plane and this is thought to allow rapid passage of ingesta (Richardson and Wooller 1990).

The rainbow lorikeet *Trichoglossus haematodus* and the swift parrot both have a relatively muscular gizzard, which may reflect an increased use of insects (Richardson and Wooller 1990, Gartrell et al 2000). The physical properties of the type of insect prey may act to determine the development of gizzard musculature (le Mar 1993). However, not all birds are capable of digesting all insects (le Mar 1993). The strength and structure of the gizzard is important for birds to be able to shatter insect exoskeletons prior to digestion (Richardson and Wooller 1986). However, this fracturing is also dependent on the physical properties of the insect carapace and body structure (le Mar 1993). The koilin layer of the gizzard has been reported to be thinner and lacking in striae in those birds that feed on soft foods (Ziswiler and Farner 1972). The koilin striae play a vital role in the disruption of insect exoskeletons prior to digestion (le Mar 1993); for example, the red wattlebird has a large gizzard with prominent koilin striae.

Intestine

The swift parrot duodenum is relatively wider than that of the green rosella and musk lorikeet. The swift parrot also retains the relatively long intestine of most granivorous parrots. The length of the intestine is necessary for the digestion of complex carbohydrates and fats from a seed or insect based diet (Ziswiler and Farner 1972, Duke 1986, Richardson and Wooller 1990, Del Rio and Karasov 1990). We speculate that this allows the swift parrot to use a wider range of food sources than previously expected outside the breeding season, possibly as an adaptation to the swift parrots' migratory habits. This may account for the species' ability to use fruit and seeds opportunistically, and to survive in captivity on a seed diet.

Sources of protein: Pollen and insects

In our research, both species of nectarivorous parrots were able to rapidly ingest large quantities of *Eucalyptus* pollen and appeared to digest it efficiently. *Eucalyptus* pollen appears to be an important dietary source of protein for these birds. Examination of wild birds indicates that pollen grain emptying occurs in wild swift parrots at comparable efficiencies to that seen in our experimental trials (~48%). This level of pollen grain emptying is similar to that seen in field studies of purple-crowned lorikeets (Wooller et al. 1988). This rate of pollen grain emptying is relatively low compared to that found in honey possums (95-100%). This difference has been attributed to the longer gut transit time in honey possums than in psittacine birds (Richardson et al. 1986). It is possible that the nectarivorous parrots have adopted a strategy of rapid gut transit and, therefore, a greater food ingestion rate, at the cost of digestive efficiency. However, pollen still represents an important source of protein to these birds.

The use of pollen may explain the differences in foraging behaviour seen between nectarivorous passerine and psittacine birds. There are many reports of nectarivorous passerines "hawking" for insects as a source of protein (Recher and Abbott 1970, Paton 1982, Oliver 1998) and some evidence that their dependence on insects increases during the rearing of juveniles (Miller 1994, Oliver 1998). There is evidence from gut content studies (Higgins 1999, Gartrell et al. 2000) that nectarivorous parrots ingest significant quantities of insects but there are no records of them "hawking" for insects. Eucalypt trees are a good source of arthropods (Recher at al. 1996) and it is likely that the parrots glean insects opportunistically as they forage. It seems likely that the birds use both pollen and insects to satisfy their protein requirements.

Conclusion

The nectarivorous parrots have adapted to their specialised diet with a number of alimentary modifications: brush tongue; larger crop; specialised proventriculus; reduced gizzard and shorter intestines. These allow the birds to take advantage of their energy rich diet and overcome its inherent protein deficiency. More research is needed to understand the physiological and biochemical mechanisms that underlie these anatomical adaptations.

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Table 1. Comparison of the gross alimentary measurements of swift parrots and musk lorikeets (Gartrell et al 2000) with the published data of Richardson and Wooller (1990).

All measurements are means.

Intestine length includes duodenum.

Species	N	Body weight (g)	Gizzard length (mm)	Gizzard width (mm)	Intestine length (mm)
Swift Parrot	25	63	13.8	8.5	402.4
Platycercinae					
Western Rosella	2	74	12.5	12.5	350
Green Rosella	4	148	19.3	13.5	661.3
Trichoglossinae					
Purple-Crowned Lorikeet	6	48	7.4	5.9	245.2
Rainbow Lorikeet	3	151	11.8	9.8	248
Musk Lorikeet	4	56	8.6	6.3	375.3