A REVIEW OF THE NUTRITION OF LORIES AND LORIKEETS

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INTRODUCTION

With approximately 50 species, the subfamily Loriinae which contains 11 genera is spread across Australasia and the Pacific. These birds inhabit a variety of habitats within this area, ranging from arid to tropical, from coastal lowland to cool, highlands and vary in size from 16 g to 250 + g (Low, 1998; Forshaw, 1998).

Wild lorikeets obtain their carbohydrates predominately from the simple sugars in nectar, and their protein from pollen. Lesser roles are filled by lerp, manna, honeydew, fruits and seeds as carbohydrate sources and insects as protein sources (Gartrell, 2000; McDonald, 2003). Lorikeets tend to be opportunistic feeders in the wild and may travel significant distances to locate suitable food sources.

We know, for example, that rainbow lorikeets (*Trichoglossus haematodus moluccanus*) in Australia may feed on 43 species of food plants (Cannon, 1984). The planting of non-indigenous native flowering plants in suburban gardens and parks has allowed them to extend their range further south on a permanent basis than previously (Smith and Lill, 2008). In the same study, Musk lorikeets (*Glossopsitta concinna*) exploited 24 plant species. A study of Stephen's lory (*Vini stepheni*) on the isolated Henderson (Pitcairn) Island, revealed that 15 species of plants were utilized as food sources.

However, there is a dearth of information about the feeding ecology of most species.

Therefore, extrapolation from the limited data available on lorikeet nutrition from the few species studied, both in the wild and in captivity, and applying it to all species of Loriinae, is fraught with potential dangers.

ANATOMICAL ADAPTATIONS TO NECTARIVORY

Lories and lorikeets have thinner and structurally weaker beaks than similarly sized granivorous parrots (Holyoak, 1973). Being primarily nectar and pollen feeders, they do not require the beak strength to crack seeds or nuts as other parrots do. However, their beaks have sufficient strength to inflict injuries upon their handlers (pers obs!!)

The tongue is modified to aid in the harvesting of nectar and pollen. It is muscular and extensible and has a specialized brush tip which contains a cluster of threadlike papillae. The papillae increase the surface area of the tongue and may also create a capillary effect, increasing the speed of nectar extraction (Churchill and Christensen, 1970; Holyoak, 1973).

The proventriculus has compound glands arranged in longitudinal rows with gland-free space to allow for the distension of the glandular stomach. This may be an adaptation to pollen digestion.

The ventriculus is characterized by a reduction in the mass of the gizzard muscle. This is most noticeable in *Glossopsitta* species, where the gizzard is barely recognizable. By contrast, rainbow lorikeets have a relatively muscular gizzard, reflecting their more generalized diet which may contain seeds and hard bodied insects at times (Richardson and Wooller, 1990, Gartrell et al., 2000). Gizzard musculature can hypertrophy or atrophy over time to adapt to seasonally available food sources.

The koilin layer of the gizzard is thin and lacks striae which are thought to aid the mechanical disruption of the insect exoskeleton.

The proventricular and pyloric openings of the lorikeet gizzard both lie in the median plane. This allows rapid passage of ingesta, increasing absorption of nectar and allowing quicker passage of pollen to the intestine where most pollen digestion occurs. This is not the case with other parrots (Richardson and Wooller, 1990).

The intestinal tract is shorter than similar sized granivores or herbivores no doubt due to the highly digestible diet (Guntert, 1981; Richardson and Wooller, 1990). The caecae are relatively undeveloped due to the low fibre content of their diet.

The high moisture content of much of their food means that lories and lorikeets must consume a large volume of food to meet their energy requirements. This results in rapid transit times of food through the gastrointestinal tract and in large volumes of faeces being produced.

Due to the high moisture of the food, the droppings also contain a lot of moisture. These birds have evolved a very forceful way of expelling their droppings, which is thought to prevent soiling of feathers around the cloaca.

Honeyeaters have adapted to the large fluid loads resulting from ingesting nectar diets by producing large volumes of dilute urine (Goldstein and Bradshaw, 1998). When ingesting concentrated diets, these birds have a massive capacity for tubular reabsorption of water (>90%) with little effect on glomerular filtration rate.

Kidney architecture also differs between honeyeaters and other passerines enabling honeyeaters to resorb large proportion of solutes and water from the glomerular filtrate (Casotti et al., 1993).

There are also differences in the anatomy of wet-zone and arid-zone honeyeaters. The renal medulla of arid zone honeyeaters has a higher percentage and absolute surface area of capillaries than those of wet-zone honeyeaters, allowing for more efficient water conservation (Casotti and Richardson, 1993).

Whether these renal modifications also occur in lories and lorikeets is unknown at this stage.

Lories and lorikeets typically possess a tight, glossy plumage which is thought to minimize feather soiling by nectar.

Dietary protein requirements are deemed to be lower than those of similar-sized granivorous parrots (Frankel and Avram, 2001). This may reflect the large volume of food eaten and the rapid passage time in the gut. Therefore, although the concentration in the food may be low, the total amount absorbed over the course of the day may meet requirements.

THE ROLE OF SUGARS AND STARCHES IN CARBOHYDRATE METABOLISM IN LORIKEETS

Nectar from flowering plants is a sugar-rich food that provides the major energy source for lorikeets and other nectarivorous species. However, it provides very low levels of amino acids, vitamins and trace minerals.

Sugars make up nearly 100% of the dry weight of nectar. The three main sugars include sucrose and its constituents, namely fructose and glucose in equal amounts. Xylose is found in nectar of Proteaceae and appears to be inefficiently digested by most nectarivores.

Sugar concentrations in nectar of Australian food plants which are bird-pollinated vary between 15% and 35% w/w sugar (Pyke, 1980; Paton, 1982). Nicolson and Fleming (2003b) suggest the approximate average nectar concentration of bird-pollinated plants is 23% w/w (weight/weight) sugar or 0.75 mol/L for honeyeaters. This differs to plants relying on insect pollinators which have higher sugar concentrations (30-74% sugar in nectar for honeybees).

The gross energy value of nectar has been reported to be 16.7 kJ/g (Luttge, 1976). Nectar flows vary between species but each flower of *Eucalyptus* and *Callistemon* can produce up to 5ml of nectar during its lifespan (Christides and Boles, 1994; Gartrell, 2000). Flowers of these species usually last 10 to 30 days.

In one study, red lories (*Eos bornea*) show a preference for sucrose over glucose or fructose when fed nectars of low sugar concentrations (0.25 mol/L), but had no preference between the three sugars at higher concentrations (0.73 mol/L) (Downs, 1997). This was found to be similar to other non-psittacine nectarivores such as sunbirds, sugarbirds, honeyeaters and hummingbirds (Martinez del Rio, 1990; Mitchell and Paton, 1990; Downs and Perrin, 1996). This was explained in terms of energy profitability- a 0.25 M/L sucrose solution yields more than double the energy of a 0.25 mol/L solution of glucose.

However, this is in direct contrast to another study (Fleming et al., 2008) in which rainbow lorikeets preferred a 1:1 glucose: fructose solution over an energetically equivalent sucrose solution when dilute nectars (<0.75 mol/L) were fed, but changed preference to sucrose when concentrated nectars (1 mol/L and 2 mol/L) were fed. At diets around the average concentration of natural nectars (23% sugar or 0.75 mol/L), rainbow lorikeets showed a significant hexose preference. The possible explanation for these findings are as follows:

- At low sugar concentrations, with rapid gut transit times, hexose is much easier to absorb than is sucrose, perhaps due to reduced sucrose hydrolysis efficiency (Fleming et al., 2008). The fact that rainbows preferred hexose at mid concentrations whereas New Holland honeyeaters and red wattlebirds showed no preference was potentially attributed to decreased sucrase activity in rainbow lorikeets. However, sucrase levels have been found by some workers to be quite high in this species (Rich G, pers comm.)

- At high sugar concentrations, sucrose may be preferred to hexose because hexose solutions have twice the osmolality of equicaloric sucrose solutions which may make excretion of built up wastes more difficult and potentially result in dehydration, or require increased water intake (Fleming and Nicolson 2003; Fleming et al., 2004).

These preferences may also merely reflect the situation in nature and what birds are used to ie natural nectars tend to contain more hexose when dilute and more sucrose when concentrated (Lotz and Schondube, 2006). There may also be differences in taste perception by the birds between different sugar sources in nectars at different concentrations.

The apparent contradiction between the red lory study (Downs and Perrin, 1996; Downs, 1997) and the rainbow lorikeet study (Fleming et al., 2008) is according to the latter author due to experimental design. Hexose nectars made up on a % w/w (weight/weight) basis actually only contain 95% of the energy content of sucrose solutions (Fleming et al., 2004). However, sugar solutions made up and matched on a molarity basis (expressed as mol/L), as was the case with Downs (1997) work, resulted in the hexose nectars having only half the energy value of the sucrose nectar. Therefore, any sucrose preference observed was most likely an energy preference, particularly with dilute nectars. Brown et al. (2008) summarized these issues in stating that when comparing “equivalent” sugar solutions, the equivalence needs to be expressed either in terms of number of molecules in solution (equimolar), weight of each sugar in solution, or amount of energy in each solution (equicaloric). Changes in sugar preferences are usually only significant when birds are fed equicaloric low sugar concentration nectars, where hexoses are preferred over sucrose (Fleming et al., 2004; Brown et al., 2008). Some of the earlier work on sugar preferences in lorikeets (eg Downs, 1997) would ideally need to be repeated comparing equicaloric sugar solutions.

The role of raffinose has been discussed by one author as a fibre source potentially promoting the colonization of bifidobacteria and lactobacillus in the lorikeet intestinal tract. This may have the benefit of inhibiting clostridial and other pathogenic infections (McDonald, 2003) However, the amount of raffinose sugars in most nectars is negligible (<1%)

Raffinose sugars are more likely to be encountered in wild plant and insect exudates and make up 5-10% of lerp and 37-48 % of manna (Basden, 1965). The role of raffinose sugars as prebiotics needs further investigation.

Lerp, the waxy protective scale secreted by psyllid insects, is composed of polymers of glucose (90%) and water 10%). Manna, the sugary exudate from damaged eucalypt leaves or woods, is composed of about 60% sugars, 16% water and 20% pectin and uronic acids.

Manna, lerp and honeydew (the sugary excretion of nymphal insects), are all primarily carbohydrate sources and are supplementary food items upon which lorikeets occasionally forage (Brooker et al., 1990). They are sought out more by the other Australian nectarivorous psittacine, the swift parrot, *Lathamus discolor*.

Sugars in general have a very high degree of digestibility in lorikeets and are almost completely digested (Downs, 1997; Wolf et al., 2007).

The digestibility of starch in artificial nectars appears to be similar to that recorded for granivorous psittacine birds fed seeds (Wolf et al., 2007). This is not surprising, given that most starch sources in artificial nectars are cereal- based

Captive lorikeets maintained solely on artificial nectar with low protein showed weight loss and reduced activity compared to those fed artificial nectar supplemented with protein which maintained weight (Cannon, 1979). The protein content of this supplement was 15.4 % protein, most of which was derived from skim milk.

(Complan website: http://www.complanfoods.com/nutrition_compla_original.php)

THE ROLE OF POLLEN

Many studies report the feeding of lorikeets on flowers, but few distinguish between nectar and pollen intake. This is because many studies are observation based, rather than relying on analysis of crop contents. Active pollen harvesting has been recorded in rainbow and purple-crowned lorikeets and in swift parrots (Churchill and Christensen, 1970; Richardson and Wooller, 1990; Gartrell, 2000).

Pollen is considered the main protein source in lorikeet diets. Insect consumption is variable between species, but appears to be more important in honeyeaters than it is in lories and lorikeets (Brooker et al., 1990; Churchill and Christensen, 1970; Ford et al., 1996; Paton, 1981; Smith and Lill, 2008).

Stomach contents of lorikeets contain few insects when the birds are harvesting nectar and pollen (Cleland, 1911; Churchill and Christensen, 1970) and lorikeets do not catch insects when suitable flowers are available (Paton, 1981). The poorly developed lorikeet gizzard makes it unlikely that they could break down the hard chitinous exoskeleton of many insects. A notable exception is the Stephen's Lory (*Vini stepheni*), which ingests a considerable amount of lepidopteran larvae (soft bodied) found on the sporangia of *Phymatosorus* ferns (Trevelyan 1995). Accidental ingestion of insects whilst feeding on flowers is also possible. Grubs of unidentified species have been identified in the gizzard of several musk lorikeets, *Glossopsitta concina,* and in a red-collared lorikeet *Trichoglossus haematodus rubritorquis* (Cleland, 1927). Soft bodied *Homoptera* insects, psyllids, *Thysanoptera* and *Diptera* adults and larvae have been found in the crops of the Papuan lorikeet (also known as Stella's lorikeet - *Charmosyna papou*) (Bosch, 1994; Forshaw 1998). Caterpillars were found in the crop of yellow-bibbed lories *Lorius chlorocercus* and musk lorikeets (Forshaw, 1998). Other unidentified small insects have been found in the crops of red lories *(Eos bornea)*, the Ponape lory (*Trichoglossus rubiginosus*), and the black-capped lory (*Lorius lory)*. Invertebrates, lerp and insect galls made up 9% of the feeding records of rainbow lorikeets and 4.8% of feeding records for musk lorikeets in one study (Smith and Lill, 2008)

Pollens contain between 16-30% protein on a dry matter basis and contain a diverse amino acid profile (Turner, 1984a,b; Stace, 1987). Banksia pollen contains 33% protein, eucalyptus pollen contains 25% protein and acacia pollen contains 24% protein (Somerville, 20010). Hibiscus pollen contains 19.1% protein (Wolf et al., 2007).

Eucalyptus and *Banksia ericofolia* pollens contain adequate levels of all amino acids except methionine (van Tets, 1998; van Tets and Hulbert, 1999). Their amino acid composition is similar to vitellogenin of egg yolk, considered to be a high quality, highly digestible protein (Gartrell, 2000).

Interestingly, methionine is also the one amino acid that rainbow lorikeets rejected when given diets offering a choice of 4 separate amino acids (Frankel, pers com).

Pollen digestibility figures vary widely and appear to be contradictory. Early reports suggested that pollen digestibility was only 4.5-6.6% in adult lorikeets, but increased up to 26% in nestlings (Brice et al., 1989).

The low digestibility was thought to be due to the difficulty in penetrating the outer exine shell of the pollen granules. It is thought that pollen digestion relies on direct enzymatic action through the pores of the outer exine shell. Pollen digestibility appears to be maximized in the presence of nectar (Rich, G pers com). This may result from the hypertonicity of the nectar having an osmotic effect causing the leaching of free amino acids from the pollen granules through the pores into the bird's intestinal tract.

Pollen digestibility may also depend on pollen viability. Arnould (1986) found that unviable Banksia was digested more readily (43-61%) than live pollen (18-22%) by eastern pygmy possums *Cercartetus nanus.*

Not only was pollen found to be poorly digested. Protein digestion overall was found to be low in lorikeets. Frankel and Avram (2001) found that protein digestibility in rainbow lorikeets was only 13.3%, but they used egg white protein as their protein source.

Further research by Delia and Frankel (2006) found that digestibility of egg white did not significantly increase when casein was added (5.6%) and that the digestibility of a commercial nectar product with a whey/casein protein base (Wombaroo Lorikeet and Honeyeater Food) was higher (7.3%) but not significantly so. These figures suggest that the protein metabolizability of artificial protein sources by rainbow lorikeets is relatively low.

Lower protein digestibility may be due to the lower pepsin activity found in lorikeets when compared to 3 week old layer chickens (Delia and Frankel, 2006). Pepsin is the proventricular enzyme which begins protein digestion in the body. Optimum pH for pepsin activity in the rainbow lorikeet is similar to the chicken (pH 2.5-3.2). However, in the same study, the general proteolytic activity of the pancreatic proteases (trypsin, chymotrypsin and carboxypeptidase A) was not different between the two species. However, no studies were performed on the activity of the small intestinal proteases such as glycyl-L-leucine dipeptidase and leucine aminopeptidase N in the rainbow lorikeet. The difference in pepsin activity in this study may possibly be attributable to the different physiological state of the two species since the lorikeets were adults and the chickens were juveniles experiencing rapid growth, where demand for protein would be expected to be higher.

Low protein metabolizability may not only be due to low proventricular pepsin activity. It may also be compounded by a rapid gastrointestinal transit time of food. The presence of free amino acids rather than protein in nectar may mean that high pepsin activities are not required in lorikeets.

The higher digestibility of pollen by nestlings suggests that pollen may be a useful addition for birds rearing young.

Pollen digestibility also varies with the source of protein (Brice et al., 1989). For example,

Casein/whey are also thought to be poorly digested protein sources (4-10%) - unpublished data.

However, these experiments were done with bee pollen which is a conglomerated pollen, and hence a much larger molecule. The pollen was also stored frozen, then used. These factors may decrease the digestibility of bee pollens. By contrast, Frankel and Delia (2007) showed that mixed *Eucalyptus* pollen had a digestibility of 17.4% in rainbow lorikeets. Wolf et al. (2007) found a high protein digestibility when using Hibiscus pollen of 51.6% in Goldie's (*Trichoglossus* goldiei) and 56.3% in Rainbow lorikeets (*Trichoglossus haematodus haematodus).*

It has been calculated by Frankel and Avram (2001) that rainbow lorikeets require as little as 2.8% protein if the protein is high quality and readily digestible, or 8.6% protein for less digestible pollen (4.5% digestibility) to fulfill maintenance requirements. This equates to a daily pollen consumption of 5-6 g DM/day for a 150 g bird.

The protein requirements of lories and lorikeets, however, may also be species- dependant. For example, Cornejo and Clubb (2005) found that *Chalcopsitta* spp. and *Lorius* spp. both chose diets higher in protein and with better amino acid profiles than did *Trichoglossus* spp or *Eos* spp. However, the total protein concentration ingested was just under the estimated minimum recommended value and the digestibility of this protein was not determined. It is uncertain if these results reflect a true higher protein requirement by these species, or merely reflect a taste preference or a learned preference for the high-protein dietary items within the foods offered.

If using pollen as a feeding supplement, the source of the pollen and its amino acid profile both need to be considered.

The role of fats in lorikeet diets has not been well investigated. Fats make up between 1-20% DM of pollen, with triglycerides and phospholipids predominating (Gartrell, 2000).

These figures do not include the indigestible long-chain lipids found in the cell wall.

Dietary fat is most likely sourced from pollen, native fruits and insects (McDonald, 2003). The minimum crude fat recommended is 4% (Brue, 1994) which is similar to the amount consumed in food in at least one study (Cornejo and Clubb, 2005), and also the amount on several commercial lorikeet food products. The actual fatty acid requirements of lories and lorikeets have yet to be determined.

Pollens contain 4-10 % carbohydrates which consist of starch, fructose, glucose and sucrose but are considered to be an insignificant source of energy for nectarivores compared to nectar.

Pollens also contain vitamin C, vitamin E, B vitamins and carotenoids-vitamin A precurors which give pollen its yellow colour. The exact amounts of these nutrients vary (Gartrell, 2000).

Minerals make up 2.5-6.5% DM of pollen. These largely consist of nitrogen, phosphorus, calcium, sulphur, sodium and magnesium and trace amounts of iron and boron (Gartrell, 2000).

THE ROLE OF FRUITS IN THE DIET OF WILD LORIES AND LORIKEETS

Native fruits make up a small percentage of the dietary items found in the crops of wild lories and lorikeets (Forshaw, 1998) and likely represent a seasonal food source. Lorikeets have been observed feeding on native figs (*Moraceae* spp.), *Schefflera*, *Podocarpus* spp., mistletoe berries (Forshaw, 1998; Gartrell 2000; McDonald 2003), although in many cases the species of fruit are not identified.

Lorikeets will also raid domestic fruit crops and quickly adapt to this food source (Forshaw, 1998; Low, 1998)

There are substantial differences between native and domestic fruits. Native Australian fruits have significantly higher protein and slightly higher fat values. However, there is the potential for decreased availability of this protein in fruits containing high tannin levels (McDonald, 2003). Domesticated fruits are higher in simple sugars and water and have poor protein levels. The fibre content of some wild fruits is similar to that of some vegetables (McDonald, 2003).

Fruits tend to contain low levels of calcium but native figs contain calcium levels which fall within the recommended range for psittacine birds (Roset et al., 2000) and have a high Ca;P ratio (McDonald, 2003). Domestic figs, on the other hand, remain calcium deficient but still maintain a positive Ca:P ratio.

Fruits in general provide good levels of provitamin A and vitamin C and have low levels of iron. Native fruits have lower vitamin C levels than domestic fruits, which may explain the susceptibility of some lory species in captivity to iron storage disease since vitamin C promotes iron absorption.

THE ROLE OF SEEDS IN WILD LORIKEETS

Although lories and lorikeets are considered to be primarily pollen and nectar feeders, seeds are also opportunistically consumed by many species. Small seeds of unidentified plant species have been found in the crops of many lorikeet species, including yellow-bibbed lories (*Lorius chlorocercus*), and Stella's lorikeets *Charmosyna papou* (Forshaw and Cooper; Bosch, 1994). Most seeds are described as being small.

The small seeds of *Casuarina* trees are favoured at particular times of the year by several lorikeet species. Rainbow lorikeets are frequently seen to feed on these seeds at certain times of the year when other favoured food plants are not flowering (Cleland, 1927; Low, 1998). Casuarina feeding has also been observed in green-naped lorikeets and in Kuhl's or Rimitara lories, *Vini kuhlii* (Low, 1998).

ENERGY REQUIREMENTS OF LORIKEETS

Smaller lorikeet species seem to have a relatively higher energy requirement than do larger species. Mitchell's lorikeets have a relatively higher energy intake (883 kJ ME/Kg 0.75 BW/d) than green-naped lorikeets (784 kJ ME/kg 0.75 BW/d) . The figures given are for medium dilution nectars but the results are the same for all dilutions (Kalmar et al., 2009). Goldie's lorikeets have a relatively higher energy requirement (0.86 MJ ME/kg BW 0.75) than do green-naped lorikeets (0.65 MJ ME/kg BW0.75) (Wolf et al., 2007).

In green-naped lorikeets fed apple and nectar, energy intake was similar regardless of degree of dilution of nectar. Feeding solely a dilute nectar to this species resulted in a considerable decrease in energy intake.

Increasing dilutions of nectar resulted in increased consumption of both nectar and apples.

In Mitchell's lorikeet, by contrast, adding apple to dilute nectar resulted in a substantial increase in energy intake. Feeding solely a dilute nectar resulted in only a slight decrease in energy intake (Kalmar et al., 2009).

In both subspecies, increasing dilution of nectar and feeding apples significantly decreased protein and thiamine intake and decreased the Ca:P ratio (Kalmar et al., 2009).

WATER INTAKE IN RELATION TO DIET

Lorikeets drink only small amounts of water when fed high moisture content foods. Conversely, water intake is maximized when pollen is the main dietary source (Wolf et al., 2007). However, this study does not measure total water intake in relation to the bird's body weight, nor to its calculated daily requirement. This information would be useful to determine whether high dry matter diets place any physiological stress on lorikeets, particularly when fed long term. Nectars are hypertonic relative to plasma (Skadhauge, 1981), so nectarivores must consume fresh water either in food or separately on a regular basis to prevent dehydration (Gartrell, 2000).

Kalmar et al. (2009) found that drinking water consumption in Mitchell's and green-naped lorikeets remained relatively constant and independent of nectar dilution or the provision of apple to the diet. Therefore, the total water intake for both species was increased when birds were fed dilute diets.

The same author noted that the smaller subspecies (Mitchell's lorikeet) had a significantly higher intake of drinking water than did the green-naped lorikeet.

There was no such correlation when total water intakes were compared between the smaller Goldie's lorikeet with the larger rainbow lorikeet in the study by Wolf et al. (2007).

The nature of the droppings produced also changed depending on the moisture content of the diet fed (Wolf et al., 2007). Birds fed nectar produced droppings that were "beige, soft and poorly shaped" and had a dry matter content of only 8%; Those fed apples had watery droppings (2% dry matter), whilst those fed pollen produced well-formed droppings (30% dry matter) with a clear demarcation between urine , urates and faeces. These droppings were comparable to those produced by seed-fed granivores (Graubohm, 1998). However, there are no studies that analyse what constitutes a "normal" dropping for wild lorikeets. If, as expected, this is dependant upon the local dietary sources, then a study showing the frequency with which droppings of varying consistencies are produced would give some valuable information in this area. Comparisons between renal and large intestinal anatomy and physiology between lorikeets and psittacine granivores would also further our knowledge in this field.

OTHER CONSIDERATIONS

Lorikeets eat approximately 10-15% of their body weight as a dry weight under captive maintenance conditions. The lower figures were seen with birds on apple diets whilst the higher figures correspond to feeding pollen (Churchill and Christensen, 1970; Cannon, 1979; Wolf et al., 2007). These figures are slightly higher than those for similarly sized granivores (DMI 7-12%).

Most seed-eating parrots have digestibility of organic matter of 75-90% on conventional diets (Graubohm, 1998; Britsch, 2002). The figures for lorikeets are roughly similar and diet dependent (Wolf et al., 2007). For example, digestibility of pollen was 55% for rainbow and Goldie's lorikeets, 82% for nectar, and >90% for apples.

FEEDING PREFERENCES OF CAPTIVE LORIKEETS

Historically, the species of lorikeets which have adapted best to captivity have been the ones which have been more adaptable in terms of diet and less specialized in their needs. Hence *Trichoglossus* spp., which have been maintained on an almost exclusively seed diet, have had a longer avicultural history than the more specialized nectar feeders such as *Glossopsitta* and *Charmosyna* spp. (Sindel and Gill, 1984; Low, 1998).

In the Solomon Islands, yellow-bibbed lories (*Lorius chlorocercus*) were more popular as pet birds and survived well on a basic diet of sweet potatoes. By contrast, cardinal lories (*Chalcopsitta cardinals),* another island endemic, would rarely survive more than 12 months on this diet (Low, 1998).

Data gathered from feeding preferences shown by captive birds can also provide useful information. However, such data can be skewed due to preferences formed by exposure to limited food types and by food-preference bias by parental birds and cage mates.

Nearly all lorikeet species accept a nectar supplement in captivity (Low, 1998; Frankel and Avram, 2001; Cornejo and Clubb, 2005; Wolf et al., 2007; Fleming et al., 2008; Kalmar et al., 2009).

Fruit is preferred to vegetables. In a study of 15 species of lories and lorikeets belonging to 4 genera (*Trichoglossus*, *Eos*, *Lorius and Chalcopsitta*), apples and oranges were the favoured fruits with *Trichoglossus* species also favouring pears (Cornejo and Clubb, 2005).

In the same study, *Chalcopsitta* spp and to a lesser extent *Lorius* sp had higher protein and essential amino acid values in the food they consumed than did *Eos* spp. and *Trichoglossus* spp. Whether this reflects an increased requirement in these species or is due to other factors related to the diet offered is unclear.

Green food in the form of chickweed, dandelion and half-ripe *se*ed heads have been eaten by many species of lories and lorikeets (Bosch J, 1995). Green food is actively sought by breeding birds and fed to youngsters. Whiskered lorikeets, *Oreopsittacus arfaki*, in particular seem to seek and eat large quantities of greenfoods when offered (Low, 1998; Jensen, 2000). Amongst other lorikeet species which have been recorded to eat greenfood, particularly when rearing young include members of the *Eos, Trichoglossus, Neopsittacus* and *Charmosyna* genera (Low, 1998) eg Mount Apo lorikeets *Trichoglossus johnstoniae* (Hubers, 2002), and Stella's lorikeet, *Charmosyna papou* (Bosch, 1994).

Other species seldom show any interest in green food eg *Chalcopsitta* spp. (Low, 1998).

Seeds are also ingested periodically by various lorikeet species but are an important dietary item for Musschenbroek's lorikeet, *Neopsittacus musschenbrokei*, emerald lorikeet, *Neopsittacus pullicauda,* and the iris lorikeet *Trichoglossus iris* (Low, 1998; 2000; Wierda, 2000). Other species which have been observed to eat seed in captivity include the red-flanked lorikeet, *Charmosyna pulchella,* Stella's lorikeet, and most species of *Trichoglossus*, including Goldie's lorikeet, *T. goldiei,,* rainbow lorikeet *T. haematodus subsp*, scaly-breasted lorikeet *T. chlorolepidotus.,* Mt Apo lorikeet, *T. johnstoniae*

Low (1998) comments that the only species which reject *Casuarina* cones and seeds are the members of the *Chalcopsitta* genus.

Soft bodied insects are also actively sought by many species. Blue crowned lorikeets, *Vini australis,* actively seek out and eat mealworms (Jensen, 2002) as do blue-streaked lories, *Eos reticulata.* Other species such as red-flanked lorikeets, Goldie's lorikeets, emerald lorikeets have all been observed eating mealworms (Wierda, 2000) and Musschenbroek's lorikeets seek waxmoth larvae when young are in the nest (Low, 2000). No doubt many species will ingest insects when given the opportunity, especially when rearing young.

Several breeders have commented that certain species of lorikeets fare better when kept on low protein diets in captivity. These species include members of the genera *Charmosyna* and *Chalcopsitta*, as well as the whiskered lorikeet (Low, 1998; Hubers, 2000). There is little scientific proof for these statements, which are based solely on observation and experiences in captivity by these breeders.

In general, from experiences with captive birds, the *Trichoglossus* spp, the dusky lory (*Pseudeos fuscata*) and the yellow-bibbed lory are considered more omnivorous in their dietary preferences than many other species of lories and lorikeets (Low, 1998).

POTENTIAL PROBLEMS WITH CAPTIVE DIETS

Many lories and lorikeets in captivity are fed home-made diets utilizing cereal-based ingredients and sugars. These have been developed over time and are based on aviculturists' experiences rather than any scientific basis. The range of ingredients used and the individual adjustments made may vary from breeder to breeder. The end result is highly variable, and the nutritional composition of the diet fed, including total energy and amino acid composition, is largely unknown. Some of these diets have even been produced and sold commercially, again with no scientific basis. Despite these limitations, many of these home-made diets are reported to be successfully used across a broad range of species (Hubers 2006 , Sindel and Gill, 2007).

If these nectars are too dilute they will pass through the gut more quickly giving less time for digestion and absorption of the nutrients within them. Therefore, diluting nectars as a means of effecting weight loss is likely to lead to nutritional deficiencies. Dilute nectars are also prone to spoilage as they have free water available which allows bacteria to multiply. Nectars in the wild have a sugar concentration of 20-25%, and those in captivity should mirror this. Producing nectars of the correct osmolality produces a bacteriostatic effect by depriving bacteria of available water. This acts as a natural preservative for the nectar. At the other extreme, nectars which are too hyperosmolar, such as those which contain mostly fructose or glucose, may cause osmotic water loss from the body and cause dehydration in birds. The ideal osmolality is 30% wt/volume (Rich, pers com).

Some breeders supplement protein by using high protein cereals with the mistaken belief that this may help counteract problems with feather plucking. Nectars are by nature low in protein because birds consume such large volumes of them over the course of a day. There is no evidence that increasing the protein content of nectars will increase protein absorption in adults, but may be of benefit for nestlings since they have a greater capacity for protein digestion as mentioned previously.

Many, but not all, commercial nectars are at least formulated by nutritionists. The end product is of known nutritional composition, assuming that quality control is of a high standard, which is not always the case. Known nutritional requirements for lorikeets are limited and much of this information is extrapolated from other psittacine birds or even poultry. How these figures apply to the large range of lory and lorikeet species kept in captivity is unknown. In addition, the nutritional requirements of nestlings are different to adults, but there are few manufacturers who produce separate diets to account for these differences. (eg The Dutch company Avesproduct produces "Loristart" for rearing young lories, as well as "Lorinectar" for adults).

However, there is great variability between the differing commercial products. Those with low energy value or low digestibility will result in the production of a greater volume of droppings which will necessitate more frequent cleaning if adequate hygiene is to be maintained.

Most people supplement lory diets with fresh fruit, with apple being the most popular type (Sindel and Gill, 1987, 2007; Cornejo and Clubb, 2005). The addition of fruit acts to dilute the total nutritional intake of the bird since most domestic fruits are high in sugar- but not as high as most nectars - and low in protein, essential fatty acids, mineral and some vitamins, as stated earlier.

There has been a trend in some countries to create dry diets for these birds. These diets were initially developed to minimize the risk of food spoilage and consequent outbreaks of bacterial and fungal infections which periodically occurred in collections fed nectar-based diets (Sindel and Gill, 1987). They also resulted in firming up of the droppings produced by the birds which was seen as an advantage by the pet industry in making these birds more popular as pet birds (Holsheimer, 1992). In the author's opinion, droppings from birds fed on predominately dry diets tend to stick more to the aviary structure and can be much harder to clean, especially once dried.

Unlike nectars, dry diets don't suffer from settling of ingredients, particularly during hot weather, which may result in the birds only ingesting the dilute liquid portion of the nectar whilst the more solid ingredients are left in the bottom of the food dish. Another advantage of dry foods is that they are less attractive to bees and wasps, but ants are still attracted to their high sugar content.

These dry foods have been successfully used for the keeping and breeding of Australian lorikeets (Sindel and Gill, 1987, 2007), but have been less successful with many of the other lorikeet species. Issues with maintaining adequate hydration in birds fed dry-based diets, even in the presence of ad libitum drinking water, may be placing physiological stresses on species which are less adapted to arid habitats than many of the Australian species are.

Increased intake of dry foods may result in slower gut transit times of food, since nutrient digestion is maximized when foods are dissolved in water (Holsheimer, 1992). If dry foods take longer to digest, intake of many essential nutrients, not just energy, may be impaired resulting in nutritional deficiencies and potentially weight loss. There is a lack of published information on feeding dry diets on lorikeets in terms of digestibility.

There are several health related issues resulting directly or indirectly from the diet fed to lorikeets. These will be summarized below.

The high sugar content of the diet can lead to yeast/fungal and bacterial infections to occur. This is evident in many post mortem findings by the author, even if only as a terminal event.

Similarly, the sticky and moist nature of the droppings and the high sugar content of the nectar, dry food and fruits fed provides an ideal environment for bacteria and yeast to proliferate on aviary structures if suitable hygiene practices are not maintained.

The high energy content of most diets combined with a lack of activity in a captive situation can lead to obesity-related disorders such as fatty liver syndrome and infertility.

High iron content as found in many human cereals and other foods used in lorikeet diets, combined with feeding foods high in vitamin C such as citrus can lead to iron accumulation in various organs but particularly in the liver, and iron storage disease. The exact nature of this problem in susceptible species requires further investigation, in particular the presence and activity of enzymes involved in iron homeostasis such as hepcidin, ferroportin and hephaestin.

There is some evidence that captive diets may contain excessive amounts of preformed vitamin A leading to hypervitaminosis A (McDonald, 2003). Clinical signs noted in lorikeets include problems with breeding, feather and beak condition and pigmentation (McDonald and Oldfield, 2002). Lower vitamin A levels supplemented with dietary vitamin A precursors may be a more suitable form of supplementation. This may also allow for adequate absorption of vitamin E, which otherwise would suffer from competitive inhibition by high dietary vitamin A levels.

CONCLUSIONS

Although nectar and pollen make up the bulk of lorikeet diets, supplemented with fruits, seeds, insects, lerp, manna and honeydew, the exact nutritional requirements for each species is largely unknown. Therefore, the marketing of commercial lorikeet diets as "complete" foods is misleading. The use of home-made diets results at best in the feeding of foods of unknown nutritional composition, and at worst in malnutrition and associated diseases. Despite this some of these appear to be successfully used with many species.

Even if the exact diet for each species in the wild could be accurately determined, its applicability to captive birds may be limited by the greatly reduced energy demands of birds kept in captivity.

Human-based foods need to be carefully considered before being chosen for use in captive lorikeet diets. Issues such as protein digestibility, levels of preformed vitamin A, iron and vitamin C, and fluid content all need to be addressed

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