Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions

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Abstract. Nectarivory has evolved many times in birds: although best known in hummingbirds, sunbirds and honeyeaters, it also occurs on an opportunistic basis in a varied assortment of birds. We present a phylogenetic analysis of the distribution of nectarivory in birds. Specialised avian nectarivores are generally small, with an energetic lifestyle and high metabolic rates. Their high degree of dependence on nectar as a food source has led to convergence in morphological, physiological and behavioural adaptations. We examine the constituents of nectar which are most important to bird consumers, and how the birds deal with them in terms of physiology and behaviour. There are still unanswered questions: for example, the dichotomy between sucrose-rich nectars in hummingbird-pollinated plants and predominantly hexose-rich nectars in sunbird-pollinated plants appears to have little to do with bird physiologies and may rather reflect patterns of nectar secretion.

Key words: Nectarivory, pollination, hummingbirds, sunbirds, sugar digestion, water balance, osmoregulation.

Nectar feeding is widespread in birds

Many bird-pollinated (ornithophilous) flowers are spectacular because of their large size and bright colours, often red or orange. They are also characterised as diurnal, unscented, and frequently possessing tubular corollas which match the narrow bills of their pollinators (Endress 1994). Alternatively, birds visit less specialised brush-like flowers with conspicuous stamens, grouped in inflorescences, like those of *Eucalyptus* and other Australian Myrtaceae. The energetic requirements of bird pollinators are met by abundant nectar which represents a significant investment by the plant, not only in terms of nectar production but also the substantial floral structures required to produce and contain it.

Convergent evolution is illustrated by three major radiations of nectarivorous birds on different continents: the Neotropical hummingbirds (Trochilidae), and two passerine families, the Meliphagidae (honeyeaters) in Australasia and Nectariniidae (sunbirds) in Africa and Asia. Hummingbirds and their tubular flowers show the most specialised interactions; sunbirds occupy an intermediate position; and honeyeaters are the least specialised, foraging on accessible brush flowers and depending more on insects (Stiles 1981). Of the three main nectarivore lineages, hummingbirds are the oldest, dating back to some 33 million years ago. Consequently, throughout the Americas, nearly 8,000 plant species of >60

families have evolved flowers whose principal pollinators are hummingbirds, and hummingbird pollination has sometimes evolved numerous times within a single genus (e.g. *Erythrina*, Baker and Baker 1982b, Bruneau 1997). Body sizes support the idea that nectar-dependant species are in general smaller than those with more varied or non-nectarivorous diets (Brown et al. 1978, Pyke 1980). Hummingbirds weigh 2–20 g (331 species, Cotton 1996), sunbirds 5–22 g (102 species, Cheke et al. 2001) and honeyeaters are the largest, ranging from 8–250 g (169 species, Frith 1977, Pyke 1980).

Numerous other families, mostly passerine or perching birds, include species that show varying dependence on nectar. These include the Hawaiian honeycreepers, flowerpiercers, and lorikeet parrots, as well as opportunistic nectar feeders such as white-eyes, weavers, Old and New World orioles, barbets, louries, mousebirds, starlings, Darwin's finches and some babblers and warblers (Fig. 1, Oatley and Skead 1972, Wolf and Gill 1986). Around 10% of all bird species may use nectar as a resource at some time (Wolf and Gill 1986). Even in Europe, which lacks ornithophilous flowers (Ford 1985), opportunistic nectar consumption can be energetically important for *Sylvia* warblers returning after long-distance migratory flights (Schwilch et al. 2001). The relationship between bill length and corolla length determines whether nectar-feeding birds are legitimate pollinators or nectar robbers, although the distinction between the two categories is becoming less clear (Maloof and Inouye 2000).

Aside from the fascination of bird-flower associations, nectar-feeding birds are excellent models for ecophysiological research because their energetics and water turnover are extreme and inseparable (Beuchat et al. 1990, Martínez del Rio et al. 2001). They are generally small, and consequently have high mass-specific metabolic rates: hummingbirds are the smallest endotherms and their hovering flight is especially expensive. Small body size also means a low capacity for energy storage, so they are

highly susceptible to energetic stress. In terms of studying digestive physiology, they eat sugar solutions, a deceptively simple food. And finally, these sugar solutions are dilute, so that water fluxes through the bodies of avian nectarivores may be extraordinarily high (Beuchat et al. 1990, Martínez del Rio et al. 2001, Nicolson and Fleming 2003).

We will examine the constituents of nectar which are most important to bird consumers, and how the birds deal with them in terms of physiology and behaviour.

Sugars

Nectar sugars are derived from sucrose translocated in phloem sap, and the final composition of nectar is determined by nectary invertase which hydrolyses sucrose to glucose and fructose. The extent of this hydrolysis, and the resulting sugar composition, vary dramatically between the nectars of hummingbird- and passerine-pollinated plants (Baker and Baker 1983). Hummingbird nectars show a left-skewed normal distribution, with an average of 64.4 ± 18.5% (S.D.) of the nectar sugar being present in the form of sucrose (Fig. 2B, n = 278 plant species). A very different bimodal pattern emerges for sugarbird- and sunbird-pollinated plants in southern Africa (n = 259 species), the majority of these producing nectar that is hexose dominant (37.0 ± 39.3% sucrose). About half (47%) of sunbird/sugarbird plants produce nectar with <10% of the sugar present as sucrose (Fig. 2D). Many produce sucrose-rich nectars, with almost a quarter of species (24%) producing >80% sucrose nectars. The sucrose-hexose dichotomy is pronounced even within genera, with *Erica*, *Protea* and *Leucospermum* nectars being either sucrose- or hexose-dominated and showing few species with mixed sugar compositions (Barnes et al. 1995, Nicolson and Van Wyk 1998, Nicolson 2002). Nectars from plants pollinated by honeyeaters and honeycreepers demonstrate an even more dramatic bimodal pattern (Fig. 2F, n = 83 species) with almost half

Parvclass	Order	Superfamily	Family	Subfamily	Tribe	Sucrase?	
Superorder Neognathae							
PICAE	Piciformes		Capitonidae				*Barbets*
COLIAE	Coliiformes		Coliidae				*Mousebirds*
PASSERAE	Psittaciformes		Psittacidae	Lorinae			**Lories/Lorikeets**
	Strigiformes		Musophagidae				*Louries*
	Apodiformes		Trochilidae			P	**Hummingbirds**
	Columbiformes		Columbidae				*Doves*
	Passeriformes						
	⌐ Tyranni						
	Tyrannida		Tyrannidae			tr	Tyrant/New World flycatchers
	⌐ *Corvida*						
	⌐ MELIPHAGOIDEA	Meliphagidae				**Honeyeaters**
	CORVOIDEA	⌐ Oriolidae				*Old World orioles*
		⌐ Dicruridae				*Drongos*
	Passerida						
	MUSCICAPOIDEA	⌐ Bombycillidae			P	**Waxwings**
		Cinclidae			·	Dippers
		Muscicapidae			·	Old World flycatchers
		Turdidae			**	Thrushes
		Sturnidae			**	*Starlings*
		⌐ Mimidae			**	*Mockingbirds*, thrashers, catbirds
	SYLVIOIDEA	⌐ Paridae				*Tits*
		Pycnonotidae			P	*Bulbuls*
		Zosteropidae				*White-eyes*
		⌐ Sylviidae	Sylviinae	Sylviini		*Old World warblers (Sylvia spp.)*
				Timaliini		*Babblers (Myzornis)*
	PASSEROIDEA	⌐ Fringillidae	Fringillinae	Drepanini		**Hawaiian honeycreepers**
			Emberizinae	Parulini	P	*New World warblers*
				Thraupini		**Tanagers, flowerpiercers, bananaquits,** *Darwin's finches*
				Cardinalini	P	Cardinals & New World buntings (*Saltator*, *Passerina*)
				Icteridini	P	*New World orioles (Icterus, Cacicus)*, grackle, blackbirds
		Passeridae	Passerinae			*Sparrows*
			Ploceinae			*Weavers*
		⌐ Nectariniidae	Promeropinae			**Sugarbirds**
			Nectariniinae	Nectariniini		**Sunbirds,** *spiderhunters*
				Dicaeini		**Flowerpeckers**

Specialised nectarivores
Occasional nectar-feeders
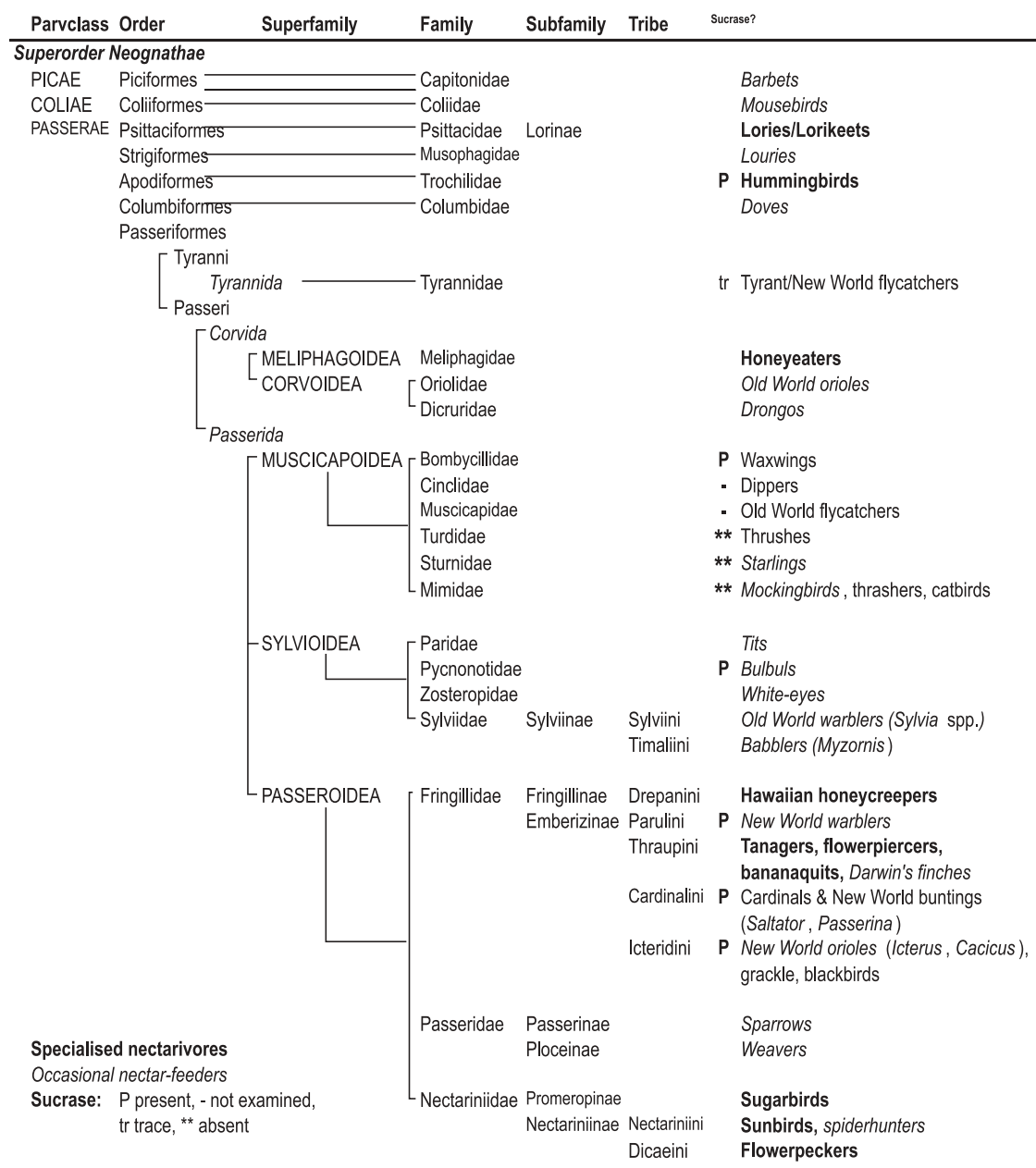**Sucrase:** P present, - not examined, tr trace, ** absent

Fig. 1. Phylogenetic distribution of avian nectarivory; phylogeny based on Sibley and Ahlquist (1990). Specialised nectarivores are indicated in bold, opportunistic or occasional nectar-feeders are indicated in italics (Oatley and Skead 1972, Wolf and Gill 1986, Schwilch et al. 2001). Some non-nectarivorous birds have been tested for the presence of sucrase and these are included in plain text. The presence of sucrase is indicated as: P present, - not examined, tr trace, and ** absent = sucrose intolerant species (Martínez del Rio et al. 1988, Martínez del Rio et al. 1989, Martínez del Rio and Stevens 1989, Martínez del Rio 1990a, Malcarney et al. 1994, I. G. van Tets, A. Green, T. McWhorter, B. Pinshow unpubl. data)

(46%) of plant species recorded with <10% sucrose and a third (37%) of species with >90% sucrose. In these plants, the sucrose-hexose dichotomy is also pronounced within genera (e.g. *Banksia* and *Grevillea*, Nicolson and Van Wyk 1998).
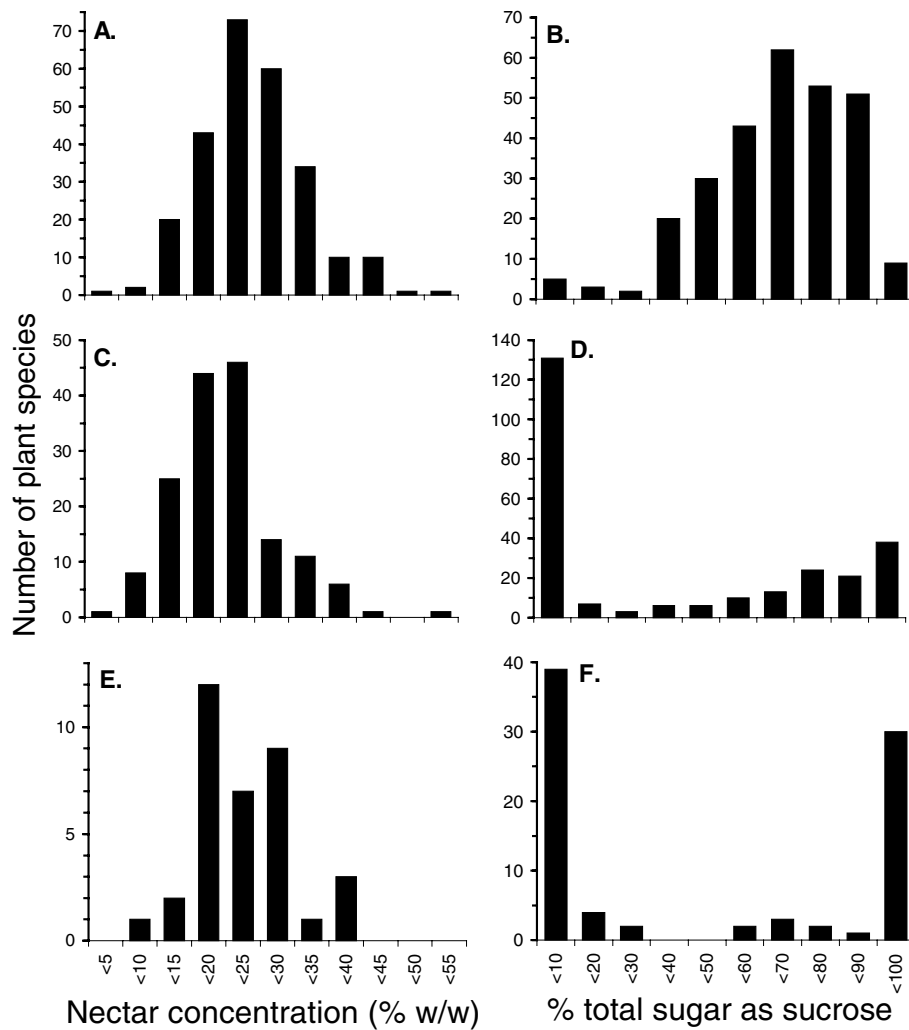
Fig. 2. Nectar concentration (% w/w sugar) and sugar composition (% total sugar as sucrose) for plant species pollinated by hummingbirds in America (A & B), sunbirds/sugarbirds in southern Africa (C & D) and honeyeaters/honeycreepers in Australia and Hawaii (E & F). Values are unpublished data (S. W. Nicolson) as well as from the literature (Percival 1965; Skead 1967; Hainsworth and Wolf 1972a, b; Hainsworth 1973, 1974; Baker 1975; Gill and Wolf 1975a, b; Stiles 1975; Wolf 1975; Hainsworth and Wolf 1976; Wolf et al. 1976; Cruden and Toledo 1977; Hainsworth 1977; Bolten and Feinsinger 1978; Bond and Brown 1979; Brown and Kodric-Brown 1979; Waser 1979; Pyke 1980; Corbet and Willmer 1981; Frost and Frost 1981; Pyke and Waser 1981; Baker and Baker 1982a, b; Feinsinger et al. 1982; Paton 1982; Collins 1983; Cruden et al. 1983; Heyneman 1983; Wiens et al. 1983; Freeman et al. 1984; Gottsberger et al. 1984; Lammers and Freeman 1986; Buys 1987; Craig and Stewart 1988; Elisens and Freeman 1988; Moncur and Boland 1989; Arizmendi and Ornelas 1990; Freeman et al. 1991; Stiles and Freeman 1993; van Wyk et al. 1993; Johnson and Bond 1994; Koptur 1994; Vos et al. 1994; Baker et al. 1998; Nicolson and van Wyk 1998; Pauw 1998; Goldblatt et al. 1999)

Differences in nectar sugar composition between hummingbird- and passerine-pollinated flowers have sparked decades of research and debate. Taste preferences and digestive limitations, such as differences in the time required to process or assimilate sugars, are affected by diet concentration, so that neither composition nor concentration can be considered independently. Bird-dispersed fruits resemble the nectars of passerine-pollinated

flowers in their hexose dominance (Martínez del Rio et al. 1992, Baker et al. 1998), and much of what we know about sugar assimilation in passerine birds comes from studies of frugivores (for review see Levey and Martínez del Rio 2001).

We might expect the high sucrose content of hummingbird nectars to reflect a high degree of sucrose preference by these birds. Unfortunately, most sugar preference trials to date have compared sugars mixed on a % weight basis, assuming them to be equicaloric (Stiles 1976, Martínez del Rio 1990b, Martínez del Rio et al. 1992, Lotz and Nicolson 1996, Jackson et al. 1998, Schondube and Martínez del Rio 2003). This convention has no doubt arisen because field nectar concentrations are measured in % (w/w) sucrose equivalents. However, the molecular mass of sucrose is not exactly twice that of glucose and fructose, and consequently hexose solutions mixed on a % weight basis will have 95% of the energy value of sucrose solutions. It is therefore not possible to distinguish between sucrose preference and preference for the greater energy value of the sucrose solutions. This point is important because hummingbirds have recently been shown to be able to discriminate between sucrose solutions differing by only 1% (Blem et al. 2000).

In contrast with reports of significant sucrose preference in hummingbirds, a more recent study (using equicaloric solutions) showed no significant sucrose preference in broadtailed hummingbirds *Selasphorus platycercus* (P. A. Fleming, B. Hartman Bakken, C. N. Lotz, S. W. Nicolson, unpubl. data). Slight preference for sucrose over hexose mixtures has been recorded for sunbirds and white-eyes feeding on moderate concentrations (Franke et al. 1998, Jackson et al. 1998, Fleming et al., unpubl. data). When offered choices between more dilute solutions (5 and 8.3%), hummingbirds, sunbirds and nectar-feeding flowerpiercers show greater preference for hexose diets (Schondube and Martínez del Rio 2003, Fleming et al., unpubl. data).

Why then are hummingbird nectars sucrose-dominant, if both hummingbirds and sunbirds show only slight preference for sucrose in the laboratory? A sucrose solution has a similar sweetness rating to a 1:1 glucose-fructose mixture (Harborne 1993), although bird perception of sweetness may differ from that of humans. Could there be differences in physiology that enable hummingbirds to cope with sucrose better? Firstly, a dietary mechanism seems an unlikely explanation for sucrose preference (Martínez del Rio 1990b). Sucrose and hexose sugars have the same energy value and are assimilated with equally high (>97%) efficiency by all nectarivorous birds examined to date (Collins et al. 1980, Martínez del Rio 1990b, Lotz and Nicolson 1996, Jackson et al. 1998). In fact, sucrose digestion involves the additional step of sucrose hydrolysis. Secondly, the osmolality of sucrose solutions is around half that of energy-equivalent hexose mixtures (Beuchat et al. 1990, Nicolson 2002): if the rate of delivery of food from crop to intestine is mediated by osmolality, then sucrose might be processed faster than hexose mixtures, but this is not the case (Martínez del Rio 1990b). The preference switch to hexoses on dilute diets, however, may be linked with the greater osmolality of hexose solutions. A third, rather unlikely, hypothesis is that birds may be imprinted on nectar sugar as chicks (Martínez del Rio 1990b); but while hummingbird chicks may be fed a little nectar, sunbird nestlings are fed very little (if any) nectar (see below).

Plant physiology must also be considered. Because energy is transported as sucrose in plants, it may be easier for plants to secrete sucrose directly in the nectaries. In the absence of a pollinator aversion to sucrose, sucrose may be the dominant nectar sugar. However, hummingbird nectars are neatly clumped around 64% of sugar present as sucrose; only 3% of hummingbird-pollinated plant species produce sucrose-dominant (>90%) nectar (Fig. 2B). Partial hydrolysis is evidently responsible for the mixed sugar composition of the majority of nectars (Baker and Baker

1982a, Baker et al. 1998), but details of nectar secretion mechanisms and the location of nectary invertase are generally lacking (Nicolson 2002). Studies such as those of Pate et al. (1985) are an exception.

Sucrose must be hydrolysed by sucrase (the animal equivalent to the plant invertase) before intestinal absorption of glucose and fructose. Hummingbirds have much higher sucrase activity (per unit intestinal area) than some other non-specialised nectar-feeding passerine birds (Martínez del Rio 1990a). All birds in the Muscicapoidea families Turdidae, Sturnidae and Mimidae (thrushes, starlings and mockingbirds) that have been examined lack sucrase expression, and are therefore sucrose intolerant (Fig. 1, Martínez del Rio et al. 1988, Martínez del Rio 1990a); accumulation of undigested sucrose in the gut causes osmotic diarrhoea (reviewed by Martínez del Rio et al. 1992). Consequently, starlings develop an aversion to sucrose in preference tests (Martínez del Rio et al. 1988). However, frugivorous cedar waxwings possess sucrase but still prefer hexoses (Martínez del Rio et al. 1989). We have no data for intestinal sucrase activity in sunbirds or honeyeaters, but their consumption of sucrose-dominant nectars certainly suggests high sucrase activity. In sum therefore, these data indicate that the absence of intestinal sucrase cannot be a factor driving the hexose-dominant nectars in plants pollinated by these groups. An interesting idea could be that high sucrose composition may have developed as a deterrent to nectar robbers in hummingbird-pollinated plants. This hypothesis would require that nectar robbers were sucrose-intolerant, but we do not know enough about the digestive capacities of these birds (Fig. 1 summarises our knowledge of the presence of intestinal sucrase in birds).

Active transport of glucose at high rates was demonstrated in hummingbirds by Diamond et al. (1986). However, recent studies on lorikeets and several species of passerine frugivore suggest that passive absorption is the predominant pathway for glucose transport in birds (Levey and Martínez del Rio

2001). The everted sleeve technique which was used in the original hummingbird experiments has recently been applied to sunbirds and found to damage the delicate intestinal tissue, so that uptake rates are likely to be underestimated (Starck et al. 2000). Both glucose and fructose may be absorbed passively by a paracellular route (Pappenheimer 1993).

Water

One of the defining characteristics of bird-pollinated flowers is that they produce copious and dilute nectar, often in the range 20–25% (w/w) (Pyke and Waser 1981, Stiles and Freeman 1993). American hummingbird nectars (25%, Fig. 2A, n = 255 plant species) are more concentrated than southern African sunbird nectars (21%, Fig. 2C, n = 158 species, ANOVA: $F_{1,411} = 16.36$, $P \leq 0.001$), although we do not know whether this difference is biologically relevant. In Australia, honeyeater nectars average an intermediate 23% (Fig. 2E, n = 35 species). Dilute bird nectars are puzzling since under laboratory conditions, both sunbirds and hummingbirds show preferences for more concentrated sugar solutions than their natural nectars, somewhere in the region of 31 to 45% (e.g. Stiles 1976, Pyke and Waser 1981, Tamm and Gass 1986, Roberts 1996, Nicolson and Fleming 2003).

A variety of hypotheses have been proposed to account for the relatively low sugar concentration of bird nectars:

1. low viscosities permit more efficient extraction of nectar by birds (Baker 1975);
2. low concentrations discourage bees (Bolten and Feinsinger 1978);
3. dilute nectars meet the water requirements of birds (Baker 1975, Calder 1979), a situation that may not be replicated to the same degree in laboratory trials;
4. nectars remain dilute owing to protection in tubular hummingbird flowers (Plowright 1987);
5. dilute nectars may encourage more bird visitations by not satiating their energy

requirements immediately (Collins and Clow 1978, Martínez del Rio et al. 2001); and

6. dilute nectars are a consequence of hydrolysis of sucrose to glucose and fructose, the subsequent increase in osmolality drawing water from the nectary (Nicolson 1998, Nicolson 2002).

The question is still unresolved, and perhaps a combination of these factors is involved. Nectar concentrations are determined by both chemical effects and microclimatic gradients, and the usual post-secretory change is an increase in concentration due to evaporation, especially in open brush-type flowers (Corbet et al. 1979, Nicolson 2002). In fact, average values in the literature obscure the fact that the diet of avian nectarivores is highly variable in concentration (Martínez del Rio et al. 2001, Nicolson 2002).

Over a wide range of diet concentrations, many nectarivorous birds show compensatory feeding, varying their food intake (and thus preformed water) in order to maintain constant energy intake (Collins 1981, Lotz and Nicolson 1999, McWhorter and Martínez del Rio 1999, Nicolson and Fleming 2003, Schondube and Martínez del Rio 2003). For the negative relationship between volumetric intake and concentration $V = aC^{-b}$ (also known as the intake response) a value of b equal to 1 indicates perfect compensation (Martínez del Rio et al. 2001). Values of b which are statistically indistinguishable from 1 have been found in various bird species (for review see Martínez del Rio et al. 2001), but these data depend on the range of sugar concentrations over which intake is measured. Sufficient dilution of the diet causes birds to shift from an intake response showing compensatory feeding to one showing physiological constraints; when intake can not be increased further, birds fail to maintain energy balance (Nicolson and Fleming 2003).

Volumetric intake is extremely high on dilute sugar nectars with low energy densities, e.g. 5.4 times body mass daily in broad-tailed hummingbirds *Selasphorus platycercus* feeding on 10% sucrose (McWhorter and Martínez del Rio 1999). In an influential review of the physiology of nectar-feeding birds, Beuchat et al. (1990) hypothesised that birds feeding on large volumes of dilute nectar may reduce intestinal water absorption and shunt some of the excess water directly through the gut, thus reducing the water load to be processed by the kidneys. This hypothesis was first tested in broad-tailed hummingbirds by McWhorter and Martínez del Rio (1999), who found that absorption through the intestine was essentially complete. In contrast, recent application of the same pharmacokinetic technique to Palestine sunbirds *Nectarinia osea* shows that water flux in these birds is indeed regulated on dilute sugar nectars (McWhorter et al. 2003). As water intake increased, the fraction of ingested water absorbed decreased to 36%. The difference between these lineages of nectar-feeding birds is exciting, though we must be cautious in extrapolating to other species of hummingbirds and sunbirds.

Even when a proportion of ingested water passes directly through the intestine, the kidneys of nectarivores have to deal with heavy water loads and these animals can be described as chronically diuretic (Calder and Hiebert 1983). Their kidneys are ideal for processing large volumes of water but contain very few mammalian-type, concentrating nephrons and a small medullary component (hummingbirds and honeyeaters, Casotti et al. 1998). Glomerular filtration rate (GFR) is a measure of the maximal possible rate of urine production by the kidney. In Palestine sunbirds *Nectarinia osea*, GFR is lower than predicted from allometry, is highly variable and not particularly sensitive to water loading (T. J. McWhorter, C. Martínez del Rio, B. Pinshow, L. Roxburgh, unpubl. data), perhaps indicating that the kidneys of these birds are capable of dealing with even greater water loads. Similarly for the red wattlebird *Anthochaera carunculata*, GFR is also highly variable and does not change with water intake (Goldstein

and Bradshaw 1998). Excreted fluid volume and osmolality are inversely correlated, and extremely low osmolalities have been measured in the cloacal fluid of birds drinking dilute nectar. Ruby-throated hummingbirds *Archilochus colubris* produced fluid with a mean osmolality of 10 mmol kg H_2O^{-1} (Beuchat 1998). Whitebellied sunbirds *Nectarinia talatala* on dilute sugar diets excreted fluid comparable to measurements of tap water at 6.2 ± 2.6 S.D. mmol kg^{-1} (Fleming and Nicolson 2003). Recovery of solutes by the kidneys and gastrointestinal tract could not be more efficient than this.

There are other physiological problems associated with feeding on dilute sugar nectar. Warming ingested food to body temperature is an expensive business for birds feeding on dilute diets because of the enormous volumes they ingest in relation to body mass. The cost is reflected in the increased metabolic rate of sunbirds feeding on dilute sugar nectars (Lotz and Nicolson 2002). This cost is a function of three factors: the volume of nectar consumed, the specific heat of the sugar solution, and the difference between body and nectar temperatures. Modeling predicts that the cost of warming nectar should increase linearly as nectar temperature decreases, and exponentially as nectar concentration decreases; experiments with rufous hummingbirds *Selasphorus rufus* have confirmed these predictions (Lotz et al. 2003). It is tempting therefore to speculate that in cold climates birds should prefer more concentrated nectars (Calder 1979, Gass et al. 1999).

At the other extreme, concentrated sugar nectars may also pose osmoregulatory problems. Although it is often assumed that nectarivorous birds do not consume drinking water, honeyeaters in arid Australia are highly dependent on drinking water (Fisher et al. 1972). When sugar concentrations in the diet are high, captive whitebellied sunbirds drink supplementary water if it is available, thereby diluting their food to around 30% w/w (Nicolson and Fleming 2003).

Ions

'Nonsugar' solutes in hummingbird nectars may account for about 9% of the apparent sugar content estimated by refractometry (Inouye et al. 1980). Of these 'nonsugar' solutes, ions are the most important, but data on nectar ion concentrations are sparse (Waller et al. 1972, Hiebert and Calder 1983, Nicolson and W.-Worswick 1990). Hummingbird nectars may have reasonably high potassium levels, but are often low in sodium: mean values of 24.7 mmol l^{-1} for K^+ and 3.4 mmol l^{-1} for Na^+ were measured in nectar of 19 plant species (Hiebert and Calder 1983). The nectar of sunbird-pollinated plants in southern Africa is generally low in both K^+ and Na^+, although ten species of *Protea* (Proteaceae), which are pollinated by the Cape sugarbird *Promerops cafer*, produce nectar with mean K^+ and Na^+ concentrations of 18.0 and 16.9 mmol l^{-1} respectively (S. W. Nicolson, unpublished data).

Rufous hummingbirds fed on dilute (salt-free) sucrose solutions excrete fluid containing 0.4 and 0.2 mmol l^{-1} of Na^+ and K^+ respectively (Lotz and Martínez del Rio 2003). The same birds were not particularly tolerant of high salt diets, retaining ions when NaCl in their food exceeded 35 mmol l^{-1} (Lotz and Martínez del Rio 2003). The ureters of birds empty into the cloaca, and on both salt-free and high salt diets, further postrenal modification occurs, additional ions being reabsorbed or added (Roxburgh and Pinshow 2002, Lotz and Martínez del Rio 2003).

Electrolyte intake of avian nectarivores is supplemented with arthropod feeding. This becomes apparent when excreted fluid is sampled from both wild-caught hummingbirds and honeyeaters; measured K^+ and Na^+ concentrations in the excreted fluid are much higher than expected from a nectar diet (Calder and Hiebert 1983, Goldstein and Bradshaw 1998).

Nitrogen

Nectar of bird-pollinated plants is a poor source of nitrogen (Baker and Baker 1982a,

Paton 1982). Amino acids occur in nectar in small quantities, but the amounts are too low to meet the protein requirements of nectarivorous birds (Martínez del Rio 1994). In particular, the relative proportions of the amino acids may differ from the birds' requirements, with low amounts of essential amino acids resulting in waste of others. Gottsberger (1990) has cautioned against attributing too much significance to measured amino acid concentrations in nectar, because of the probability of amino acids leaching from contaminating pollen grains. Certainly for plants like *Eucalyptus*, it is difficult to imagine how honeyeaters can remove nectar without dislodging pollen from the numerous anthers.

Adult nectarivorous birds appear to have unusually low daily protein requirements compared with other bird species (around 1.5% of daily diet on a dry mass basis, Paton 1982, Brice and Grau 1991, Brice 1992, Roxburgh and Pinshow 2000, Van Tets and Nicolson 2000). Adult Anna's hummingbirds *Calypte anna* can survive for long periods (up to 10 days) with no protein intake (Brice and Grau 1991). Despite low daily protein requirements, nectarivorous birds are unable to meet their nitrogen requirements on an exclusively nectar diet (Martínez del Rio 1994). Other nitrogen sources include insects (Paton 1982, Brice 1992) and pollen (Wooller et al. 1988, Van Tets and Nicolson 2000). However, net rates of energy gain from hawking insects are small (usually < 20 J/min, certainly lower than energy gain from nectar feeding) and sometimes negative (Paton 1982). Therefore, provided that nectar is available, it would be expected that birds would not invest more time on insect feeding than is required to meet daily nitrogen requirements (Roxburgh and Pinshow 2000), contributing to strong selection for low nitrogen requirements. Pollen ingestion requires less energy than insect feeding, as pollen will be encountered while foraging on nectar. However, birds vary in their ability to extract nutrients from pollen, hummingbirds being less efficient than some other nectar-

feeders (Wooller et al. 1988, Brice et al. 1989, Richardson and Wooller 1990, Van Tets and Nicolson 2000). Pollen protein constituents also vary between plant groups, with some essential amino acids lacking (Martínez del Rio 1994), perhaps limiting the usefulness of pollen as a diet component.

Protein requirements of nestlings, on the other hand, are very high due to growth, and nestlings are fed an almost exclusively arthropod diet (Markman et al. 1999). As a consequence, nesting female hummingbirds and honeyeaters may switch to spending a greater proportion of their time feeding on insects than non-breeding birds (Pyke 1980, Paton 1982). Interestingly, even though nectar is not fed to young, the quality (concentration) of nectar resources available to parents significantly increases the degree of parental care that they can invest in offspring (Markman et al. 2002).

"Toxic" substances

The ecological significance of toxic nectar has recently been reviewed by Adler (2000). Of various theories proposed to explain the existence of toxic compounds in nectar, one that has received little attention is that secondary compounds involved in herbivore resistance may be present in nectar as a consequence of their presence in phloem (Adler 2000). A possible example is the pentose sugar xylose, which occurs in nectar of *Protea* and *Faurea* (Proteaceae) at concentrations up to 39% of total sugars (Nicolson and Van Wyk 1998). Xylose is not palatable to bird or insect pollinators and its presence in nectar may be a result of plant physiology (xylose passing untransformed through the nectaries) rather than pollinator preferences (Jackson and Nicolson 2002).

Occasional toxic compounds in nectar are most likely to be discovered when bees make poisonous honey. Sometimes nectar is toxic to honeybees but without apparent ill effects on birds. The New Zealand kowhai *Sophora microphylla* is pollinated by honeyeaters but

alkaloids in the nectar are toxic to honey bees (Clinch et al. 1972). Amygdalin is a cyanogenic glycoside occurring in fruit and nectar which does not deter frugivorous birds (Struempf et al. 1999) but is unpalatable to honeybees (London and Eisikowitch, this volume). These examples illustrate that toxicity to one taxon should not be extrapolated to another, and in fact very little is known about the role of secondary metabolites in bird-plant interactions (Levey and Martínez del Rio 2001).

Conclusion

In summary, despite the strong co-evolution between birds and plants, the patterns of this relationship are not easily read. The influence of other pollinators with conflicting requirements could be one reason, an incomplete understanding of both plant and bird physiologies could be a second. Certainly, some interesting questions arise.

Firstly, is there a connection between the ability of sunbirds to shunt water through the intestine (McWhorter et al. 2003) and their habit of feeding on very dilute nectars? Water load may limit uptake of energy-dilute solutions in hummingbirds more than in sunbirds, due to relative differences in metabolic rate. More comparative work is needed, especially on the Meliphagidae, which is the largest family of passerine birds in the Australasian region (Keast 1985).

Secondly, one of the curious patterns in nectar sugar composition is why so few bird-pollinated plants produce nectar with 10–30% of the sugar as sucrose (Fig. 2B, D & E). Why is there such a distinct dichotomy in sugar composition of both sunbird/sugarbird and honeyeater/honeycreeper nectars, with so many nectars consisting of either pure sucrose or pure hexoses, even within a single genus? Could the mixed sugar composition of hummingbird nectars in tubular flowers be related to rates of nectar secretion and sucrose hydrolysis by invertase?

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