Sugar Preferences in Nectar- and Fruit-Eating Birds: Behavioral Patterns and Physiological Causes[1]

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ABSTRACT

Sucrose, glucose, and fructose are the three sugars that commonly occur in floral nectar and fruit pulp. The relative proportions of these three sugars in nectar and fruit in relation to the sugar preferences of pollinators and seed dispersers have received considerable attention. Based on the research of Herbert and Irene Baker and their collaborators, a dichotomy between sucrose-dominant hummingbird-pollinated flowers and hexose-dominant passerine flowers and fruits was proposed. Data on sugar preferences of several hummingbird species (which prefer sucrose) vs. a smaller sample of passerines (which prefer hexoses) neatly fitted this apparent dichotomy. This hummingbird–passerine dichotomy was strongly emphasized until the discovery of South African plants with sucrose-dominant nectars, which are pollinated by passerines that are able to digest, and prefer sucrose. Now we know that, with the exception of two clades, most passerines are able to assimilate sucrose. Most sugar preference studies have been conducted using a single, relatively high, sugar concentration in the nectar (*ca* 20%). Thus, we lack information about the role that sugar concentration might play in sugar selection. Because many digestive traits are strongly affected not only by sugar composition, but also by sugar concentration, we suggest that preferences for different sugar compositions are concentration-dependent. Indeed, recent studies on several unrelated nectar-feeding birds have found a distinct switch from hexose preference at low concentrations to sucrose preference at higher concentrations. Finally, we present some hypotheses about the role that birds could have played in molding the sugar composition of plant rewards.

RESUMEN

Sacarosa, glucosa y fructosa son los azúcares mas comunes en néctar floral y pulpa de fruta. La proporción relativa de estos azúcares en néctar floral y la pulpa de fruta han sido estudiadas en relación a las preferencias de azúcar de polinizadores y dispersores de semillas. Basandose en estudios de Herbert e Irene Baker y colaboradores se propuso la existencia de una dicotomía entre plantas con néctares ricos en sacarosa que son polinizadas por colibríes, y plantas con néctares y frutos ricos en hexosas que son polinizadas por paserinos. Datos sobre la preferencia de azúcares en varias especies de colibríes (que prefieren sacarosas) comparados con una pequeña muestra de paserinos (que prefieren hexosas) apoyan la existencia de la dicotomía propuesta. La dicotomía colibrí-paserino fue enfatizada por más de una década, hasta el descubrimiento de plantas sudafricanas con néctares ricos en sacarosa que son polinizadas por paserinos que prefieren sacarosa. Hoy sabemos que la mayoría de los paserinos, salvo los miembros de dos clados, pueden asimilar la sacarosa. La mayoría de los estudios sobre preferencias de azúcares han sido conducidos usando una sola concentración de azúcares en el néctar (*ca* 20%). Por lo tanto, carecemos de información sobre el papel que juega la concentración de azúcares en las preferencias de estos por las aves. Debido a que muchos procesos digestivos son afectados, no solo por la composición de azúcares, sino también por su concentración, sugerimos que las preferencias por diferentes azúcares dependerán de su concentración. Efectivamente, estudios recientes indican que diferentes aves prefieren alimentarse de hexosas a bajas concentraciones, y de sacarosa a altas concentraciones. Finalmente, presentamos algunas hipótesis sobre el papel que las aves pudieron haber tenido en la evolución de la composición de azúcares del néctar y la fruta que consumen.

THE SUGAR COMPOSITION AND CONCENTRATION OF FLORAL NECTAR AND FRUIT PULP varies widely among plant species (Widdowson & McCance 1935; Whiting 1970; Nagy & Shaw 1980; Pyke & Waser 1981; Baker & Baker 1983a, b; Freeman & Worthington 1989; Baker *et al.* 1998; Nicolson & van Wyk 1998; Nicolson 2002). Twenty years ago, Baker and Baker (1982, 1983b) presented a large data set on sugar composition of nectar. Their results suggested a marked correlation between nectar sugars and the bird taxa acting as pollinators of the plants. The hummingbird-pollinated flowers from this data set generally contained sucrose-dominant nectars, whereas the passerine-pollinated flowers contained hexose-dominant nectars. Since this influential review was published, a plethora of authors have examined both the behavioral preferences for sugars of different nectar- and fruit-eating birds, and the physiological causes of these preferences in relation to the evolution of bird–plant interactions (see Appendix 1; Martínez del Rio *et al.* 1992, 2001; Baker *et al.* 1998; Nicolson & Fleming 2003; Schondube & Martínez del Rio 2003a).

The main goal of this review is to link the digestive mechanisms of nectar- and fruit-eating birds with their sugar preferences. First, we briefly summarize observed patterns of sugar composition in floral nectar and fruit pulp among plants that are visited by different bird taxa. Second, we describe sugar selection by birds and examine the underlying physiology that may cause their preferences. Third, we discuss complicating factors that have thwarted our

understanding of sugar selection by nectar- and fruit-eating birds. In particular, we speculate on how sugar concentration may affect bird physiology and, in turn, affect preferences among foods with different sugar compositions. Finally, we discuss the ecological and evolutionary significance of avian sugar preferences in nectar and fruit.

THE SUGAR COMPOSITION OF FLORAL NECTAR AND FRUIT PULP

It has been widely accepted that there are only three major sugars in floral nectar and fruit pulp. These are the disaccharide sucrose and the hexose monosaccharides glucose and fructose. Until recently, these "big three" were the only sugars detected in significant quantities in thousands of plant species surveyed (Percival 1961; Whiting 1970; Baker & Baker 1982, 1983b; Freeman *et al.* 1984; Lammers & Freeman 1986; Barnes *et al.* 1995; Baker *et al.* 1998). However, van Wyk and Nicolson (1995) found that the pentose monosaccharide xylose comprised up to 40 percent of the total nectar sugar of several South African Proteaceae species (see also Nicolson & van Wyk 1998). Minor sugars detected in nectar and fruit include maltose, melezitose, arabinose, galactose, mannose, gentiobiose, lactose, melibiose, trehalose, raffinose, and stachyose (Whiting 1970, Baker & Baker 1982, van Wyk & Nicolson 1995).

The significance of xylose as a nectar sugar has been investigated since its discovery as an important sugar of nectar secreted by several South African species in the Proteaceae (Nicolson & van Wyk 1998). One of the most obvious hypotheses was that it attracted sugarbirds (Promeropidae), a southern African family of virtually obligate Proteaceae nectar-feeders. However, Jackson *et al.* (1998a, b) found that Cape Sugarbirds (*Promerops cafer*) avoided xylose when offered a choice between it and any of the "big three" nectar sugars. Representatives of the two other main African nectar-feeding bird families (Lesser Double-collared Sunbirds, *Nectainia chalybea*, and Cape White-eyes, *Zosterops pallidus*) are also averse to xylose (Appendix 1; Lotz & Nicolson 1996, Franke *et al.* 1998). Lesser Double-collared Sunbirds drink xylose only when mixed with favored sugars and when offered no other choice (Lotz & Nicolson 1996). Also, chickens (*Gallus gallus*) showed aversion to xylose, strongly preferring water to xylose solutions (Kare & Medway 1959).

Like birds, two insect pollinators, Protea Beetles (*Trichostetha fascicularis*) and Cape Honey-bees (*Apis mellifera capensis*), are also averse to xylose (Jackson & Nicolson 2002). The only pollinator tested to date that does not show a very strong aversion to this nectar sugar is the Namaqua Rock Mouse (*Aethomys namaquensis*). A few individuals of this species preferred this sugar to other nectar sugars in laboratory experiments (Johnson *et al.* 1999). However, most rock mouse individuals still revealed a preference for other nectar sugars over xylose, so this animal species cannot pose strong selective pressure for xylose production in nectar. The presence of xylose in nectar remains a mystery, and because we lack information on the importance of this sugar in fruit pulp, this review will focus only on the effects that sucrose, glucose, and fructose have on bird physiology and behavior.

NECTAR.—Many flowers contain all three major nectar sugars. Baker and Baker (1983b) reported that 649 out of 765 nectars sampled contained all three sugars in detectable amounts. However, one or two of the sugars quite commonly constitute most of the total sugar in the nectar of a particular plant species. The proportion of sucrose to hexose in different nectars has been the focus of a considerable amount of research (*e.g.*, Baker & Baker 1982, 1983a, b; Freeman *et al.* 1991; Stiles & Freeman 1993; van Wyk 1993; Baker *et al.* 1998; Nicolson & van Wyk 1998; Perret *et al.* 2001; Dupont *et al.* 2004). Of the 140 hummingbird-pollinated plants surveyed by Baker and Baker (1983b), 122 of them produced nectar containing higher proportions of sucrose than of hexoses. On the other hand, only 2 of the 75 species of passerine-pollinated flowers from both the New World and the Old World contained nectar with more than 50 percent sucrose. This perceived dichotomy between hummingbird- and passerine-pollinated floral nectar became firmly entrenched in the literature since Baker and Baker published their first review on the composition of floral nectar (Baker & Baker 1982). A decade after Baker and Baker's (1982) initial review, with a few new data, the pattern was again strongly emphasized by Martínez del Rio *et al.* (1992). The generality of this widely accepted pattern was questioned 3 years later when Barnes *et al.* (1995) discovered that 29 passerine-pollinated *Erica* species in South Africa had sucrose-dominant nectar, and only 8 had hexose-dominant nectar. Nicolson and van Wyk (1998), however, found that South African and Australian Proteaceae species that were pollinated by passerines had hexose-dominant nectar, unlike insect- and mammal-pollinated species, but argued that other factors apart from pollinator type (such as plant phylogeny) were important factors to explain nectar composition in these plants.

FRUIT.—The pulp of fruits consumed by birds, both in the Old and in the New World, is rich in the hexoses fructose and glucose (Martínez del Rio *et al.* 1992, Baker *et al.* 1998). The sucrose content of passerine-consumed fruits averages only 8 percent of total sugars (Baker *et al.* 1998). Baker *et al.* (1998) found that from a sample of 65 species of Old World plants distributed in 27 families, only 2 plants had fruits that were sucrose-rich. They found a similar pattern among members of 37 New World plant families. The sugar content of fruits ingested by most non-passerine frugivorous birds, a diverse group that includes among others, pigeons, trogons, quetzals, hornbills, turacos, tucans and a large array of species distributed in 59 genus of 12 families (Snow 1981), remains largely unknown. Most studies that deal with the nutrient content of bird-consumed fruits explore the amounts of protein, lipids, and nonstructural carbohydrates in pulp (*e.g.*, Foster 1977, Wheelwright *et al.* 1984, Herrera 1985, Johnson *et al.* 1985, Jordano 1995), and do not include information on their specific sugar composition.

SUGAR PREFERENCES OF NECTAR- AND FRUIT-EATING BIRDS

Despite the high functional diversity found among non-passerine birds, information on their sugar preferences is limited to some species of fowl (chickens, *G. gallus*; and Japanese quail, *Coturnix coturnix japonica*; family Phasianidae; Jukes 1938, Kare & Medway 1959, Harriman & Milner 1969, among others), some members of the Trochilidae (hummingbirds, see below), and one parrot (Red Lory, *Eos bornea*; Downs 1997a). Chickens and Japanese quails were able to distinguish sweet flavors and preferred sucrose, glucose, or fructose solutions to pure water (Kare & Medway 1959, Harriman & Milner 1969). When facing diets with sucrose or glucose at a 20 percent concentration (weight/volume), both species preferred sucrose (Jacobs & Scott 1957) or were indifferent (Jukes 1938). Despite their seed-based diet (that does not contain sucrose), these two species had sugar preferences similar to those found in the specialized nectar-feeding hummingbirds.

While some hummingbird species show behavioral preferences for sucrose over hexoses in laboratory studies (Appendix 1; Stiles 1976, Hainsworth & Wolf 1976, Martínez del Rio 1990a, Martínez del Rio *et al.* 1992), other species are indifferent to the sugar composition of nectar (Martínez del Rio 1990a, Schondube & Martínez del Rio 2003a, Fleming *et al.* 2004). However, all but the most recent of these experiments have been performed using relatively high sugar concentrations, and there are physiological reasons why preferences for sucrose over hexoses may reverse when nectar is more dilute (discussed later). Recently, authors have begun studying sugar preferences over a whole range of nectar concentrations, and the trend indeed seems to be a switch from preferring sucrose or being indifferent at high concentrations to a hexose preference at low concentrations (Schondube & Martínez del Rio 2003a, Fleming *et al.* 2004). Moreover, nectars dominated by the hexoses glucose and fructose tend to be more dilute than those dominated by sucrose (Nicolson 1998, 2002). Hummingbird field preference data are scarce, but they do support a general, although not strong, preference of these birds for sucrose (van Riper 1958, Stiles 1976).

Early studies of several fruit-eating passerines, in contrast to hummingbirds, revealed marked preferences for hexoses over sucrose, or even complete aversion to sucrose (Appendix 1; Martínez del Rio *et al.* 1988, 1989, 1992; Martínez del Rio & Stevens 1989; Martínez del Rio 1990a; Brugger & Nelms 1991; Brugger *et al.* 1993). These bird preference studies attractively fitted the notion of Baker and Baker (1983b) that there was a distinct dichotomy in the composition of floral nectar between hummingbird- and passerine-pollinated plants worldwide. A paradigm shift came when Barnes *et al.* (1995) discovered high frequencies of sucrose-dominant nectar in South African passerine-pollinated flowers. We now know that at a nectar concentration of 20 percent sugar, several South African nectar-feeding passerines either show no preference for hexoses over sucrose (Cape Sugarbirds), or actually prefer sucrose (Lesser Double-collared Sunbirds, and Cape White-eyes; Appendix 1; Lotz & Nicolson 1996; Jackson *et al.* 1998a, b; Franke *et al.* 1998). Moreover, two specialized nectar-feeding passerines show a reversal from hexose preference at low concentrations, to being indifferent

(White-bellied Sunbirds, *Nectarinia talatala*; Fleming *et al.* 2004) or preferring sucrose at higher concentrations (Cinnamon-bellied Flowerpiercers, *Diglossa baritula*; Schondube & Martínez del Rio 2003a). Fruit-eating Azure-winged Magpies (*Cyanopica cyana*) and Brown-eared Bulbuls (*Hypsipetes amaurotis*) displayed no preferences between sucrose and hexose when offered agar cubes with 12 percent sugar (Appendix 1; Lane 1997), and three species of nectar-feeding tanagers (*Dacnis cayana, Chlorophanes spiza, Cyanerpes nitidus*) were indifferent for sucrose or glucose solutions at a 20 percent concentration (Schaefer *et al.* 2003).

While many groups of nectarivorous birds including hummingbirds, orioles (Icteridae), sunbirds, honeyeaters, flowerpiercers, and tanagers preferred sucrose over hexoses, or were indifferent when tested at a 20 percent concentration (weight/volume; Martínez del Rio 1990a, b; Lotz & Nicolson 1996; Jackson *et al.* 1998a, b; Schaefer *et al.* 2003; Schondube & Martínez del Rio 2003a), their preference patterns among different hexoses are not clear. Different species have been found to display different orders of preference among glucose, fructose, and glucose–fructose mixtures (see Appendix 1).

PHYSIOLOGICAL CAUSES OF SUGAR PREFERENCES

Sucrose.—Are the observed behavioral preferences and aversions of birds for different sugar compositions caused by underlying physiology or by superficial taste preferences? Aversion, at least, appears to be caused by an inability to assimilate particular sugars. Martínez del Rio and Stevens (1989) discovered that some omnivorous birds that include fruit in their diet such as European Starlings (*Sturnus vulgaris*) completely lack the enzyme sucrase. Birds lacking this enzyme suffered from osmotic diarrhea when fed sucrose solutions because of accumulation of high concentrations of unabsorbed sugar in the intestine, and developed a behavioral aversion to this sugar. Hummingbirds, on the other hand, digest and absorb sucrose with almost 100 percent efficiency (Appendix 1; Martínez del Rio 1990a, b). The use of sucrose-rich nectars and fruits by birds is clearly linked to the birds' ability to assimilate this sugar. Less clear from physiology is why hummingbirds and some other nectar-feeding birds display a preference for sucrose over the sugars that it is hydrolyzed into, glucose and fructose.

Martínez del Rio *et al.* (1992), and more recently Schondube and Martínez del Rio (2003a), hypothesized that the perceived hummingbird–passerine dichotomy in nectar sugar composition and behavioral preferences for sucrose over hexoses had a physiological basis. These authors were partially correct: the first passerines studied were found either to completely lack the enzyme sucrase, or like Cedar Waxwings (*Bombycilla cedrorum*) to at least have reduced sucrase activity compared to hummingbirds (Appendix 1; Martínez del Rio *et al.* 1988; Martínez del Rio & Stevens 1989; Martínez del Rio *et al.* 1989; Martínez del Rio 1990b; Brugger & Nelms 1991; Brugger 1992; Martínez del Rio *et al.* 1992; Brugger *et al.* 1993). Martínez del Rio *et al.* (1992) stated in their review that the digestive traits and sugar preferences of specialized Old World
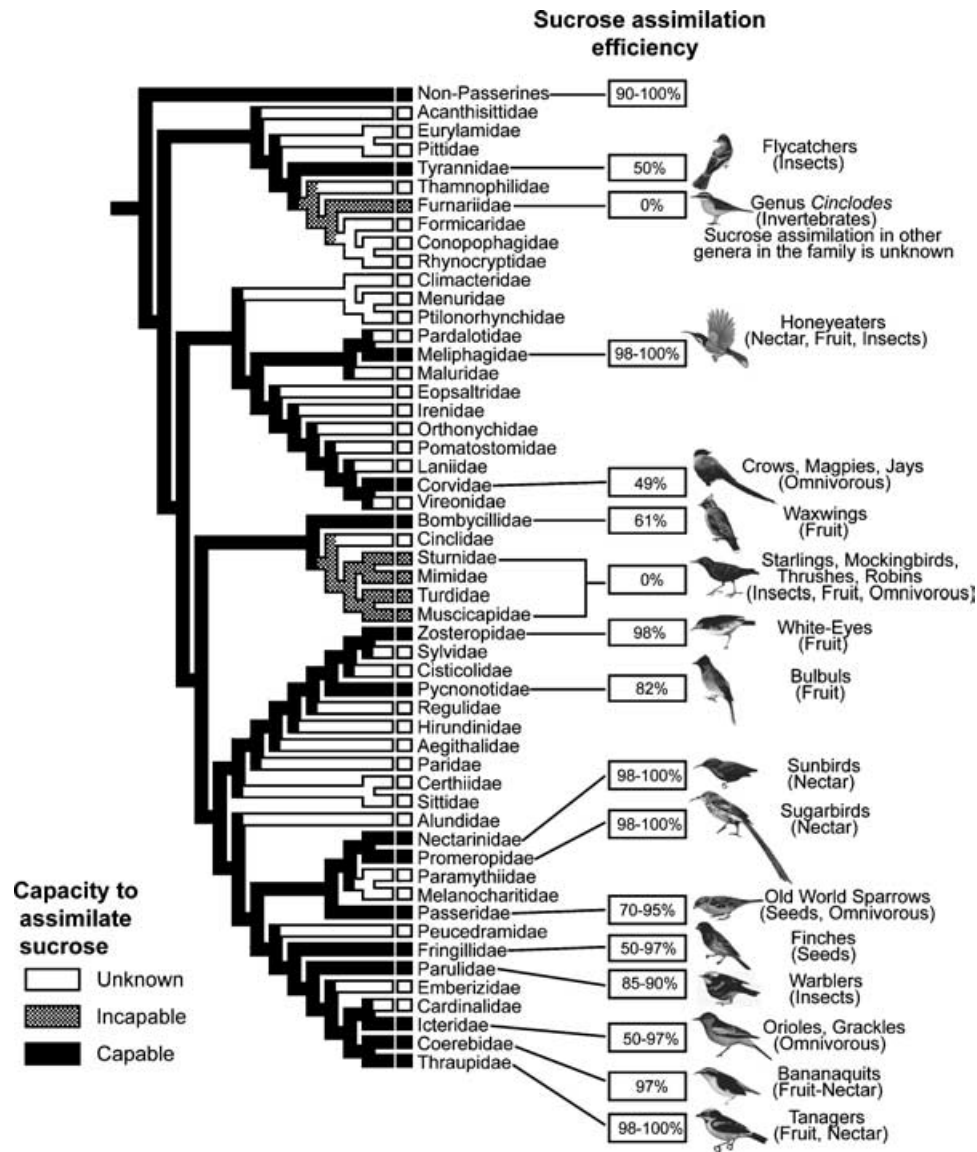
Sucrose assimilation efficiency

FIGURE 1.   Sucrose assimilation in passerine birds. Our knowledge of sucrose assimilation efficiency in birds is limited. Outside of the passeriformes, chickens and quail (Phasianidae), hummingbirds (Trochilidae), and some parrots (Psittacidae) assimilate sucrose with 90–100 percent efficiency, suggesting that the ancestral ability to assimilate sucrose in passerines is in that range. From the passerine clades tested for sucrose assimilation, only two seem to lack the enzyme sucrase and thus cannot assimilate sucrose at all. These clades include *Cinclodes* (family Furnariidae), and thrushes, robins, catbirds and starlings (families Turdidae, Mimidae, and Sturnidae). Members of the family Bombycillidae have intermediate abilities to assimilate sucrose. Capacity to assimilate sucrose clearly has a primary phylogenetic explanation in birds. Variation in sucrose assimilation efficiency is related to diet, with nectar- and fruit-eating species showing the highest capacities to assimilate this sugar. Names of bird families from Dickinson (2003), phylogenetic relationships among families from Sibley and Ahlquist (1990).

nectar-feeding passerines were at that time largely unknown. Our knowledge has significantly advanced in the last decade, and it is now known that Australasian honeyeaters as well as African sugarbirds and sunbirds, all specialized nectar-feeding passerines, are all equally efficient (97–100%) at assimilating sucrose as hummingbirds. Even a passerine that feeds predominantly on fruit, the Cape White-eye, has been found to be virtually 100 percent efficient at assimilating this sugar. Another frugivore, the Brown-eared Bulbul, assimilates sucrose with 82 percent efficiency (Collins & Morellini

1979; Collins *et al.* 1980; Lotz & Nicolson 1996; Downs 1997b; Lane 1997; Franke *et al.* 1998; Jackson *et al.* 1998a, b).

Even though our knowledge of sucrose assimilation among bird taxa is limited (see Fig. 1), it is now clear that a passerine–hummingbird dichotomy in sucrose assimilation efficiency does not exist. Rather, it seems that only two monophyletic clades within the Passeriformes lack the enzyme sucrase and thus cannot assimilate sucrose at all (Fig. 1; Martínez del Rio *et al.* 1992). These clades are the Furnariidae and the Muscicapidae–Sturnidae lineage.

While the information we have on the Furnariidae is limited to one genus (*Cinclodes*; Sabat 2000), and requires further investigation, we know that the members of the Muscicapidae–Sturnidae lineage (that includes starlings, true thrushes, and catbirds; see Appendix 1) do not express this enzyme (Vonk & Western 1984). Fruit-eating Cedar Waxwings and Azure-winged Magpies, both closely related to this sucrase-lacking clade, have intermediate abilities to assimilate sucrose. Waxwings strongly prefer hexoses, but the magpies do not show preferences between sucrose and different hexoses (Martínez del Rio *et al.* 1989, Lane 1997). Nestled within clades that are 97–100 percent efficient at assimilating sucrose (white-eyes, Zosteropidae; sunbirds, Nectariniidae; and honeyeaters, Meliphagidae) are representatives of three other passerine families that have intermediate sucrose assimilation efficiencies. All of these representatives eat fruit and/or nectar as a supplement to their primary diet of insects and/or grain, and when feeding on fruit or nectar they tend to ingest those that are rich in hexoses (Martínez del Rio 1990b).

Outside of the Passeriformes, not only the hummingbirds, but also two nectar-feeding parrots, the Rainbow Lorikeets (*Trichoglossus haematodus*) and Red Lories (*Eos bornea*), assimilate sucrose with 90–100 percent efficiency (Karasov & Cork 1996, Downs 1997a). Members of a basal group of birds, the Phasianidae, present high assimilation efficiencies for sucrose that are related to intermediate values of sucrase activity (Biviano *et al.* 1993). The capacity to assimilate sucrose of the members of the basal family Phasianidae, and two more derived non-passerines families (Trochilidae and Psitacidae), suggests that the ability to digest this sugar is present throughout non-passerines and represents the ancestral digestive condition for passerines (Schondube & Martínez del Rio 2004). This phylogenetic hypothesis needs to be tested by sampling sucrase activity in different groups of non-passerines like turacos (Musophagidae), mousebirds (Coliidae), swifts (Apodidae), trogons (Trogonidae), and woodpeckers (Picidae), and some basal clades of passerines.

We hypothesize that although sucrose-digesting ability clearly has a primary phylogenetic explanation, the diet to which a species is adapted may explain why some groups within clades have reduced sucrase activity relative to sister taxa. It would be exciting to test this hypothesis by ascertaining sugar preferences of bird subspecies in different geographical regions that feed on nectar or fruit containing different proportions of sucrose.

XYLOSE.—Like sucrose, aversion to xylose can readily be explained by physiology. Although xylose is a monosaccharide and thus does not have to be digested like sucrose, birds are very inefficient at assimilating it. Both nectar-feeding Cape Sugarbirds and Lesser Double-collared Sunbirds, and frugivorous Cape White-eyes are only 53–61 percent efficient at assimilating xylose, even though they are 98–100 percent efficient at assimilating the "big three" nectar sugars (Appendix 1; Lotz & Nicolson 1996; Downs 1997b; Franke *et al.* 1998; Jackson *et al.* 1998a, b). This poor assimilation of xylose may be due either to it (1) not being absorbed efficiently, or (2) being absorbed efficiently but then being excreted before being metabolized, the latter occurring in humans (Jackson & Nicolson

2002). Chickens and sunbirds get osmotic diarrhea when fed xylose (Lotz & Nicolson, pers. comm., Kare & Medway 1959), just like starlings fed sucrose (Martínez del Rio & Stevens 1989).

HEXOSES.—There is no consistent pattern in behavioral preferences among different hexose sugars. It is possible that this is related to the fact that both glucose and fructose are invariably absorbed with virtually 100 percent efficiency by nectar- and fruit-eating birds (Appendix 1). Without significant physiological limitations, behavioral preferences may be determined by superficial taste preferences for the commonest sugars in the flowers or fruits with which particular birds interact. However, although overall assimilation efficiencies may be the same for glucose and fructose, the processing rates of these two sugars may differ. Moreover, these processing rates may differ between bird species, and this could at least partly explain species-specific preferences. Glucose and fructose are absorbed across the intestine by independent carrier systems (Sigrist-Nelson & Hopfer 1974, Karasov & Debnam 1986, Karasov *et al.* 1986, Martínez del Rio & Karasov 1990). Different bird species may differ in their proportions of intestinal glucose and fructose transporters. These differences may be either genetic or a result of dietary acclimatization. Phenotypic intestinal plasticity is known to occur in birds (Diamond 1991, Starck 1996, Sabat *et al.* 1998, Starck & Rahmaan 2003). Also, there is evidence that much absorption of simple sugars in nectar-feeding Rainbow Lorikeets and other birds is passive (Karasov, pers. comm., Karasov & Cork 1994). In Rufous (*Selasphorus rufus*) and Anna's (*Calypte anna*) hummingbirds, on the other hand, passive absorption of glucose appears to be minimal, but active uptake of glucose is the highest measured in any bird species (Karasov *et al.* 1986). The possibility of passive fructose absorption remains untested. Preferences for hexoses could be caused by genetic or plastic phenotypic differences in glucose vs. fructose transport (both active and passive components), which lead to differing processing rates. These hypotheses can be tested by comparing preferences, overall assimilation rates, and transport of glucose vs. fructose in different bird species. To date, only behavioral preferences and overall absorption efficiencies have been compared (Appendix 1).

There may also be differences in processing rates between glucose, fructose, and glucose–fructose mixtures that are more universal and thus not species-specific. Two mechanisms may account for these differences. First, the independent intestinal glucose and fructose carriers of birds may differ in their transport rates. Second, because of sugar carrier saturation when sugar concentrations are high, overall sugar transport rate may be higher when birds ingest a mixture of glucose and fructose rather than either pure glucose or pure fructose. This second point is discussed below in relation to possible concentration-dependence of sugar-type preferences.

SUGAR CONCENTRATION: DOES IT AFFECT PHYSIOLOGY, SUGAR PREFERENCES, AND EVOLUTION?

Few authors have considered the possibility that sugar composition preferences may change with sugar concentration. Until very

recently, preference experiments had invariably been performed using only a single, relatively high, sugar concentration (Appendix 1). However, nectar-feeding Lesser Double-collared Sunbirds were found to prefer lower concentrations of glucose (10% or 20%) than a higher concentration (30%), but to prefer higher concentrations of sucrose and fructose to lower concentrations (30% = 20% > 10%; Lotz & Nicolson 1996; Jackson *et al.* 1998a, b). It was therefore deemed plausible that sunbirds would show a preference for glucose over sucrose and fructose when these sugars are offered at low concentrations, even though they prefer sucrose and fructose to glucose when the sugar concentration is offered at 20 percent (Lotz & Nicolson 1996, Jackson *et al.* 1998a,b). Indeed, current data reveal a trend in both passerines (Cinnamon-bellied Flowerpiercers, *D. baritula*) and hummingbirds (Magnificent Hummingbird, *Eugenes fulgens*) for a marked switch from sucrose preference at high concentrations to hexose preference at low concentrations (Schondube & Martínez del Rio 2003a).

Based on the physiological mechanisms explained in the last section, we propose that many nectar-feeding birds may have the following orders of preference for different sugars at high and low sugar concentrations, respectively: S > GF > G = F, and GF = G = F > S. As mentioned previously, glucose and fructose are transported across the intestine by independent carrier systems. This means that at high sugar concentrations when the glucose and fructose transporters are near saturation, a glucose–fructose mixture should be absorbed at a faster rate than an equicaloric solution of either pure glucose or pure fructose (Martínez del Rio 1990a). This effect should be reduced when the sugar concentrations are lower. Sucrose first has to be hydrolyzed into glucose and fructose before being absorbed through the intestine (Martínez del Rio 1990b). Thus, an advantage of sucrose over pure glucose or fructose at high sugar concentrations is that its hydrolysis leads to a glucose–fructose mixture that can be rapidly absorbed (Schondube & Martínez del Rio 2003a). However, sucrose digestion may be a rate-limiting step (Martínez del Rio *et al.* 2001). McWhorter and Martínez del Rio (2000) found that Broad-tailed Hummingbirds (*Selasphorus platycercus*) ingested sucrose at almost the same rate as the total sucrase activity of their intestines. When ambient temperature was reduced, this hummingbird species failed to increase food intake and lost body mass, presumably because they were constrained by their total sucrase activity. Remarkably, Fleming *et al.* (2004) found that nectar intake of *S. platycercus* was equally limited irrespective of whether hummingbirds were fed sucrose or a glucose–fructose mixture. This implies that absorption rates of glucose and fructose must match sucrose hydrolysis rates, making absorption just as limiting as hydrolysis. Similarly, Martínez del Rio (1990a) found that the processing rates of sucrose and of equicaloric glucose–fructose mixtures were equal in three other hummingbird genera, but that pure glucose was processed more slowly. Consistent results were obtained irrespective of whether the solutions were offered at 17.1 or at 34.2 percent (weight/volume). We hypothesize that glucose–fructose absorption rate matches sucrose hydrolysis rate as an energy-conserving strategy, so that birds do not synthesize more intestinal absorption proteins than necessary. This would also mean that when fed pure glucose or pure fructose, carrier-mediated

uptake would be limited and absorption rates would be lower than when birds feed on sucrose or a glucose–fructose mixture.

Why do many birds show a strong behavioral preference for sucrose over glucose–fructose mixtures (at least at high sugar concentrations), when sucrose first has to be digested? Beuchat *et al.* (1990) suggested that an advantage of sucrose nectar is that it contains double the energy content per unit of osmotic concentration than glucose–fructose nectar. Reduced osmotic concentration may in turn increase gastric emptying rate and thus post-ingestional intestinal energy delivery rate (Karasov & Cork 1994; Jackson *et al.* 1998a, b; Schondube & Martínez del Rio 2003a). The unregulated delivery of solutions with high osmotic concentration into the intestinal lumen can also cause osmotic diarrhea (as in birds feeding on nonassimilable xylose, or in asucrotic birds feeding on sucrose). Thus, when nectar concentrations are high, sucrotic birds may reduce their osmotic stress by feeding on sucrose rather than hexose. At lower nectar concentrations, this effect will be less important. This would provide an alternative explanation to sugar digestion to explain the finding that birds reverse their preference for sucrose when nectar concentration is reduced (Schondube & Martínez del Rio 2003a, Fleming *et al.* 2004).

Nicolson (1998) observed that nectars in the field that are dominated by sucrose are more concentrated than predominantly hexose nectars. This pattern may be the result of hexose solutions evaporating more slowly than sucrose solutions (Corbet *et al.* 1979). A complementary explanation, proposed by Nicolson (2002), assumes that osmotic effects can explain the correlation between sucrose dominance and high sugar concentration in nectar. Sucrose-rich phloem sap is either hydrolyzed by acid invertase or secreted without prior hydrolysis into nectaries. Sucrose hydrolysis increases nectar osmolality, causing water to move from the nectary walls into nectar resulting in more dilute nectars.

The relationship between sugar composition and concentration may have adaptive significance for pollinators, for the reasons discussed above. However, taste may also explain preference for sucrose over hexose (discussed in Stiles 1976 and Martínez del Rio 1990a, b). It would not be surprising then to find that birds prefer sucrose at high concentrations, but prefer hexose at low concentrations, simply because this is the pattern found in floral nectar. Thus, an alternative hypothesis is that there is no physiological basis for the frequently observed preference of birds for sucrose over glucose–fructose.

ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF SUGAR PREFERENCES IN BIRDS

Martínez del Rio *et al.* (1992) reviewed several aspects of the evolution between nectar and fruit sugar composition and the sugar preferences of avian pollinators and seed dispersers. They suggested that the sugar preferences of birds acted as a selective pressure that molded the sugar composition of plant rewards. Baker *et al.*'s (1998) data set clearly shows the existence of a correlation between pollinator and seed-disperser type and the sugar composition of nectar

and fruit pulp, supporting the hypothesis of Martínez del Rio *et al.* (1992). Although many researchers have investigated nectar and fruit sugar composition, phylogenetic approaches to determine the role of birds in shaping the sugar composition of their food sources are rare (but see Bruneau 1997, Nicolson & van Wyk 1998, Dupont *et al.* 2004). As a result, we do not know if bird physiology can act as a selective pressure on plants, or if sugar preferences in birds are the result of an adaptation to the sugar composition of their diet.

To determine if pollinators and seed dispersers played an important role in the evolution of the sugar composition of floral nectar and fruit pulp in different plant clades, we need to address the following questions using a phylogenetic approach on a clade-by-clade basis: (1) What was the ancestral state of sugar composition in nectar and fruit?; (2) Who were the original pollinators/seed dispersers of these flowers/fruits, and what effect did they play on the sugar composition of nectar and fruit?; and (3) Are evolutionary switches between pollinator/seed-disperser type associated with changes in nectar and fruit sugar composition? Also we need to understand the effect that an evolutionary shift in diet has on the physiology and sugar preferences of pollinators/seed dispersers. New discoveries in plant and animal phylogenetics and physiology provide us with preliminary information to answer some of these questions.

Whereas it was believed that flower and fruit morphology could change rapidly in response to pollinators and seed dispersers, the sugar composition of nectar and fruit pulp was thought to be a conservative trait (van Wyk 1993, Baker *et al.* 1998, Perret *et al.* 2001; but see Bruneau 1997). Recent studies have shown that sugar composition in both nectar and fruit is controlled by the action of the enzyme acid invertase, and that in some fruits its activity is regulated by one gene that follows simple Mendelian inheritance rules (Muller-Rober *et al.* 1992, Chetelat *et al.* 1993, Nicolson 2002, De la Barrera & Nobel 2004). Plants with high acid invertase activity have hexose-rich nectars or fruits, whereas plants with low levels of the enzyme have sucrose-rich ones (Yelle *et al.* 1991, Chetelat *et al.* 1993, Nicolson 2002). Hybridization of two species of tomato with low acid invertase activity (*Lycopersicon chmielewskii* and *L. hisutum*) resulted in F_1 plants that had sucrose-rich fruits, suggesting a common genetic basis for the trait in both species (Chetelat *et al.* 1993). Segregation for sucrose accumulation in these tomato hybrids is consistent with the action of a single recessive gene, and suggests that the sugar composition of fruit and maybe nectar is an evolutionarily labile trait (Bruneau 1997, Dupont *et al.* 2004).

Two phylogenetic studies also suggest that the sugar composition of nectar is a labile trait, and that changes in sugar composition are correlated with changes in pollinator type (Bruneau 1997, Dupont *et al.* 2004). Bruneau (1997) studied the evolution of bird pollination in the genus *Erythrina* (Leguminosae). *Erythrina* is a pantropical genus of over 100 species, all of which are either hummingbird- or passerine-pollinated. Basal members in this genus experienced a shift from insect pollination, prevalent in the Phaseoleae, to passerine pollination (Galetto *et al.* 2000, Etcheverry & Trucco Alemán 2005). By mapping pollinator type and sugar composition of nectar over a phylogeny of the genus, Bruneau (1997) found that shifts from the ancestral passerine-pollinated state to hummingbird pollination have occurred at least four times. Each

time a pollinator shift occurred, it was accompanied by a change in sugar composition, from hexose-rich nectars in passerine-pollinated plants to sucrose-rich ones in species visited by hummingbirds. The second study (Dupont *et al.* 2004) explored the effect that shifts from insect to passerine pollination had on the sugar composition of the plants of the Canary Islands. Dupont *et al.* (2004) studied 23 species of plants representing seven lineages, and found that the evolution of nectar type was correlated with mode of pollination: plants visited by specialized pollinators (insects) had sucrose-rich nectar, while species visited by nonspecialized passerine birds were hexose-rich. Because in most Canarian plant lineages the ancestral sugar composition of nectar was sucrose, they concluded that nectar characteristics may have evolved readily, possibly in response to visits by opportunistic nectarivorous birds living on the islands. To our knowledge, the expression of acid invertase in nectaries of plants and its relationship to pollinator identity have not been studied. The genus *Erythrina* and the Canarian plant lineages studied by Dupont *et al.* (2004) offer an unparalleled opportunity to investigate the biochemical bases that accompany pollinator shifts in plants.

Are the evolutionary changes in nectar sugar composition in these lineages the result of selective pressure exerted by pollinator type? We believe that in some cases they are. In particular, we hypothesize that nonspecialized passerine birds act as a selective pressure for plants to produce hexose-rich nectar and fruit. There are various reasons why we should expect plants visited by passerines to exhibit hexose-rich nectars and/or fruits. First, the asucrotic Sturnid–Muscicapid clade is extremely speciose. Members of this lineage are abundant throughout Africa, Eurasia, and the New World, and could have played an important role in selecting against sucrose-rich nectar and fruit pulp. Another hypothesis was proposed by Martínez del Rio *et al.* (1992). They speculated that the high proportions of hexose sugars in many fruits may be linked to the need for birds to rapidly dispose of undigestible seeds. This assumes that fast passage rates are needed to dispose of undigestible materials, and therefore the birds' efficiencies to hydrolyze sucrose would be reduced. Their prediction was supported by Afik and Karasov (1995), who found that Yellow-rumped Warblers (*Dendroica coronata*) have shorter gut transit times when feeding on fruit (46 min) compared with insects (62 min) or seeds (114 min). The reduction in gut transit time was accompanied by a reduction in their capacity to assimilate sucrose (from 85% to 58%). The work of Afik and Karasov (1995) suggests that it is advantageous for frugivorous birds to feed on hexose-rich fruits. Finally, because hexoses are readily assimilated while sucrose is not, birds with intermediate abilities to digest sucrose should present higher energy intakes while feeding on glucose–fructose mixtures than when feeding on a sucrose-rich diet. Specialized nectarivorous Cinnamon-bellied Flowerpiercers (*D. baritula*), even though they assimilate sucrose with 99 percent efficiency, have levels of sucrase activity that limit the amount of sucrose they can ingest per unit of time. As a result, they ingested 10 percent less energy when feeding on sucrose than when feeding on a glucose–fructose diet (Schondube & Martínez del Rio 2003a). We hypothesize that most nectarivorous and frugivorous passerines would show lower food intake rates when feeding on sucrose than when feeding on hexoses. Sunbirds are an exception

to this prediction as they have sucrase activity levels similar to those of hummingbirds (McWhorter & Schondube, pers. obs.). If our hypothesis is correct, we can expect birds with intermediate sucrase activity levels, even if they have high assimilation efficiency for this sugar, to potentially act as selective agents for hexose-rich nectar and fruit.

While it seems clear why birds would benefit from the existence of hexose-rich nectars and fruits, it remains puzzling why birds would prefer to feed on, and act as a selective pressure for, sucrose-rich plant rewards. Hummingbirds and sunbirds have identical intake rates when feeding on sucrose or 1:1 glucose–fructose mixtures (Schondube & Martínez del Rio 2003a, Fleming *et al.* 2004). This indicates that the ability to feed on sucrose does not provide birds with an energetic advantage. Moreover it has an extra cost: it requires the existence and maintenance of the biochemical machinery necessary to digest sucrose. Considering this evidence, it is not surprising that most species of specialized nectarivorous birds with high sucrase activity (hummingbirds, sunbirds) tend to be indifferent to the sugar composition of nectar when tested at concentrations close to 20 percent (weight/volume). We hypothesize that, in most cases, specialized nectar-feeding birds do not act as a selective pressure for sucrose-rich nectars. Supporting our hypothesis is the fact that sucrase activity levels of hummingbirds and sunbirds, that are ten times higher than those of other birds, seem to be the result of a physiological adaptation to their sucrose-rich diets (McWhorter & Schondube pers. comm., Schondube & Martínez del Rio 2004). The presence of sucrose-rich nectars in bird-pollinated plants could be the result of selective pressures exerted by insects before the plants were pollinated by birds, as suggested by Dupont *et al.* (2004). Also, species of nectar-feeding birds with a high capacity to digest sucrose could have released the selective pressure of nonspecialized nectarivorous birds for hexoses, allowing some clades of plants to produce sucrose-rich nectars. Plants that secrete hexose-rich nectars avoid the cost of synthesizing invertase and may be selected for if the pollinators do not prefer hexoses.

In the Americas, most bird-pollinated flowers seem to have nectar with high proportions of sucrose, presumably to attract hummingbirds and maybe to discourage opportunistic nectarivorous passerines (Martínez del Rio *et al.* 1992, Baker *et al.* 1998). Hummingbirds are suitable pollinators because they are abundant, diverse (331 species in 107 genera), and obligate nectar-feeders (Brice 1992). Far fewer New World flowers seem to contain hexose-dominant nectar, and perhaps these flowers evolved as a response to pressures exerted by nonspecialized passerine visitor, as Baker and Baker (1983b), Baker *et al.* (1998), and Dupont *et al.* (2004). In fact, in the New World, hummingbird-pollinated *Erythrina* and *Puya* species contain far higher sucrose to hexose ratios than do passerine-pollinated ones (Baker & Baker 1983b, Martínez del Rio *et al.* 1992, Bruneau 1997, Nicolson 2002). There are few obligate nectar-feeding passerines in the New World, and the main ones (flowerpiercers; genus *Diglossa*) are robbers of sucrose-dominant hummingbird nectars (Martínez del Rio *et al.* 1992, Arizmendi *et al.* 1996, Schondube & Martínez del Rio 2003b). However, a few New World plant species may have evolved to attract opportunistic nectar-feeders such as orioles, bananaquits, and honeycreepers,

which have intermediate sucrase activity (Martínez del Rio 1990b, Schondube & Martínez del Rio 2004; see above). A similar scenario could have occurred in the Old World between specialized nectarivorous birds (sunbirds, sugarbirds, and some honeyeaters), and generalist species of passerines (white-eyes and some frugivorous honeyeaters).

Clearly, behavioral preferences for different sugars show highly diverse patterns in birds. Some of this behavioral variation can be explained by known physiological constraints, such as sucrose digestion or xylose assimilation. However, much of the variation remains mysterious, and could either stem from as yet very poorly studied physiological mechanisms (such as differences in processing rates among sugars, or concentration-dependence of several physiological processes), or from more superficial taste preferences. We have drastically changed our paradigms about avian sugar preferences in the two decades since the pioneering work of Herbert Baker and Irene Baker, and we have now reached a point where we have numerous novel hypotheses to test.

ACKNOWLEDGMENTS

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APPENDIX 1.   *Sugar preferences and sugar assimilation efficiency of nectar-feeding birds and mammalian pollinators. S = sucrose, G = glucose, F = fructose, X = xylose. All concentrations are in percent (weight of sugar/volume of solution).*

Taxon	Main diet/ ecological role	Order of preference	Nectar concentration	Assimilation efficiency	References
Birds					
Phasianidae					
Chicken (*Gallus gallus*)	Seeds	(1) S, G, F > H$_2$O (2) S = G	(1) 5, 10, 15, 20 and 25% (2) 20%		(1) Kare and Medway (1959) (2) Jukes (1938)
Japanese Quail (*Coturnix coturnix japonica*)	Seeds	S = G	20%		Harriman and Milner (1969)
Psittacidae					
Red Lory (*Eos bornea*)	Specialized nectar-eater, pollen/pollinator	(1) S = G = F (2) S > G or F	(1) 30% (2) 10%	S 99–100%	Downs (1997a)
Rainbow Lorikeet (*Trichoglossus haematodus*)	Specialized nectar-eater, pollen/pollinator			S 90.5%, G 80%	Karasov and Cork (1994), 1996
Trochilidae					
Black-chinned Hummingbird (*Archilochus alexandri*)	Specialized nectar-eater/ pollinator	SFG = SF > S > FG > SG > F > G	S: 17.1%; Hexoses: 18%		Hainsworth and Wolf (1976)
Ruby-throated Hummingbird (*Archilochus colubris*)	Specialized nectar-eater/ pollinator	SFG = SF > S > FG > SG > F > G	S: 17.1%; Hexoses: 18%		Hainsworth and Wolf (1976)
Anna's Hummingbird (*Calypte anna*)	Specialized nectar-eater/ pollinator	S > G > GF > F	30%		Stiles (1976)
Cinnamon Hummingbird (*Amazilia rutila*)	Specialized nectar-eater/ pollinator	S > GF > G > F	17.1%	S 97–99%	Martínez del Rio (1990a)
Golden-crowned Emerald (*Chlorostilbon canivetii*)	Specialized nectar-eater/ pollinator	S > GF > G > F	17.1%	S 97–99%	Martínez del Rio (1990a)
Broad-billed Hummingbird (*Cynanthus latirostris*)	Specialized nectar-eater/ pollinator	S > GF > G > F	17.1%	S 97–99%	Martínez del Rio (1990a)
Magnificent Hummingbird (*Eugenes fulgens*)	Specialized nectar-eater/ pollinator	(1) SFG = SF > FG > SG > F > G (2) S > GF (3) S = GF (4) GF > S	(1) S: 17.1%; Hexoses: 18% (2) 40% (3) 20% (4) 5%	(1, 2, 3) S 99%, GF 99%	(1) Hainsworth and Wolf (1976) (2–4) Schondube and Martínez del Rio (2003a)
Blue-throated Hummingbird (*Lampornis clemenciae*)	Specialized nectar-eater/ pollinator	SFG = SF > S > FG > SG > F > G	S: 17.1%; Hexoses: 18%		Hainsworth and Wolf (1976)
Meliphagidae					
Singing Honeyeater (*Lichenostomus virescens*)	Specialized nectar-eater/ pollinator			S 99%	Collins and Morellini (1979)
Brown Honeyeater (*Lichmera indistincta*)	Specialized nectar-eater/ pollinator			S 99%	Collins et al. (1980)
Corvidae					
Azure-winged Magpie (*Cyanopica cyana*)	Fruit	S = GF = G = F	12%	S 49%, GF 96%	Lane (1997)
Pycnonotidae					
Brown-eared Bulbul (*Hypsipetes amaurotis*)	Fruit	S = GF = G = F	12%	S 82%, GF 92%	Lane (1997)
Bombycillidae					
Cedar Waxwing (*Bombycilla cedrorum*)	Fruit	GF = G > F > S	15%	S 61%, GF 92%	Martínez del Rio et al. (1989)
Turdidae					
American Robin (*Turdus migratorius*)	Fruit, insects	G = GF > F > S	15%		Brugger and Nelms (1991)
Rufous-backed Robin (*Turdus rufopalliatus*)	Fruit, insects			S 0%	Martínez del Rio (1990b)
Orange-billed Nightingale-trush (*Catharus auratiirostris*)	Fruit, insects			S 0%	Martínez del Rio (1990b)

APPENDIX 1. *Continued.*

Taxon	Main diet/ ecological role	Order of preference	Nectar concentration	Assimilation efficiency	References
Mimidae					
Gray Catbird (*Dumetela carolinensis*)	Omnivore	GF > S	15%	S 0%	Malcarney *et al.* (1994)
Sturnidae					
Purple-headed Glossy Starling (*Lamprotornis pupureiceps*)	Omnivore	GF > S	15%		Malcarney *et al.* (1994)
Red-winged Starling (*Onychognathus morio*)	Omnivore			S 0%	Bosque and Lotz (pers. comm.)
White-cheeked Starling (*Sturnus cineraceus*)	Omnivore	GF = G = F > S	12%	S 0%, GF 77%	Lane (1997)
European Starling (*Sturnus vulgaris*)	Omnivore	(1) GF > S (2) 1 tube test: GF > S (3) 2 tubes test: GF > S at all sucrose concentrations (4) S = water, GF > water	(1) 5.9, 11.9 and 23.9% (2) 15% (3) one tube had always 15% GF, the other tube had different concentrations of S (0, 3.75, 7.5, 11.25, and 15%) (4) 11.9, and 23.9%	(1) S 0%	(1) Martínez del Rio and Stevens (1989) (2–4) Brugger *et al.* (1993)
Zosteropidae					
Cape White-eye (*Zosterops pallidus*)	Fruit, opportunistic nectar-eater/ pollinator	S > GF = G = F > X	20%	S 98%	Franke *et al.* (1998)
Nectariniidae					
Lesser Double-collared Sunbird (*Nectarinia chalybea*)	Specialized nectar-eater/ pollinator	(1) S = GF = F > G > X (2) S > GF = F > G	(1, 2) 20%	(1, 2) S 97%	(1) Lotz and Nicolson (1996) (2) Jackson *et al.* (1998a,b)
Malachite Sunbird (*Nectarinia famosa*)	Specialized nectar-eater/ pollinator			S 99%	Downs (1997b)
Palestine Sunbird (*Nectarinia osea*)	Specialized nectar-eater/ pollinator			(1) S 99% (2) GF 99%	(1) McWhorter (pers. comm.) (2) Roxburgh and Pinshow (2002)
Black Sunbird (*Nectarinia amethystina*)	Specialized nectar-eater/ pollinator			S 99%	Downs (1997b)
Peromopidae					
Gurney's Sugarbird (*Promerops gurneyi*)	Specialized nectar-eater/ pollinator			S 99%	Downs (1997b)
Cape Sugarbird (*Promerops cafer*)	Specialized nectar-eater/ pollinator	S = GF = F = G	20%	S, G, F 99.8%, X 52.9%	Jackson *et al.* (1998a,b)
Thraupidae					
Cinnamon-bellied Flowerpiercer (*Diglossa baritula*)	Specialized nectar-eater/ nectar robber	(1) S > GF (2) S = GF (3) GF > S	(1) 40% (2) 20% (3) 5%	S 99%, GF 99%	Schondube and Martínez del Rio (2003a)
Blue Dacnis (*Dacnis cayana*)	Specialized nectar-eater/ pollinator	S = G	20%		Schaefer *et al.* (2003)
Green Honeycreeper (*Chlorophanes spiza*)	Specialized nectar-eater/ pollinator	S = G	20%		Schaefer *et al.* (2003)
Short-billed Honeycreeper (*Cyanerpes nitidus*)	Specialized nectar-eater/ pollinator	S = G	20%		Schaefer *et al.* (2003)
Coerebidae					
Bananaquit (*Coereba flaveola*)	Specialized nectar-eater/ pollinator, nectar robber	S = G = F	18%	S 97%, G 97%, F 97%	Mata and Bosque (2004).

APPENDIX 1. *Continued.*

Taxon	Main diet/ ecological role	Order of preference	Nectar concentration	Assimilation efficiency	References
Parulidae					
Yellow-rumped Warbler (*Dendroica coronata*)	Insect, fruit			S 85%	Afik and Karasov (1995)
Yellow-breasted Chat (*Icteria virens*)	Insects	GF > S	15%	S 88%, GF 98%	Martínez del Rio *et al.* (1992)
Icteridae					
Yellow-winged Cacique (*Cassiculuss melanicterus*)	Fruit, insects	GF > S	15%	S 88%, GF 98%	Martínez del Rio *et al.* (1992)
Common Grackle (*Quiscalus quiscula*)	Omnivore	S > water	5.9%, 11.9%, and 23.9%		Martínez del Rio *et al.* (1988)
Streak-backed Oriole (*Icterus pustulatus*)	Opportunistic nectar-eater, insects/pollinator	S = GF	15%	S 98%	Martínez del Rio *et al.* (1992)
Red-winged Blackbird (*Agelaius phoeniceus*)	Seeds	(1) S = water (2) S > water (3) Water > sucrose	(1) 5.9% (2) 11.9% (3) 23.9%		Martínez del Rio *et al.* (1988)
Fringillidae					
House Finch (*Carpodacus mexicanus*)	Seeds	(1) S = GF (2) S = GF (3) GF > S (4) GF > S	(1) 2% (2) 4% (3) 6% (4) 10%	S ≈ 97% GF ≈ 96%	Avery *et al.* (1999)

Bird families from Dickinson (2003).