Ecological and evolutionary implications of digestive processes: Bird preferences and the sugar constituents of floral nectar and fruit pulp

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Abstract. Plants pollinated and dispersed by different groups of birds offer different kinds of sugars in nectar and fruit pulp. The preferences and physiological traits of avian pollinators and seed dispersers are broadly correlated with the sugar composition of the nectar and fruit that they feed on and appear to have influenced the evolution of the sugar composition of the rewards that plants offer. Hummingbirds prefer sucrose whereas many nectar- and fruit-eating passerines prefer glucose and fructose. Preference for hexoses in passerines seems to be associated with poor sucrose assimilation resulting from two physiological mechanisms: lack of intestinal sucrase activity and fast passage rates. Sucrase activity absence appears to be restricted to a single phylogenetic group (the sturnid-muscicapid lineage). Fast passage rates seem to be characteristic of many small frugivores and to hinder the assimilation of complex nutrients that require hydrolysis before absorption. Hummingbirds have extremely specialized digestive traits that allow them to assimilate sucrose at high rates and with extremely high efficiency. These specialized digestive traits appear not to be present in many nectar-feeding passerines.

Key words. Bird feeding preferences; digestion; intestinal enzymes; sucrase; fruit; nectar.

The evolution of flower and fruit diversity and its obvious relationship to pollination and seed dispersal has been studied for over a hundred and fifty years[5]. The forces and constraints that mold and maintain the array of floral and fruit characteristics, however, have received comparatively little attention. Researchers have recognized that characteristics such as morphology, color and smell associate flowers and fruits with specific groups of pollinators and seed dispersers[22], but they have rarely tried to explain why or how unrelated plants have evolved convergent syndromes in response to common groups of pollinators and dispersers.

Because flowers and fruit are 'prey that want to be eaten'[31], ecologists generally assume that their characteristics are a consequence of a pollinator's or disperser's choice[34]. The physiological and behavioral processes that determine the feeding choices of different groups of pollinators and seed dispersers, however, are largely unknown[48]. The chemical composition of the rewards that plants offer is a good example of the diversity usually assumed to be molded by the preferences of animals[14, 34]: plants pollinated or dispersed by different groups of animals offer different kinds and concentrations of sugars, amino acids, and lipids[7, 34, 49]. Here we will focus on the sugar constituents of nectar and fruit to examine this assumption and to try to resolve why plants offer different rewards to different kinds of animals.

This paper summarizes our work on the chemical composition of plant rewards (H. G. and I. Baker) and on the behavior and physiology of birds (C. Martínez del Rio). It integrates ecological, behavioral, and physiological information in an evolutionary context: We describe an ecological pattern (the apparent convergence in sugar composition in the rewards offered by plants with common pollinators or dispersers); postulate a process that can account for the maintenance of this pattern (the variation in sugar preferences among birds); and investigate the physiological and ethological mechanisms presumably responsible for this process. Finally we integrate information from these three levels in hypotheses about the evolution of sugar preferences in birds and their influence on sugar composition in nectar and fruit pulp. We suggest that appropriate tests of these hypotheses require knowledge about the phylogenetic history of both plants and animals in addition to detailed knowledge about bird physiology and behavior. Because the sugar composition of nectar and fruit has been reviewed in detail elsewhere[7, 8], here we emphasize the behavior and digestive physiology of birds. Data on plants are provided only as necessary background.

Sugar constituents of floral nectar and fruit pulp

Nectar

The three most common sugars in nectar and fruit pulp are the disaccharide sucrose and the monosaccharides glucose and fructose[54]. Analyses of the nectar sugar constituents of over 200 species of bird-pollinated plants reveal that plants pollinated by different groups have contrasting compositions: hummingbird-pollinated plants secrete predominantly sucrose-dominated and sucrose-rich nectars, whereas passerine-pollinated plants secrete, almost without exception, hexose-dominated nectars[7] (table).

This dichotomy in the chemical composition of nectars is well illustrated by the genus *Erythrina* (Fabaceae)[6], in which Old World and New World passerine-pollinated species are hexose-dominant, and hummingbird-pollinated species are sucrose-rich or sucrose-dominant (fig. 1). Similar patterns have been described for *Puya* (Bromeliaceae; table 1)[56], *Campsis* (Bignoniaceae; table)[7], *Fuchsia* (Onagraceae; Berry, pers. comm., table), and *Fritillaria* (Liliaceae)[13].

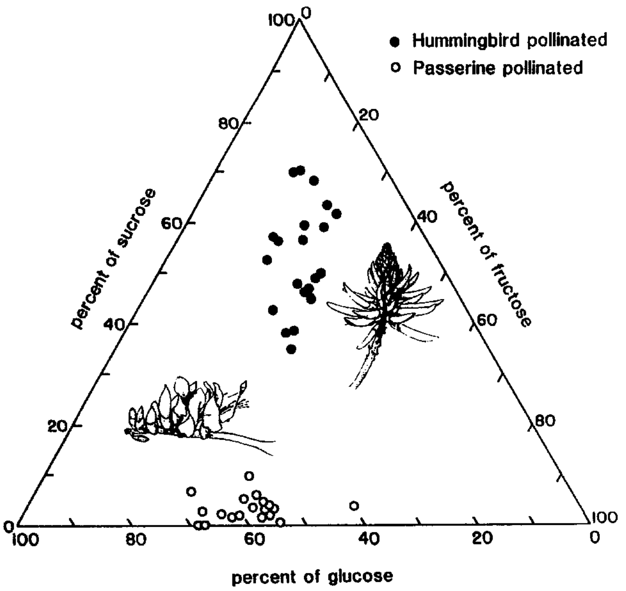

Figure 1. Triangular chart showing the sugar composition of nectar in hummingbird and passerine pollinated plants in the genus *Erythrina*. Data are from Baker and Baker[6] and I. and H. G. Baker, unpublished measurements. *Erythrina coralloides* and *Erythrina breviflora* are shown as examples of hummingbird and perching bird pollinated plants. Note the contrasting floral morphologies.

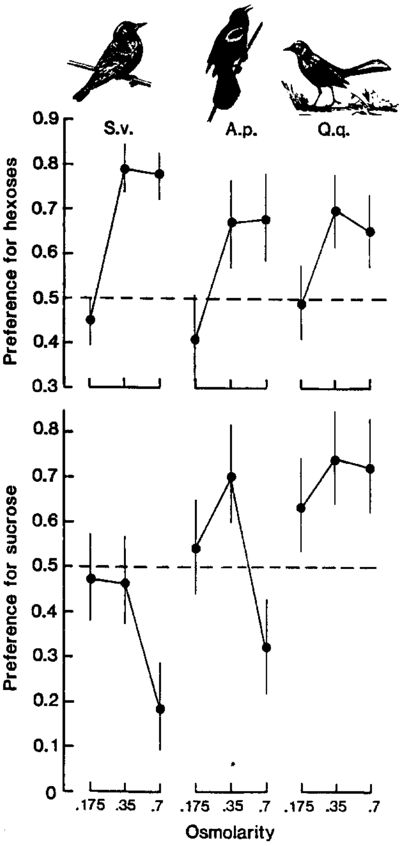

Figure 2. Preferences for a 1 : 1 mixture of glucose and fructose (above) and sucrose (below) against water in European starlings (S.v.), red-winged blackbirds (A.p.) and common grackles (Q.q.). Preference is defined as the ratio of test solution to total amount of fluids consumed. Bars are 95% confidence intervals for 16 birds. Dashed line at 0.5 indicates no preference. Figure modified from Martínez del Rio et al.[46] with permission from The University of Chicago Press.

Proportion of sucrose in the sugars of *Erythrina, Puya, Campsis* and *Fuchsia* species pollinated by hummingbirds and passerines (data from Baker and Baker[6, 7] and unpublished, and Scogin and Freeman[56])

	Hummingbird pollinated	Passerine pollinated Old World	New World
Erythrina			
Mean, (n, spp)	0.53, (21)	0.04, (11)	0.03 (8)
Range	0.45–0.69	0.02–0.07	0.02–0.05
Puya			
Mean, (n, spp)	0.59, (4)	—	0.08, (2)
Range	0.41–0.71	—	0.07–0.08
Campsis			
Mean, (n, spp)	0.63, (1)	0.01, (1)	—
Fuchsia			
Mean, (n, spp)	0.56, (4)	0.06, (2)	—
Range	0.43–0.84	0.03–0.09	—

Fruit-pulp

The pulp of most bird-dispersed fruits is rich in glucose and fructose but contains only very small amounts of sucrose[8]. Cultivated fruits used for human consumption and mammal-dispersed fruits contain significantly higher sucrose proportions[8, 24]. This broad pattern in the composition of fruit pulp appears also to hold within restricted phylogenetic groups. In the Rosaceae, for example, mammal-dispersed fruits have significantly higher sucrose proportions (mean ± SD = 0.13 ± 0.01, n = 8) than bird-dispersed fruits (mean ± SD = 0.041 ± 0.03, n = 14; t = 15.3, $p < 0.05$, I. and H. G. Baker unpubl. data).

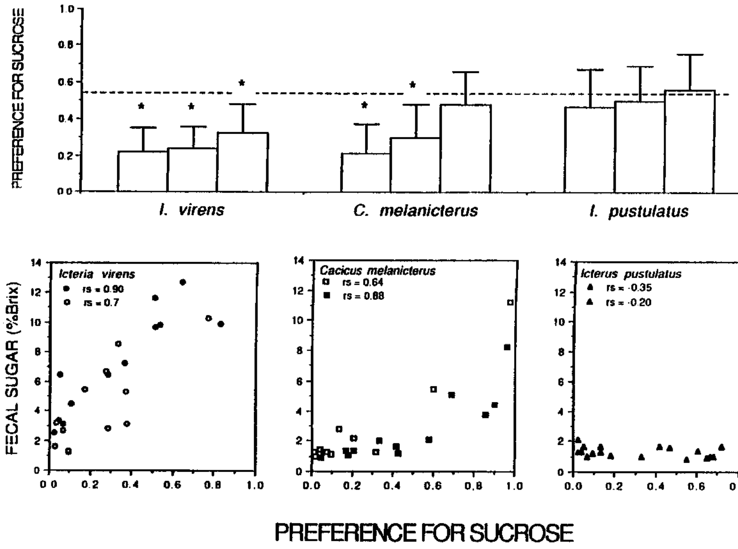

Figure 3. Sugar preferences and fecal sugar as a function of sugar preferences in three species of emberizids. Birds were offered a 15% (wt/wt) sucrose solution paired with a 15% mixture (1 : 1) of glucose and fructose (10 replicates/bird). Error bars are 95% confidence intervals for each individual. Individuals that exhibited significant preference for the hexose mixture are starred. The dotted line is the line of equal preference. Lower graphs plot fecal sugar measured with a refractometer as a function of preference for the hexose mixture. The positive spearman rank correlations indicate lower sugar assimilation (i.e. more sugar in excreta) when sucrose was preferentially ingested (the $p < 0.05$ cutoff point for 10 replicated measurements is $r_s = 0.56$). Different symbols represent individual birds.

Sugar preferences in birds

Why do plants pollinated or dispersed by different groups of birds contain different kinds of sugars in their nectar and fruit pulp? Conventional ecological wisdom suggests that the sugar composition of the rewards that plants offer should be the result of selection by pollinators and seed dispersers that vary in their preferences for simple sugars[7,44]. Do different groups of birds vary in their preference for sucrose, glucose, and fructose? Preference tests conducted with a variety of bird species reveal a surprising amount of variation in sugar preferences.

Passerines

Martínez del Rio et al.[46] studied the preferences of European starlings *(Sturnus vulgaris*: Sturnidae), red-winged blackbirds *(Agelaius phoeniceus*: Emberizidae), and common grackles *(Quiscalus quiscula*: Emberizidae) and found dramatic interspecific differences. Starlings reject concentrated sucrose solutions ($>$ 0.7 M; fig. 2), and develop a conditioned aversion for even relatively dilute (0.175 M) sucrose solutions. Red-winged blackbirds are indifferent to weak sucrose solutions (0.175 M $\leq$), prefer intermediate solutions (0.35 M), and reject concentrated ones ($\geq$ 0.70 M). Common grackles significantly prefer sucrose solutions over water at all the concentrations tested (fig. 2). The three species avidly drink solutions containing a 1 : 1 mixture of glucose and fructose.

We examined the preferences for sucrose over a 1 : 1 mixture of glucose and fructose in three species of neotropical flower-visiting passerines: yellow-breasted chats *(Icteria virens:* Emberizidae), yellow-winged caciques *(Cacicus melanicterus:* Emberizidae), and streak-backed orioles *(Icterus pustulatus:* Emberizidae). The chats and the caciques prefer the mixture over sucrose, but the orioles are indifferent (fig. 3). Sugar preferences apparently vary even within a single family of passerine birds. The sugar preferences of cedar waxwings *(Bombycilla cedrorum:* Bombycillidae) and American robins *(Turdus migratorius:* Muscicapidae), two of the most heavily frugivorous species in temperate North America, were examined by Martínez del Rio et al.[47] and Brugger and Nelms[12]. In paired choice tests cedar waxwings and American robins prefer glucose, fructose and a 1 : 1 mixture of glucose and fructose over sucrose. Preferences for simple sugars are ranked as follows: glucose = mixture of hexoses $>$ fructose $>$ sucrose. In addition, robins develop a conditioned aversion to sucrose (fig. 4)[11].

Hummingbirds

The heterogeneity in sugar preferences shown by passerines contrasts with the uniform preferences of hummingbirds. Hummingbirds show relatively weak preferences among sugars in brief exposure tests (30 min)[30], but strong preferences in long exposure tests ($\geq$ 240 min)[43,67]. The combined results from Stiles[67] and Martínez del Rio[43] indicate that in long exposure tests the preference ranking of sugars in five species of hummingbirds is sucrose $>$ 1 : 1 mixtures of hexoses $>$ glucose $>$ fructose. Free-ranging broad-tailed hummingbirds *(Selasphorus platycercus)* show the same ranking of sugar preferences as captive birds[70]. Of 6 species examined in captivity, only one *(Archilochus alexandri)* deviates from this ranking in that it shows no significant preference for sucrose over mixtures of glucose and fructose[67]. The preference of hummingbirds for sucrose seems to be very persistent. Attempts to reverse it by exposing hummingbirds for extended time periods (20 days) to the non-preferred diet (a glucose + fructose mixture) have been unsuccessful[43,67].

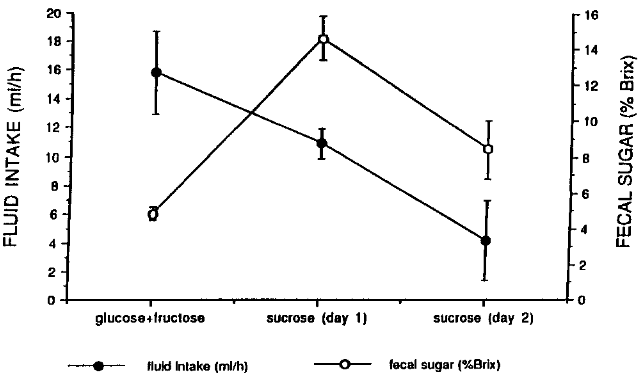

Figure 4. Development of sucrose aversion in American robins *(Turdus migratorius)*. Birds (8) were exposed to a 15% 1 : 1 mixture of glucose and fructose (4 h/day, two consecutive days), and then to a 15% sucrose solution in two consecutive days (4 h/day). Mean sucrose ingestion decreases significantly from day 1 to day 2. Note that fecal sugar tracks the amount of sucrose ingested. Bars are SEM. Data from Brugger[11].

Summarizing, all bird species tested seem to find the hexoses glucose and fructose acceptable. The response for sucrose, in contrast, ranges from aversion in starlings and robins to preference over other sugars in hummingbirds. The preferences of birds show a good, but not perfect, fit with the kinds of sugars that they receive from plants. Hummingbirds prefer sucrose over glucose and fructose; the frugivorous cedar waxwings, American robins and starlings prefer glucose and fructose over sucrose; and two out of three species of passerine nectarivores examined also preferred glucose and fructose over sucrose.

Sucrose, glucose, and fructose differ in chemical structure but have very similar energy contents per unit gram, and from the point of view of current standard foraging theory should have identical foraging profitabilities. Why then do birds show such strong and contrasting preferences for these sugars?

Mechanisms underlying sugar preferences

Differences in the efficiency and speed at which different sugars are processed in the digestive system can account for the sugar preferences of birds. Sucrose, glucose, and fructose have different modes of intestinal transport and produce different metabolic effects after ingestion and absorption[1,60]. Sucrose is a disaccharide and to be absorbed has first to be hydrolyzed into its monosaccharide components, glucose and fructose, by the intestinal enzyme sucrase[57]. Glucose and fructose, on the other hand, are absorbed directly by the intestine[58].

Sucrose hydrolysis as the rate-limiting step

Sugar preferences are probably determined by relative rates of energy assimilation which are the result of the interplay between sucrose hydrolysis, glucose and fructose uptake, and intestinal retention time[44]. Animals lacking intestinal sucrase activity cannot use ingested sucrose as an energy source. Undigested sucrose in the intestinal lumen can induce severe osmotic diarrhea and produce a feeding aversion[69]. For instance, Martínez del Rio and Stevens[44] and Brugger and Nelms[12] have shown that birds lacking intestinal sucrase activity, such as starlings and American robins, strongly prefer glucose and fructose to sucrose and develop a conditioned feeding aversion to sucrose (fig. 4).

Lack of sucrase is a sufficient but not necessary condition for birds to prefer hexoses over sucrose. The extremely fast passage rates of some frugivores[38] may preclude the efficient hydrolysis and absorption of sucrose relative to the hexoses glucose and fructose, even in the presence of significant intestinal sucrase. Cedar waxwings show intestinal sucrase activity but prefer glucose and fructose over sucrose[47]. Cedar waxwings absorb 92% and 88% respectively, of the glucose and fructose that they consume, but only 60% of the sucrose[47]. Time at first appearance of marked food in cedar waxwings is about ten minutes, and mean retention times of fluid markers are approximately 30 minutes (fig. 5)[40]. Fast passage rates probably do not provide the processing time required to assimilate complex substrates such as sucrose, that must be hydrolyzed to be absorbed[42,44]. The preference for the monosaccharides glucose and fructose over sucrose may be a consequence of the constraint imposed by high food passage rates.

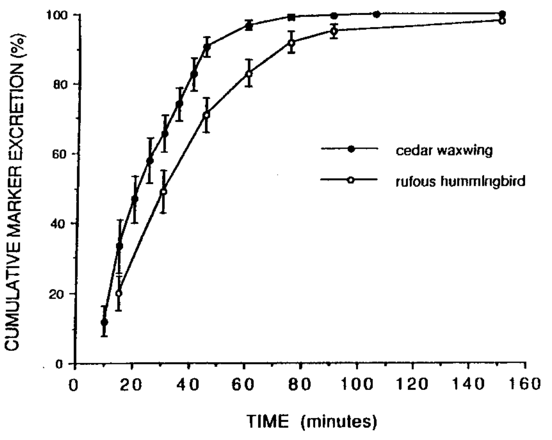

Figure 5. Cumulative excretion of water-soluble impermeant ■ markers in cedar waxwings (*Bombycilla cedrorum*, data from Levey and Grajal[40]) and rufous hummingbirds (*Selasphorus rufus*, data from Karasov et al.[36]). Marker mean retention times are shorter for cedar waxwings (30 min) than for rufous hummingbirds (47 min). Because retention time is an allometric function of body weight[35], and cedar waxwings are about an order of magnitude heavier than hummingbirds, this result illustrates the extremely fast food passage rates in cedar waxwings. Bars are SEM.

Sugar digestion and sugar preferences in hummingbirds

The digestive system of hummingbirds is exquisitely suited to digest and absorb a sucrose diet. Hummingbirds have the highest rates of carrier-mediated intestinal glucose transport reported among vertebrates[36] and their rates of intestinal sucrose hydrolysis are also extremely high[42]. These digestive traits allow them to use sucrose as efficiently as 1 : 1 mixtures of glucose and fructose[43]. Sucrose, glucose, and fructose are assimilated by hummingbirds with equally high efficiency (> 97%)[43]. Also, sucrose and equicaloric mixtures of glucose and fructose are processed at the same rate. The preference of hummingbirds for sucrose over hexose mixtures does not seem to be a result of hummingbirds assimilating sucrose more efficiently or digesting it faster than mixtures of glucose and fructose. The preference of hummingbirds for sucrose is puzzling. Female hummingbirds feed nestlings and fledglings a fluid mixture of arthropods and presumably sucrose-rich nectar[15]. Martínez del Rio[43] hypothesized that nestling hummingbirds may become 'imprinted' to the sucrose-rich foods regurgitated by their mothers. Many animals prefer foods experienced early in life over those experienced later[21]. In analogy with filial imprinting, Hess[33] called this phenomenon 'food imprinting'. It remains to be established if the sucrose preferences of hummingbirds can be explained by subtle, and not yet detected, differences in the physiological effect of different sugars or by food imprinting.

Sugar preferences, digestive constraints and the evolution of the sugar composition in nectar and fruit pulp

Gilbert and Raven[26] have pointed out the difficulty of integrating ecological and evolutionary time in coevolutionary studies. Coevolutionary relationships are by definition the product of historical change, yet this historical change is still proceeding. The approach that we used to guide our work emphasizes ecological time and therefore includes an implicit equilibrium assumption; it assumes that current mechanisms and processes are responsible for maintaining a given coevolutionary pattern. The results of history, however, rarely specify their initial causes unambiguously[28]. In consequence, our chosen approach does not provide many insights on the evolutionary origins of the mechanisms and processes that underly the peculiar distribution of the sugar constituents of nectar and fruit pulp. In the following sections we formulate what we believe are the necessary ingredients for an evolutionary explanation of the distribution of sugars in nectar and fruit pulp. At the outset of our research we hypothesized that the chemical composition of the rewards that plants offer was a result of an evolutionary adjustment to the preferences of pollinators and seed-dispersers[7,44]. Why, however, have different groups of birds evolved different sugar preferences? We deal with the evolution of sugar preferences in nectar- and fruit-eating birds and its consequences for plants in different sections.

Nectar-feeding birds

By morphological, behavioral and physiological criteria, hummingbirds are the most specialized nectar-feeding birds (see table 3 in Stiles[68]). We hypothesize that the digestive physiology of hummingbirds is specialized as well. Specifically we suggest that the digestive traits of hummingbirds are well suited for a sucrose diet whereas the digestive physiology of nectar-feeding passerines are not. We predict that an exception to this hypothesis will be *Coereba flaveola* and several species of *Diglossa* which feed parasitically on the sucrose-dominated nectar of hummingbird-pollinated plants[41,68]. These species are highly specialized and dependent upon flower nectar as an energy source. We hypothesize that their digestive traits have converged with those of hummingbirds from an ancestral frugivorous-insectivorous condition[63].

In the New World, passerine-pollinated plants are visited by birds such as warblers (Parulinae: Emberizidae), tanagers (Thraupinae: Emberizidae), and orioles (Icterinae: Emberizidae) that are generalists, consuming much fruit and insects as well as varying amounts of nectar[20,29]. Our scanty data on the digestive traits and sugar preferences of New World nectar-feeding passerines provide some support to the hypothesis that they prefer hexoses and have poor sucrose-digesting abilities (fig. 3). In Australasia, Africa, and Hawaii, several families of passerines have independently evolved sophisticated morphological specializations that enhance their ability to feed on nectar[19,55]. The digestive traits and sugar preferences of these more specialized and nectar-dependent Old World nectarivores are largely unknown. We predict that they prefer hexoses over sucrose and that they assimilate sucrose poorly or more slowly than glucose and fructose. To our knowledge no data are available to falsify this hypothesis. Collins and Morellini[18] and Collins et al.[17] reported that sucrose assimilation was extremely high in two honeyeater species (*Meliphaga virescens* and *Lichmera indistinta*, Meliphagidae) but did not compare the rate of sucrose processing with that of hexoses. Much more data on the sugar preferences and digestive abilities of passerine nectar-feeding birds are needed.

Why should the digestive traits of hummingbirds be different from those of the relatively specialized Old World nectarivorous birds? At the moment we do not have a convincing answer. We suspect, however, that the contrasting pollination spectra of the floras with which hummingbirds and passerines evolved may hold the key to this question. Hummingbird-pollinated flowers are mostly derived from large bee- and butterfly-pollinated flowers[27,68], both of which secrete sucrose-rich or sucrose-dominant nectars[7]. Presumably, proto-hummingbirds had to evolve the digestive adaptations to feed on sucrose before they became the 'most effective pollinators' (sensu Stebbins[66]) of these plants. Large flower-visiting bees are scarcer in Australia and Africa than in the New World[3,50], and in the Old World, bird-pollinated flowers are derived from a variety of other syndromes, including small-bee, fly and mammal pollination[23]. Flowers in these syndromes tend to secrete nectars with lower sucrose/hexose ratios than large bee and butterfly flowers[7]. Phylogenetic analyses, currently unavailable for the majority of ornithophylous plants, are a critical element for the historical reconstruction of the evolution of nectar chemistry.

Seed dispersal and the chemical composition of fruit-pulp

We have identified two mechanisms that can account for the preference for hexoses over sucrose in frugivorous birds: fast passage rates and lack of intestinal sucrase. In this section we explore the evolutionary causes and consequences of the first of these mechanisms.

Fruits are the vehicles used by plants for seed dispersal and are by necessity bulky. Nutritionally, many fruits are characterized by a nutrient-dilute pulp and a large proportion of seeds[52]. The presence of seeds in fruit reduces total gut capacity and imposes a heavy undigestible load to flying fruit-feeding dispersers[39]. Levey and Grajal[40] have suggested that the fast gut passage rates typical of frugivores evolved as a mechanism to void the ballast that undigestible seeds represent. Fast passage rates apparently do not provide the necessary processing time for complex substrates such as sucrose, that must be hydrolyzed to be assimilated, and hence impose a severe digestive constraint on frugivorous birds[47]. Levey and Grajal[40] argue that frugivores may have selected for nutrients in fruit pulp that can be rapidly assimilated, such as monosaccharides and free amino acids, and against complex nutrients that require digestion prior to absorption such as sucrose, polysaccharides, and polypeptides (see also Milton[51]).

The low sucrose/hexose ratios found in the fruit pulp of bird-dispersed fruits are probably the result of the need of birds for rapid disposal of seeds. Fast passage rates, therefore, may causally link frugivory and seed dispersal with the preference of bird frugivores for glucose and fructose. We hypothesize that the absence of sucrose – and presumably other complex substrates – in fruit pulp is the result of diffuse coevolution (sensu Futuyma and Slatkin[25]) between birds and plants, and to be mediated by the digestive adaptations of birds to a fruit diet. An evolutionarily meaningful examination of this hypothesis requires testing that short retention times are derived traits in frugivorous bird species (or lineages[9,16]), that short retention times are more advantageous, i.e. provide higher rates of energy assimilation, in the processing of fruit than the ancestral condition (longer retention times in granivory or insectivory[35]), and that short retention times hinder the efficient assimilation of sucrose. Although rapid processing of fruit-pulp and seeds is frequently invoked as an advantageous trait shared by volant frugivores[32,38,53] the comparative evidence is still scanty.

Lack of sucrase: a phylogenetic singularity with ecological consequences?

Martínez del Rio[42] noted that lack of sucrase among birds appears to be restricted to thrushes (Muscicapidae), starlings (Sturnidae), and thrashers (Mimidae). These three families are members of a single phylogenetic lineage[61,63] that includes many nectarivorous and frugivorous species (fig. 6). The cosmopolitan family Muscicapidae contains the largest number of seed-dispersing genera and species in the Nearctic and Palearctic realms[32,64,72]. The families Mimidae and Sturnidae also include many highly frugivorous species in the New and the Old World[65,72]. Sucrose-intolerance appears to be taxonomically restricted among birds but to be quite widespread geographically. In present-day communities, the preferences of sucrose-intolerant species may be a strong selective force that contributes to the maintenance of low sucrose concentrations in nectar and fruit pulp. Lack of sucrase may be a good example of a phylogenetic constraint with significant behavioral and ecological consequences[42]. In order not to contribute to the current chaos in constraint terminology[2], we define a phylogenetic constraint as a derived ('apomorphic') trait in a monophyletic lineage, whose current utility is less than the ancestral ('plesiomorphic') condition, which we hypothesize is the presence of intestinal sucrase activity. We hypothesize that intestinal sucrase activity was lost in the presumably insectivorous ancestor of robins and starlings before they radiated into frugivorous and nectarivorous habits. According to this hypothetical scenario, lack of intestinal sucrase in fruit- and nectar-feeding species of starlings and robins is a 'secondary nonadaptation'[9]. It is likely that hexose dominance in fruit pulp originally evolved in response to fast passage rates, and subsequently permitted the development of frugivory in the asucrotic sturnid-muscicapid lineage, facilitating a successful frugivorous and nectarivorous radiation. In present-day communities, the relative importance of fast-passage rates and lack of intestinal sucrase activity in maintaining hexose dominance in fruit probably depends on the taxonomic composition of a plant's dispersers coterie.

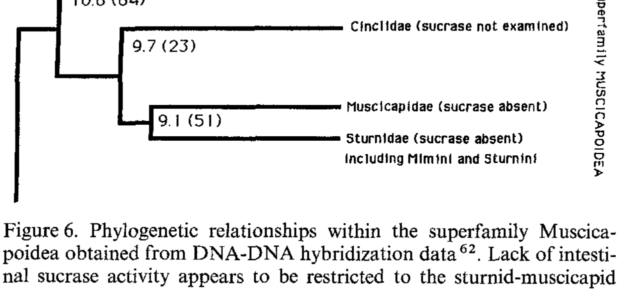

Figure 6. Phylogenetic relationships within the superfamily Muscicapoidea obtained from DNA-DNA hybridization data[62]. Lack of intestinal sucrase activity appears to be restricted to the sturnid-muscicapid clade.

The molecular bases of lack of intestinal sucrase activity in the sturnid-muscicapid lineage are not known. It is not known if it is the consequence of mutations in the sucrase gene, in its promotor, in a regulatory gene, or of defective homing of pro-sucrase between Golgi and the intestinal brush border. All these mechanisms have been reported in humans exhibiting congenital sucrase-isomaltase deficiency[59]. Starling and robins exhibit substantial isomaltase activity apparently independent of a glucoamylase[45] suggesting a back mutation to a double isomaltase as hypothesized for sea lions[71]. Congenital sucrase deficiency is a rare condition in most human populations, but occurs commonly among Eskimos[59]. Because starlings and robins are such abundant and convenient laboratory animals, they may serve as an excellent model to study the molecular causes and physiological consequences of congenital sucrase deficiency.

Digestive physiology and bird-plant interactions: a new direction in vertebrate physiological ecology?

Vertebrate ecological physiologists have devoted a considerable amount of effort into documenting the correspondence between the physiological capacities of animals and the environment[8,37]. Much less effort has been devoted to examine how physiological traits can act as selective influences on the characteristics of other animal species or on the plants with which animals interact[48]. Our research on sugars and birds provides an example of the insights that physiology can contribute to the study of animal-plant interactions, and illustrates the influence that our understanding of the physiological diversity in animals can have for explanations about the evolution of plant traits. The digestive physiology of pollinators and seed dispersers will almost certainly play a crucial role in the development of explanations to the enormous diversity of their interactions with plants[48]. Ecological physiologists can benefit from viewing physiological traits not only as the result of environmental influences, but also as forces that contribute to shape the environments (biotic and abiotic) in which animals live.

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1 Alpers, D. H., Digestion and absorption of carbohydrates and proteins, in: Physiology of the Gastrointestinal Tract, vol. 2, pp. 1469–1486. Ed. L. R. Johnson. Raven Press, New York 1987.
2 Antonovics, J., and van Tienderen, P. H., Ontoecogenophyloconstraints. Trends in Ecol. Evol. *6* (1991) 166–167.

3 Baker, H. G., Evolutionary relationships between flowering plants and animals, in: Tropical Forest Ecosystems in Africa and South America: A Comparative Review, pp. 149–159. Eds P. J. Meggers, E. Ayensu and W. D. Duckworth. Smithsonian Institution Press, Washington D.C. 1972.

4 Baker, H. G., Sugar concentrations in nectars from hummingbird flowers. Biotropica *7* (1975) 37–41.

5 Baker, H. G., Anthecology: Old Testament, New Testament, Apocrypha. N. Z. J. Bot. *17* (1979) 431–440.

6 Baker, H. G., and Baker, I., Some chemical constituents of floral nectars of *Erythrina* in relation to pollinators and systematics. Allertonia *3* (1982) 25–37.

7 Baker, H. G., and Baker, I., Floral nectar sugar constituents in relation to pollinator type, in: Handbook of Experimental Pollination Ecology, pp. 131–171. Eds C. E. Jones and R. J. Little. Scientific and Academic Editions, New York 1983.

8 Baker, I., Baker, H. G., and Hodges, S. A., Patterns in the sugar composition of nectar and fruit juices taken by Microchiroptera and Megachiroptera. Biotropica (in press).

9 Baum, D. A., and Larson, A., Adaptation reviewed: a phylogenetic methodology for studying character macroevolution. Syst. Zool. *40* (1991) 1–18.

10 Bennet, A. F., The achievements of ecological physiology, in: New Directions in Ecological Physiology, pp. 1–10. Eds M. E. Feder, A. F. Bennett, W. W. Burggren and R. B. Huey. Cambridge Univ. Press, New York 1987.

11 Brugger, K. E., Sucrose as a fruit repellent to American robins *(Turdus migratorius)*. J. Wildl. Mgmt (in press).

12 Brugger, K. E., and Nelms, C. O., Sucrose avoidance by American robins *(Turdus migratorius)*: implications to control of bird damage in fruit crops. Crop Protect. *10* (1992) 455–460.

13 Búrquez, A., Blue tits, *Parus caeruleus*, as pollinators of the crown imperial, *Fritillaria imperialis*, in Britain. Oikos *58* (1989) 335–340.

14 Calder, W. A., On the temperature dependency of optimal nectar concentration for birds. J. theor. Biol. *78* (1979) 185–196.

15 Carpenter, F. L., and Castronova, J. L., Maternal diet selectivity in *Calypte anna*. Am. Midl. Nat. *103* (1980) 175–179.

16 Coddington, J. A., Cladistic tests of adaptational hypotheses. Cladistics *4* (1988) 3–22.

17 Collins, B. G., Cary, G., and Packard, G., Energy assimilation, expenditure and storage by the brown honeyeater *Lichmera indistinta*. J. comp. Physiol. *137* (1980) 157–163.

18 Collins, B. G., and Morellini, P. C., The influence of nectar concentration and time of day upon energy intake and energy expenditure by the singing honeyeater *Meliphaga virescens*. Physiol. Zool. *52* (1979) 165–175.

19 Collins, B. G., and Paton, D. C., Consequences of differences in body mass, wing length and morphology for nectar-feeding birds. Aust. J. Ecol. *14* (1989) 269–289.

20 Cruden, R. W., and Toledo, V. M., Oriole pollination of *Erythrina breviflora* (Leguminosae): evidence for a polytypic view of ornithophily. Pl. Syst. Evol. *126* (1977) 393–403.

21 Dethier, V. G., and Goldrich, N., Blowflies: alteration of adult taste responses by chemicals present during development. Science *173* (1971) 242–244.

22 Faegri, K., and van der Pijl, L., The principles of pollination ecology. Pergamon Press, New York 1966.

23 Ford, H. A., Paton, D. C., and Forde, N., Birds as pollinators of Australian plants. N.Z. J. Bot. *17* (1979) 509–519.

24 Freeman, C. E., and Worthington, R. D., Is there a difference in the sugar composition of cultivated sweet fruits of tropical/subtropical and temperate origins? Biotropica *21* (1988) 219–222.

25 Futuyma, D. S., and Slatkin, M., Epilogue: the study of coevolution, in: Coevolution, pp. 459–464. Eds D. S. Futuyma and M. Slatkin. Sinauer, New York 1983.

26 Gilbert, L. L., and Raven, P., Coevolution of Animals and Plants. Univ. of Texas Press. Austin, Texas 1975.

27 Grant, K. A., and Grant, V., Hummingbirds and Their Flowers. Columbia University Press, New York 1968.

28 Gould, S. J., The Panda's Thumb. W. W. Norton and Co., New York 1980.

29 Gryj, E., Martínez del Rio, C., and Baker, I., Avian pollination and nectar use in *Combretum fruticosum* (Loefl.). Biotropica *22* (1990) 266–271.

30 Hainsworth, F. R., and Wolf, L. L., Nectar characteristics and food selection by hummingbirds. Oecologia *25* (1976) 101–113.

31 Heinrich, B., Energetics of pollination. A. Rev. Ecol. Syst. *6* (1975) 139–170.

32 Herrera, C. M., Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology *65* (1984) 609–617.

33 Hess, E. H., Imprinting in birds. Science *146* (1964) 1128–1139.

34 Howell, D., Bats and pollen: physiological aspects of the syndrome of Chiropterophily. Comp. Biochem. Physiol. *48*A (1979) 236–276.

35 Karasov, W. H., Digestion in birds: chemical and physiological determinants, and ecological implications, in: Avian Foraging: Theory, Methodology, and Applications, pp. 391–415. Eds M. L. Morrison, C. J. Ralph, J. Verner and J. R. Jehl Jr. Studies in Avian Biology No. 13, Cooper Ornithological Society, Lawrence, Kansas 1990.

36 Karasov, W. H., Phan, D., Diamond, J. M., and Carpenter, F. L., Food passage and intestinal nutrient absorption in hummingbirds. Auk *103* (1986) 453–464.

37 Karasov, W. H., and Diamond, J. M., Interplay between physiology and ecology in digestion. BioScience *38* (1989) 602–611.

38 Karasov, W. H., and Levey, D. J., Digestive trade-offs and adaptations of frugivorous birds. Physiol. Zool. *63* (1990) 1248–1270.

39 Levey, D. J., Seed size and fruit-handling techniques of avian frugivores. Am. Nat. *129* (1987) 471–485.

40 Levey, D. J., and Grajal, A., Evolutionary implications of fruit processing and intake limitation in cedar waxwings. Am. Nat. *138*: 171–189.

41 Lyon, D. L., and Chadek, C., Exploitation of nectar resources by hummingbirds, bees *(Bombus)*, and *Diglossa baritula* and its role in the evolution of *Penstemon kunthii*. Condor *73* (1971) 246–248.

42 Martínez del Rio, C., Dietary and phylogenetic correlates of intestinal sucrase and maltase activity in birds. Physiol. Zool. *63* (1990) 987–1011.

43 Martínez del Rio, C., Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. Condor *92* (1990) 1022–1030.

44 Martínez del Rio, C., and Karasov, W. H., Digestion strategies in nectar- and fruit-eating birds and the composition of plant rewards. Am. Nat. *136* (1990) 618–637.

45 Martínez del Rio, C., and Stevens, B. R., Physiological constraint on feeding behavior: intestinal membrane disaccharides of the starling. Science *243* (1989) 794–796.

46 Martínez del Rio, C., Stevens, B. R., Daneke, D., and Andreadis, P. T., Physiological correlates of preference and aversion for sugars in three species of birds. Physiol. Zool. *61* (1988) 222–229.

47 Martínez del Rio, C., Levey, D. J., and Karasov, W. H., Physiological basis and ecological consequences of sugar preferences in cedar waxwings. Auk *106* (1989) 64–71.

48 Martínez del Rio, C., and Restrepo, C., Ecological and behavioral consequences of digestion in frugivorous animals. Vegetatio (in press).

49 McKey, D., The ecology of coevolved seed dispersal systems, in: Coevolution of Animals and Plants, pp. 159–192. Eds L. E. Gilbert and P. H. Raven. Univ. of Texas Press, Austin 1975.

50 Michener, C. D., Superfamily Apoidea, in: The Insects of Australia, pp. 943–951. Ed. C.S.I.R.O., Melbourne University Press, Melbourne 1970.

51 Milton, K., Food choice and digestive strategies of two sympatric primate species. Am. Nat. *117* (1981) 496–505.

52 Moermond, T. C., and Denslow, J. S., Neotropical avian frugivores: patterns of behavior, morphology, and nutrition with consequences for fruit selection, in: Neotropical Ornithology, pp. 865–897. Eds P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridley and F. G. Buckley. Ornithological Monographs 45, Allen Press, Lawrence, Kansas 1985.

53 Morrison, D. W., Efficiency of food utilization by fruit bats. Oecologia *45* (1980) 270–273.

54 Percival, M. S., Types of nectar in angiosperms. New Phytol. *60* (1961) 235–281.

55 Rand, A. L., The flower-adapted tongue of a timaliine bird and its implications. Fieldiana (Zool.) *51* (1967) 53–61.

56 Scogin, R., and Freeman, C. E., Floral pigments and nectar constituents in the genus *Puya* (Bromeliaceae). Aliso *10* (1984) 617–619.

57 Semenza, G., Intestinal oligosaccharidases and disaccharidases, in: Handbook of Physiology, sect. 6, vol. 5, pp. 2543–2566. Ed. C. F. Code. American Physiological Society, Washington D.C. 1968.

58 Semenza, G., and Corcelli, A., The absorption of sugars and amino acids across the small intestine, in: Molecular and Cellular Basis of Digestion, pp. 381–412. Eds P. Desnuelle, H. Sjöstrom and A. Norén. Elsevier Science Publishers B. V., New York 1986.

59 Semenza, G., and Auricchio, S., Small-intestinal disaccharidases, in: The Metabolic Basis of Inherited Disease, pp. 2975–2997. Eds C. R. Scribner, A. L. Beaudet, W. S. Sly and D. Valle. McGraw Hill, New York 1989.

60 Shafir, E., Effects of sucrose and fructose on carbohydrate and lipid metabolism and the resulting consequences, in: Regulation of Carbohydrate Metabolism, pp. 95–140. Ed. R. Beiner. CRC Press, Boca Raton, Florida 1985.
61 Sibley, C. G., and Ahlquist, J. E., The relationships of the starlings (Sturnidae: Sturnini) and the mockingbirds (Sturnidae: Mimini). Auk *101* (1984) 230–243.
62 Sibley, C. G., and Ahlquist, J. E., Phylogeny and classification of birds. Yale University Press, New Haven 1990.
63 Sibley, C. G., Ahlquist, J. E., and Monroe, B. L., A classification of the living birds of the world based on DNA-DNA hybridization studies. Auk *105* (1988) 409–423.
64 Snow, B. K., and Snow, D. W., Birds and Berries. T. Poyser and A. D. Poyser, Calton, England 1971.
65 Snow, D. W., Tropical frugivorous birds and their food plants: a world survey. Biotropica *13* (1981) 1–14.
66 Stebbins, G. L., Adaptive radiation of reproductive characteristics in angiosperms, I. Pollination mechanisms. A. Rev. Ecol. Syst. *1* (1970) 307–326.
67 Stiles, F. G., Taste preferences, color preferences and flower choice in hummingbirds. Condor *78* (1976) 10–26.
68 Stiles, F. G., Geographical aspects of bird-flower coevolution, with particular reference to Central America. Ann. Mo. bot. Gdn *68* (1981) 323–351.
69 Sunshine, P., and Kretchmer, N., Intestinal disaccharidases: absence in two species of sea lions. Science *144* (1964) 850–851.
70 Van Riper, W., Hummingbird feeding preferences. Auk *75* (1958) 100–101.
71 Wacker, H., Aggeler, R., Kretchmer, N., O'Neill, B., Takesue, Y., and Semenza, G., A two-active site one-polypeptide enzyme: the isomaltase from sea lion small intestinal brush border membrane (its possible phylogenetic relationship with sucrase isomaltase). J. biol. Chem. *259* (1984) 4878–4884.
72 Willson, M. F., Avian frugivory and seed dispersal in eastern North America. Curr. Orn. *3* (1986) 223–279.

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The matches, achieved by natural selection, between biological capacities and their natural loads

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Abstract. Natural selection tends to eliminate unutilized capacities because of their costs. Hence we ask how large are the reserve capacities by which biological capacities exceed natural loads, and how closely are related biological capacities matched to each other. Measured capacities (V_{max} values) of small intestinal brush-border nutrient transporters are typically around twice their natural loads (dietary intakes of their substrates); the ratio is higher for a transporter of a hyperessential nutrient. Preliminary evidence suggests matching of capacities between different steps in carbohydrate metabolism, and between the intestine, liver, kidneys, and spleen. Symmorphosis – the postulated matching of capacities to each other and to loads – is a testable hypothesis of economic design, useful in detecting and explaining cases of apparently uneconomic design.

Key words. Small intestine; brush border; nutrient absorption; sugar absorption; lactation; cold exposure; symmorphosis; safety margin; reserve capacity.

Introduction

This paper examines the quantitative match between biological capacities and the natural loads upon those capacities, and also the match between related capacities. As examples of capacities, we have measured the maximal reaction velocities (V_{max} values) of intestinal nutrient transporters and hydrolases; and as examples of corresponding loads, the daily dietary intakes of the substrates of those transporters and hydrolases. However, one could pose the same question for the strengths of bones in relation to the natural stresses on bones, or for the lung's oxygen diffusing capacity in relation to actual oxygen consumption[18], or for any other biochemical, physiological, or anatomical capacity. For each such comparison we ask whether the biological system is designed with some reserve capacity, such that actual capacity exceeds natural loads by some margin of safety. In effect, Darwin showed that biological capacities are qualitatively matched to their loads; we now ask about the quantitative match.

At the outset, one might wonder why natural selection or God did not endow animals with large reserve capacities in all systems, such that the animal's body could never limit the animal's behavior. The answer surely is that any biological capacity incurs costs (such as allocations of biosynthetic energy and space), but that animals have access to only finite biosynthetic energy, and that the space within an animal's body, cell membranes, and cytoplasm is utilized almost to the limit of standing-room-only. An animal squandering resources on one system thus draws down the resources available to other systems. Hence such an uneconomical animal would tend to be replaced by economical ones.

Many familiar examples illustrate the evolutionary outcome that disused capacities tend to become eliminated by natural selection. Cave animals tend to lose functional eyes, while some volant birds (especially rails) colonizing remote and predator-free islands tend rapidly to lose the ability to fly. The large and energetically costly flight