Sugar Preference across Butterfly Families

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ABSTRACT

Adult butterflies have a carbohydrate-based diet, acquiring their sugars mostly from nectar or from rotting fruits. Fruit-eating butterflies most often encounter fructose and glucose (Omura and Honda, 2003), while nectarivorous butterflies may encounter hexose-rich nectars in short-corolla flowers or sucrose-rich nectars in long-corolla flowers (Baker and Baker, 1983). This study explores the possibility that butterfly species exhibit certain sugar preferences that reflect not only their diet but their phylogeny as well, since feeding habits are often the result of co-evolution with pollination syndromes in the case of nectar-feeding butterflies. Butterflies from as many species as possible were given a solution of either 20% sucrose by weight or a 20% solution of combined glucose and fructose. The amount imbibed was recorded for the 26 species caught. No obvious preference for either sucrose or hexose nectars were uncovered. Butterflies would drink from either solution, indicating that fruits and flowers offering either sugar would be acceptable to most butterflies and that sugar preference is not as rigidly an evolved trait as was thought. However, minor trends towards sucrose preference are compelling grounds for further study.

RESUMEN

Las mariposas tienen una dieta basada en carbohidratos, consiguen los azucares principalmente en la forma fructosa y glucosa, de nectar o de frutos en decomposición. Las mariposas nectarívoras encuentran néctar rico en hexosa en flores con corolas cortas o néctar rico en sucrosa en flores con corolas largas. Este estudio explora la posibilidad de que algunas mariposas exhiban alguna preferencia por azucares que refleje no solo su dieta pero también su filogenia, ya que los habitos alimenticios a veces son el resultado de co-evolución con los sindromes de polinización. Mariposas de varias especies fueron alimentadas con sucrosa al 20% o una solución al 20% de glucosa/fruxtosa. La cantidad consumida fue medida para 26 especies. No se detecto ninguna preferencia. Esto indica que las flores y frutos ofreciendo cualquiera de los azucares serán aceptados por la mayoría de las mariposas, y que la preferencia de azúcar no es un carácter evolutivo tan rigido con se pensaba.

INTRODUCTION

Most adult butterflies depend on sugar solutions for their diet, which they get either from nectars (Romeis and Wackers, 2002) or juices of rotting fruit (Omura and Honda, 2003). The nectar-feeding butterflies are important pollinators of the plants they depend on, and certain pollination syndromes have evolved to ensure a tighter relationship between flower and butterfly (Baker and Baker, 1983). While flower shape and color are agreed to be important components of pollination syndromes, the importance of the content of the nectar is less certain.

Baker and Baker (1983) found that plants are fairly constant within a species in terms of sucrose-dominance or hexose-dominance of their nectars, regardless of variation

in the environment. Plants with the same pollinator type exhibit similarities in sugar ratios even without being taxonomically related. This strongly suggests that pollinators, like butterflies, have important sugar preferences that can shape the evolution of nectars. Most nectars contain sucrose, glucose and fructose; only a few have only one detectable sugar, and none of these contain fructose alone, or sucrose and fructose without glucose. In general, Percival (1961) noted that families with deep-tubed flowers tend to be sucrose-rich while shallow-tubed or cupped flowers are most often hexose-rich. Baker and Baker (1983) distinguish butterfly-visited flowers into two groups: those with deep narrow corollas characteristically rich in sucrose and visited primarily by butterflies, and those smaller short-tubed hexose-rich flowers visited equally by bees and butterflies.

Sugar preference studies have been done in birds (Martinez del Rio et al., 1992), showing that nectar-feeding hummingbirds have specialized on sucrose, but that most fruit-eating passerines cannot digest sucrose and instead show a preference for fruits containing the monosaccharide sugars fructose and glucose. Plants pollinated and dispersed by different birds thus use different types of sugars in their nectars and fruit pulps as rewards. If birds exhibit such diet-related preferences for sugar types, one would expect fruit-eating butterflies to possibly specialize on fructose and glucose, while nectar-feeding butterflies of at least long-corolla flowers may prefer sucrose.

Baker and Baker (1983) did a survey of plant families and found that pollinator syndrome is the most important component of which sugar type a flower offers. Hummingbird pollinated flowers are sucrose rich and hummingbirds prefer sucrose. The case for butterflies and their flowers is still unknown. Butterflies may exhibit sugar preferences that reflect their diet, on fruit or either type of nectar. These patterns of preference may fall along taxonomic lines if mechanisms like the enzyme deficiencies reported in birds (Martinez del Rio et al., 1992) exist in butterflies. Another possibility, that most butterflies have the enzymatic ability to use sucrose and hexose sugars, would explain why butterfly flowers supply either sugar type.

Some studies have been done to determine sugar preference in individual butterfly species, but one does not get an idea of big-picture trends from them. Watt et al. (1974) found no preference in *Colias* sp., as it was found that this genus has enzymes to process both hexose and sucrose sugars. *Pieris brassicae*, a species of Pierid, was found to prefer sucrose to fructose (Romeis and Wackers, 2000), as Battus philenor in Erhardt's 1991 feeding experiments. Even though fructose ands glucose were the major sugars found in the fruits eaten by *Nymphalis xanthomelas*, *Kanisca canace*, and *Vanessa indica*, sucrose was the most effective feeding stimulant in these species, with fructose following close behind (Omura and Honda 2003). Ithomiines specialize on members of Asteraceae and Boraginaceae (Baker and Baker, 1983), which have hexose-rich nectars, so it is hypothesized that they prefer hexose sugars to sucrose. Besides these findings, few studies have been devoted to discovering sugar preferences in butterfly species let alone in multiple butterfly families.

This experiment aims to see if a relationship between sugar preference and butterfly family phylogenies exists. Butterflies in this study were fed a solution containing only the sugars of interest, without presenting flower options. Though other monosaccharide and disaccharide sugars may be present in nectars, they occur in minute amounts, which is why this study focuses on sucrose, glucose and fructose in terms of sugar preference in butterflies.

MATERIALS AND METHODS

Study Site

The experiment was conducted at the Selvatura butterfly garden and the Monteverde Butterfly Garden, both in Monteverde. Butterflies were collected from inside the gardens, while feedings were conducted in a separate room at the Monteverde Butterfly Garden, and in an eclosion chamber at Selvatura.

Preparation of Sugar Solutions

The sucrose solution consisted of 20% sucrose by weight. The hexose mix consisted of 10% fructose by weight and 10% glucose by weight. Both solutions were stored in capped containers and remade every other day.

Catching and Storing

Butterflies were caught using a simple butterfly net, and then transferred to a 1 m tall cylindrical holding net, where they were kept for at least two hours before feeding, or overnight in the case of most of the morphos and heliconiines. This delay ensured that the butterflies would be less active and more inclined to eat the sugar solution presented to them without trying to escape. Butterflies were caught in the late morning between 8 and 11 a.m. when they are most active, and were identified using *The Butterflies of Costa Rica and their Natural History* (DeVries, 1987).

Feeding

Butterflies were transferred individually to the feeding room, where they were placed on wax paper in front of a bead of 100μL of sugar solution. While a nearby light bulb shone on the butterfly in order to heat it and induce it to feed, the butterfly was held lightly by the wings and its proboscis was unrolled with an unbent paperclip to place the tip of the proboscis in the liquid. At this point, if the butterfly immediately started to feed, I would release its wings and let it feed until it was ready to fly away; otherwise, I would continue keeping its proboscis extended in the sugar solution until it kept it extended on its own for at least three seconds. Every butterfly that did not start feeding immediately was given three chances to eat. At the end of a feeding session, when the butterfly was satiated or had used up its three chances, the remaining sugar solution was sucked up by 20μL microcapillary tubes and the volume measured. The wax paper would then be cleaned, a new bead of 100μL would be applied by blowing sugar solution out of a microcapilllary tube, and a new butterfly would be pulled from the holding net. This same feeding process was used for sucrose feedings and hexose feedings, though they were conducted on separate pieces of wax paper and with separate microcapillary tubes in order to avoid contamination.

RESULTS

Thirty three species from the families Pieridae, Papilionidae and Nymphalidae were tested. Of these, 26 species of three families and five nymphalid subfamilies were surveyed for both sugar solutions. Mean hexose volumes were subtracted from mean sucrose volumes for all species that had representatives from both feedings, giving positive or negative values. Differences of <5% were listed as zero and discounted. The result of the Sign Test pointed to 14 cases where a species preferred sucrose and nine cases where a species preferred the fructose-glucose mixture. In three cases there was little or no difference. Overall, butterflies do not show a preference for sucrose or hexose-rich sugars (Sign test, n=14 plus, 9 negative, p> 0.05).

For all three Papilionid species tested, mean sucrose consumption was greater than mean hexose consumption, though in one trial, the difference was just 7 µL. Three of four Pierid species seemed to prefer sucrose to hexose. In these cases, there were too few species to test trends statistically.

With eight negative and eight positive points for the Sign Test, no trend could be found in sugar preference, either in Nymphalidae as a family, or within the subfamilies Ithomiinae, Morphinae, Heliconiinae and Nymphalinae.

Further Observations

On the whole, the Pierid butterflies were very finicky eaters, and it was difficult to get them to take up even a little of either sugar solution. The Papilionids and certain members of Heliconiines were hard to feed as well, but to a lesser extent. Ithomiines and Morphos would readily eat, but whereas the smaller glass-wing Ithomiines took half an hour to eat about 30µL, the Morphos would eat the entire hundred µL to the point where I had to start feeding them more until they were satiated.

Parides individuals and most Pierid individuals were extraordinarily active when caught, but could not be stored overnight since they would die, so they were only stored between two and four hours.

TABLE 1. Sugar consumption in three butterfly families. Members of the family Nymphalidae are shown in red, Papilionidae in green, and Pieridae in blue. Butterfly individuals were collected from the Monteverde Butterfly Garden and the butterfly garden at Selvatura.

Species	Sucrose Number fed	Sucrose Mean volume eaten (µL)	Hexose Number fed	Hexose Mean volume eaten (µL)
Greta oto	5	30.682	5	26.788
Ithomia heraldica	1	36.05	1	36.8
Pteronymia fumida	1	40.26	0	—
Morpho granadensis	4	58.2875	3	62.544
Morpho peleides	5	83.364	5	78.474
Caligo eurilochus sulanus	1	33.4	1	400
Caligo memnon memnon	1	346.3	2	344.2

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Danaus plexippus	1	89.7	1	76.6
Dione moneta poeyii	3	55.089	2	44.737
Dryadula phaetusa	6	30.2183	1	49.5
Dryas iulia	2	40.791	3	58.3
Eueides isabella	4	31.91	5	34.788
Heliconius charitonius	3	29.123	3	31.929
Heliconius hecale zuleika	2	70.13	3	65.878
Heliconius sapho leuces	4	23.51	4	26.117
Heliconius sara fulgidus	2	23.29	2	24.08
Heliconius erato	2	35.79	2	26.449
Catonephele numilia esite	3	56.228	3	31.053
Myscelia cyaniris cyaniris	3	30.263	3	36.404
Siproeta steleres	2	103.553	2	59.6
Battus polydamas polydamas	4	49.212	4	24.5
Parides lycimenes lycimenes	2	77.434	1	59.145
Parides arcas mylotes	0	—	1	12.1
Parides iphidamas iphidamas	0	—	1	68.4
Parides erithalion	0	—	1	11.3
Papilio astyalus pallas	1	89.47	1	81.3
Papilio polyxenes	1	36.3	0	—
Papilio thoas nealces	0	—	1	177.6
Ascia limona	1	43.16	1	59.2
Phoebis sennae	2	46.316	3	23.86
Phoebis philea philea	1	59.5	1	55.5
Anteos clorine	0	—	1	92.6
Appias drusilla	1	42.1	2	18.421
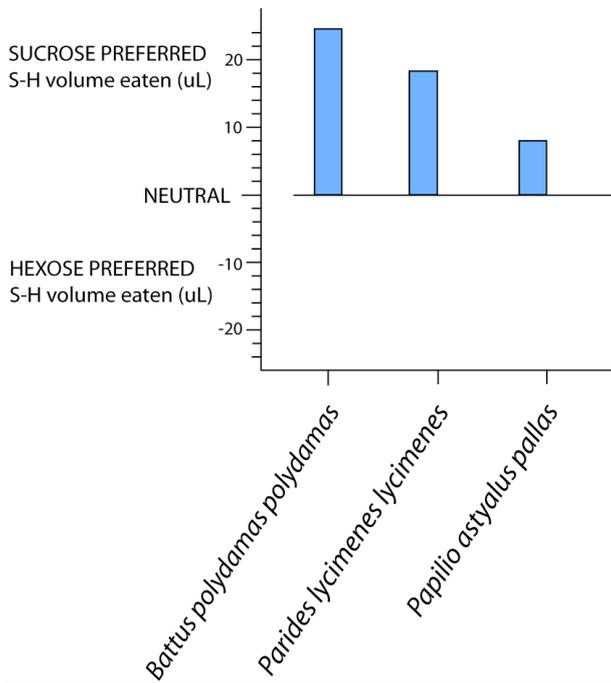
FIGURE 1. Preference of sugar types by Papilionidae. Bars show results of a Sign Test where the mean volume of hexose solution eaten was subtracted from the mean volume of sucrose eaten. Bars pointing toward sucrose preference represent positive results. Negative results indicate hexose preference.
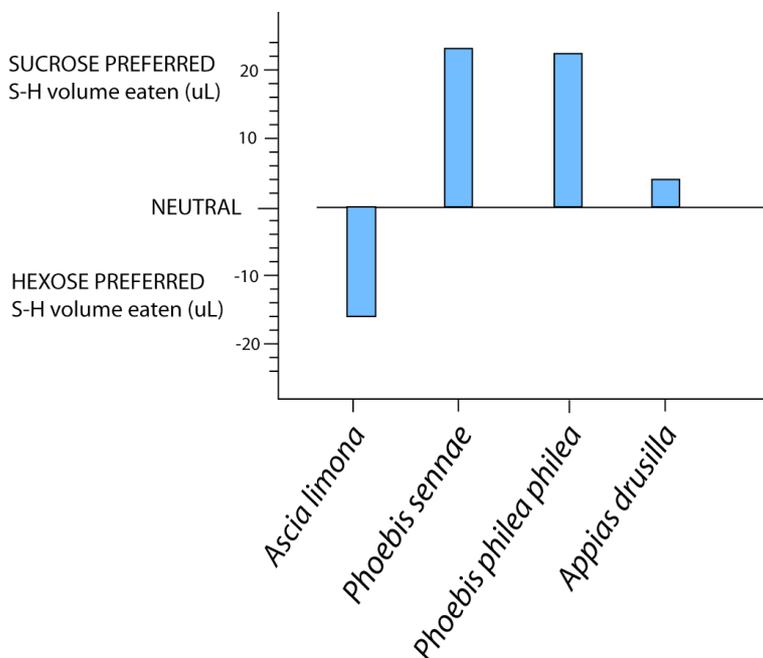

FIGURE 2. Preference of sugar types by Pieridae. Positive results of a sucrose-minus-hexose Sign Test are shown as bars pointing to sucrose preference, while negative results point to hexose preference.
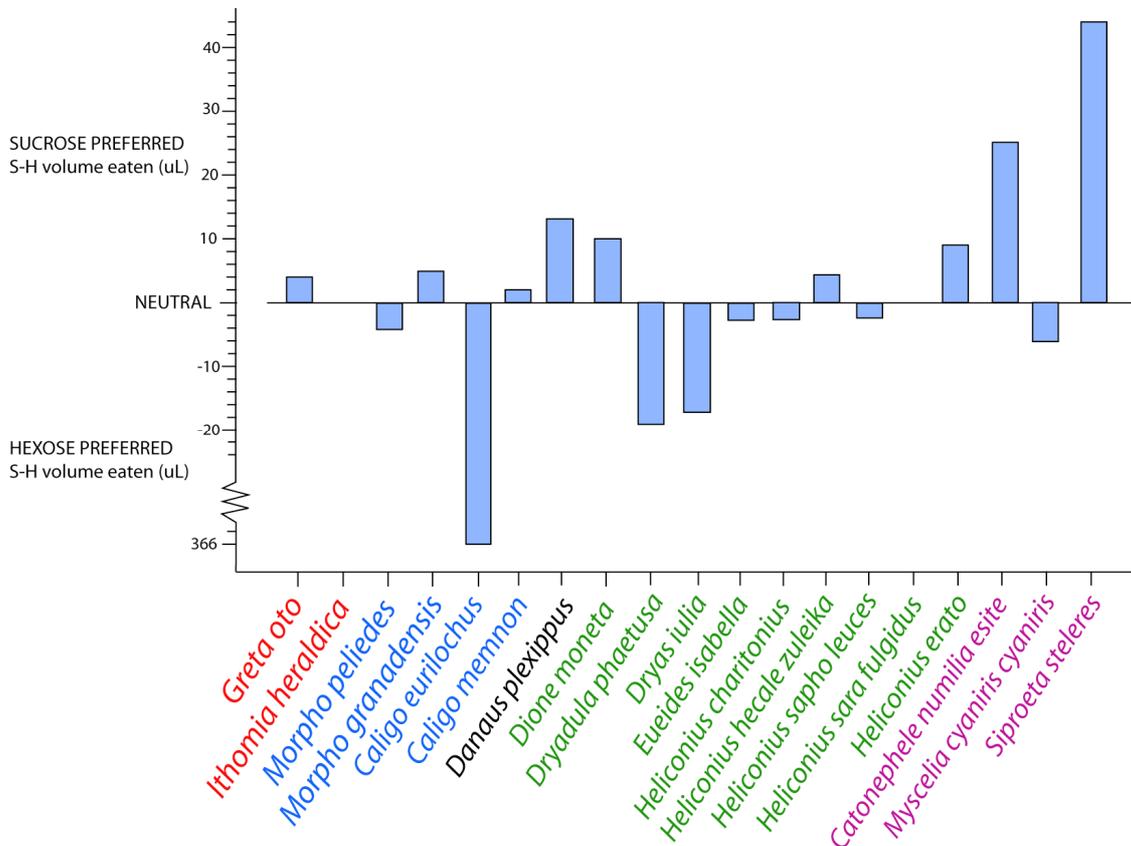
FIGURE 3. Preference of sugar types by Nymphalidae. Subfamily Ithomiinae shown in red, Morphinae in blue, Danainae in black, Heliconiinae in green and Nymphalinae in purple. Positive results of a Sign Test indicate sucrose preference; negative results indicate hexose preference. Neutral preference indicates <5% difference in mean consumed volumes.

DISCUSSION

Even though the Sign Test showed no overall sugar preference across butterfly species, this is to be expected. The butterflies examined include three familes and several subfamilies within Nymphalidae, some of which feed on fruits and some of whom have longer and shorter proboscides. What is perhaps most surprising is that, despite possible preferences, all species readily took both sugar types, suggesting that both would serve as an acceptable reward for any of the species in the survey.

　　　　Within the broader pattern, there were some trends worth investigating further. For example, all three Papilionidae species fed exhibited a preference for sucrose. Indeed, this finding supports Erhardt's (1991) study of *Battus philenor*, where individuals preferred both sucrose and fructose to glucose, but preferred sucrose to fructose. Confirmation of sucrose preference would also tie in to DeVries' observations (1987) that

the genus *Parides* feeds on flowers of the families Balsamaceae and Rubiaceae, which have fairly long tubes and therefore are probably sucrose-rich.

Three of the four genera of Pierid butterflies fed in this study also preferred sucrose to hexose, so it would be interesting to see if further studies corroborate a preference for sucrose over hexose, since there currently are conflicting lines of evidence for Pierid sugar preferences. Romeis and Wackers' 2000 study of *Pieris brassicae* revealed a preference for sucrose over fructose, but interestingly enough, Romeis and Wackers (2002) also found that *Pieris brassicae* fecundity is compromised by sucrose, and glucose is the only sugar with a positive effect on both longevity and fecundity. Furthermore, according to DeVries (1987), Pierids feed on red flowers in general, and as many red flowers are hummingbird pollinated, one would expect them to be sucrose-rich. Pierids also feed on shallow-tubed *Lantana camara*, however, which according to Percival (1961) points toward a hexose-rich nectar. If hexoses are good for Pierids, we might expect to see a hexose preference, but there is a possibility that the *Pieris brassicae* preference for sucrose can be expanded to the whole family. Again, further study is necessary to determine if there is a family trend for sucrose preference.

The Nymphalidae did not show a strong preference for either sucrose or hexose, but even if future studies corroborate this lack of feeding preference pattern, it would not be entirely unexpected, since certain subfamilies of Nymphalids have become specialized on different diets. For example, adults of the subfamily Morphinae do not visit flowers, and instead feed exclusively on plant sap and the juices of rotted fruits and fungi (DeVries, 1987); meanwhile, Heliconiines and Ithomiines eat nectar, often from *Lantana camara*. There might then be patterns within smaller clades, but the family as a whole would not have a single evolved preference.

Ithomiines have specialized on members of the families Boraginaceae and Asteraceae, whose nectars are predominantly hexose-rich (Baker and Baker, 1983). This corresponds with Percival's (1961) observations that shallow flowers, usually found in inflorescences, tend to be hexose dominant. However, those observations do not correspond with this study's findings, wherein *Greta nero* ate more sucrose and *Ithomia heraldica* had no discernable preference. Clearly more feeding experiments need to be carried out.

Morphinae species are specialized fruit eaters, so one would expect them to prefer fructose and glucose, as these sugars are the most common sugars in fruit (Omura and Honda, 2003); however, this is not what was found. Two of the four Morphinae species studied (*M. peliedes* and *C. eurilochus*) preferred the hexose solution, while *M. granadensis* on average ate more sucrose solution and *C. memnon* showed no discrimination between sugar solutions at all. Looking again at Omura and Honda's 2003 study, where they found that sucrose was the preferred sugar but that fructose was also a very good feeding stimulant and occurred in higher quantities, perhaps concentration plays a role in sugar feeding preferences. Part of the problem could also be that Morphos have a tendency to eat the entirety of the volume of solution they are presented with, which made it hard to find a pattern in terms of preference. One way to possibly overcome this would be to feed them until they are fully satiated, which would require one to put down far more than 100μL at a time. Future experiments on Morphinae sugar preference might consider feeding them solutions of fructose, a hexose mixture, and sucrose, each with the necessary ethanol and acetic acid compounds to entice feeding.

Two of the three Nymphalinae species preferred sucrose, and five Heliconiinae species preferred sucrose as opposed to three heliconiines that preferred hexose. The genus *Heliconius* eat pollen *from Gurania costaricense* (Gilbert, 1983), but nothing is mentioned about the sugars they get from nectar, and any conjecture is made more complicated by the fact that hummingbirds may also visit *G. costaricense*. I was unable to find any literature on the feeding habits of adult Nymphalinae species that would point to either a sucrose or hexose preference Again, more studies should be carried out to find out if Heliconiines and other Nymphalid butterflies exhibit preferences for specific sugar types.

Overall, data presented here cannot conclusively say that butterflies as a whole appear to favor one sugar type over the other even though there were more positive (i.e., sucrose preference) results from the Sign Test than negative results. A Omura and Honda (2003) point out, much of the existing literature concerning butterfly feeding habits points to a trend of sucrose preference over fructose, and fructose preference over the remaining sugars, but there are not enough studies of multiple butterfly families for one to really get a sense of a pattern.

Successful attraction of pollinators is complex, relying on many factors other than nectar sugar type. Pollinators will ignore one flower if other flowers with more desirable nectar are present (Vansell et al., 1942), and will feed on less desirable flowers of attractive competitors are not present (von Frisch, 1950). It could very well be that butterflies will eat sugars from whatever flowers are available to them, and their sugar "preference" will change as the composition of flower species in their environment changes. If butterflies also have the ability to digest multiple types of sugars as Watt et al. found (1974), sugar preferences would be further confounded. In this case, future studies would end up with similarly inconclusive results in terms of sucrose vs. hexose preference, and no pattern would be found relating butterfly phylogeny to adult dietary preference. In any event, butters flies do not seem constrained to one or few sugar types as was found for some frugivorous and nectarivorous birds (Martinez del Rio et al., 1992).

The ecological implications of these findings for nectar flowers are rather curious. Despite the strong patterns shown by Baker and Baker (1983) with regards to nectar composition, there seems to be no cause for specified sugar compositions in butterfly-pollinated flowers. Sugar preference works really well for hummingbirds, as they really strongly prefer sucrose and the hummingbird flowers are all sucrose, but if butterflies don't really have a sugar preference, why would butterfly-pollinated flowers be constrained to sugar types within families and pollination syndromes? Why should long-corolla flowers have sucrose-rich nectar and short corolla flowers have hexose-rich nectar? One explanation could be that the long-corolla flowers being pollinated by butterflies are also pollinated by hummingbirds, necessitating the production of a sucrose-rich nectar. Another similar explanation has to do with bee sugar preference. Apparently long-tongued bees tend to be rewarded with sucrose rich nectar, while short-tongued bees rarely are rewarded with sucrose (Baker and Baker, 1983). It could well be that certain flowers contain either sucrose or hexose in order to reward bee pollinators, and butterflies have jumped on the existing pollination-syndrome wagon. However, this

hypothesis is not without problems: many of the long-tongued bee flowers come from a few set families characterized by sucrose-rich nectar while the short-tongued bee-flowers are from hexose-rich families like Asteraceae, so it is hard to say if the flowers are producing specific nectars to conform to bee preference, or the other way around. Finally, one might want to explore the costs of producing sucrose as opposed to hexose nectars, as this might give insight into which pollinators are dictating the composition of sugar nectars.

One major limitation of the study was that all of the butterflies had to be caught individually, which was time consuming and gave an uneven distribution of representatives from certain families (the Heliconiines are much more numerous than the Papilionids). The caught individuals were also much more energetic and resistant to being force fed, so I had to institute a waiting period before feeding in order to let them calm down and get hungry. The *Parides* and Pierid individuals in particular were difficult to feed since they could only be contained for two to four hours without food, which was not enough time for them to become hungry and less agitated.

A way to improve this study would be to acquire at least twenty individuals of each species as pupae, feed them one of the solutions after they hatched, contain them for a day or two, and then feed them the other solution. This would greatly increase the evenness of representation between species. Such experiments would be incredibly valuable, since to my knowledge, no other studies have been done looking at adult feeding preferences across butterfly families, relating dietary preference to phylogeny or ecology. Further studies could be undertaken to look at the biology of butterfly digestion that may also shed light on evolved dietary preferences.

ACKNOWLEDGEMENTS

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APPENDIX

APPENDIX 1. Phylogeny of Lepidoptera from Janz and Nylin (1998).
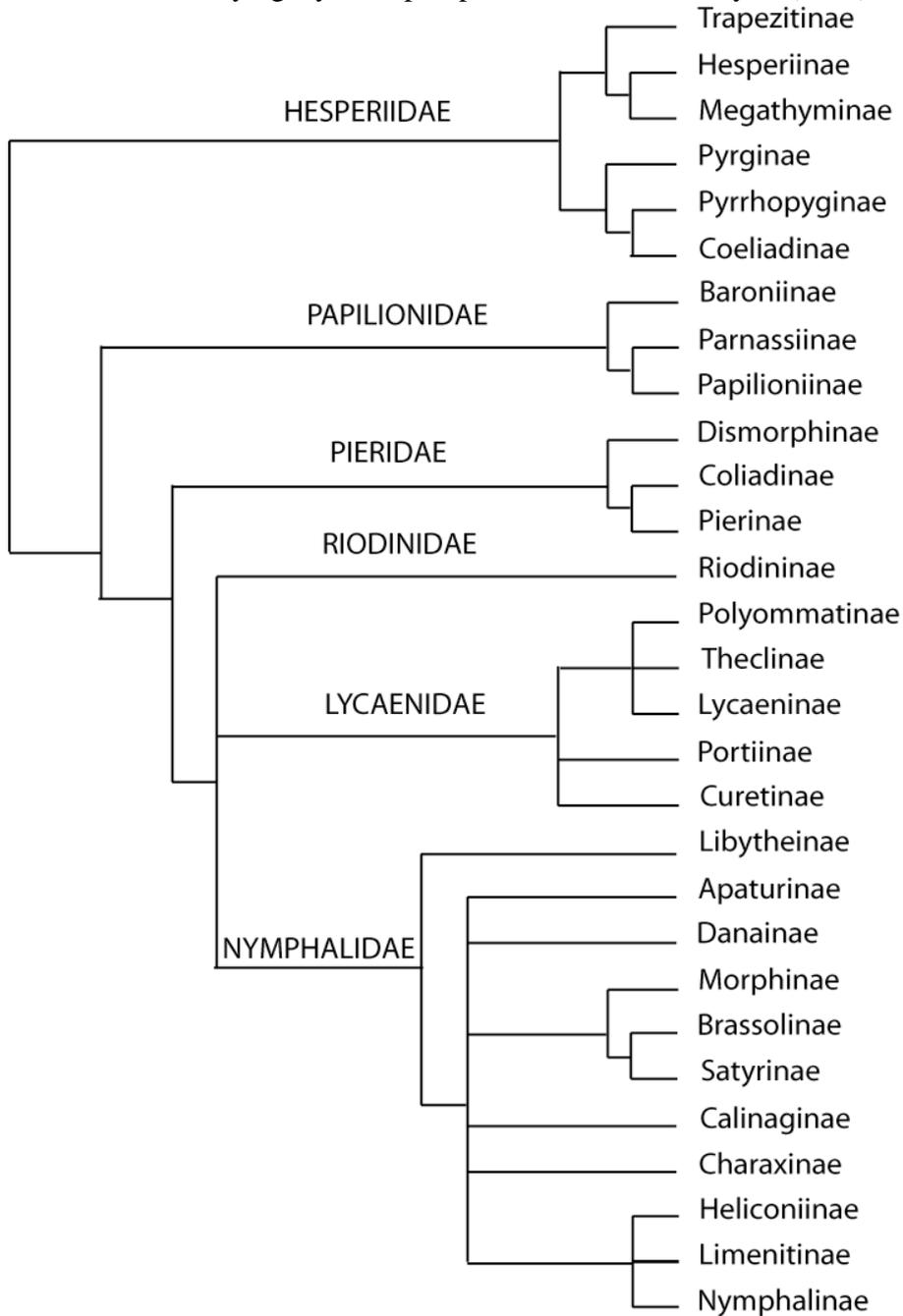
APPENDIX 2. Sign Test Results

Subfamily	Species	Sucrose mean volume (µL)	Hexose mean volume (µL)	Sign of S-H
Ithomiinae	*Greta oto*	30.68	26.79	+
	Ithomia heraldica	36.05	36.8	0
Morphinae	*Morpho granadensis*	58.29	62.54	—
	Morpho peleides	83.36	78.47	+
	Caligo eurilochus sulanus	33.4	400	—
	Caligo memnon memnon	346.3	344.2	0
Danainae	*Danaus plexippus*	89.7	76.6	+
Heliconiinae	*Dione moneta poeyii*	55.09	44.74	+
	Dryadula phasetusa	30.22	49.5	—
	Dryas iulia	40.79	58.3	—
	Eueides isabella	31.91	34.79	—
	Heliconius charitonius	29.12	31.93	—
	Heliconius hecale zuleika	70.13	65.88	+
	Heliconius sapho leuces	23.51	26.12	—
	Heliconius sara fulgidus	23.29	24.08	0
	Heliconius erato	35.79	26.45	+
Nymphalinae	*Catonephele numilia esite*	56.23	31.05	+
	Myscelia cyaniris cyaniris	30.26	36.4	—
	Siproeta steleres	103.55	59.6	+
Papilioninae	*Battus polydamas polydamas*	49.21	24.5	+
	Parides lycimenes lycimenes	77.43	59.15	+
	Papilio astylaus pallas	89.47	81.3	+
Pierinae	*Ascia limona*	43.19	59.2	—
	Appias drusilla	42.1	18.42	+
Coliadinae	*Phoebis sennae*	46.32	23.86	+
	Phoebis philea philea	59.5	55.5	+

Total positive: 14
Total negative: 9

Family Pieridae
Positive: 3
Negative: 1

Family Papilionidae
Positive: 3
Negative: 0

Family Nymphalidae
Positive: 8
Negative: 8

APPENDIX 3. Sucrose Feeding Data

SPECIES	Vol. Sucrose Eaten (µL)
Pteronymia fumida	40.26
Dryadula phaetusa	68.16
Morpho peliedes	55.26
Morpho peliedes	99.73
Heliconius charitonius	20
Greta oto	25.79
Ascia limona	43.16
Heliconius hecale zuleika	72.89
Heliconius sapho leuces	23.68
Eueides isabella	58.16
Heliconius charitonius	40.79
Greta oto	21.84
Heliconius sara fulgidus	26.84
Heliconius erato	50.53
Greta oto	34.47
Heliconius hecale zuleika	67.37
Heliconius sapho leuces	44.47
Heliconius charitonius	26.58
Heliconius sara fulgidus	19.74
Heliconius erato	21.05
Eueides isabella	24.74
Eueides isabella	13.42
Eueides isabella	31.32
Heliconius sapho leuces	10.26
Heliconius sapho leuces	15.63
Ithomia heraldica	36.05
Morpho peliedes	62.1
Greta oto	44.21
Morpho peliedes	100
Morpho peliedes	99.73
Morpho granadensis	99.73
Dryadula phaetusa	32.1
Morpho granadensis	74.47
Papilio astyalus pallas	89.47
Phoebis argante	0
Dione moneta poeyii	55.53
Parides lycimenes	68.95
Battus polydamas	99.74
Battus polydamas	66.05
Dione moneta poeyii	50.79
Morpho granadensis	43.95
Dryadula phaetusa	8.95
Dryadula phaetusa	21.05
Morpho granadensis	15
Dryadula phaetusa	42.63
Dryadula phaetusa	8.42
Appias drusilla	42.1

Greta oto	27.1
Dryas iulia	48.95
Parides lycimenes	29.47368421
Battus polydamas	74.73684211
Danaus plexippus	89.73684211
Parides lycimenes	27.89473684
Catonephele numilia esite	90.26315789
Caligo eurilochus sulanus	33.42105263
Dione moneta poeyii	58.94736842
Papilio polyxenes	36.31578947
Myscelia cyaniris cyaniris	41.31578947
Myscelia cyaniris cyaniris	32.10526316
Phoebis sennae	80.26315789
Catonephele numilia esite	41.05263158
Caligo memnon memnon	346.3157895
Dryas iulia	32.63157895
Myscelia cyaniris cyaniris	17.36842105
Phoebis sennae	12.36842105
Siproeta steleres	131.5789474
Catonephele numilia esite	37.36842105
Siproeta steleres	75.52631579
Battus polydamas	69.21052632
Phoebis philea philea	59.47368421

APPENDIX 4. Glucose-Fructose Feeding Data

SPECIES	Vol. Hexose Eaten (µL)
Heliconius charitonius	26.84
Eueides isabella	22.63
Heliconius charitonius	37.63
Eueides isabella	32.89
Heliconius erato	35.53
Heliconius hecale zuleika	60
Greta oto	17.1
Heliconius sapho leuces	16.84
Dryadula phaetusa	36.32
Greta oto	41.05
Greta oto	43.16
Heliconius hecale zuleika	44.74
Heliconius sapho leuces	33.68
Greta oto	20.53
Greta oto	12.1
Heliconius sara fulgidus	28.95
Heliconius sapho leuces	15.78947368
Papilio astyalus pallas	81.31578947
Morpho granadensis	73.94736842
Phoebis sennae	26.84210526
Parides lycimenes	40.52631579
Heliconius charitonius	31.31578947
Morpho granadensis	64.73684211

Dryas iulia	61.31578947
Dryas iulia	53.94736842
Heliconius sara fulgidus	19.21052632
Heliconius sapho leuces	38.15789474
Eueides isabella	44.73684211
Eueides isabella	43.68421053
Heliconius hecale zuleika	92.89473684
Heliconius erato	17.36842105
Morpho peleides	2.631578947
Morpho peleides	100
Morpho granadensis	48.94736842
Dryadula phaetusa	49.47368421
Eueides isabella	30
Morpho peleides	100
Morpho peleides	100
Morpho peleides	89.73684211
Anteos clorine	92.63157895
Battus polydamas	46.31578947
Battus polydamas	98.94736842
Appias drusilla	15.78947368
Appias drusilla	21.05263158
Dione moneta poeyii	33.15789474
Dione moneta poeyii	56.31578947
Ascia limona	59.21052632
Catonephele numilia esite	30.52631579
Parides lycimenes	24.47368421
Caligo eurilochus	400
Papilio thoas nealces	177.6315789
Battus polydamas	87.36842105
Myscelia cyaniris cyaniris	29.47368421
Myscelia cyaniris cyaniris	45.52631579
Catonephele numilia esite	20
Dryas iulia	59.73684211
Caligo memnon memnon	391.5789474
Phoebis sennae	25.26315789
Parides arcas mylotes	12.10526316
Myscelia cyaniris cyaniris	34.21052632
Phoebis sennae	19.47368421
Parides iphidamas iphidamas	68.42105263
Siproeta steleres	87.63157895
Danaus plexippus	76.57894737
Parides erithalion	11.31578947
Catonephele numilia esite	42.63157895
Caligo memnon memnon	296.8421053
Battus polydamas	3.947368421
Siproeta steleres	31.57894737
Phoebis philea philea	55.52631579
Ithomia heraldica	36.84210526