Sugar discrimination and gustatory thresholds in captive-born frugivorous Old World Bats

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Summary. – In general, preference for different sugars in nectarivores and frugivores is related to the composition of their food. We determined individual preferences in *Cynopterus brachyotis* and *Pteropus rodricensis,* and group preferences in one group of *P. rodricensis* and two mixed groups of *P. rodricensis, P. pumilus, P. vampyrus,* and *P. hypomelanus.* Most bats were born in captivity and received a diet with a composition of sugars of sucrose = glucose > fructose during 1 to 6 years before the experiment. We tested the hypothesis that diet composition influences food preferences, and predicted that bats would not discriminate between sucrose and glucose, and would prefer sucrose and glucose over fructose. Individuals and groups consistently favored sucrose over glucose and fructose, and fructose over glucose. We also determined gustatory thresholds for (0.15 % weight/weight) than fructose (> 0.5 %) and glucose (0.5 %). Food preferences, in general, did not match the composition of the diet. Gustatory thresholds may be a valid proximate reason to explain preference for sucrose over glucose and fructose, but not for preference for fructose over glucose.

Résumé. – La préférence pour différents sucres chez les nectarivores et frugivores dépend en général de la composition de leur nourriture. Nous avons déterminé les préférences individuelles chez *Cynopterus brachyotis* et *Pteropus rodricensis,* la préférence du groupe dans un groupe de *P. rodricensis,* et dans deux groupes mélangés *P. rodricensis, P. pumilus, P. vampyrus* et *P. hypomelanus.* La plupart des chauves-souris sont nées en captivitée et élevées avec un régime alimentaire composé de sucre (saccharose = glucose + fructose) pendant 1 à 6 années avant l'expérience. Nous avons testé l'hypothèse que la composition du régime alimentaire des chauves-souris peut influencer leurs préférences alimentaires, que les chauves-souris ne discriminent pas entre saccharose et glucose, et qu'elles préfèrent le saccharose et le glucose au fructose. Les individus comme les groupes ont préféré le saccharose au glucose et au fructose, ou le fructose au glucose. Nous avons déterminé aussi les seuils gustatifs pour des solutions de saccharose, de glucose et de fructose dans trois groupes de chauves-souris. Le saccharose a eu un seuil gustatif inférieur (0.15 % poids/poids) à celui de fructose (> 0.5 %) ou du glucose (0.5 %). Les préférences alimentaires en général ne concordent pas avec la composition du régime alimentaire. Le seuil gustatif peut expliquer la préférence pour le saccharose ou le glucose et le fructose, mais ne permet pas d'expliquer la préférence pour le fructose sur le glucose.

KEY WORDS : plant-animal interactions, frugivory, nectarivory, food preferences, taste thresholds, sugars.

Mammalia, t. 64, n° 2, 2000 : 135-143.

INTRODUCTION

Fruits and nectars consumed by different guilds of frugivores and nectarivores present consistent patterns in the composition of their sugars (Baker and Baker 1982 ; Baker *et al.* 1998). The existence of such patterns suggests that animals prefer the sugar that predominates in their foodstuff. Most studies have found a positive relationship between preferences of frugivores and nectarivores and the composition of their food (Stiles 1976 ; Martinez del Rio 1990 ; Erhardt 1991 ; Martinez del Rio *et al.* 1992). A few of them, however, did not detect clear patterns in preferences (Law 1994) or found that the animals had a preference for the sugar that was less common in their food (Herrera 1999a, b). It seems, then, that factors other than food composition as an ultimate cause might determine the sugar preferences of some animals.

Experimental tests of the relationship between preferences for different sugars and composition of food have been conducted with animals captured in the wild (Stiles 1976 ; Martinez del Rio 1990 ; Erhardt 1991 ; Martinez del Rio *et al.* 1992 ; Herrera 1999a). Results of studies with wild animals, in general, allow discussing the significance of their finding in the evolution of the biochemical composition of plant rewards. There is, however, a certain level of uncertainty about the composition of the food that the experimental subjects have actually eaten. Studies with captives animals offered a diet with known composition of sugards are, then, a valuable alternative to test the relationship between preferences and composition of the food, and to complement the findings of studies with wild animals.

Here, we assessed preferences for different sugars in individuals and groups of captive pteropodid frugivores to test the hypothesis that composition of sugars in the diet influences food preferences. Most bats induded in this study were captive-born and a few of them were caught in the wild. Bats had been in captivity from 1 to 6 years, and diet during this period had a sugar composition of 24 % fructose, 38 % glucose, and 38 % sucrose. We predicted, then, that bats in this study favor sucrose and glucose over fructose, but show ne preference when offered sucrose and glucose. Because the difference in the contribution to the diet between fructose and the other sugars is not particularly large, the experimental diet may be alternatively considered as homogeneous in sugar composition and predict no preference for a particular sugar. However, there is no empirical test of how different the percent contribution of different sugars needs to be in order to have a significant effect on the preferences of the animal.

Digestive traits of the animal have been partly successful at providing proximate explanations of preference patterns. For example, preferences in New World passerine birds are associated with different assimilation efficiencies of sugars (Martinez del Rio *et al.* 1992). In contrast, preferences by hummingbirds and phyllostomid bats do not seem to have apparent digestive basis (Martinez del Rio 1990 ; Herrera 1999a). A factor that has not been previously studied is the relative sweetness of the sugar and its relation with sugar preferences when there is no apparent digestive constraints. Old World frugivorous bats but their sugar receptors may be stimulated differently by each sugar.

We determined the gustatory thresholds for solutions of glucose, fructose, and sucrose in three groups of *Pteropus* in an attempt to find a proximate explanation of our results. Gustatory thresholds are considered as an index of taste sensitivity in animals. We hypothesized that preferred sugars would have lower gustatory thresholds and, consequently, higher relative sweetness.

MATERIAL AND METHODS

Experiments were conducted at the Lubee Foundation in Gainesville, Florida, USA, which maintains seven species of pteropodid bats in captivity for research, educational, and breeding purposes. Most of the bats included in this study were born in Lubee (56 bats born in Lubee, five born in other zoos, and four born in the wild). Details of the origin of the bats are given below.

Preferences of Sugar.

We offered the bats pairs of equicaloric solutions of sugars (20 % weight/weight) individually and/or in groups. Procedures are described separately for each species or group of bats. Weights of the bats are given as mean ± standard deviation.

Cynopterus brachyotis. – Eight individually caged adults (five males and three females, 36.1 + 3.6 g) were offered the following diet choices during eight consecutive nights : sucrose (S) *versus* glucose (G) (1 st 4 nights), and S *versus* fructose (F) (last 4 nights). Cages were 48.3 by 39.1 by 39.1 cm. Thirty ml of each solution were placed in 60-ml plastic feeders (originally designed for passerine birds) at 1900 h. The amount consumed was measured to the nearest ml with a 100-ml graduated cylinder, feeders were refilled and their position switched at 2300 h. Amount consumed was again measured at 0700 h. Feeders were adjacent to each other, ca. 5 cm apart. Two additional feeders were placed outside the cage to account for evaporation. The bats were also offered their standard diet (apple, pear, cantaloupe, grapes, greens, carrot, dry primate biscuit, vionate, and calcium carbonate) and water in separate containers from 1700 to 1900 h and from 2300 to 0700 h. All *C. brachyotis* were born in Lubee between 1991 and 1994.

Pteropus rodricensis. – Eight individually caged bats (8 males, 309 ± 46 g) were offered s *verus* F during four consecutive nights in one pair of 400 ml metal bowls. Cages were triangular, with the base 6 by 6 by 5.5 m and a height of 2.5 m. Procedures were the same as for *Cynopteris,* except that the volume offered of each solution was 150 ml and the separation between feeders was 15 cm. The standard diet (apple, pear, banana, cantaloupe, grapes, greens, carrots, dry primate biscuit, vitamin E, and calcium carbonate) and water were offered from 2300 to 0100 h. The S *versus* G comparison was not completed because the bats began to show signs of stress by the 5th day of experimentation and stopped consuming the sugar solutions. This comparison was not included in the analysis. All *P. rodricensis* were born in Lubee between 1992 and 1995.

Group 1. – Fifteen *P. rodricensis* (14 adult females and 1 male young, 242.5 ± 5.24 g for adults and 83.5 g for the young) were housed in an octagonal cage, ca. 9 m in diameter and 2 m high. The group was offered pairs of solutions of sugar (150 ml each) in two pairs of 400-ml metal bowls placed at opposite walls in the cage.

Separation between feeders was 15 cm. Three painwise comparisons were conducted during 12 consecutive nights in the following order : S *versus* F (4 nights), S *versus* G (4 nights), and F *versus* G (4 nights). The comparisons were processed in the same way as described for *Cynopterus,* except for F *versus* G. In the F *versus* G comparison, the solutions (300 ml each) were offered at 1700 h, measured to the nearest ml at 0700 h, and their positions were switched in the following trial. Intake was measured with a 100-ml graduated cylinder. The standard diet for *Pteropus* and water was offered from 1700 to 0700 h. Eleven bats were born in Lubee between 1994 and 1996, and the other four were born in the Jersey Preservation Trust.

Group 2. – Seven female *P. rodricensis* (305.5 ± 46.5 g), nine female *P. pumilus,* (191.5 ± 14.8 g) and two female *P. vampyrus* (972.5 ± 10.6 g) were housed in an octagonal cage and offered two pairs of 400-ml metal bowls with three painwise comparisons during 10 consecutive nights. The order of the comparisons was the following : S *versus* G (2 nights), S *versus* F (4 nights) and F *versus* G (4 nights). Solutions (300 ml each) were offered at 1700 h measured to the nearest ml at 0700 h, and their position swithched in the following trial. The standard diet for *Pteropus* was offered from 1700 to 0700 h. All the *P. rodricensis* and *P. vampyrus* were born in Lubee between 1991 and 1994 ; eight *P. pumilus* were born in Lubee between 1993 and 1995 and one *P. pumilus* was caught in the Philippines and brought to Lubee in 1992. All individuals in this group were adults.

Group 3. – Nine male *P. rodricensis* (305.5 ± 46.5 g) and seven male *P. hypomelanus* (601.8 ± 40.2 g) were housed in an octagonal cage and offered three painwise comparisons during 12 consecutive nights in the following order: S *versus* G (4 nights), S *versus* F (4 nights), and F *versus* G (4 nights). The rest of the experimental protocol was identical to group two. Eight *P. rodricensis* were born in Lubee between 1991 and 1994, and one in the Blackriver/London Zoo (in Lubee since 1990) ; three *P. hypomelanus* were caught in Indonesia and brought to Lubee in 1990, the other four *P. hypomelanus* were born in Lubee between 1992 and 1995. All individuals in this group were adults.

Gustatory Thresholds for Sugars

We determined taste thresholds for sucrose, glucose, and fructose in groups 1, 2 and 3 after the preference experiments were completed. We considered taste thresholds as the lowest concentration at which each solution was preferred over water. One hundred and twenty ml of water and each solution of sugar were presented at 1800 h in two separate 400-ml metal bowls, and the volume consumed from each feeder was measured to the nearest ml with a 100-ml graduated cylinder at 0800 h.

This procedure was repeated during 5-7 consecutive nights, and the position of the feeders was switched before each trial. We first conducted painwise comparisons of water *versus* 0.5 % G, F, or S with each one of the groups. We then compared water *versus* lower concentrations of one of the three sugars in a randomly assigned group of bats. This second series of comparisons was ended at the concentration at which the bats did not show a preference for the sugar over water. Accordingly, water *versus* 0.25 % G was compared in group 1, water *versus* 0.25 and 0.15 % S in group 2, and water *versus* 0.25 F in group 3. Bats were allowed to eat their standard diet during experiments.

Statistical Analysis

Preference for sucrose in the S *versus* F, and S *versus* G comparisons, and for fructose in the F *versus* G comparison was calculated as : preference for solution A = volume of A consumed (ml)/total volume of and B consumed (ml). We tested the hypothesis that the observed value was not significantly different from 0.5 (the value of the ratio at which there is no preference) using one-sample t-tests (Sokal and Rohlf 1995). Data was arcsine-transformed for analysis. We used the mean of the mean preference values and its standard deviation for each bat when preferences were tested individually. For the group preferences, we used the preference values for each pair of feeders to calculate the mean preference value and its standard deviation. Because several simultaneous tests *(k)* were conducted, the significance level was adjusted using the sequential Bonferroni method (Rice 1989). This method is not as conservative as the standard Bonferroni method but does not increase the probability of a type-I error. After selecting a significance level ([224] = 0.05), *P.* values associated with each t-test ranked from smallest (P_1) to largest (P_k). The corresponding t-test was considered significant only if $P_1 \leq$ [224]/(k) and significance of the remaining tests was evaluated in this fashion until the inequality $P_i \leq$ [224]/($1 + k - i$) was not met. We collectively analyzed all comparisons conducted in this part of the study ($k = 12$). The same procedure was followed to test for preference for each sugar over water except that we adjusted [224] separately for number of tests involving each sugar (glucose = 4 ; fructose = 4 ; sucrose = 5).

RESULTS

Sugar Preference

There were consistent preferences for sucrose over fructose and glucose, and for fructose over glucose in all species and groups of bats tested. *C. brachyotis* preferred sucrose over glucose and fructose (Table 1) and individual *Pteropus rodricensis* preferred sucrose over fructose (Table 1). The three groups of *Pteropus* preferred sucrose over glucose and fructose, and fructose over glucose (Table 1).

TABLE 1. – Preference ratio[a] (mean ± SD) for sugars by individuals of *Cynopterus brachyotis* and *Pteropus rodricensis,* and by three groups of *Pteropus.*

Species or Group	Sucrose vs. Glucose	Sucrose vs. Fructose	Fructose vs. Glucose
C. brachyotis	0.92 ± 0.02 t = 32.8, P < 0.001 d.f. = 7, α = 0.005	0.84 ± 0.14 t = 5.16, P = 0.006 d.f. =5, α = 0.006	
P. rodricensis		0.74 ± 0.11 t = 5.6, P < 0.001 d.f. = 7, α = 0.008	
Group 1 (*P. rodricensis*)	0.87 ± 0.13 t = 8.63, P < 0.001 d.f. = 15, α = 0.004	0.82 ± 0.12 t = 5.35, P < 0.001 d.f. = 15, α = 0.0045	0.92 ± 0.15 t = 6.49, P < 0.001 d.f. = 7, α = 0.007
Group 2 (*P. rodricensis, P. pumilus* and *P. vampyrus*)	0.90 ± 0.05 t = 11.3, P = 0.003 d.f. = 3, α = 0.01	0.82 ± 0.16 t = 4.77, P = 0.004 d.f. = 7, α = 0.012	0.83 ± 0.10 t = 7.67, P < 0.001 d.f. = 7, α = 0.0055
Group 3 (*P. rodricencis* and *P. hypomelanus*)	0.88 ± 0.10 t = 6.67, P < 0.001 d.f. = 7, α = 0.006	0.79 ± 0.24 t = 3.06, P = 0.023 d.f. = 6, α = 0.025	0.77 ± 0.27 t = 2.80, P = 0.029 d.f. = 7, α = 0.006

[a] Preference ratios > 0,5 indicate preference for sucrose in the sucrose vs glucose, and fructose comparisons, and for fructose in the fructose vs glucose comparison. Significance levels (α) were adjusted for each one-sample t-test using the sequential Bonferroni technique (Rice 1989).

Gustatory Thresholds for Sugars

All groups of *Pteropus* preferred 0.5 % sucrose over water, but only groups 2 and 3 discriminated 0.5 % glucose from water and no group discriminated 0.5 % fructose from water (Table 2). Only sucrose was preferred over water when lower concentration were used ; the lowest concentration at which sucrose was preferred was 0.15 % (Table 2).

TABLE 2. – Preference ratio[a] for sugars over water by three groups of *Pteropus*.

		Sugar Concentración		
		0.5%	0.25%	0.15%
Sucrose	Group 1	0.73 ± 0.10 t = 4.4, P = 0.008 d.f. = 5, α = 0.016	0.83 ± 0.15 t = 3.65, P = 0.02 d.f. = 4, α = 0.05	0.58 ± 0.05 t = 4.67, P = 0.006 d.f. = 6, α = 0.012
	Group 2	0.81 ± 0.08 t = 7.5, P < 0.001 d.f. = 5, α = 0.01		
	Group 3	0.87 ± 0.11 t = 4.8, P = 0.009 d.f. = 4, α = 0.025		
Glucose	Group 1	0.75 ± 0.12 t = 4.95, P = 0.005 d.f. = 6, α = 0.012		
	Group 2	0.56 ± 0.09 t = 1.72, P > 0.10 d.f. = 6, α = 0.025	0.43 ± 0.19 t = 0.86, P > 0.40 d.f. = 5, α = 0.05	
	Group 3	0.82 ± 0.16 t = 3.5, P = 0.016 d.f. = 5, α = 0.016		
Fructose	Group 1	0.52 ± 0.12 t = 0.37, P > 0.50 d.f. = 5, α = 0.05		
	Group 2	0.66 ± 0.13 t = 3.97, P = 0.023 d.f. = 6, α = 0.01		
	Group 3	0.57 ± 0.23 t = 0.97, P > 0. 30 d.f. = 6, α = 0.016	0.39 ± 0.25 t = 1.03, P > 0.30 d.f. = 4, α = 0.025	

[a] Preference ratios > 0,5 indicate preference for sucrose in the sucrose vs glucose, and fructose comparisons, and for fructose in the fructose vs glucose comparison. Significance levels (α) were adjusted for each one-sample t-test using the sequential Bonferroni technique (Rice 1989).

DISCUSSION

Preferences for sugars

If diet influences food choices, then preferences for different sugars will follow patterns that reflect the composition of sugars in the food. Accordingly, we predicted that bats in this study would favor sucrose and glucose over fructose, and show no discrimination between sucrose and glucose. Our findings, however, were only partly concordant with our predictions. Individuals and groups of all species of bats tested preferred sucrose over fructose and over glucose, and fructose over glucose.

Preferences for sugars in captive animals may reflect genetically determined trends or are a learned behavior. If preferences were genetically determined, then animals would have a fixed preference for sugars that predominate in the food with which the species has interacted in an evolutionary time. If preferences were a behavior learned during the lifetime of the animal, it would favor the sugar that predominates in its diet since it was born.

Nectars consumed by pteropodids in the wild are in average 33 % fructose, 26 % glucose, and 41 % sucrose, whereas fruits are 42 % fructose, 36 % glucose, and 22 % sucrose (Baker *et al.* 1998). The predicted preference patterns are, then, sucrose > fructose > glucose for nectar-eaters, and fructose > glucose > sucrose fort fruit-eaters. Both *C. brachyiotis* and *Pteropus* spp. have a mixed diet of fruits and nectars in the wild, but fruits seem to be the predominant food item (Marshall 1983 ; Tan *et al.* 1998). For example, fruits from several species of *Ficus,* a hexose-rich genus, are considered as key components in the diet of *C. brachyotis* (Tan *et al.* 1998). The natural diet of the species of bats in this study may be predominantly rich in hexoses. Consequently, they should present the predicted pattern for frugivores if their preferences reflect the evolutionary effect of their interaction with their food sources.

The preferences of individual *C. brachyotis* and *P. rodricensis,* and the mixed groups of *Pteropus,* in general, did not match the patterns of the artificial diet, or of their hypothetical natural diet. This conclusion may be re-evaluated if more information on the composition of sugars of the natural food consumed by these species shows that sucrose is the predominant sugar (for example, if sucrose-rich nectars of fruits represent the bulk of their diet).

Gustatory thresholds

Previous studies with other nectarivores and frugivores have tried to find the proximate reasons that explain preferences for a particular sugar. Physiology of the digestive system has been partly successful as an explanation of the preference patterns of birds (Martinez del Rio *et al.* 1992). There are, however, some groups for which digestive physiology is not enough to understand preference patterns (Martinez del Rio 1990 ; Herrera 1999a). In this study, digestion physiology of different sugars by pteropodids was not determined but it is likely that they digest the three sugars equally well, as is the case in phyllostomid bats (Herrera, 1999a).

We tried to find proximate reasons of the food preferences of pteropodids in the sensitivity with which their sugar receptors detect sucrose compared to fructose and glucose. Bats in this study had lower gustatory thresholds (0.15 %) than fructose (> 0.5 %) and glucose (0.5 %). Other mammals detect sucrose at significantly lower concentration than glucose and at slightly lower concentrations than fructose (Cameron 1947 ; Jakinovich 1985 ; Ramirez 1990 ; Laska *et al.* 1996). A similar pattern is also found in insects (Omand and Dether 1969 ; Hansen 1978). Lower gustatory thresholds, then, may be the proximate reason of preference for sucrose over glucose and fructose in pteropodid bats.

On the other hand, fructose was consistently preferred over glucose, but the groups of bats studied had lower gustatory thresholds for glucose than for fructose. In contrast, other vertebrates have lower gustatory thresholds for fructose than for glucose (Jakinovich 1985 ; Kemnitz and Neu 1986 ; Jakinovich and Sugarman 1988 ; Laska *et al.* 1996). Fructose preference over glucose in pteropodid bats resemble the results of previous studies with honey possums (Landwehr *et al.* 1990) and butterflies (Ehrardt 1991). However, it cannot be explained by the ability to detect the sugar by the sugar receptors of the animal.

CONCLUSIONS

Sugar preferences by captive pteropodids do not seem to be the result of a learned process. Preferences did not match the composition of their hypothetical natural diet and do not seem to be the result of an evolutionary interaction with their food sources. Lower gustatory thresholds may be the proximal reason that explains preference for sucrose over glucose and fructose. This argument, however, cannot be used to explain preference for fructose over glucose. This study provides a first attempt to assess individual and group food preferences in captive-born pteropodid bats. Determination of preferences of wild pteropodids and more information about the composition of their food are necessary to understand the ultimate reasons of their food preferences. Once we have these elements, we will be in a better position to evaluate the ecological and evolutionary significance of the composition of fruits and nectars consumed by pteropodids and other groups of animals.

ACKNOWLEDGMENTS

We thank T.H. Fleming, E. Dierenfield, J. Reitor, and J. Seyjagat for assistance in preparation of this manuscript and the Lubee Foundation, for financial and logistic support. We also thank M. Chag, A. Millwood, C. Cooke, and B. Pope for kindly helping conduct part of the experiments. G. Méndez helped with the French translations. This is publication number 46 of the Lubee Foundation.

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