Sugar Preferences and Xylose Metabolism of a Mammal Pollinator, the Namaqua Rock Mouse (*Aethomys namaquensis*)

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ABSTRACT

The sugar preferences of 10 Namaqua rock mice, *Aethomys namaquensis*, were assessed using pairwise combinations of 30% (w/w) solutions of sucrose, glucose, fructose, xylose, and a mixture of equal parts of glucose and fructose. The tests were designed to control for side biases that were apparent in preliminary experiments. The mice preferred sucrose to fructose and glucose. Xylose, although the least preferred sugar, was willingly consumed by the rodents (up to 5.8 mL in 24 h). This contrasts with the strong rejection of xylose by nectarivorous birds on which similar preference tests were performed. The efficiency of xylose absorption and metabolism by *A. namaquensis* was investigated by measuring dietary intake, blood xylose levels, and urinary and fecal xylose output. Again in contrast to the birds, the apparent absorption efficiency of xylose was found to be very high at 97%, but exactly how the xylose is metabolized requires further study. Xylose is thought to be only slowly metabolized by mammals, and it is possible that intestinal bacteria may serve this purpose, like the ruminal bacteria that break down xylans in plant tissue.

Introduction

Many species of the Proteaceae are pollinated by nonflying mammals. In Australia these mammals are predominantly small arboreal marsupials, while in South Africa the mammal pollinators of *Protea* are rodents (Rourke and Wiens 1977; Wiens et al. 1983; Carthew and Goldingay 1997). Although some evidence indicates that pollen is an important food item (van Tets 1997; van Tets and Whelan 1997), the major attractant for these mammals is undoubtedly nectar.

The principal sugars in floral nectar are sucrose and its component hexoses, glucose and fructose. Recently, however, the pentose sugar xylose was reported as being a common and important constituent of the nectar of *Protea* and *Faurea* in the family Proteaceae, occurring in concentrations of up to 39% of total sugar (van Wyk and Nicolson 1995). A more comprehensive survey, including 147 species from seven South African and nine Australian genera of Proteaceae, has shown that xylose is restricted to nectar of the related genera *Protea* and *Faurea* (Nicolson and van Wyk 1998). Within the genus *Protea*, the large and showy bird-pollinated flowers produce hexose nectars containing little xylose, while the cryptic flowers pollinated by small mammals have more balanced nectars, with sucrose up to 79% and xylose up to 28% of total sugar (Nicolson and van Wyk 1998).

Sugar preferences and sugar absorption efficiencies have been investigated in the three major families of nectarivorous birds in southern Africa: the lesser double-collared sunbird *Nectarinia chalybea*, the Cape sugarbird *Promerops cafer*, and the Cape white-eye *Zosterops pallida* (Lotz and Nicolson 1996; Franke et al. 1998; Jackson et al. 1998*a*, 1998*b*). All three species show similar preferences for sucrose, glucose, and fructose, which they digest with great efficiency, but show a strong aversion to xylose, which they assimilate poorly and apparently do not utilize. Honeybees are potentially important pollinators of both *Protea* and *Faurea* but show a similar aversion to xylose when provided with a range of glucose/xylose mixtures, and their survival time decreases as the proportion of xylose increases (Allsopp et al. 1998). The occurrence of xylose in *Protea* and *Faurea* nectar does not seem to be related to pollination by birds or bees.

The Namaqua rock mouse, *Aethomys namaquensis*, readily forages from flowering heads of *Protea amplexicaulis* and *Protea humiflora* and is thought to be an important pollinator of these species (Wiens et al. 1983; van Tets 1997). In this study we have investigated whether the sugar preferences of this rodent and its ability to digest xylose differ from those found in our previous studies of the birds feeding on *Protea* nectar. The only previous study of the sugar preferences of nonflying mammal pollinators is that of Landwehr et al. (1990) on the western pygmy possum, *Cercatetus concinnus*, and the honey possum, *Tarsipes rostratus*, in Australia. Xylose is absent from the nectars available to these marsupials.

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Material and Methods

Namaqua rock mice (*Aethomys namaquensis*) were caught in live traps on the foothills of Jonaskop on the western edge of the Riviersonderendberge (33°56′S 19°31′E). *Protea humiflora* is common at this site, and *Protea amplexicaulis* can be found nearby. The mice (mean body mass 59 g, SE 2.2) were kept in standard rodent cages in a room in which the temperature ranged from 17° to 22°C. Except during feeding trials, the mice were fed on water and rat chow.

Preference Tests

Sugar solutions were presented to the animals in 25-mL glass pipettes, modified at the bottom end to form a spout from which the mice could drink. We used 30% (w/w) solutions because mammal-pollinated species of *Protea* produce more concentrated nectars than the bird-pollinated species (Wiens et al. 1983).

In previous sugar preference tests on birds, individuals often exhibited a positional bias, sometimes so strong that it overrode taste preferences (Hainsworth and Wolf 1976; Franke et al. 1998; Jackson et al. 1998*a*). Thus, it was important to check for possible positional biases in the mice. When the animals were accustomed to drinking from the feeders, five of them were given water and another five 30% sucrose in two test feeders placed 2 cm apart. The volumes consumed were recorded every 24 h for 1 wk. From these trials, it was evident that some of the mice had strong side preferences; the extreme case being one individual that consumed a mean of 0.2 and 10 mL of sucrose solution from the left and right feeders, respectively.

The 20-d feeding trial was designed to control for these side preferences and followed the protocol of Jackson et al. (1998*a*). The five test solutions were 30% sucrose, glucose, fructose, xylose, and a mixture of equal parts of fructose and glucose (15% fructose and 15% glucose). Ten animals were offered a choice of two solutions over a period of 48 h. Food pellets (rat chow) were included in the diet, but water bottles were removed. During the 48-h period, we controlled for possible positional biases by switching the positions of the two test solutions (left vs. right) after 24 h. A sugar type preference was indicated if the individual changed feeders to "follow" the sugar. Every possible pairwise combination of the five test solutions was presented to all 10 animals, and the order of presentation of combinations was randomized. Volumes consumed were recorded every 24 h. Sugar preferences were calculated as ([volume of left-hand sugar consumed/total volume consumed] × 100). The term "left-hand sugar" refers to the solution in the feeder on the left-hand side in the cage. Values near 50, therefore, indicate no preference, values close to 100 a strong preference, and those close to 0 an aversion.

The significance of the preferences of *A. namaquensis* within each pair of sugar solutions was tested using the Wilcoxon paired-sample test (Zar 1996). The mean volume of each sugar solution consumed by the mice over the course of the trials was also compared using a single-factor ANOVA. Tukey's HSD test (Zar 1996) was used to identify differences between means.

Xylose Absorption and Metabolism

To ascertain how efficiently the mice absorb and digest xylose, the animals were moved to metabolism cages to facilitate the separation and collection of urine and feces. The metabolism cages were made from inverted 2-L glass bottles (Howell 1974). A glass bulb was suspended below the cage so that feces would be deflected into a beaker, while urine was collected separately in a vial containing 4 mL of liquid paraffin to prevent evaporation. Test feeders containing sugar solutions were inserted into the metabolism cages through a wire mesh cover. Rat chow was offered in commercial pet feeders.

After an acclimatization period of 2 d, a 2-d experimental trial was started. Control animals ($n = 3$) were given water and food pellets, and the experimental animals ($n = 8$) were given the 30% xylose solution and food pellets. Urine was collected separately for two 24-h periods, and at both collections the volume of xylose solution consumed was recorded. After the first 24 h, the mice were anesthetized by intraperitoneal injection of xylazine. The anesthetic consisted of 100-mg/μL ketamine in 20-mg/μL xylazine, and the dosage administered was 1.45 μL g/body mass. Blood samples were taken by cardiac puncture after sterilization of the skin with 70% ethanol; 0.1 mL of blood was drawn from each mouse using a syringe fitted with a heparinized needle. Urine and blood samples were centrifuged at 11,000 rpm for 2 min to remove contaminants from the urine and separate the plasma. The xylose content of the urine and plasma was then measured using a colorimetric assay. The assay involves incubation of 10-μL aliquots of fluid with 1 mL of color reagent, containing 1-g phloroglucinol in 200-mL glacial acetic acid and 20-mL concentrated HCl, for 4 min at 100°C, followed by reading of the absorbance at 554 nm on a spectrophotometer (Jackson et al. 1998*b*).

In a subsequent experiment, eight mice were fed only the xylose solution and no food pellets, while two control animals were given water but no food. Fecal pellets were collected twice over 48 h, dried overnight in an oven at 60°C, and then ground with a pestle and mortar. Dried ground material was soaked in 80% ethanol for 1 h (1-g dried material to 100-mL ethanol) and filtered through filter paper (Whatmans no. 1). The filtrate was then analyzed for xylose content, as earlier.

Table 1: Sugar preferences of 10 *Aethomys namaquensis*

Animal	SG*	SF*	SM	SX*	GF	GM*	GX*	FM	FX*	MX
1:										
Day 1	100	13	15	99	2	98	0	98	99	3
Day 2	99	11	5	99	1	99	2	99	100	0
2:										
Day 1	81	100	2	98	97	13	84	0	89	100
Day 2	83	98	31	100	83	3	71	1	84	100
3:										
Day 1	83	21	69	100	5	0	96	21	90	100
Day 2	89	13	98	94	4	1	100	58	99	100
4:										
Day 1	98	4	99	95	3	99	98	97	99	6
Day 2	3	99	1	4	97	2	78	1	4	98
5:										
Day 1	100	99	0	99	2	5	100	100	96	8
Day 2	92	81	0	98	3	1	97	93	95	9
6:										
Day 1	99	95	30	98	2	10	90	14	99	58
Day 2	100	94	85	100	2	15	98	30	100	93
7:										
Day 1	58	99	99	98	81	7	95	0	88	100
Day 2	70	54	65	98	4	30	97	60	96	98
8:										
Day 1	91	96	95	95	99	0	82	5	89	91
Day 2	99	100	99	97	54	6	98	20	97	97
9:										
Day 1	76	60	3	93	15	13	90	0	89	95
Day 2	96	100	99	97	98	59	72	97	95	98
10:										
Day 1	27	96	82	80	75	12	71	31	97	94
Day 2	39	99	55	92	75	0	98	6	96	87

Note. Preference values ([volume of left-hand sugar consumed/total volume consumed] × 100) for 30% sugar solutions offered in pairs to *Aethomys namaquensis*. The column headings list the sugar combinations offered, with the left sugar first (S = sucrose, G = glucose, F = fructose, M = hexose mixture, and X = xylose). On day 2, the test solutions were switched. Asterisks denote significant preferences (Wilcoxon paired-sample test, $P < 0.05$).

Results

Sugar Preference Tests

Preference values for the different sugars are reported in Table 1 as the preference values for the first (left) sugar of the combination in question. Left and right sugars were switched on the second day to control for positional biases. A significant difference between consecutive days suggests that the animal changed feeders in response to the change in the sugar type, thus exhibiting a preference for one sugar over the other.

The mice showed significant preferences for sucrose over fructose, glucose, and xylose, for the hexose mixture over glucose, and for glucose and fructose over xylose (Table 1). These sugar preferences are very like those of the sunbird *Nectarinia chalybea* (Jackson et al. 1998*a*). The most notable change was the lack of a significant difference between the hexose mixture and xylose, as a result of two mice that preferred xylose (animals 1 and 5 in Table 1) and one mouse that did not show a preference for either solution (animal 4 in Table 1). The exceptionally strong side bias of the latter individual is evident in the very different preference values for consecutive days (even when sucrose was being compared with xylose). The maximum volume of 30% xylose consumed by individual mice throughout the 20-d trial ranged from 0.6 to 5.8 mL. The total volume drunk by the mice was usually lower when xylose was one of the test solutions.

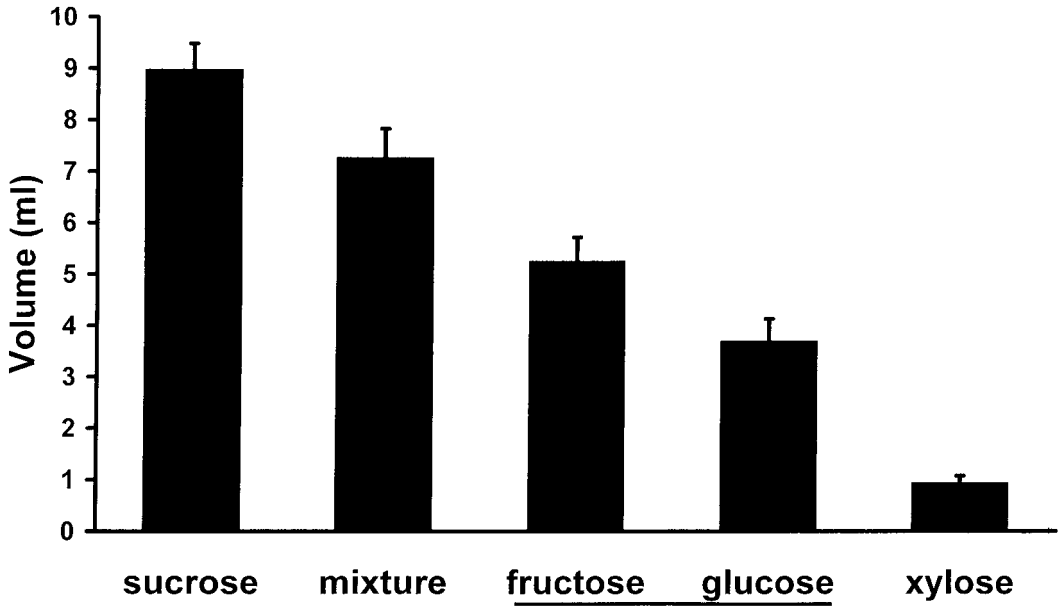

Figure 1. Mean volume of each sugar solution consumed by *Aethomys namaquensis* ($n = 10$) during the preference tests. The error bars indicate SEs. Means that were not significantly different are indicated by underlining (fructose and glucose; Tukey's HSD test, $P > 0.05$).

These sugar preferences are further supported by the mean volumes of each sugar type consumed by the mice during the preference tests (Fig. 1). The mean volume of sucrose consumed was significantly greater than that of the hexose mixture (Tukey's HSD test, $P < 0.05$). It, in turn, was greater than that of fructose. There was no significant difference between glucose and fructose, and the mean volume of xylose consumed was lower than that for each of the other sugars.

Xylose Absorption and Metabolism

To determine the apparent absorption efficiency of xylose, the quantities of xylose consumed, excreted, and present in the blood were measured (see Table 2). In both 24-h periods, the amounts of xylose consumed are much greater than the amounts that appear in the urine and the blood. The apparent absorption efficiency of xylose can be calculated as ([mg xylose in food] − [mg xylose in urine])/(mg xylose in food) × 100, giving values of 96.8% and 97.1% for days 1 and 2, respectively. Although the three control animals were not given xylose solutions, after 24 h xylose was found to be present in their urine and blood at 0.67 ± 0.32 mg/mL and 0.16 ± 0.03 mg/mL, respectively.

In the subsequent experiment that checked for xylose in the feces, results from the analysis revealed negligible amounts of xylose: day 1, 0.43 ± 0.16 mg ($n = 8$); day 2, 0.29 ± 0.08 mg ($n = 4$). (The fecal samples of the other four mice were too small for analysis on the second day.) Again the controls, although not given xylose solutions, were found to have some xylose in their feces (0.01 ± 0.004 mg, $n = 2$).

Discussion

The sugar preferences of the Namaqua rock mouse are consistent with the mixed sugar composition of the nectar in the flowers it pollinates, *Protea amplexicaulis* and *Protea humiflora* (Nicolson and van Wyk 1998). Sucrose is the most abundant sugar in the nectar as well as the most preferred. The order of preference sucrose → fructose → glucose → xylose corresponds to the relative amounts of the four sugars in the nectar of *P. amplexicaulis* and *P. humiflora*. It is interesting that multiple sampling of the nectars of these two species showed consistently more fructose than glucose, although equal amounts would be expected from the hydrolysis of sucrose in the nectary (Nicolson and van Wyk 1998). Our results for *Aethomys namaquensis* support the proposal of Baker and Baker (1983) that the proportion of sugars in the nectar is reflected in the sugar preferences of the plant's pollinator.

The only previous study of the sugar preferences of nonflying mammal pollinators is that of Landwehr et al. (1990) in Australia. These authors found no significant preferences in the western pygmy possum, *Cercatetus concinnus*, but the honey possum, *Tarsipes rostratus*, which feeds only on nectar and pollen, preferred sucrose and fructose to glucose. Distinct pref-

Table 2: Data used to calculate xylose absorption efficiency in *Aethomys namaquensis*

	Day 1	Day 2
Food:		
Volume consumed (mL)	3.3 ± .3	2.9 ± .6
Xylose concentration (mg/mL)	300	300
Xylose consumed (mg)	979 ± 82	855 ± 189
Urine:		
Volume (mL)	2.0 ± .3	1.6 ± .5
Xylose concentration (mg/mL)	15 ± 2.3	12.6 ± 3.1
Xylose excreted (mg)	31 ± 7.2	25 ± 10.5
Feces:		
Mass (mg)	97.3 ± 2.2	70.3 ± 1.4
Xylose excreted (mg)	.43 ± .16	.29 ± .08
Blood:		
Xylose concentration (mg/mL)	.2 ± .04	...

Note. Xylose concentrations of urine were measured at 24 and 48 h and xylose concentrations of blood at 24 h. All values are mean ± SE; $n = 8$ (except for values for feces on day 2: $n = 4$).

erences for sugar types were not apparent in another mammal pollinator, the Queensland blossom bat, *Syconycteris australis* (Law 1993). However, both of these were preliminary studies in which the animals were tested in groups, and the protocol of our sugar preference tests was much more rigorous.

The most exciting result of the preference tests was the willingness of the mice to drink pure xylose solutions. The Namaqua rock mouse did not show as great an aversion to xylose as the nectarivorous birds studied previously in this laboratory (Lotz and Nicolson 1996; Franke et al. 1998; Jackson et al. 1998*a*, 1998*b*). Both sunbirds and sugarbirds showed a strong aversion to xylose and would not consume it in pure form, only in mixtures with the other nectar sugars. The rodents in this study willingly consumed pure xylose, although in lower quantities than the other sugars (Fig. 1). It should be pointed out that the response of the mice to xylose may be different when it is mixed with other sugars as in nectar. Valenstein et al. (1967) reported interactions between sweet tastes in laboratory rats that consumed far greater amounts of a glucose-saccharin mixture than of either substance alone.

Xylose appears to have been utilized very efficiently by *A. namaquensis*. The apparent absorption efficiency of sucrose, glucose, and fructose for nectarivorous birds was close to 100% (Lotz and Nicolson 1996; Franke et al. 1998; Jackson et al. 1998*b*), but for xylose it was markedly lower. The most accurate measures of sugar absorption efficiency in nectar-feeding animals are those obtained by measuring the volumes of ingested and excreted fluids and the concentrations of individual sugars in the excreted fluid, rather than using refractometry (Jackson et al. 1998*b*). Using this method, values of 53% and 61% were obtained for the apparent absorption efficiency of xylose in sugarbirds and white-eyes (Franke et al. 1998; Jackson et al. 1998*b*). This contrasts with the 97% efficiency for Namaqua rock mice.

The pentose sugar xylose is absorbed across the gut wall of hamsters and rats (Alvarado 1965; Salem et al. 1965). However, xylose is not rapidly metabolized in mammalian tissues, and in humans this is the basis of the xylose absorption test for intestinal disease (Zilva and Pannall 1984). In this study, the low xylose content of the blood, urine, and feces of Namaqua rock mice fed 30% (w/w) xylose solutions suggests that the xylose was being metabolized. In contrast, Cape sugarbirds fed a xylose/glucose mixture had blood xylose concentrations of 12.5 mM (1.9 mg/mL), almost 10 times the value in *A. namaquensis* consuming xylose solutions.

Ruminants are the only mammals that have been shown to use xylose efficiently. The utilization of xylose by their ruminal bacteria has been extensively studied (e.g., Turner and Robertson 1979; Hespell et al. 1987; Matte et al. 1992; Marounek and Kopecny 1994), and it appears that the metabolism of xylose by ruminal bacteria occurs more rapidly and efficiently than the metabolism of xylose by vertebrates. Xylans are xylose polymers that are major components of the hemicellulose found in plant cell walls. When the ruminant consumes plant material, ruminal bacteria degrade the xylan to xylose and then metabolize the xylose. The pathways for xylan degradation (outside the microbial cell) and xylose utilization (inside the cell) by ruminal bacteria are discussed in detail by Matte et al. (1992).

When we investigated xylose absorption and metabolism, the

control animals were given water instead of xylose solutions, but small amounts of xylose were detected in their blood, urine, and feces. This xylose can only be a result of hydrolysis of xylans in the rat chow, which consists primarily of plant material. This strongly supports a pathway of xylose metabolism in the Namaqua rock mouse that involves intestinal bacteria. The most likely site for such bacteria would be the cecum, where the breakdown of the cellulose in the animals' natural diet would be accompanied by the release of xylan.

However, one cannot discard the possibility that the Namaqua rock mouse is able to metabolize xylose without the help of bacteria. As xylose readily crosses the gut wall in other rodents, it would be surprising if this were not the case in *A. namaquensis*. The very low levels of xylose in the blood and the urine suggest that any absorbed xylose was, for the most part, metabolized. Unfortunately, our measurement of the apparent absorption efficiency of xylose does not differentiate between xylose metabolized by the gut flora and xylose absorbed and metabolized by the animal itself.

It seems likely that *A. namaquensis* uses a combination of its own and its bacterial flora's metabolic processes to break down xylose. To confirm this, further experiments are necessary. The use of nonabsorbable antibiotics to eliminate the gut flora (van der Waaij and Sturm 1968) and the use of radiolabeled xylose are two approaches that spring to mind. However, at this early stage it is still worth considering whether the general assumption that mammalian tissues are poor at metabolizing xylose is perhaps not so general after all.

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