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Sugar preferences of nectarivorous bats

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ABSTRACT

Groups of flowers pollinated by the same subset of species will have general characteristics in common. These characteristics, when considered together, are called flower syndromes. For example, flowers that are bat pollinated open at night and are often drab, pale, and green with a musty odor, and contain hexose-rich nectar. Baker and Baker (1983) findings demonstrate that all bat-pollinated flowers have hexose-rich or hexose-dominated nectar. Four feeders were hung outside of the Hummingbird Gallery in the Monteverde Reserve. Each feeder contained a different type of sugar solution: one of fructose, one of glucose, the third of honey (a mixture of glucose and fructose) and the last, a solution of sucrose. The number of visits to each feeder was observed nightly. Results indicate a significantly greater preference for solutions of glucose and fructose (Kruskal Wallis, $p = 0.0005$). Number of visits to honey was not significantly higher over sucrose due to the lower concentration of the honey solution. Preference for hexose sugars in nectarivorous bats may reflect the evolution of nectarivory from frugivory.

RESUMEN

Flores polinizadas por el mismo grupo de especies tienen características generales en común. Estas características, cuando se consideran al mismo tiempo, se llaman síndromes de las flores. Por ejemplo, flores polinizadas por Murcielagos se abren durante la noche, tienen olor fuerte y son de color pardo pálido o verde. También tienen azucares como glucosa y fructuosa. Baker y Baker (1983) encontraron que todas las flores de Murcielagos tienen azucares con mas glucosa y fructuosa que sucosa. Suspendí cuatro comederos fuera de la Galería Colibrí en Monteverde, Costa Rica y cada uno tenía un azúcar diferente: uno con fructuosa, uno con glucosa, uno con sucosa y el último con miel (glucosa y fructosa). Conté las visitas de los Murcielagos en cada comedero. Prefirieron las soluciones con fructuosa y glucosa mas que sucosa o miel (Kruskal Wallis, $p = 0.0005$). La miel no tuvo muchas visitas pues tenia una menor concentración. Es posible que la preferencia por azucares con glucosa y fructosa refleja la evolución de los nectarívoros de cuando eran frugívoros.

INTRODUCTION

While flowers may receive a wide range of visitors, usually only one or two taxonomic classes or families will act as effective pollen vectors (Bawa 1990). Therefore, interactions between plants and animals often lead to floral syndromes that favor specific pollinators. For example, flowers commonly visited by hummingbirds tend to be red in color, with tubular corollas. In addition, the nectars tend to be high in sucrose and they are scentless since flower-visiting birds have little or no sense of smell, (Proctor et al 1996). These traits will not be attractive to the majority of visitors and will select specifically for hummingbirds.

The bat flower syndrome is well-documented. Opening at night, these flowers commonly attractive to bats are often drab, pale and green with a musty odor. In shape, they are often have radial symmetry and are flat with a “shaving brush” such as Bombacaceae or deep tube such as Bignonicaceae. They are often found hanging on a branch or trunk (Howe and Westley 1988). In the Neotropics, bats are common pollinators of Margraviaceae, Bombacaceae, Bignoniaceae, and Cactaceae (Murray et al 2000).

Chiroptera, the order to which bats belong, is composed of two suborders, Microchiroptera and Megachiroptera. Megachiroptera are found only in the Old World while Microchiroptera are found in both Old and New Worlds. However, it is only in the New World Microchiroptera family Phyllostomidae that bats have evolved flower and fruit visitation (Baker et al. 1998). Seventy-one species of bats inhabit the areas surrounding Monteverde, with seven of these species of bats being primarily nectarivorous (Murray et al 2000). Almost exclusively small, they usually have long, pointed heads and long tongues with brush-like tips that are adapted for obtaining nectar from flowers (Nowak and Paradiso 1983).

Flowers offer different rewards to pollinators who come to visit: oils, perfume, pollen and nectar. These may vary the contents of these rewards to select for different subsets of pollinators. For example, flower scents can be divided into three categories: ‘flowery’ scents, insect pheromone mimicking scents, and unpleasant dung or carrion-like smells. Each of these scents will attract different subsets of pollinators (Proctor et al 1996). Just as plants will vary their scents, they will also vary their nectar sugar contents. Flower nectar usually contains a mixture of three different sugars: sucrose, fructose, and glucose at varying ratios. For instance, one flower’s nectar may proportionally contain more sucrose while another flower’s nectar may be high in the hexose sugars of glucose and fructose.

Baker and Baker (1983) studied 765 species for nectar sugar contents. They found that the relative amounts of fructose, glucose, and sucrose differed by floral syndrome. Hummingbird pollinated flowers tend to contain nectar that is proportionally high in sucrose sugars. Likewise, those flowers pollinated by short-tongued bees tend to contain nectar with a greater content of sucrose than hexose sugars as do hawkmoth (Sphingidae) flowers. Flower syndromes have indicated preferences such as in the case of avian groups where the sugar constitutes found in flowers match fairly well with sugar preferences.

In contrast, Baker and Baker (1983) found that New World bat nectars are consistently hexose-rich or hexose-dominated in composition (Table 1). The question as to whether nectarivorous bats will prefer solutions of hexose sugars remains to be answered. I predicted that when various sugar solutions are offered, bats will prefer the hexose sugars of glucose and fructose to a solution of sucrose sugar.

MATERIALS AND METHODS

Study Site

Research was conducted in the Monteverde Cloud Forest Preserve, Costa Rica outside of the Hummingbird Gallery where bats frequently come to forage from the feeders at night. The Monteverde Cloud Forest Preserve is located at approximately 1500 meters in elevation in the lower montane wet forest region (Clark, et al 2000). The study was carried out from mid-October to mid-November, 2000, which falls at the end of Costa Rica's wet season.

Mist Netting

Mist netting was conducted for two days, on October 21 and on October 24, outside of the Hummingbird Gallery. This was done in order to determine the composition of nectarivorous bats that were most likely to be visiting the hummingbird feeders at night.

Sugar Preference

In order to measure sugar preference of nectivorous bats, four feeders were filled, each with a difference sugar type. These four sugars, one of fructose, one of sucrose, another of honey (a mixture of fructose and glucose), and the last of glucose. Glucose and fructose were obtained from Sigma chemicals, while granulated, refined sugar was used as the source of sucrose. Honey was obtained from the supermarket. Each solution was prepared by adding 120 g of the sugar source to 600ml of water. Thus, fructose, glucose and sucrose were 20% solution by weight. Honey, because of its water content, was mistakenly made at 15% concentration. The hummingbird feeders were standard plastic coke bottle feeders approximately 8 inches in diameter at the bottom with four feeder holes located at 90-degree intervals around the base of the feeder.

The feeders were hung by a single wire in a straight line, each approximately one meter away from the neighboring feeder. Only glucose, fructose, and sucrose were observed for the first four nights. For the remaining observation nights, a honey solution was added. The feeders were always kept in the same sequence so that the bats would be able to learn where each sugar could be located nightly. Between 6:30p.m. and 9:30p.m., visitation frequency to each individual feeder was observed. Every ten minutes, the number of visits to each feeder was added and recorded.

After data collection was completed, the results were analyzed using a Kruskal Wallis Nonparametric Analysis to determine the significance of visitation to the four feeders.

RESULTS

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RESULTS

Mist-Netting

The nectarivorous bats: *Anoura cultrata*, *Anoura geoffroyi*, *Choeroniscus godmani*, *Glossophaga commissarisi*, *Glossophaga soricina*, *Hylonycteris underwoodi*, and *Lonchophylla robusta* are all found in the Monteverde area (Timm and Laval 2000). Mist netting captured bats of the species *Hylonycteris underwoodi* (nine captured), *Glossophaga commissarisi* (five captured), and *Anoura geoffroyi* (one captured). All three are common species in Monteverde (Fig. 1).

Sugar Preferences

Significant differences were found for the type of sugar and the visitation (Fig. 2, Kruskal-Wallis, $p = 0.0005$). Mean visitation for the four sugars during the 13 days were as follows: fructose 30.615 (sd 27.100), sucrose 6.077 (sd + 6.589), glucose 28.077 (sd + 22.028), and honey 15.333 (sd + 10.356). Rank sum tests show that there were a significantly higher number of visits to fructose feeders over both sucrose and honey feeders. Likewise, bats visited glucose feeders at a significantly higher rate than feeders containing sucrose and honey. No significant difference could be found between the visitation rates of sucrose and honey and glucose and fructose using rank sum analyses.

Evidence was also showed that bats learned quickly which feeders to re-visit to obtain the desired sugars. When analyzing figure 3, one can see a trend for a preference of glucose and fructose after the third day. This indicates that bats were able to tell the difference between sugars by taste and then remember where to find that sugar again.

DISCUSSION

A Baker and Baker's finding that bat flowers often contain hexose-rich sugars predicts a preference of the bats for these sugars. As shown here, bats have a taste preference for solutions of both fructose and glucose, over the sugar solution that was made with sucrose. Floral syndrome predictions have also indicated sugar preferences in other pollinator species. For example, in the case of avian groups, the sugar constitutes found in flowers match fairly well with sugar preferences (Thompson 1994).

One may ask why the bats did not also show stronger selection for the feeder containing the honey solution. This result may be attributed to a measurement error in the concentration of the honey solution. The fact that honey is not a straight mixture of glucose and fructose, but also already contains water was not taken into consideration initially. The honey solution was found to have not a 20 percent concentration but in fact, only a 15 percent concentration. According to Sullivan (2000), bats do, in fact, show preferences for solutions of greater sugar concentration. Thus, bats may not have visited the honey solution as often because the reward of visitation to the honey was not as great.

Why might nectarivorous bats prefer hexose rich nectars? One theory developed by Baker and Baker (1983) state that since many nectar-drinking bats also chew fleshy or juicy fruits to obtain the liquid contents, they may have developed a preference for the same hexose sugars in nectar that are found in the fruits. According to Richard Laval, all nectarivorous bats, to some extent, eat both fruits and nectar (pers. comm). Proctor et al. states that flower-visiting bats almost certainly evolved from those that feed on fruit (1996). This theory may evolutionarily explain why nectarivorous bats prefer hexose sugars, as fruits are often rich in hexose sugars and the preference of hexose sugars may be a residual trait. This study further demonstrates that bats may in fact, have taste preferences for fructose and glucose.

The strong preference for the sugars of glucose and fructose may also be explained, in part, by analyzing digestive tracts. Passerine birds prefer fructose and glucose to sucrose. This preference is associated with a low assimilation of sucrose (Gerardo and Herrera 1999). Some avian families lack intestinal sucrose and as a result, cannot use sucrose. In addition, sucrose cannot be hydrolyzed fast enough due to the rapid passage of food through the guts of some frugivorous passerines (Thompson 1994). Although, it has not been shown, bats may possess the same characteristic that prevents them from consuming too much sucrose and driving them to forage on hexose rich nectars. Perhaps nectarivorous bats, as passerine birds, have an easier time processing hexose-rich sugars.

Plants may take advantage of the preference of bats for hexose rich sugars by producing hexose rich nectars to specifically attract bats. This process may have several advantages for the plant. The first advantage of producing hexose rich sugars is the conservation of energy expenditure. Each formation of a saccharide bond, the bonds that combine monosaccharides together, costs the plant high-energy phosphate (Baker and Baker 2000). Unlike fructose and glucose sugars, which are only monosaccharides, sucrose is a disaccharide and therefore to form a sucrose molecule over that of a hexose, requires a plant to break three high energy bonds. Less energy is expended when forming a hexose sugar than the formation of a sucrose molecule. It is advantageous to keep the production of sucrose as comparatively low as possible and still attract pollinators. By selecting for bat pollination, which utilizes hexose-rich nectar, a plant is conserving energy. Since most flowers which are pollinated by bats are large and heavy, requiring a considerable amount of energy, the energy that is saved by producing hexose sugars instead of sucrose is valuable (Proctor et al 1996).

Evidence that has been gathered shows that bats are strong fliers and may travel long distances. This makes bat pollination desirable since pollen will be able to reach areas farther than the local vicinity where many of the plant's close relatives may be. Furthermore, bat fur is able to carry large quantities of pollen. These two traits make bats effective and desirable pollinators (Proctor et al 1996).

In addition, because of the high degree of specialization needed for effective pollination, plants wish to attract a smaller subset of pollinators (Proctor et al. 1996). This way, there will be a more distinctive target for the pollen, and the plant need not deal with the pollen from another species. By selecting for hexose nectar, plants that have open flowers at night are selecting for the subset of bats. Flowers pollinated by the night-foraging hawkmoth contrast strongly with the bat-pollinated flowers in the ratio of sugars they contain. Hawkmoths show a preference for the high sucrose content in certain flowers (Howe and Westley 1988). Bat pollinated plants, by selecting hexose sugars exclude hawkmoths and avoid potential competition between bats and hawkmoths for their nectar.

Future studies should analyze the rates of food passage through the guts of nectarivorous bats and the effects of sucrose on their digestive tracts. In addition, further studies need to look at evolutionary processes of nectarivory and frugivory. This research would give more insight as to why nectarivorous bats prefer hexose sugars over those of sucrose-rich sugars and would determine if bats prefer hexose-rich nectars because their bodies will not assimilate it or if it is simply a residual taste preference.

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Table 1. Proportions of flower species pollinated by New World bats in each of the four sugar-ratio categories. All flowers pollinated by New World bats possess nectar that is either rich in or dominated by hexose sugars.

		S / (G +F)		
	.1	0.1 to 0.499	0.5 to 0.999	>0.999
NEW WORLD BATS	0.33	0.67	0	0

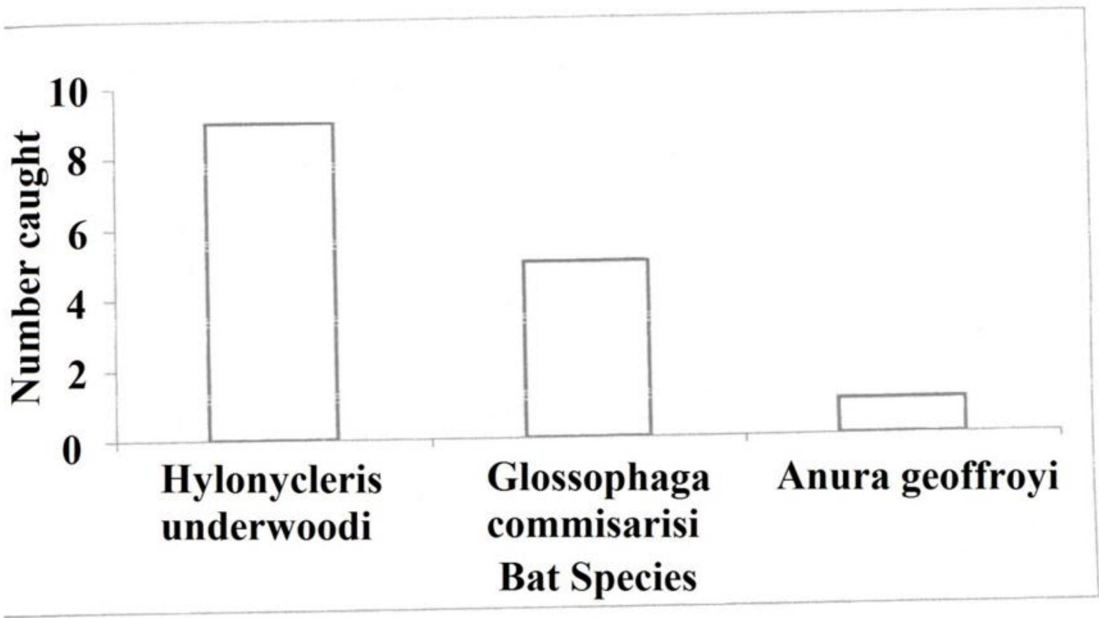

Figure 1. Number of captures per species with mist nets at the Hummingbird Gallary, Monteverde Cloud Forest Reserve.

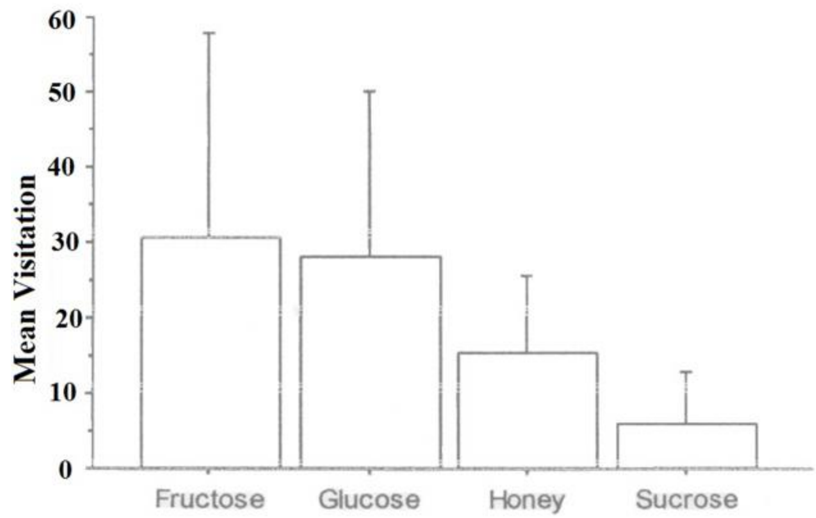

Figure 2. The mean visitation of nectarivorous bats to fructose, glucose, honey, and sucrose in Monteverde, Costa Rica.

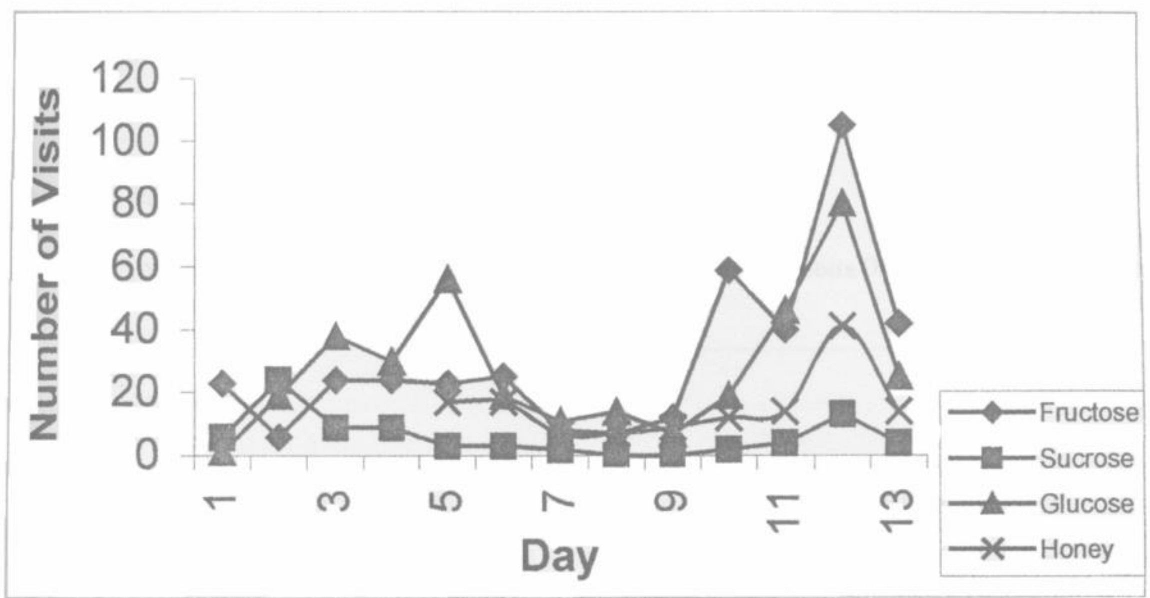

Figure 3. Number of visits per day to feeders of different sugar solutions in Monteverde, Costa Rica.