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Tropical Bees (*Trigona hockingsi*) Show No Preference for Nectar with Amino Acids¹

ABSTRACT

We offered Australian tropical stingless bees (*Trigona hockingsi*) artificial nectar (30% sucrose w/v) either with or without added amino acids (3.30 mM). Bees showed no preference for nectar type, suggesting that sugars, rather than amino acids, play a greater role in nectar choice by this species.

Key words: amino acid; feeding choice; nectar; Queensland, Australia; Trigona.

NECTAR IS AN IMPORTANT BIOLOGICAL RESOURCE that is utilized by a wide variety of animals. Insects are the most abundant floral visitors, but some vertebrates also regularly take nectar. These include flying animals such as birds and bats as well as nonflying animals (*e.g.*, primates, marsupials, and reptiles). Along with pollen, nectar can be regarded as a reward to the floral visitor in return for the pollinating service. Although composition of nectar is dominated by sugars, being in the range of 10 to 40 percent w/v, amino acids form a ubiquitous and substantial component of floral nectar, occurring at millimolar concentrations (Baker & Baker 1973). This discovery initiated a series of investigations into the concentration and composition of amino acids in nectar, and provoked debate concerning their ecological role as a resource (Baker & Baker 1975, 1982, 1983, 1986; Baker 1977; Gottsberger *et al.* 1984, 1989).

To date the role of nectar amino acids as a resource for pollinators has not been satisfactorily resolved, but the consensus view is that plants that are adapted to pollination by butterflies show high concentrations of amino acids. Plants pollinated by birds exhibit low concentrations of amino acids. The ecological rationale behind this is that butterflies are specialized liquid feeders as adults and nectar is their only source of nitrogen. Birds, however, are able to capture insects and so gain nitrogen in the form of protein (Brice & Grau 1991, Brice 1992). Bees are able to eat and digest pollen; plants that they pollinate form an intermediate group.

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A key element in any debate concerning the ecological role of amino acids in nectar is the element of choice exhibited by floral visitors. If pollinating animals can detect amino acids at natural concentrations and exhibit any preference, then this could affect natural selection and floral evolution. Amino acids can stimulate the chemosensory cells of insects (Schoonhoven 1969, Shiraishi & Kuwabra 1970) and the few receptors insects possess can produce a rich array of responses (Dethier 1971). This information has led to a variety of studies that have examined insect preference for solutions containing amino acids. An early experiment on honeybees (*Apis mellifera*) showed a mixed response (Inouye & Waller 1984), but the study used only single amino acids rather than a nectar mimic of more complex composition. A later experiment using a nectar mimic showed that honeybees preferred amino acid-enhanced solution over sugar-only solution (Alm *et al.* 1990). The work of Roubik *et al.* (1995) focused on several species of tropical bees. Their study found that amino acids (added singly) had little effect on bee foraging but certain amino acids, including glycine, were repellent to *Melipona* species. A more recent study has shown that glycine elicited a feeding response in honeybees (Kim & Smith 2000). Potter and Bertin (1988) found that the flesh fly *Sarcophaga bullata* preferred some amino acid–sugar mixtures to sugar-only controls but a later study found this preference only if animals were deprived of other protein sources (Rathman *et al.* 1990), pointing to a role in nutrition for this taxon.

Other experiments have focused on lepidopteran pollinators, with variable results. Some studies have shown that flower-visiting butterfly species prefer sugar solutions enhanced with amino acids (Alm *et al.* 1990, Erhardt & Rusterholz 1998), while others could find no preference (Erhardt 1991, 1992; Romeis & Wackers 2000). More recent work on the Adonis blue butterfly (*Lysandra bellargus*) showed that in the wild, the sexes forage on different plant species, with females choosing those containing a higher concentration of amino acids than males (Rusterholz & Erhardt 2000).

A variety of choice experiments have been conducted using ants (Koptur 1979; Lanza & Krauss 1984; Lanza 1988, 1991; Lanza *et al.* 1993). Various ant species were permitted to examine series of artificial nectaries containing two solutions, plain sugar and sugar plus amino acids in a mixture to mimic nectar of a commonly available plant. Results showed that some species of ant did not discriminate while other species preferred amino acid-enhanced sugar solutions to sugar-only solutions. Although ants are associated with extrafloral nectaries in mutualistic defense relationships with plants, the results show that some insects are capable of detecting nectar amino acids.

Although early evidence suggested that the amino acid composition of individual plant species was constant (Baker & Baker 1977), more recently it was shown that there is substantial variation within species (Lanza *et al.* 1995, Gardener & Gillman 2001b). Furthermore, environmental variables such as atmospheric CO₂ (Rusterholz & Erhardt 1998) and soil fertilizer (Gardener & Gillman 2001a) have been shown to alter the composition and concentration of amino acids in nectar. This demonstrates that the resource available to pollinators is variable, not only between species but also within. The choices that foraging insects exhibit may provide valuable information about the plant–pollinator interaction.

Previous studies have focused on competition between species in the tropics (Roubik 1980, 1983) but few studies have examined the preference of a tropical bee species for nectar amino acids (*cf.* Roubik *et al.* 1995). Bees of the genus *Trigona* are widespread throughout the tropics. They generally form small colonies of several thousands of individuals; favored nest sites are hollow logs. *Trigona carbonaria* can be trained to artificial feeders and exhibits a preference for artificial nectar with high sugar concentration (Bartareau 1996).

The experiment was conducted on a hive of *Trigona hockingsi* bees kept in the grounds of the James Cook University campus, Townsville, Queensland, Australia during November 2000. This species of bee is common in northern Australia, occurring throughout tropical Queensland and parts of Northern Territory. Like other members of the genus, *T. hockingsi* is a generalist feeder, visiting a wide variety of plants (Dollin *et al.* 2000). It forms small colonies of 3000 to 4000 individuals.

Two artificial nectar solutions were made. The first, designated “sugar,” was composed of 30 percent w/v sucrose in distilled water. The second solution, designated “amino,” was identical to “sugar,” except with the addition of amino acids to produce a total amino acid concentration of 3.3 mM (see Table 1 for the list of amino acids). Very little is known about how different amino acids taste to bees, although it is known that glycine can elicit a feeding response in honeybees (Kim & Smith 2000). Given that the responses of some fly species to different amino acids can be classified into a small number (4) of taste classes (Shiraishi & Kuwabra 1970), it is possible to characterize the nectar of any plant species by its

TABLE 1. *Amino acids used to produce artificial nectar types. These compounds are typically found in the nectar of forage plants. The final "amino" solution prepared by adding sucrose to produce a 30 percent w/v solution mimicking nectar in common forage plants.*

Compound	Concentration (mM)	mg in 1 liter
Alanine	0.250	22.28
Arginine	0.250	43.55
Asparagine	0.200	26.42
Glutamic acid	0.250	36.775
Glutamine	0.350	51.135
Glycine	0.250	18.77
Proline	0.500	57.55
Serine	0.250	26.275
Threonine	0.250	29.78
Tyrosine	0.250	45.30
Valine	0.500	58.55

potential taste (Gardener & Gillman 2002). In this experiment, the range of amino acids was chosen to produce a solution that was neutral (*i.e.*, was balanced between the taste classes). Before the experiment was conducted, the amino acid composition of locally available plant species was unknown and so amino acids were added to produce a concentration typical of many nectars commonly occurring in Europe (Gardener & Gillman 2001b). Early work has suggested that the amino acid concentration of bee-visited flowers was in the region of 0.7 mM (Baker & Baker 1973) but the range was large (0–12 mM). A concentration of 3.3 mM was used in this experiment. This is somewhat lower than that used in previous studies (Alm *et al.* 1990: 16 mM; Roubik *et al.* 1995: 35–80 mM), but subsequent analysis of locally available nectar showed that the amino acid concentration and composition of the experimental solution matched quite well with locally available nectar (MCG, RJR, and MPG, pers. obs.). The two solutions were aliquoted into 5 ml plastic vials and frozen at -20°C until use. Feeders were constructed by using disks of Whatman no. 2 filter paper on plastic discs (80 mm diam). Because the plastic disks (blue in color) were mostly obscured by the filter paper, it is unlikely that color itself affected bee visitation as both feeders were identical. A vial of artificial nectar was inverted onto the paper disk. As bees fed from the solution on the paper, capillary action withdrew fresh solution from the vial.

Each morning throughout the study, a feeding station was set up close to the hive. The distance (*ca* 3 m) and direction were randomized each day. A tripod was used to present a blue plastic tray upon which the training solution was placed. This was a plain sucrose solution. A small amount of frangipani oil was added to the outside of the vial to act as an olfactory cue because addition of a floral odor has been shown to dramatically decrease the time taken for recruitment to the experimental feeders (Bartareau 1996). After *ca* 30 minutes, sufficient numbers of bees were seen foraging at the station to replace the single training vial with the two test solutions, which were separated by 10 cm. The orientation of the two solutions was randomized each day. After *ca* 20 minutes, the number of bees foraging at each feeder was deemed sufficient to begin data collection. At five-minute intervals the number of bees at each feeder was recorded, producing a snapshot of visitation for the preceding time interval. Data collection continued for approximately two hours; by this time the levels of solution in the vials were very low. The number of animals at each feeder was totaled and the relative proportion of bees visiting each feeder was calculated. During the experiment, bees were observed to visit feeders freely. Even when there were many other individuals at a particular feeder there was plenty of room for others, although occasional fights were seen to break out. Individuals were also seen switching from one feeder to the other in one foraging bout.

A total of 2180 visits was recorded over nine days (sequential). The visitation data are summarized in Table 2. A Mann–Whitney *U*-test was used to analyze the proportion of bees visiting each solution. The bees showed no preference for either nectar type ($U = 34$, $P = 0.566$, $N = 9$; Fig. 1). The median value for the "sugar" solution was slightly higher, but there was little suggestion that the bees actively avoided the "amino" solution; mean values were closer ($A = 0.49$, $S = 0.51$) and the total number of visits quite similar ($A = 1063$, $S = 1117$). There is a suggestion of pseudoreplication in this experimental

TABLE 2. Visitation data for *Trigona hockingsi* at artificial feeders containing nectar mimics with sugar only (30% w/v) or sugar plus amino acids (3.3 mM). Visits = total visits during that day; Per 5-min = average visitation rate throughout day; SE = Standard Error; Prop = proportion of visits to feeder; Feed = type of feed (i.e., S = sugar only; and A = amino acid-enhanced).

Day	Visits	Per 5-min	SE	Prop	Feed
1	96	3.8	0.77	0.42	A
	135	5.4	1.08	0.58	S
2	136	5.9	1.23	0.58	S
	97	4.2	0.88	0.42	A
3	115	4.6	0.92	0.60	A
	78	3.1	0.62	0.40	S
4	100	4.5	0.97	0.44	S
	129	5.9	1.25	0.56	A
5	121	4.8	0.97	0.47	S
	137	5.5	1.10	0.53	A
6	79	3.3	0.67	0.40	A
	120	5.0	1.02	0.60	S
7	117	6.9	1.67	0.56	S
	93	5.5	1.33	0.44	A
8	183	9.2	2.05	0.63	A
	109	5.5	1.22	0.37	S
9	201	10.6	2.43	0.60	S
	134	7.1	1.62	0.40	A

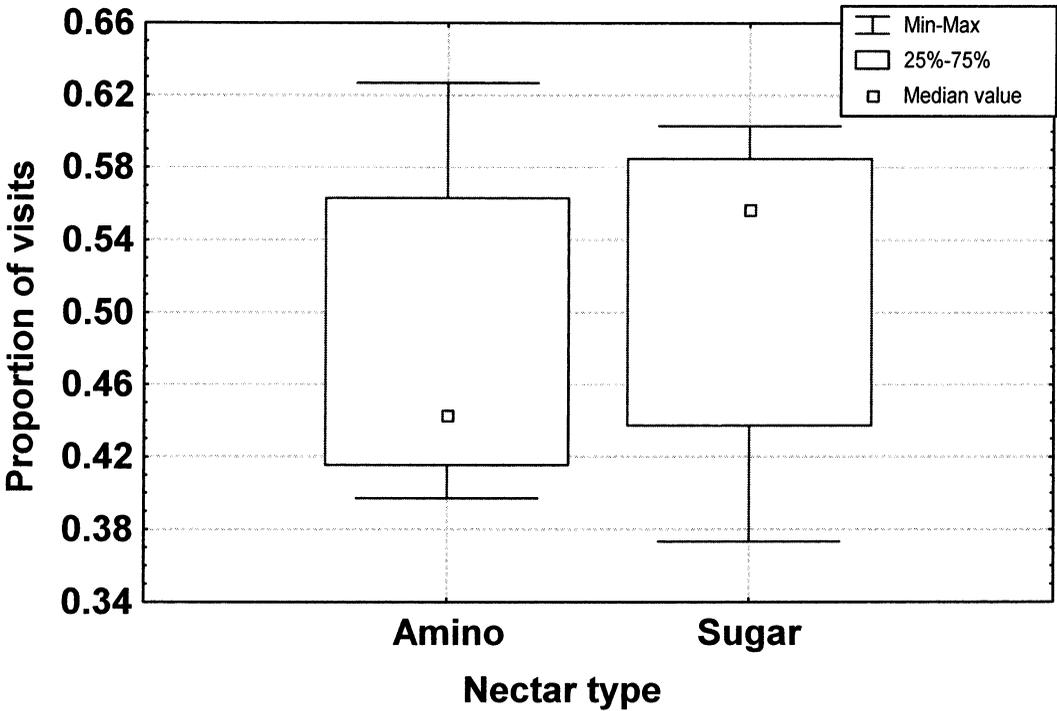


FIGURE 1. Proportion of visits by tropical stingless bees (*Trigona hockingsi*) to feeders containing artificial nectar. Sugar = 30% w/v sucrose solution. Amino = 30% sucrose plus 3.3 mM amino acids.

design (Hurlbert 1984), which would make estimation of the *P*-value less accurate; however, a large number of foragers visited the feeders on subsequent days and it is likely that each repeat of the experiment attracted a different cohort of visitors, with some overlap, which would ameliorate this problem. At the time of the experiment a wide range of plant species were in flower, which provided the colony with plenty of feeding options.

Bees feed on pollen, a rich source of amino acids (Stanley & Linskens 1965, Linskens & Schrauwen 1969, Erhardt & Baker 1990); so it is perhaps not surprising that the *T. hockingsi* used in this study exhibited no preference. Their protein requirements can be met from pollen, a resource that most lepidopteran pollinators are unable to utilize. Other bee species may exhibit a similar feeding choice, as they too feed upon pollen, but experiments using complex mixtures of amino acids (as found in natural nectar) are lacking (*cf.* Alm *et al.* 1990). This, however, was only one colony and its nutrient status or requirements were unknown and so the result must be viewed with a little caution.

The lack of preference by *T. hockingsi* for either nectar type in this study does not necessarily indicate an inability to detect amino acids or to discriminate between solutions with or without them. Taste of nectar may influence choice; perhaps a different taste would elicit a different response. The mixture of amino acids used in this experiment was chosen to give a neutral taste (Gardener & Gillman 2002). Some amino acids stimulate the sugar-cell taste receptors (*e.g.*, Val, Leu, Ile, Met, Phe, and Trp; Shiraishi & Kuwabara 1970). Perhaps, given the preference of *Trigona* species for higher sugar content (Bartareau 1996), nectars rich in these amino acids would be preferred. In a previous study (Roubik *et al.* 1995), *Melipona* species avoided certain amino acids (Glu, Gly, Ser, Ala, and Pro) when added singly to a sugar solution (none of these are thought to be sugar-cell stimulatory; Shiraishi & Kuwabara 1970). It would be interesting to test the response of *Trigona* species to these amino acids and also to the sugar-cell stimulating amino acids.

It may be that different species have different preferences and exhibit different responses to amino acids. The responses of bee species to various combinations of amino acids and the composition of the nectar of forage plants are areas of study that remain largely unexplored. Further study will aid our understanding of the role played by nectar amino acids, which currently remains unclear. Also, examination in this area will inevitably yield important information about the foraging decisions of pollinators and the coevolution of plants and their pollinators.

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Benthic Community Structure and Invertebrate Drift in a Pacific Island Stream, Kosrae, Micronesia¹

ABSTRACT

Tropical Pacific island streams have poorly understood communities that deserve scientific attention. We examined benthic macroinvertebrates and fishes of the Inem River on Kosrae, Federated States of Micronesia. Larval chironomids, lepidopterans, odonates, and freshwater shrimps dominated the benthos and drift. Diel periodicity in drift was not evident. Nine fishes, two shrimps, and one snail species were identified. Kosrae's stream fauna appears even more depauperate than other Pacific high islands, possible due to its extreme isolation.

Key words: amphidromy; freshwater shrimps; migration; Oceania; tropical rivers; volcanic high-island.

PERENNIAL STREAMS DRAINING MANY of the geologically young, volcanic high-islands of the Pacific Ocean have extremely depauperate communities that are very poorly understood (Resh & de Szalay 1995, Craig *et al.* 2001). Isolation from other island systems and continental landmasses (often involving distances of hundreds of kilometers) results in stream communities that are dominated by marine-derived, diadromous taxa (*i.e.*, fishes, shrimps, and snails; Resh *et al.* 1992). In contrast to continental streams, aquatic insects are not major components of Pacific island stream communities, and insect assemblages are composed only of those species able to colonize over huge distances (Resh & de Szalay 1995). Despite being of great biogeographic and ecological interest, Pacific island streams have received comparatively little scientific attention with the exception of Hawaii (Kido 1996, Zink *et al.* 1996, Englund & Polhemus 2001). Improved understanding of their community structure and invertebrate drift patterns could benefit ecological theory (Craig *et al.* 2001) and guide regional water resource management (Benstead *et al.* 1999).

In October 2000, we conducted a short-term study of the Inem River on Kosrae, located in the eastern Caroline Islands in the equatorial western Pacific Ocean (5°16'–5°22'N, 162°54'–163°02'E). Kosrae is the easternmost island-state in the Federated States of Micronesia, and is a small (112 km²) volcanic high-island (maximum elevation 629 m) between 1.2 and 2.6 million years old (Keating *et al.* 1984). Annual mean temperature is 27°C and average annual rainfall ranges from 5000 mm at the coast to 7500 mm in the interior (Whitesell *et al.* 1986). Marked seasonality in temperature and rainfall is not evident on Kosrae (Ewel *et al.* 1998). The Inem is a small (third order) stream that flows into the Pacific on Kosrae's eastern side. Its catchment vegetation consists of undisturbed upland forest (dominated by the canopy tree *Camptosperma brevipetiolata*), with some agroforestry at lower elevations (Whitesell *et al.* 1986). Our study site was a 100-m reach situated at *ca* 20 m elevation on the main stem of the stream. Riparian vegetation was dominated by *C. brevipetiolata* and *Hibiscus tiliaceus*. The channel was *ca* 7 m wide and the substratum was mostly cobble, with some boulders, gravel, and sand. While intense

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