Original article

On optimal nectar foraging by some tropical bees (Hymenoptera: Apidae)

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Summary — Sugar concentration in nectar foraged by 13 Euglossini, 16 Meliponini and 8 Centridini (Apidae) was monitored in floristically rich habitats. For 6 Meliponini, sugar solution profitability by imbibement rate was compared to nectar choice (figs 1–4, tables I–IV). In addition, foraging assays tested meliponine response to 10 amino acid solutions (table V, fig 5). Optimal nectars were 35–65% sugar among bees, and apparently their modal forage. Bees also accepted suboptimal nectar, or were 'rate maximizers'. Two species had modes well below the means, indicating facultative selection of dilute nectars. For pollination, heterogeneity and optimal nectar sweetness are likely key mechanisms causing forager fidelity. Mean sugar contents were 38, 44 and 48 for Euglossini, Meliponini and Centridini, respectively; modes averaged 3–4% higher. All bees used nectars of 30–45% sugar; some also used nectars of 10–15 or 65–70% sugar; others did not use nectar of over 60% sugar. Amino acid solutions of 35–80 mM concentration did not generally affect attractiveness, but *Melipona* avoided glutamic acid, glycine, serine, alanine and proline, responding comparably to 20–40% sugar solutions contrasted with 50% concentration.

nectar composition / optimal foraging / pollination

INTRODUCTION

An intringuing question was posed by Eickwort and Ginsberg (1980): is energy alone an appropriate measure of fitness for foraging bees? Bees often do not receive optimal sugar reward from flowers (Roubik and Buchmann, 1984). Considering the wide range in nectar concentration, total sugar per flower, and nectar composition among angiosperms, we know little about why certain flowers are chosen by foraging bees, or even what resources are normally available. Bees provide a means of sampling

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nectar on a community-wide basis. Because nectar recently stored within the bee's crop is not dehydrated, a sample taken from a forager shows mean sugar concentration in flowers. Whereas nectars used by varied classes of pollinators, such as birds, bats and insects, seem to show differences in concentration, divisions between 'large and small' or 'long-tongued and short-tongued' bees have rarely been assessed (Baker, 1978; Baker *et al*, 1983). Larger bees evidently use high-sucrose nectar, while smaller bees take nectars of all kinds (sucrose-poor, balanced fructose/glucose/sucrose solutions, sucrose-rich, and sucrose-dominant; Southwick *et al*, 1981). However, comparative data on sugar concentration preference are needed for both solitary and social species. The economy of daily metabolic demands may have a greater effect on solitary, non-food-storing species because they cannot exchange dilute nectar for more profitable 'fuel' at the home base, nor do they make honey from watery nectar. Nonetheless, studies of several temperate and tropical *Apis,* and 4 species of *Melipona* show these social foragers profit most from nectar having 45–60% or slightly higher sugar (Roubik and Buchmann, 1984; Roubik, 1994). Similarly, Harder (1986) discussed influence of proboscis and body size, lapping rate, and corolla tube dimensions for temperate-zone *Bombus,* making a theoretical prediction that the bees prefer nectar of 50–65% sugar. Are significant nectar feeding constraints imposed by tongue or body size, and have flowering plants responded evolutionarily to nectar quality sought by different bees? Tropical habitats, whose flora show the range in sugar concentration comparable to temperate areas, are ideal for study of such questions. Not only are many kinds of flowers and bees present, lowland conditions remove constraints imposed on smaller or non-thermoregulating bees by cold weather, wind and cloud cover (Eickwort and Ginsberg, 1980; Roubik, 1989; Kearns

and Inouye, 1993; Endress, 1994). Here we present data on nectar selection by 37 bee species of the long-tongued family Apidae (Roig-Alsina and Michener, 1993). These include Euglossini, whose tongue lengths reach 4.5 cm (D Roubik, unpublished data), a variety of Meliponini (see also Roubik and Buchmann, 1984; Roubik *et al,* 1986) and *Centris* (Centridini). The bees ranged from permanently social to solitary, and from very small to very large (*ca* 8–1 000 mg, table I). We measured profitability directly for several meliponines by assaying caloric intake rate at sucrose solutions, and for certain euglossines (Kato *et al,* 1992) or meliponines by choice studies with artificial feeders. We also made tests of forager response to 10 nectar amino acids, using sucrose solutions (Inouye and Waller, 1984).

MATERIALS AND METHODS

Following the methods of Roubik and Buchmann (1984); we studied nectar harvest through the day by capturing bees and extracting their crop contents from mouthparts, using either 20 or 50 μl calibrated microcapillary tubes, while pressing bees dorsoventrally. Less than 1% of Meliponini and none of the other bees carried liquid of less than 5% TDS (total dissolved solids), which may have been water. These samples were not included. Euglossine males, which readily fly to chemical attractants (Roubik and Ackerman, 1987), were used in place of their relatively rare females. Meliponine foragers were sampled as they returned to their nests. Stinging bees, female *Centris,* were killed quickly in cyanide collecting jars, after which nectar remained in the crop but could be expelled. The *Centris* were collected at Malpighiaceae, and thus their nectar came from other flowers. Sugar content in solutions was determined with an Atago hand-held refractometer (National Co, Japan) corrected for temperature. Our study included nectar that may have been rich in amino acids, thus sugar content in nectar would be lower than that recorded on the refractometer, but likely by no more than a few percent (Inouye *et al,* 1980).

Study sites were primarily forested or relatively undisturbed lowlands. Nectar collections

Table I. Nectar foraged by Euglossini, Meliponini, and Centridini [a] in neotropical habitats.

Bee species	Bee size (mm)	Sugar (TDS [b], wt/wt solution)			
		Mean	Mode	Range	N
Euglossini					
Euglossa sapphirina Moure/					
crassipunctata Moure	9	41	46	12–52	35
Euglossa mixta Friese/*analis* Westwood	10	36	41	16–50	50
Euglossa tridentata Moure	10.5	36	32	24–47	50
Euglossa chalybeata (Friese)	14	36	39	17–46	61
Eufriesea aniosochlora (Kimsey)	14.5	29	33	17–40	50
Euglossa imperialis Cockerell	15	36	40	20–59	333
Euglossa flammea Moure	15	39	39	31–42	72
Eufriesea pulchra (F Smith)	19.5	41	41	29–54	30
Eulaema nigrita Lepeletier	21	37	40	20–49	45
Exaerete frontalis (Guérin)	24	36	40	28–45	12
Eulaema meriana (Olivier)	28	39	38	27–47	38
Meliponini					
Paratrigona ornaticeps (Schwarz)	4	44	49	11–60	61
Nannotrigona testaceicornis (Cresson)	4.5	53	53	20–63	55
Partamona aff *cupira* (Smith)	5.5	20	21	11–49	79
T (Tetragona) dorsalis Friese	6	48	55	19–65	99
Trigona necrophaga Camargo & Roubik	6	55	63	19–65	16
Trigona ferricauda Cockerell	6	37	43	14–55	61
Trigona muzoensis Schwarz	6	41	43	27–57	45
Trigona fulviventris Guérin	7	32	17	5–59	265
Scaptotrigona barrocoloradensis (Schwarz)	6	42	51	10–61	149
Scaptotrigona pectoralis (Latreille)	6	49	56	22–59	39
Scaptotrigona luteipennis (Cockerell)	6.5	44	48	19–66	95
Cephalotrigona capitata (Cockerell)	7.5	45	54	19–63	199
Melipona micheneri Schwarz	9	48	64	31–64	28
Melipona favosa (Fabricius)	9	61	63	52–65	19
Melipona beecheii Bennett	9.5	48	62	19–67	120
Melipona panamica Cockerell	10	41	28	19–63	157
Centridini					
Centris decolorata Lepeletier/					
versicolor (Fabricius)	15.5	45	41	39–52	28
Centris spp	15–17	52	56	31–67	241

[a] Bees of each tribe are listed from the smallest to the largest; 2 species were combined twice in the euglossine data, because they were almost identical in size, tongue length, and were the same phylogenetic group. The *Centris* spp from Hermosillo were *C flavofasciata* Friese, *C aethyctera* Snelling, *C eisenii* W Fox, *C transversa* Pérez, *C cockerelli* W Fox and *C angustifrons* Snelling (det R Snelling, 1992). [b] Total dissolved solids.

were made both during the wet and dry seasons at the Panama sites, and during the wet season at all other sites. Studies took place from 1976 to 1992, as detailed below. Meliponines were studied at Barro Colorado Island, Parque Nacional Soberania, Pipeline Road, and Curundu (Panama); San Bernadino, Quintana Roo (Mexico), and near Kourou (French Guyana). Sites used for Centris were northeastern Puerto Rico (coastal habitat), and the Centro Ecológico of Hermosillo (Mexico). Euglossines were studied at Parque Nacional Soberania, Nusagandi, Cerro Campana, Montaña de Chepo, Herrera Province, and Howard Air Base (Panama); Parque Nacional Braulio Carrillo (Costa Rica); Parque Nacional Amacayacu (Colombia); Degrad Saramaca, Kourou (French Guyana) and Felipe Carrillo Puerto, Quintana Roo (Mexico). Ambient temperatures during the day were 27–34°C at lowland sites, while at Montaña de Chepo and Cerro Campana (Panama) temperatures were approximately 7°C cooler.

Assays of imbibement rate at sugar solutions also followed Roubik and Buchmann (1984), with some modifications. Artificial nectar droplets were presented to bees that climbed or alighted directly by slight depressions in either paraffin or plastic discs of gray or whitish color. Discs held either 20 or 10 µl droplets, used for bees of different sizes. For Scaptotrigona, Trigona and Cephalotrigona, we measured the time to completely consume a droplet of 10 µl for 15 individual bees at 15, 30, 45 and 60% sucrose solutions. For Melipona beecheii, 30 bees were scored at 25, 35, 45, 55 and 65% sugar. The ambient temperature was 26–32°C. In both sets of assays, some bees were scored more than once, but probably not more than 3 times. This procedure produced 'pseudoreplication' (Hurlbert and White, 1993) but does not affect our statistical results. The sugar content of sucrose solutions on a volume basis was calculated from a table given in Kearns and Inouye (1993: p 172). This allowed energy intake to be quantified as calories consumed per second (where 1 mg sucrose provides 3.938 calories), which seemed preferable to the alternative notation, joules per second (Watts). Either 1 or 2 colonies were used of each meliponine species, for which studies were made in both the dry and wet seasons of 1983 and 1990.

Foraging stingless bee response to amino acids was compared to control solutions of both 25 and 50% sugar concentration, and generally followed Inouye and Waller (1984). Solutions of 35–80 mM amino acid concentrations were prepared for the 25 or 50% solutions, respectively, of valine, isoleucine, leucine, glutamic acid, threonine, alanine, glycine, serine, arginine and proline. These are not necessarily essential amino acids for bees but all are found in floral nectar (Baker et al, 1983). Solutions were presented on randomly placed artificial feeders in a grid of 6. One control and 5 sucrose/amino acid solutions were on saturated yellow or light blue sponges, 4 mm thick, 6 cm square, within whitish plastic dishes. Grids were rotated 180° each 5 min to prevent position effects. The number of bees on each feeder was counted each 5 min during 1 h, after bees had been trained to 50% sugar solutions on the previous day. Sponges and feeders were washed in boiling water after each replicate, and no sponge was used more than 4 times. The grid was also used with only sucrose solutions of 10, 20, 25, 30, 40 and 50%, to compare directly the response to sugar with response to amino acids in the experimental setting. From 1 to 4 colonies of each of the 8 species was used, either on Barro Colorado Island or at Curundu, Panama. The studies were made in 1981. Replication was 1–9 times for the pure sucrose solutions, and 3–26 times for the sucrose/amino acid solutions (see fig 5 below).

Taxonomic studies resulted in name changes and some new data are incorporated here (D Roubik, unpublished results, see also Roubik, 1992): T amalthea Olivier is the correct name for Panamanian and Central American bees formerly called T silvestriana Vachal (holotype in Paris, National Museum of Natural History), the senior synonym of T truculenta Almeida. T muzoensis Schwarz is the correct name for bees from Panama formerly called T pallens or T pallida. T necrophaga Carmago & Roubik, from Panama and Costa Rica, was originally referred to as T hypogea Silvestri in Panama studies. M panamica Cockerell is the correct name for M 'fasciata' Latreille from Panama, from which Schwarz (1932) unfortunately designated the lectotype for a Mexican Melipona of another species. Subspecies of M panamica include M p fuscopilosa Moure & Kerr, M p indecisa Cockerell, M p costaricensis Cockerell and M p melanopleura Cockerell (see Roubik, 1992, Camargo, 1994), and thus its geographic range extends at least from Brazil to Nicaragua. M micheneri Schwarz was formerly called M marginata micheneri.

RESULTS

Nectar harvest in nature

Nectar statistics in table I and figures 1–4 give the mean, mode and ranges of concentrations used by 3 bee tribes, and are compared to time of day. Nectar gathered by Meliponini (16 species) averaged 44%, Euglossini (13 species) averaged 37%, and Centridini (2 groups) had a mean of 48% sugar. Euglossine means ranged from 22 to 48%, with individual extremes of 12–59%, while a greater range of means, 20–61% (extremes 5–67%) was found for meliponines (figs 2 and 4). Centris ranged from 31 to 67% (fig 3). Associations between sugar concentrations and bee group were highly significant (contingency table test, χ^2 = 634, P < 0.0001, table II). However, nectar concentrations differed temporally only for Meliponini (χ^2 = 214, P < 0.0001), while they were stable through the day for Euglossini (χ^2 = 0.26, P = 0.88) and Centridini (χ^2 = 0.17, P = 0.92, table III and fig 4).

Although bee tribes showed nectar differences, stingless bees of varied size and genera harvested the highest mean sugar content. M favosa Fabricius collected nectar averaging 61%, T necrophaga 55%, and Nannotrigona testaceicornis Cresson 53% sugar, compared with Centris spp averaging 52%. However, the samples of Centris species were limited. Both Centris and M beecheii Bennett foraged nectar of 67% sugar, while the highest sugar content taken by Euglossini was 59% (table I). Mode nectar sugars were generally greater than means, particularly for Meliponini and Euglossini, although T fulviventris Guérin and M panamica displayed modes lower than means (table I).

Table II. Nectar concentration distribution for Euglossini, Meliponini and Centridini: relative size and direction of deviation from expected values indicated with '+' or '−'.

Bee tribe	Sugar concentration		
	≤ 35%	36–50%	> 50%
Euglossini	334	643++	11 --
Meliponini	503+	430--	397+
Centridini	9--	81-	152++

Table III. Nectar concentration frequency and time of day for Euglossini, Meliponini and Centridini.

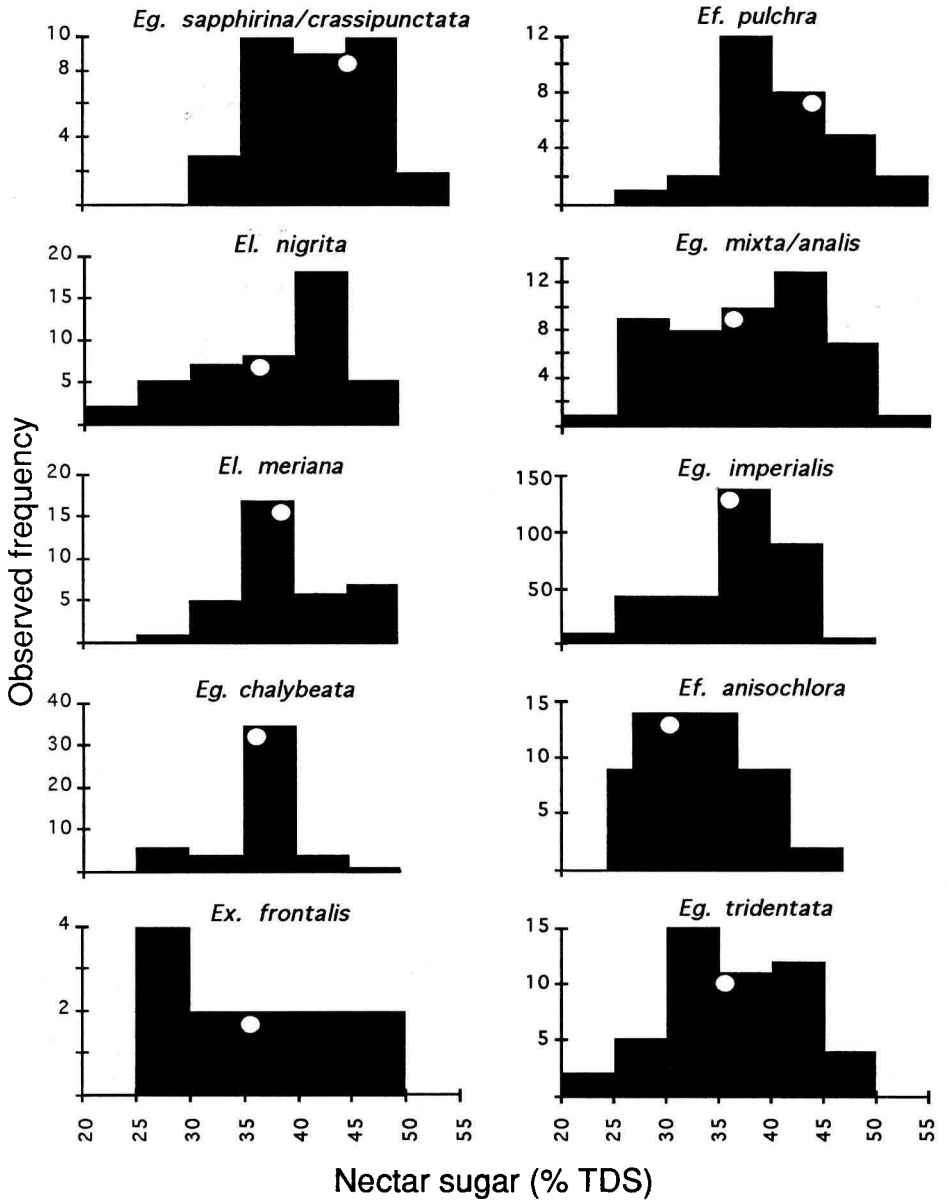| Bee tribe	Time	Sugar concentration		
		≤ 35%	36–50%	> 50%
Euglossini	≤ 11.00	251	484	9
	> 11.00	83	159	2
Meliponini	≤ 11.00	326	141	74
	> 11.00	176	293	323
Centridini	≤ 11.00	4	31	61
	> 11.00	5	50	91

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Fig 1. Nectar sugar concentration (wt sucrose/wt solution) found in foraging Euglossini in neotropical forests. Abbreviations are as follows: Eg = *Euglossa*, El = *Eulaema*, Ef = *Eufriesea*, Ex = *Exaerete*. White circles indicate means.
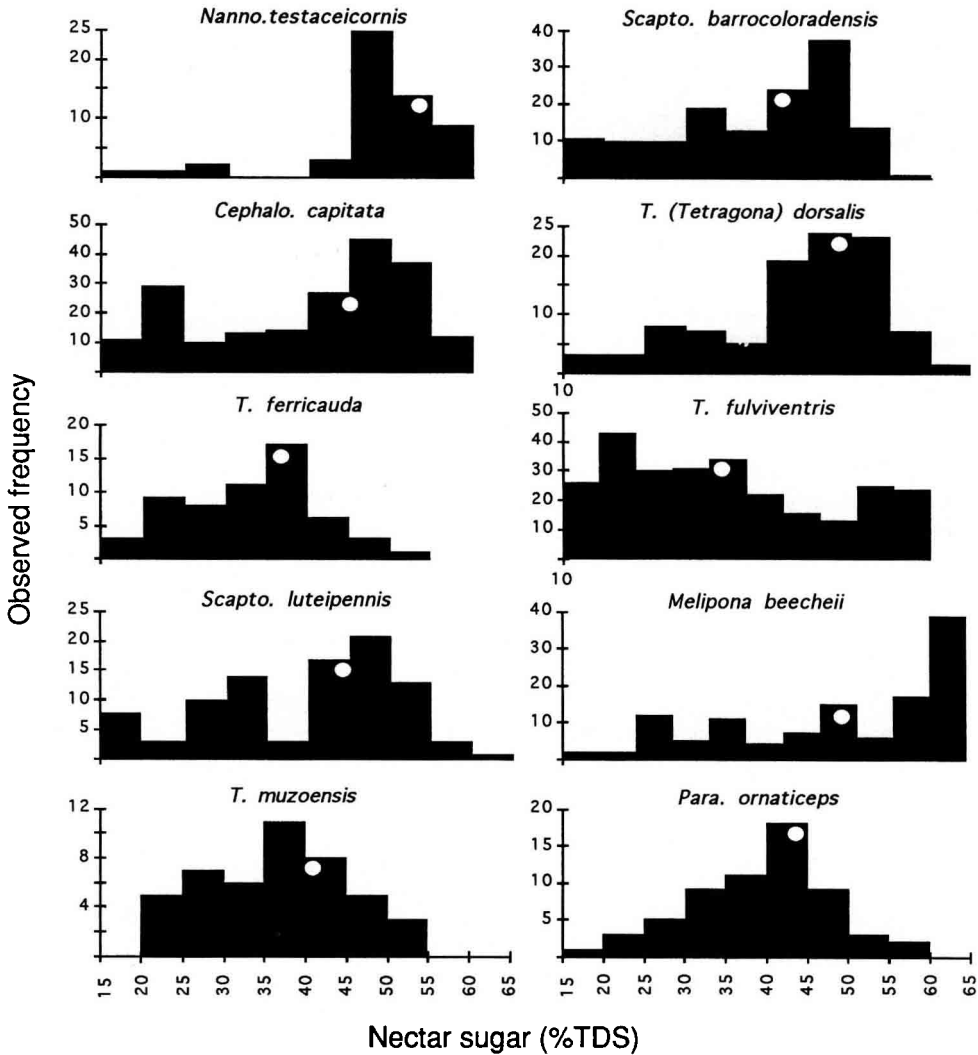
Fig 2. Nectar sugar concentration found in foraging Meliponini in neotropical forests. Abbreviations are in the following form: *Nanno = Nannotrigona, etc; T = Trigona sensu stricto.* White circles indicate means.

Profitability of nectar having different sugar concentrations

Artificial nectars were imbibed at rates that increased with bee body size (tables I and IV). The greatest rate of caloric intake tended to be at relatively high concentrations for the larger bees. However, samples were relatively small, and thus variation was not significant (Anova and Tukey's highly significant difference test) for *T muzoensis* at 30–45% sucrose solutions, *T fulviventris*
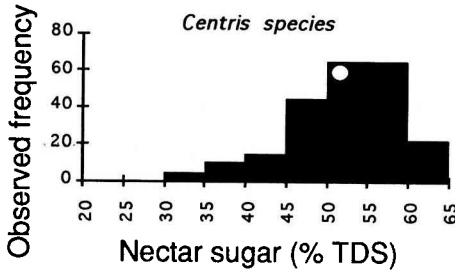
Fig 3. Nectar sugar concentration found in foraging Centridini at Hermossilo, Mexico. White circle indicates mean.

at 30–60% solutions, *Scaptotrigona luteipennis* Friese at 45–60% solutions, nor *M beecheii* foraging 35–45% sugar solutions. *M beecheii* attained highest caloric reward at 65% solutions, while *Cephalotrigona capitata* Cockerell and *S luteipennis* did so at 45–60% solutions. *T muzoensis* obtained the greatest reward from 30–45% solutions. Figure 5 provides another view of profitability from feeders presented simultaneously. The figure suggests most species, including *T*

muzoensis, preferred solutions of at least 50% sugar in this experimental setting, with an exception in *T corvina* Cockerell.

Response to amino acids

All 8 Meliponini used amino acid/sucrose solutions in largely the same way as solutions of pure sucrose (fig 5, table V). Results from 50 and 25% sugar solutions were combined for analysis, due to similar foraging at amino acid solutions and the sugar controls. Although glutamic acid often depressed colony foraging (fig 5), statistical analysis of individual replicates by Anova showed significant effect only for *M fuliginosa* Lep (table V). This species also foraged substantially less at solutions containing serine, glycine, alanine, and arginine (table V). *M panamica* also avoided proline. For the significant differences (Anova), the amino acids were less in foragers to an extent comparable to that of a 0.2–0.6 decrease in sugar content between pure sucrose solutions (fig 5).
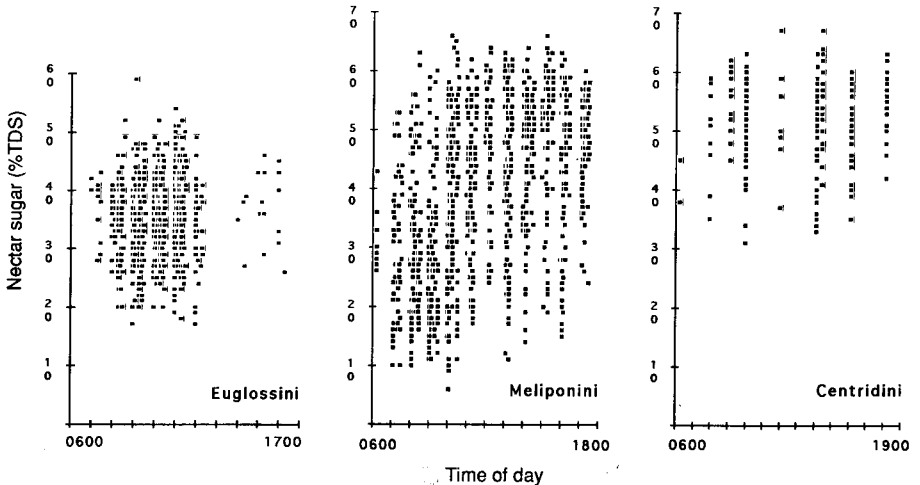

Fig 4. Nectar sugar concentration foraged by 1 905 neotropical bees plotted against time of day.

Table IV. Sucrose concentration profitabilities for 6 Meliponini in experimental settings.

Bee species	Mean calories imbibed per second at indicated							
	Sugar concentration (% TDS, wt/wt)							
	15	25	30	35	45	55	60	65
T muzoensis	0.21		0.37		0.31		0.22	
T fulviventris	0.39		0.69		0.67		0.67	
S pectoralis	0.43		0.77		0.98		0.81	
S luteipennis	0.78		0.98		1.47		1.50	
C capitata	0.68		1.64		2.08		2.27	
M beecheii		1.81		2.34	2.74	3.52		3.99

Table V. Significant results from Anova of forager number at amino acid and control sucrose solutions.

Bee species	Solutions compared	N	STP[a] results
M panamica	prol/cont, arg/prol	19	$P < 0.05$
M fuliginosa	ga/cont, val/ga, isol/ga, thr/ga, leu/ga	11	$P < 0.01$
M fuliginosa	ser/cont, gly/cont, ala/cont, prol/ser, arg/gly	10	$P < 0.01$

[a] Non-parametric multiple comparisons tests by STP (Sokal and Rohlf, 1981: p 438) *a posteriori* tests for significant differences between each pair of treatments when a model I Anova showed significant (≤ 0.05) differences.

DISCUSSION

Considering nectar quality for 37 species, tropical bees specialize on nectar of 17–63% sugar. Excluding 5 species using the most dilute nectars, the modes were no lower than 39%. These figures are modes of arithmetic means, *ie* the sugar concentration in bee foraging loads. Therefore, ranges of acceptable nectar sweetness for individuals are hidden, but likely expressed in the extremes among bees. Euglossine species used less concentrated nectars and so ranges averaged 22–48%, compared to 20–61% for Meliponini, while no Centridini foraged nectar with less than 31% sugar. Flowers and floral morphology used by each bee group consist primarily of species used little by the other 2 (Roubik, 1989). Euglossines had extended tongue lengths (from mentum base to tip of glossa) of 12–38 mm, while those of the stingless bees were 2–6 mm, and those of *Centris* were 11–14 mm. Nectar of flowers with long, tubular corollas used by euglossines tends to have a lower sugar concentration, remaining relatively constant through the day, in marked contrast to smaller more open flowers, including those of short, fused corollas or exposed to sunlight (Corbet *et al*, 1979;
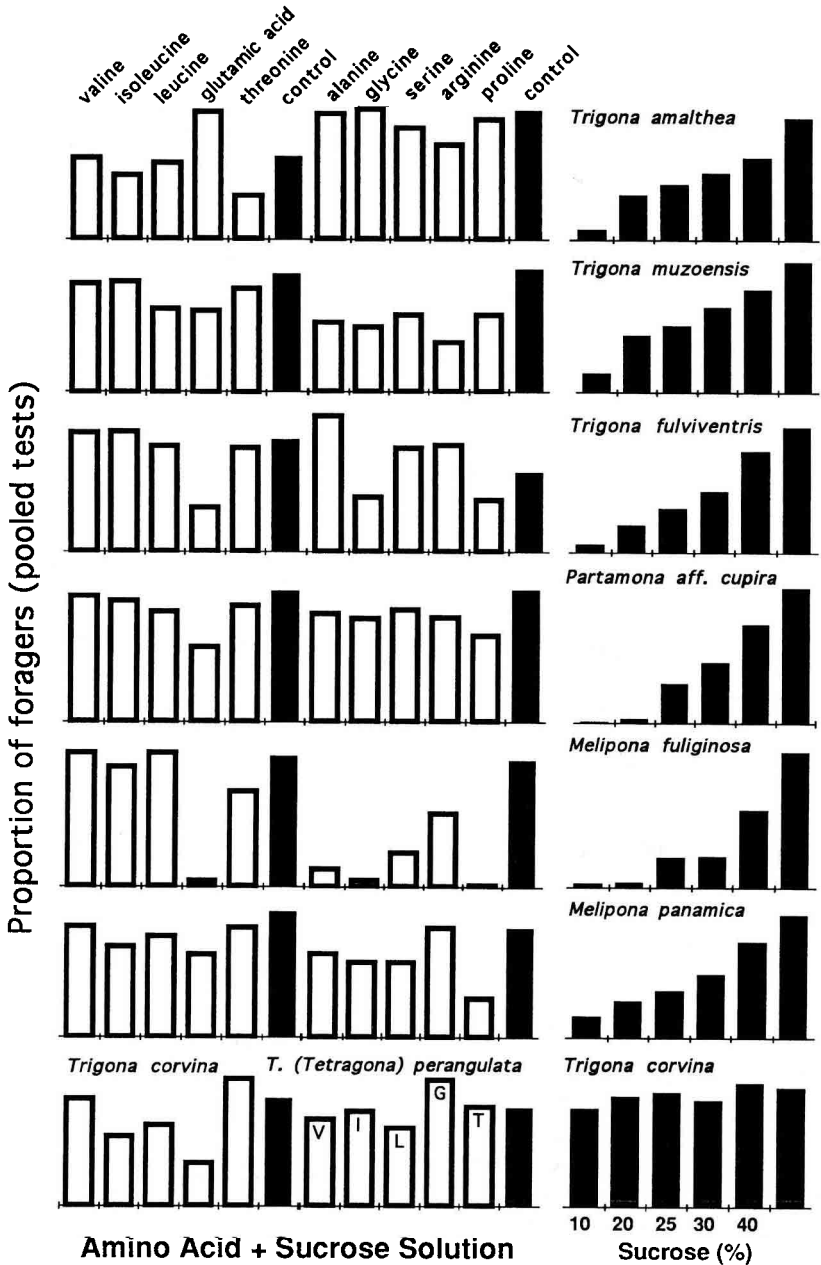
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Fig 5. Results of amino acid/sucrose solution assays for 8 stingless bee species studied in Panama. The number of replicates (d) and total bees scored for each species are: *T amalthea* (9, 5 278); *T muzoensis* (34, 17 859); *T fulviventris* (23, 46 661); *Partamona* aff *cupira* (24, 68 330); *M fuliginosa* (12, 1 560); *M panamica* (25, 13 581); *T corvina* (4, 4 948); *T (Tetragona) perangulata* (5, 1 673).

Baker *et al,* 1983). These characteristics are indicated by consistency in daily nectar concentration for euglossines, its changing daily values for Meliponini, and lower sugar concentrations in euglossine nectars (tables I, III, fig 4). Nectar in tropical dry forests may range from 5–80% in sugar concentration, where bees may visit flowers in dry season averaging 46% sugar (Baker, 1978; Baker *et al,* 1983). If there are 'nectar-niches' determined by sweetness, these may occur in the range of >60% sugar and <30% sugar, which were rare among large bees for Euglossini and Centridini, respectively. Meliponini seem to use all kinds of nectar, with individual extremes of 5 and 67% sugar. We assume that mean and mode nectar concentration used by individual bees are similar, *eg,* foraging loads were not bimodal, with 30% sugar derived primarily from floral nectars of 15 and 45%.

Do bees forage for optimal nectar concentration? Our data indicate that they do. Whether they were social or solitary, large or small, often had no apparent relevance to the end result. We predict that a sizeable proportion of flowers must have nectar of optimal sweetness for pollinating bees, regardless of flower nectar volume. The 6 Meliponini for which imbibement rates were recorded had different ranges of optimal profitability (table IV). Smaller species had lower uptake rates, similar to trends among solitary bees and *Bombus* (Harder, 1983). The smallest Meliponini seemed less likely to profit from viscous nectar. Whereas *T muzoensis* fed most profitably at solutions of 30–45% sugar, *M beecheii* did so at concentrations near 65% sugar. *T fulviventris* benefitted equally from concentrations of 30–60%. Concentrations of 45–60% were optimal for the other species.

Comparison between species' performance in feeding experiments and their mode and mean nectar sugar harvest in nature suggests modes are good predictors of optimal caloric value. Examining the majority

trend in foraging behavior is justified, because arithmetic means may have no actual representation among individual cases. However, mode and mean averages usually fell within ranges predicted by imbibement experiments (tables I, IV). All species profited least at the dilute solutions of 15 or 25% sugar, although for *T muzoensis,* 15 and 60% solutions were equally profitable (table IV). Mode and mean averages of nectar differed slightly less for Euglossini (modes averaged 1.06 times the mean) than for Meliponini (modes were 1.07 times the means), while combined species of *Centris* showed comparable mean and mode (table I).

Mode average nectar selection may be near the optimum, and bees differing primarily in size may have predictable nectar selection differences, but further qualifications are needed. Despite potential behavioral differences between social and solitary bees, and the problems that small bees or those with extremely long proboscides may have when imbibing very viscous nectar, small singless bees such as *Nannotrigona* occasionally specialized on nectar of the same quality as large bees like *Centris* of *Melipona* (table I). For Euglossini, choice experiments (Kato *et al,* 1992) suggest these bees prefer 51 over 34% sugar solutions. However, their nectar flowers (see Roubik, 1989), being tubular and unlikely to change in sugar concentration through evaporation through the day (table III) very seldom contain nectar of >50% sugar. This added constraint implies that Euglossini are less likely to forage optimal nectars, but only because these are seldom available.

In addition to bee tongue length, other aspects of feeding structure likely affect nectar profitability. The flabellum of *T fulviventris* is enlarged and very different from other meliponines (Michener and Roubik, 1993), which may allow them to load the proboscis using 30–60% sucrose with equal profit (see Harder, 1986, 1988), and also accept more dilute solutions (tables I, IV). *Tetragona* have

a relatively wide proboscis, which may allow them to specialize in more viscous sugar solutions (*T dorsalis*, table I). *T necrophaga*, with its liquified flesh foraging habit (Camargo and Roubik, 1991), is therefore accustomed to imbibing viscous substances and also appears to use very viscous nectar. It apparently uses only non-floral nectar sources (D Roubik, unpublished data, pollen analyzed from honey). Among the 6 *Melipona* now studied, 4 can be called high sugar specialists. The 2 others, *M panamica* and *M fuliginosa*, profit from nectars of varying quality and appear to have the most rapid forager recruitment capability.

In the above examples, some stingless bees harvest nectar ignored by other foragers. Small bees like *Nannotrigona* would gain by using resources unattractive to others, because the proportion of a full foraging load from single flower could compensate both time and effort. Despite higher caloric values, such nectar is likely to be relatively scarce or inaccessible. Conversely, when potential caloric harvest rate is very rapid, cooperating social bees may be more willing to accept less profitable nectar, performing as 'rate maximizers' (Stephens and Krebs, 1986). Long-term rate maximizers apparently forage inefficiently for some periods, but net caloric intake is acceptable to them. Roubik and Buchmann (1984) give examples of nectar concentration being similar all day for *Melipona* collection 20 or 60% sugar, which demonstrates 2 extremes in foraging. Therefore, some flowers do offer nectar near the optimal concentration for bees through the day. Others offer nectar of low sugar concentration, or gradually increase the sugar concentration (Corbet *et al*, 1979). Increases of 35–60% are known in tropical flowers, despite high humidity and low insolation (*eg, Hybanthus prunifolius* [Schult] Schulze, Violaceae, see Roubik and Buchmann, 1984). Data for *Verbesina gigantea* Jacq, Coll (Compositae, D Yanega and D Roubik, unpublished results) show

such sugar concentration changes in insolated flowers visited by *Melipona*.

Suboptimal nectar is frequently taken by socially foraging species. Bees that perforate the flower to obtain nectar–virtually all of *Trigona* ss but also some *Partamona*–often used low-sugar nectars. This resource is even less rewarding, due to the extra investment made in removing floral tissue and defending the resource. These bees also visit flowers normally, but sugar concentration in their nectars, along with those of non-robbing *M panamica,* displayed mode averages much lower than the means (table I). This result agrees with previous data for *T ferricauda* Cockerell (18.4% mean, in the wet season) and *Partamona peckolti* Friese (given as *T musarum*), with a wet season mean of 19.3% sugar (Roubik *et al*, 1986), and also for *M panamica* (Roubik and Buchmann, 1984*). T corvina* is an aggressive group forager that apparently did not discriminate resource quality in small patches (fig 5). All appear to profit more than do other species from dilute nectar. If relatively high rates of harvest are realized, then caloric reward is comparable to that obtained from sweeter nectars harvested at slower rates. Bees are behaving as rate maximizers.

The amount of nectar within flowers is measured by foragers, along with the sugar concentration; their product can indicate profitability (Real, 1981; Southwick, 1982). Risk aversion has been detected for *Bombus* (Real, 1981), defined as avoidance of flower species that vary greatly in reward at a given time. However, such flowers may still be visited if their nectar sugar concentration increases (Southwick, 1982; Roubik and Buchmann, 1984). The studies of Real (1981) and recent studies of risk-sensitive foraging (Banschbach and Waddington, 1994) use sugar concentrations below optimality or modes that we observed; thus their results should be tested using more profitable nectar.

Non-sugar nectar components have been thought to affect optimal foraging (Baker, 1978). In our study, amino acids did not have a deterrent effect for robbing bees like *Trigona* and *Partamona*. Because the concentrations we prepared were up to 10 times that observed among neotropical flowers (Baker *et al*, 1983), the amino acids seem unlikely to serve either as attractants or repellents.

Bee pollination management strategies and selective breeding programs for nectar sugar content in crops (Davis, 1995) might focus on the mode average sugar content in nectar taken by the target pollinator under favorable conditions. All Euglossini, and some Meliponini likely to perform as thieves or robbers will rarely visit flowers providing nectar sugar concentrations over 60%. Desirable pollinators would seek greater rewards.

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Résumé — Du butinage optimal de nectar par certaines abeilles tropicales (Hymenoptera: Apidae). Dans des habitats riches du point de vue floristique, on a étudié la concentration en sucres du nectar butiné par 13 espèces d'Euglossini, 16 espèces de Meliponini et 8 de Centridini (Apidae). Pour 6 espèces de Meliponini on a calculé la rentabilité des solutions sucrées (énergie consommée) en conditions expérimentales et on l'a comparée avec la teneur en sucres des nectars récoltés en conditions naturelles (figs 1–4 ; tableaux I–IV). Des tests de butinage ont permis d'étudier la réaction des abeilles à 10 solutions d'acides aminés (tableau V, fig 5). La teneur en sucres des nectars optimaux se situait entre 35 et 65%, ce qui correspond au butinage modal (fréquence la plus élevée de nectar naturellement butiné). Les abeilles ont accepté aussi des nectars non optimaux et optimisaient le taux de prélèvement. Chez 2 espèces, le mode était nettement situé en-dessous de la moyenne, ce qui prouve qu'elles sélectionnent à l'occasion des nectars dilués. Pour la pollinisation, l'hétérogénéité et la douceur optimale du nectar sont vraisemblablement des mécanismes clés pour fidéliser les butineuses. Les Euglossini préféraient en moyenne une teneur en sucres de 38%, les Meliponini de 44% et les Centridini de 48%. Toutes les abeilles ont récolté des nectars à 30–45% de sucres, certaines aussi des nectars à 10–15% ou 65–70% de sucres. D'autres n'ont pas butiné de nectar ayant plus de 60% de sucres. Les solutions d'acides aminés aux concentrations comprises entre 35 et 80 mM n'ont pas affecté l'attractivité, mais *Melipona* a évité l'acide glutamique, la glycine, la sérine, l'alanine et la proline. Ceci correspond à une réaction à une solution sucrée à 20–40% par rapport à une solution sucrée à 50%.

nectar / composition chimique / butinage optimal / pollinisation / zone tropicale / Apidae

Zusammenfassung — Optimales Nektarsammeln von einigen tropischen Bienen (Hymenoptera, Apidae). Für 13 Arten der Euglossini, 16 Arten der Meliponini und 8 Arten der Centridini (Apidae) wurde die Zuckerkonzentration von in floristisch reichen Habitaten gesammeltem Nektar ermittelt. Für 6 Arten der Meliponini wurde die Profitabilität von Zuckerlösungen anhand der Aufnahmeraten ermittelt und mit dem Zuckergehalt von natürlich gesammeltem Nektar verglichen (Abb 1–4, Tabellen I–IV).

Darüberhinaus wurde die Reaktion von Meliponini-Arten auf 10 Aminosäure-Lösungen in Sammel-Testanordnungen untersucht (Abb 5, Tabelle V). Der Zuckergehalt von optimalem Nektar lag je nach Art zwischen 35–65%, dies entsprach jeweils dem Modus des natürlich gesammelten Nektars. Die Bienen nahmen allerdings auch unteroptimale Nektare an, in manchen Fällen optimierten sie die Aufnahmerate. Bei zwei der Arten lag der Modus deutlich unter dem Mittelwert, was auf die gelegentliche Auswahl von niedrig-konzentrierten Nektaren hindeutet. Hautpmechanismen zur Erreichung von Blütenstetigkeit zur Bestäubung sind wahrscheinlich die Verschiedenartigkeit und die optimale Süße des Nektars. Die Euglossini bevorzugten im Mittel einen Zuckergehalt von 38%, die Meliponini 44% und die Centridini 48%; die Modi lagen im Mittel 3–4% höher. Nektare mit 30–45% Zuckergehalt wurden von allen Bienen gesammelt. Einige der Bienen nutzten sogar Nektare mit 10–15% oder 65–70% Zucker, während andere Arten keinen Nektar mit über 60% Zucker sammelten. Aminosäurelösungen von 35–80 mM hatten keinen generellen Einfluß auf die Attraktivität, allerdings vermied *Melipona* Glutaminsäure, Glycin, Serin, Alanin und Prolin; ihre Reaktion entsprach dabei etwa der von 20–40% Zuckerlösung im Kontrast zu 50% Zuckerlösung.

Nektar / chemische Zusammensetzung / optimales Sammeln / Bestäubung / Tropen / Apidae

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