BIOTROPICA 30(2): 179–189 1998

Facultative Ant-Plant Interactions: Nectar Sugar Preferences of Introduced Pest Ant Species in South Florida[1]

Suzanne Koptur and **Ni Truong**

Department of Biological Sciences, Florida International University, Miami, Florida 33199, U.S.A.[2]
Fairchild Tropical Garden, Miami, Florida 33156, U.S.A.

ABSTRACT

We observed nectar use by native and exotic ant species in nature, garden, and urban situations, and found ants utilizing floral and extrafloral nectar of a variety of flowering plant species. We collected 31 plant nectars (29 floral, 2 extrafloral) and used them in feeding preference tests against standard solutions of sugars (20 percent fructose, glucose, and sucrose, and their mixture), 10 trials for each nectar-ant comparison. We compared time-to-discovery and total ant visits to each droplet using ANOVA, and found that both trial and solution contributed significantly to the variation in most experiments. Seven of the floral nectars tested were significantly more attractive to certain ant species than the sugar solutions. Not only do ants use floral nectar, but it appears that some floral nectars contain compounds that are especially attractive to ants.

RESUMEN

Se observó que varias especies de hormigas nativas y exoticas utilizaban nectar de flores y nectar extrafloral de varias especies de plantas en floración, localizadas en jardines, en el casco urbano y en areas naturales. Se colectaron 31 nectares de plantas y su preferencia fué comparada con soluciones de azucar (20 perciento de fructosa, glucosa, y sucrosa, y sus mezclas). Esta comparación fue realizada 10 veces para cada combinacion de nectar y hormiga. Se utlizó el Analisis de Varianza para comparar el tiempo que le tomaba a las hormigas en descubrir las soluciones y el número de visitas a cada gota de nectar o solución. El analisis estadistico demonstró que tanto el número de replicaciones como la clase de solución contribuía significativamente a la variacion de la mayoría de los experimentos. Siete de los nectares florales fueron mas significativos a algunas especies de hormigas que las soluciones de azucar. Evidentamente, algunos nectares florales contenian algunas substancias especialmente atrayentes a las hormigas.

Key words: *ants; feeding; Florida; nectar; preference.*

Ants are ubiquitous and perform many important functions in the ecology of plants in tropical and temperate areas (Huxley & Cutler 1991). Ants are often attracted to plants to collect exudates from extrafloral nectaries or from insects consuming the plants. Flowers often contain nectar as the floral reward, and Janzen (1977) posed the question "Why don't ants visit flowers?", hypothesizing that floral nectar must contain ant repellents to protect it for pollinators. Nearly one hundred years earlier, A. Kerner von Marilaun (1878) had described many ways in which plants can exclude nectar-thieving ants, including extrafloral nectaries, sticky stems, dense hairs, water traps, and distasteful substances in floral tissue. Van der Pijl (1955) used the term "myrmecophoby" for the deterrence of ants from flowers, hypothesizing the existence of volatile, ant-repellent substances in petal tissues of plants, and demonstrated their existence in a simple experiment.

The Bakers (1978) were the first to respond to Janzen's hypothesis, pointing out their observations of chemicals in nectars such as alkaloids, phenolics, and nonprotein amino acids that may serve as deterrents to nectar theft. Feinsinger and Swarm (1978) tested the acceptability of nectar to ants of four common plant species in Trinidad, and found that responses of ants varied widely. Schubart and Anderson (1978) offered freshly cut-open flowers of three plant species to ants in Brazil, and found all to be readily consumed; though ants may have been excluded from flowers by structural barriers, ant-repellent nectars were not indicated. Guerrant and Fiedler (1981) compared the acceptability of floral nectars and floral tissue extracts to sugar solutions, and analyzed the plant substances chemically to detect deterrent substances; they found that floral nectars were attractive to ants, but floral tis-

[1] Received 10 April 1997; revision accepted 29 September 1997.
[2] address for correspondence.

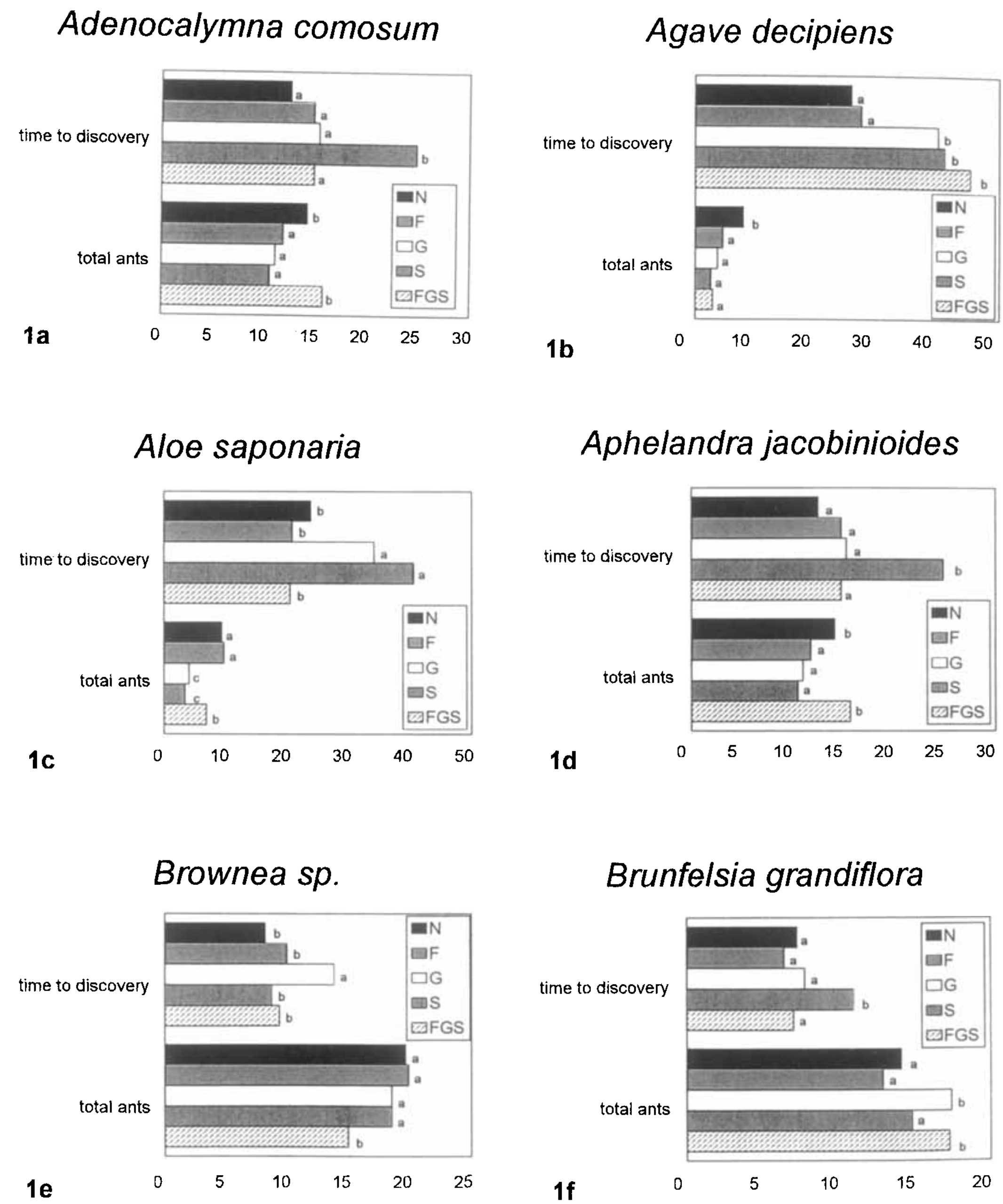


FIGURE 1. Results of feeding experiments with crazy ants, *Paratrechina longicornis*. Bars represent the means of ten trials for each experiment (variation not shown). The upper set of bars represents the time-to-discovery of the solution in minutes; the lower set of bars represents the total number of ants to visit that solution during the one hour that the experiment ran. EFN = extrafloral nectar. Solutions are abbreviated as: N = nectar, F = fructose, G = glucose, S = sucrose, and FGS = fructose, glucose, and sucrose. Significant differences shown by Analysis of Variance and Tukey post hoc tests are indicated by lower case letters, in which case bars with different letters are significantly different within that data set.

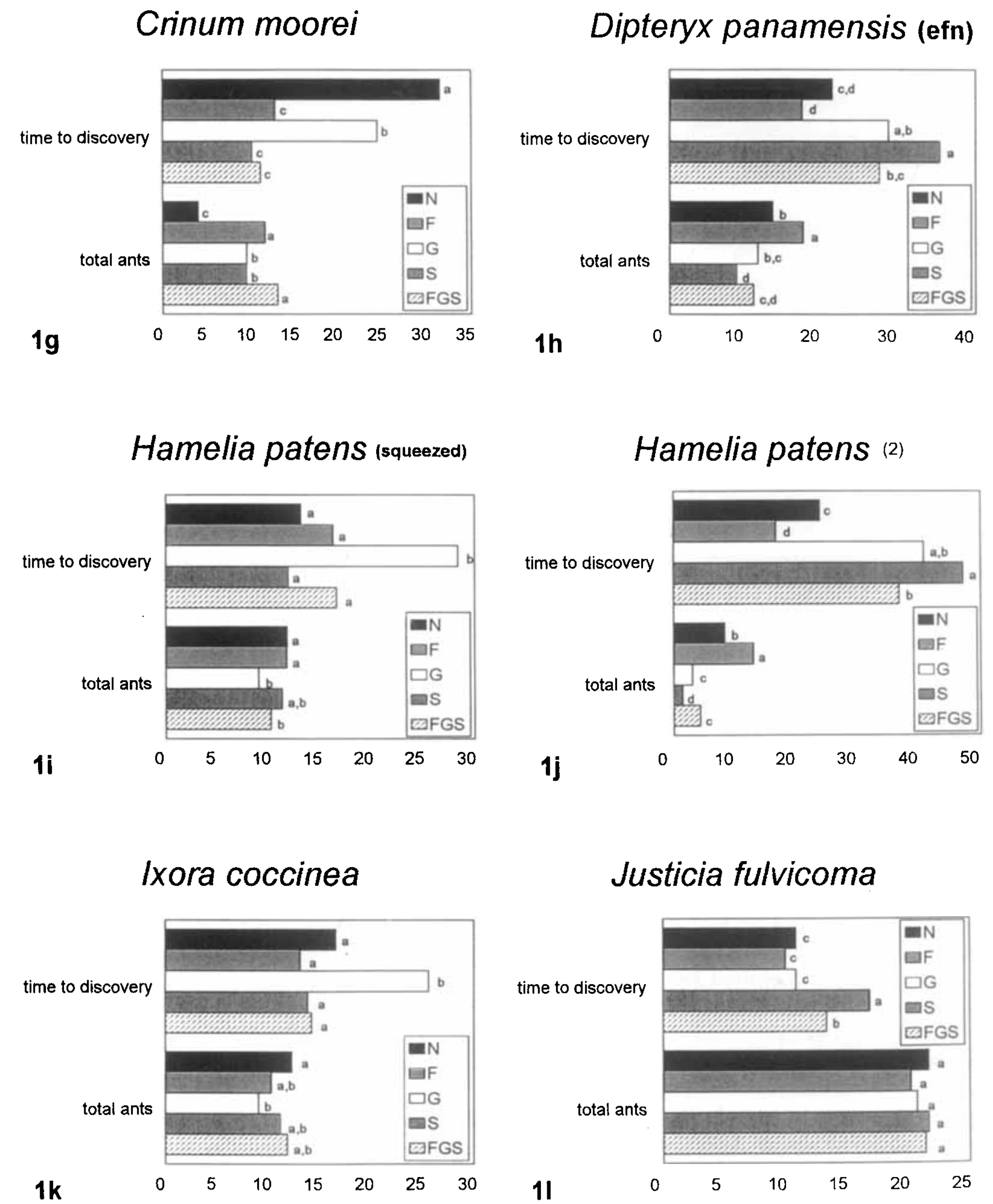


FIGURE 1. *Continued.*

sues showed highly variable palatability. Haber *et al.* (1981) had observed ants taking floral nectar from many species of plants in the lowland dry forest of Costa Rica, and tested many of these by placing nectar droplets on branches of trees and noting whether or not they were consumed by ants within five minutes; all but two tested were readily consumed, and many of those enjoyed by ants were known to have phenolics and/or alkaloids. Many nectars, therefore, are readily consumed by ants when they are offered out of their flowers, if they have been collected carefully so as to not contaminate them with any repellents present in the floral parts.

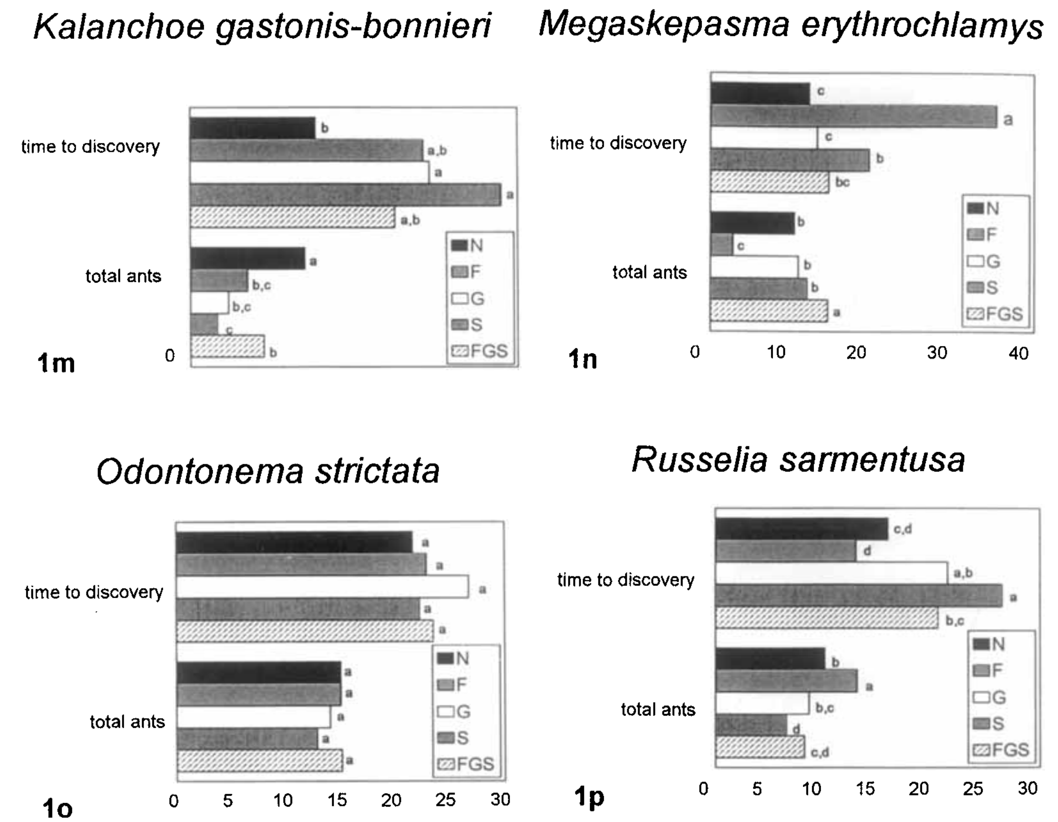


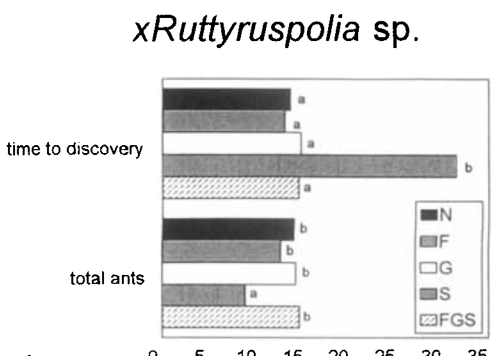
FIGURE 1. *Continued.*

In this study we document the use of nectars of a variety of cultivated tropical species by native and exotic ants, and investigate the attractiveness of the nectars to noncoevolved pest ant species in subtropical south Florida. In conducting the experiments we obtained information on the relative preferences of these ants for the various sugar solutions used in our controls as well as their different responses to the nectars tested. The facultative associations observed suggested nectars that might be attractive to ants; we compared the acceptability of these nectars to standard sugar solutions in order to determine if any of these nectars were exceptionally attractive. Sugar solutions are nonvolatile, and ants discover them by touch and taste; floral nectars may have other components that attract ants from a distance, or affect their taste once they are tried. We do not presume that there are necessarily coevolved positive relationships between ants and floral nectars in natural communities. Unlike the other social Hymenoptera, ants are usually visiting flowers as nectar robbers, and are unimportant as pollinators since most have antifungal metapleural secretions (*e.g.*, myrmicacin) that kill pollen (Beattie 1985). Our study relates primarily to the abilities of ants to obtain food, and to whether or not the nectars tested might have nonsugar constituents rendering them exceptionally attractive to ants.

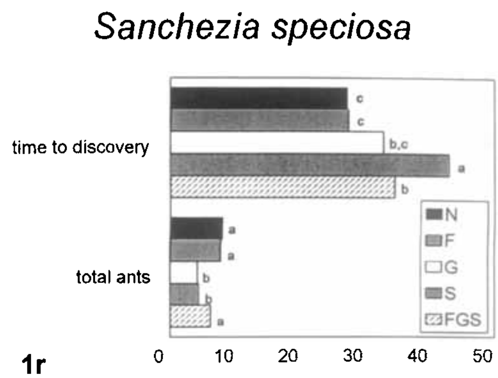
MATERIALS AND METHODS

Observations were made over two years in the collection of Fairchild Tropical Garden and, to a lesser extent, the University Park campus of Florida International University. We documented all ants using nectars, collecting ant specimens for determination and later verification.

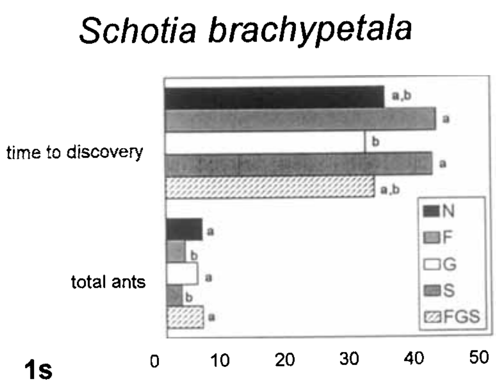
Several milliliters of nectar were collected into a tiny centrifuge tube, and its concentration measured using a hand-held refractometer (Bellingham & Stanley brand, reading percent sugar on a weight/weight scale). Nectars were diluted with distilled water to a concentration of 20 percent, unless



1q



1r



1s

FIGURE 1. *Continued.*

they were less than 20 percent sugar to begin with, in which case more dilute sugar solutions were prepared.

For each nectar-ant comparison, we ran ten trials of the following design. Standard solutions of 20 percent fructose (F), 20 percent glucose (G), 20 percent sucrose (S), and a mixture of 20 percent fructose, glucose, and sucrose (FGS) were made fresh each month and kept refrigerated, removing only small quantities to use for daily experiments. We made circular styrofoam trays (10 cm diameter) with 20 uniformly spaced depressions around the edge, and in each depression placed a large droplet (*ca* 0.1 ml) of one of the solutions or of the nectar being tested. Each solution and nectar were represented by four droplets. We prepared a tray and set it down near a colony of whatever ant species we were testing (usually on concrete substrate) and observed it for 1 h, recording the number of ants on each droplet every 5 min. For each trial, the tray was placed in a different location (presumably with a different colony of ants). We did not replace the droplets if they were used up before the end of the trial (except for reruns of *Hamelia patens,* which initially was consumed very quickly; see below). Trials that were interrupted by external factors (disturbance by urban wildlife, inclement weather) were not included.

For each droplet we figured time-to-discovery (time from initial placement to when it was first observed with ants) and the total number of ants observed during the hour's observation. Ants were counted at each 5 min interval and the total of these observations was tallied for each droplet, although the same ant may have been counted more than once.

Data were entered in files for each ant-nectar interaction, and analyzed using ANOVA, enabling us to see if either the solution or the trial had a significant effect. We used a Tukey post hoc test to determine which solutions were significantly different from each other. Solutions with the shortest

TABLE 1. *Observations of nectar use by pest ant species in south Florida. EFN = extrafloral nectar.*

Plant species (family)	Crazy	Carpenter	Fire	Ghost	White-footed
Adenocalymma comosum (Bignoniaceae)	x	x	x		
Agave decipiens (Agavaceae)	x				
Aloe saponaria (Liliaceae)	x				
Allamanda nerifolia (Apocynaceae)		x			
Allamanda violacea (Apocynaceae)		x			
Aphelandra jacobiniana (Acanthaceae)	x				
Brownea sp. (Fabaceae)	x				x
Brunfelsia grandiflora (Solanaceae)	x				
Calliandra haematocephala (Fabaceae)			x		
Callistemon lilacinus (Myrtaceae)		x			
Callistemon viminolus (Myrtaceae)				x	
Clerodendrum myricoides (Verbenaceae)		x	x	x	
Clerodendrum speciosissimum (Verbenaceae)		x	x	x	
Clerodendrum wallichii (Verbenaceae)		x			
Cornutia obovata (Verbenaceae)		x			
Dipteryx panamensis (Fabaceae) EFN	x				
Hamelia patens (Rubiaceae)	x		x		
Hibiscus tiliaceus (Malvaceae) EFN		x	x	x	
Ixora coccinea (Rubiaceae)	x			x	
Justicia fulvicoma (Acanthaceae)	x				
Kalanchoe gastonis-bonnieri (Crassulaceae)	x				
Megaskepasma erythrochlamys (Acanthaceae)	x				
Odontonema strictata (Acanthaceae)	x		x		
Russelia equisetiformis (Scrophulariaceae)		x	x		
Russelia sarmentusa (Scrophulariaceae)	x				
xRuttyruspolia sp. (Acanthaceae)	x		x		
Sanchezia speciosa (Acanthaceae)	x		x		
Schotia brachypetala (Fabaceae)			x	x	
Solandra grandiflora (Solanaceae)					x
Tecoma stans (Bignoniaceae)		x			
Thunbergia erecta (Acanthaceae)			x		

average time-to-discovery and the largest total number of ants were interpreted as being the most acceptable to the ants being tested.

RESULTS

Pest ant species.—Five of the major pest ant species in the Miami area were observed taking nectars and used in our feeding preference tests. These species (in alphabetical order of their common names) were: **carpenter ants** [*Camponotus abdominalis* var. *floridanus* (Buckley)]; **crazy ants** [*Paratrechina longicornis* (Latreille)]; **fire ants** (*Solenopsis invicta* Buren); **ghost ants** [*Tapinoma melanocephalum* (Fabricius)]; and **white-footed ants** [*Technomyrmex albipes* (F. Smith)].

Nectar use by pest ants.—We observed ants taking nectar of 31 different cultivated plant species (2 bearing extrafloral nectaries and 29 bearing floral nectaries). Crazy ants utilized the nectar of 17 species of cultivated plants (Table 1), while carpenter ants and fire ants were each recorded taking 11 nectars. Less frequently encountered were ghost ants (in five nectar-producing species) and white-footed ants (only observed in two species).

Feeding preference tests.—The number of nectar-ant preferences investigated reflects the relative abundance of the pest ant species and a similar pattern to the observed nectar use above. We tested 18 nectars with crazy ants, 8 with fire ants, 6 with carpenter ants, 3 with ghost ants, and 2 with white-footed ants. Since we performed ten trials of each ant-nectar interaction, it was easiest to test many nectars with the more common ants.

Using horizontal bar graphs provides an easy way to visualize the results of the feeding preference tests. Each bar represents the mean of ten trials, and so has some variation around it (not shown in the figures). Analysis of variance and a Tukey post hoc test revealed if there were significant differences among the solutions being tested, and these are represented by lower-case letters in the figures. We

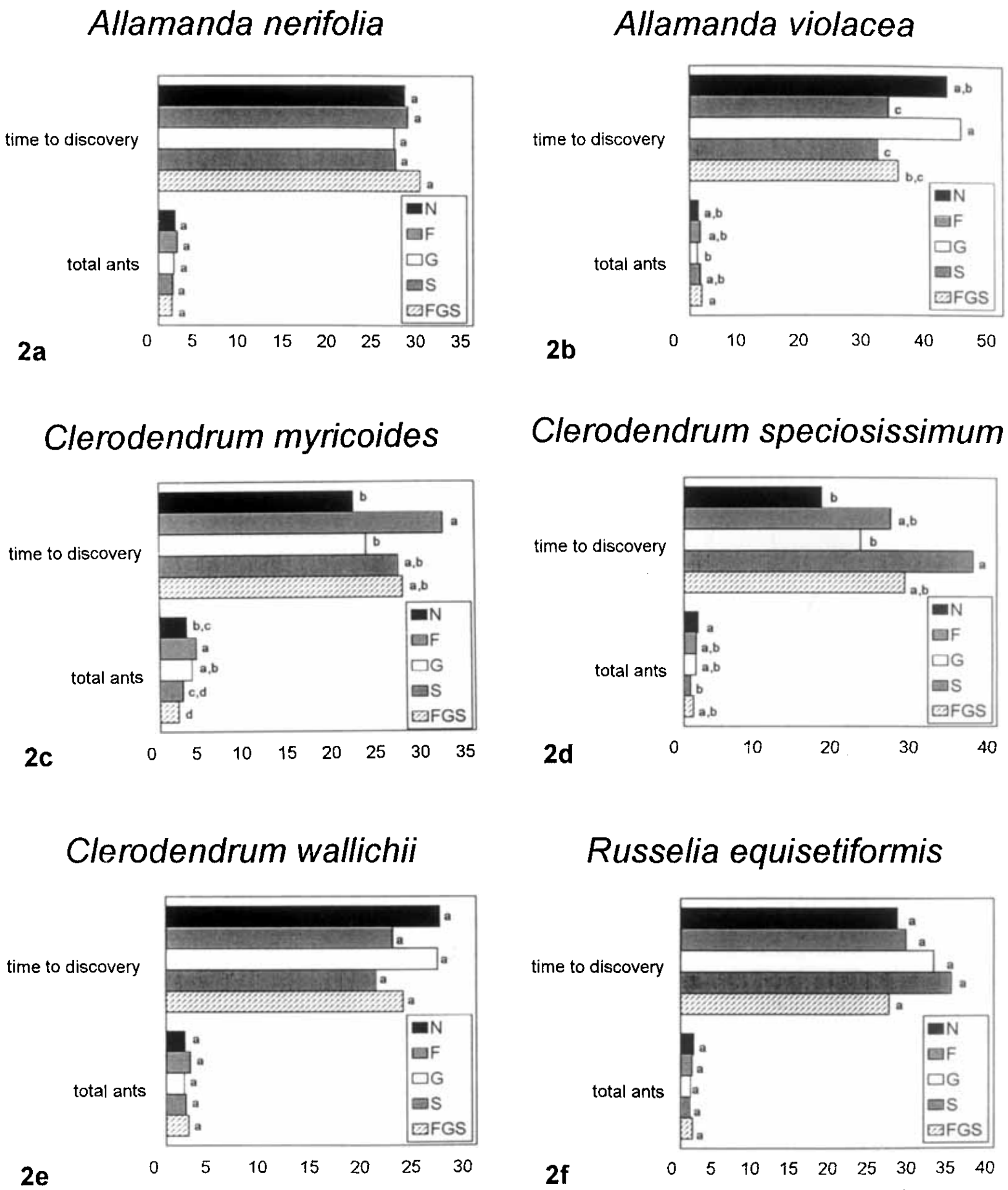


FIGURE 2. Results of feeding experiments with carpenter ants, *Camponotus abdominalis floridanus*. For explanation see Figure 1 legend.

have grouped the tests by ant species and by alphabetical order of the plant species within these groups. Certain nectars were tested with more than one ant species, but not all possible nectar-ant tests were performed because we did not always obtain enough nectar for all desired tests before the plant in question went out of bloom, and at some times could not find the desired ants for experimentation.

Significant preferences by crazy ants (Fig. 1) were shown for nectar of *Agave decipiens, Hamelia patens,* and *Kalanchoe gastonis-bonnieri.* For *Agave decipiens* (Fig. 1b), time-to-discovery for nectar was not significantly shorter than that of fructose, but the total number of ants was greatest. *Kalanchoe gastonis-bonnieri* nectar time-to-discovery was low (Fig. 1m), but not significantly different from fruc-

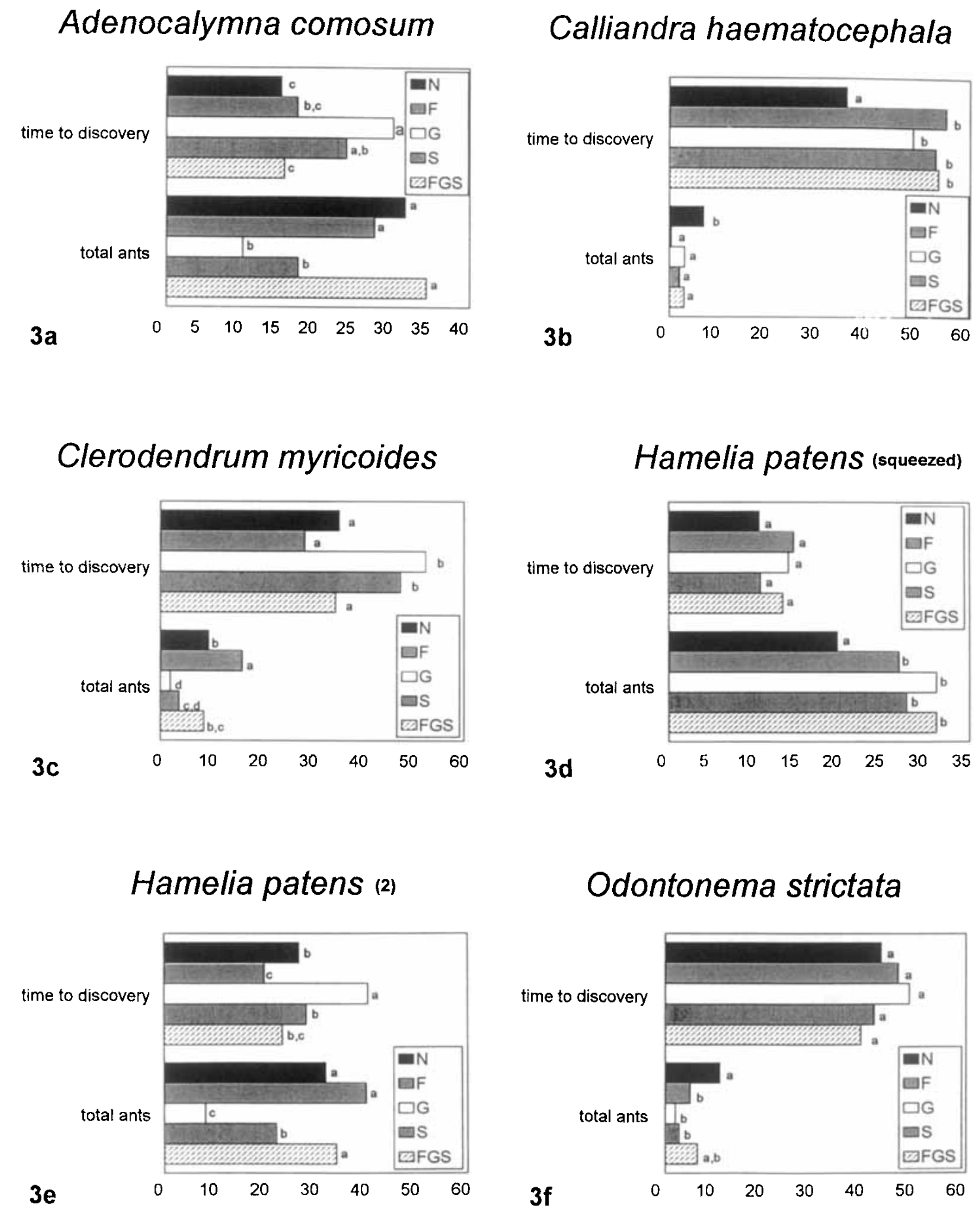


FIGURE 3. Results of feeding experiments with fire ants, *Solenopsis invicta*. For explanation see Figure 1 legend.

tose or from the FGS mixture, although the total number of ants was significantly greater than for all the other solutions. *Hamelia patens* nectar provided us with an interesting insight: our initial trials showed ants to have a great preference for the nectar over the sugars (and the nectar disappeared within 15 or 20 min in all cases). Analyzing results in the normal manner could not take this extreme preference into account, so we ran the experiments again, replacing the nectar drops when they were completely consumed. The first retest round showed the nectar to actually appear repellent (Fig.

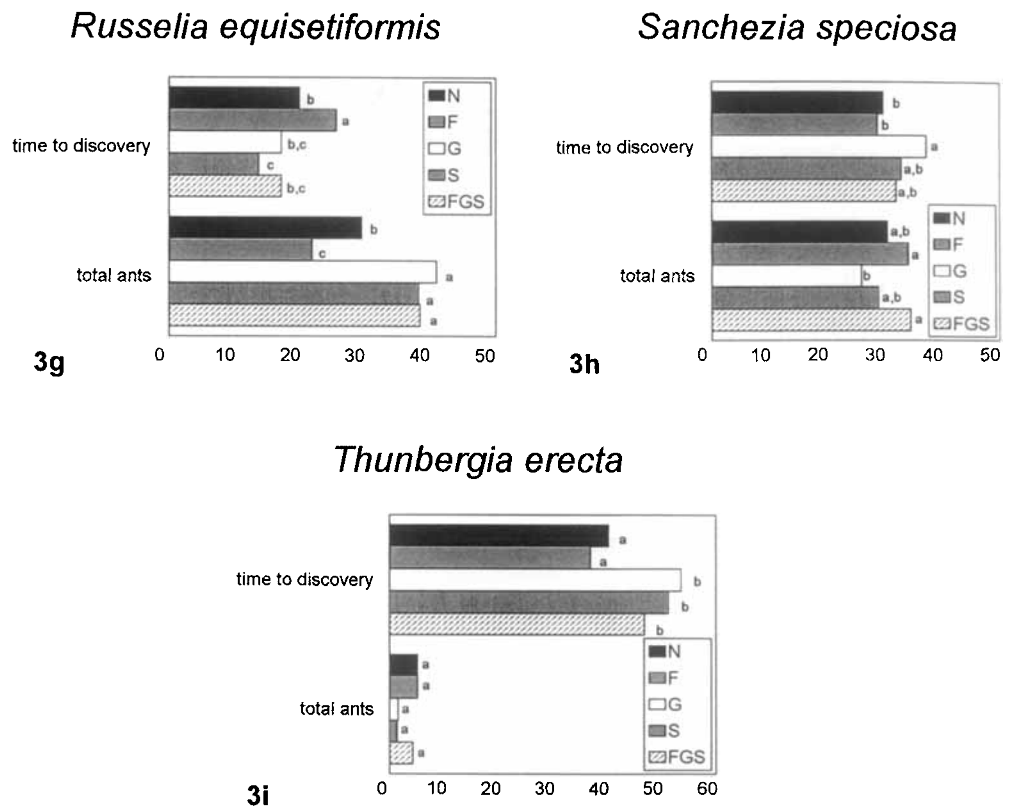


FIGURE 3. *Continued.*

1i), but it was discovered that the nectar had been contaminated by squeezing the corollas to expediently collect larger quantities of nectar; retesting with carefully collected nectar did not reveal the marked preference shown by the ants in our earliest trials (Fig. 1j), though the nectar was preferred over all the other solutions except for fructose. The nectar of *Crinum moorei* (Fig. 1g) had the greatest time-to-discovery, and significantly fewer ants than any of the sugar solutions, suggesting that this nectar has some repellent properties. In some of the experiments (Figs. 1j, 1p), fructose was preferred over the other sugar solutions. No other marked preferences were demonstrated.

Of the six nectars tested with carpenter ants (Fig. 2), none were preferred substantially over the sugar standards. No preferences among the sugar standards were exhibited in our tests.

Fire ants showed a preference for the nectar of *Calliandra haematocephala*; this nectar had the shortest time-to-discovery and the largest total number of ants (Fig. 3b). Though previous studies using sucrose solutions have shown fire ants to have a preference for more concentrated sugar solutions, fire ants did not exhibit a preference for sucrose in our experiments, but rather for fructose, in cases where there was a difference among the sugars (Figs. 3c, 3d, 3f).

Ghost ants showed significant preferences for nectars of *Bauhinia acuminata* and *Schotia brachypetala* (Fig. 4). Though the time-to-discovery of the *Bauhinia* nectar was not significantly different from that of the sucrose solution, the total number of ants was significantly different (Fig. 4a). For *Schotia,* time-to-discovery of the nectar was not significantly shorter than that of the FGS mixture, but the total number of ants was significantly greater than all the sugar solutions (Fig. 4c). No preferences for any of the sugar solutions were shown in the three experiments conducted.

Only two species were tested with white-footed ants, and neither had exceptionally attractive nectar (Fig. 5). In these two experiments, fructose and the nectars were more attractive than the other sugar solutions.

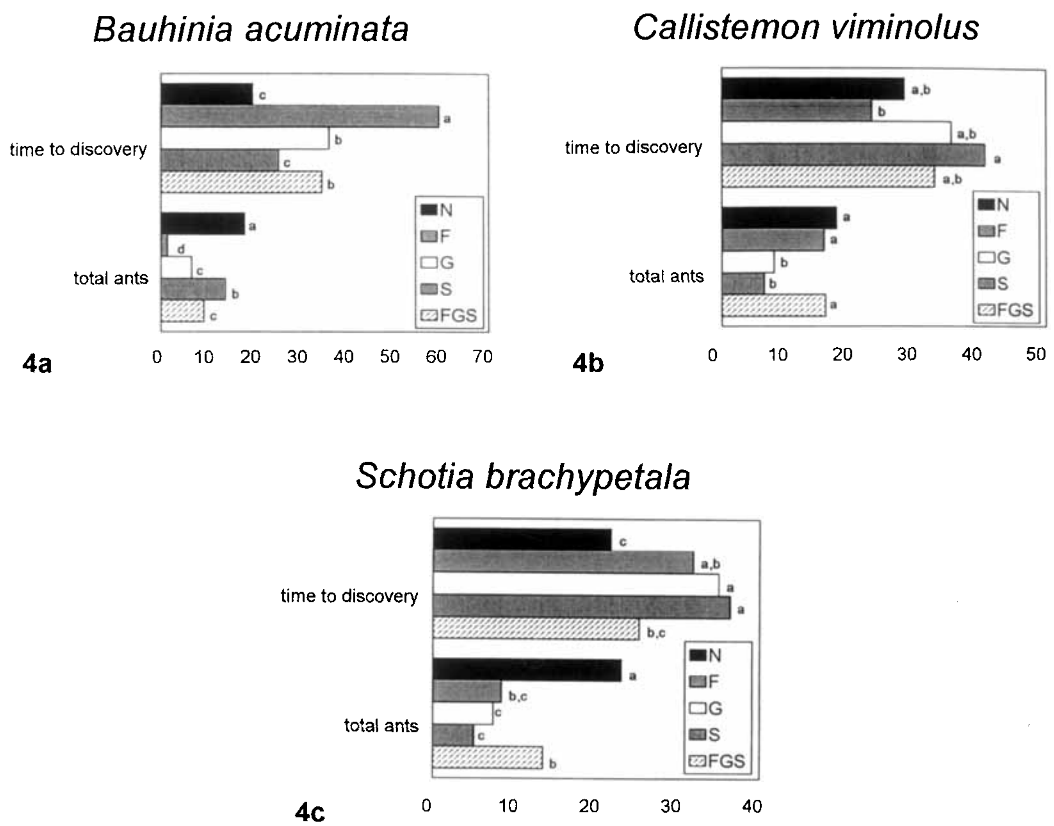


FIGURE 4. Results of feeding experiments with ghost ants, *Tapinoma melanocephalum*. For explanation, see Figure 1 legend.

DISCUSSION

It appears that, in most cases, the nectars we studied were accepted as well as sugar solutions by ants. In only one case (*Crinum moorei*) was the nectar less attractive than the sugars; and in numerous cases the nectar was more attractive than sugars to one or more pest ant species. The floral nectars used in our experiments are produced by plants with very showy flowers, used to beautify tropical landscapes. The nectars of these flowers have presumably coevolved with pollinators, not ants, and their use by ants (especially pest species) is facultative. Our observations concur with those of Guerrant and Fiedler (1981) that floral nectars are not, in general, ant repellent; however, there are some floral tissues that contain repellent substances (*e.g., Hamelia patens*), and when the corollas are damaged while collecting the nectar, the nectar is tainted with the repellent substance.

Few of the species we studied have morphologies that exclude crawling visitors from flowers, such as narrow tubes constricted at the mouth (*Brunfelsia grandiflora, Clerodendrum* spp., *Ixora coccinea*). Many of the species we studied have long, tubular corollas with wide openings (*Aloe saponaria, Kalanchoe gastonis-bonnieri, Justicia fulvicoma, Russelia sarmentusa, Thunbergia erecta*) and we often found ants taking nectar from the intact flowers. Though nectar is a valuable commodity produced by plants for the purpose of rewarding pollinators, an overabundance may often be produced as insurance to attract visitors in the face of few available pollinators or serious competition from other plant species. The relatively small amount lost to ants may not warrant protective measures in species that make an abundance of nectar; in some cases the plants may even benefit from the presence of ants utilizing their floral nectar, as when they use extrafloral nectar (Keeler 1989, Koptur 1992). Such potential facultative protective relationships warrant future investigation.

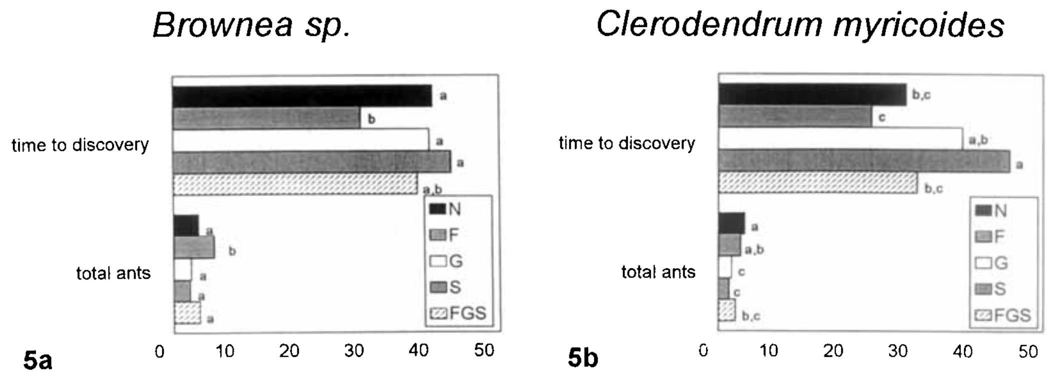


FIGURE 5. Results of feeding experiments with white-footed ants, *Technomyrmex albipes*. For explanation, see Figure 1 legend.

ACKNOWLEDGMENTS

We would like to thank Maria Cristina Rodriguez and Emiliano Granado for help in the laboratory, and Mark Deyrup for initial determination of the ant specimens. Don Bieman and Jules Silverman provided valuable discussion and facilitated support of this research by the Clorox Company. The manuscript was improved by comments from Paulo Oliveira and two anonymous reviewers, and Jorge Peña aided in Spanish translation. This paper is contribution 001 to the Program in Tropical Biology at Florida International University.

LITERATURE CITED

BAKER, H. G., AND I. BAKER. 1978. Ants and flowers. Biotropica 10(1): 80.

BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, England.

FEINSINGER, P., AND L. A. SWARM. 1978. How common are ant-repellent nectars? Biotropica 10(3): 238–239.

GUERRANT, E. O., JR., AND P. L. FIEDLER. 1981. Flower defenses against nectar-pilferage by ants. Biotropica (Reproductive Botany Supplement): 25–33.

HABER, W. A., G. W. FRANKIE, H. G. BAKER, I. BAKER, AND S. KOPTUR. 1981. Ants like flower nectar. Biotropica 13(3): 211–214.

HUXLEY, C. R., AND D. F. CUTLER. 1991. Ant-plant interactions. Oxford University Press, Oxford, England. 601 pp.

JANZEN, D. H. 1977. Why don't ants visit flowers? Biotropica 9(4): 252.

KEELER, K. H. 1989. Ant-plant interactions. *In* W. G. Abrahamson (Ed.). Plant-animal interactions, pp. 207–242. McGraw-Hill, New York, New York.

KERNER VON MARILAUN, A. 1878. Flowers and their unbidden guests. Translated into English and edited by W. Ogle. C. Kegan Paul & Co., London, England. 164 pp.

KOPTUR, S. 1992. Interactions between insects and plants mediated by extrafloral nectaries. *In* E. Bernays (Ed.). Insect/plant interactions. Volume 4, pp. 85–132. CRC Press, Boca Raton, Florida.

SCHUBART, H. O. R., AND A. B. ANDERSON. 1978. Why don't ants visit flowers? A reply to D. H. Janzen. Biotropica 10(4): 58–61.

VAN DER PIJL, L. 1955. Some remarks on myrmecophytes. Phytomorphology 5: 190–200.