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David W. Roubik; James D. Ackerman; Christine Copenhaver; Brian H. Smith

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# STRATUM, TREE, AND FLOWER SELECTION BY TROPICAL BEES: IMPLICATIONS FOR THE REPRODUCTIVE BIOLOGY OF OUTCROSSING *COCHLOSPERMUM VITIFOLIUM* IN PANAMA<sup>1</sup>

DAVID W. ROUBIK

Smithsonian Tropical Research Institute, APDO. 2072, Balboa, Panama

JAMES D. ACKERMAN<sup>2</sup>

Department of Biological Science, Florida State University,  
Tallahassee, Florida 32306 USA

CHRISTINE COPENHAVER

Department of Biology, University of Utah,  
Salt Lake City, Utah 84112 USA

AND

BRIAN H. SMITH

Department of Entomology, University of Kansas,  
Lawrence, Kansas 66045 USA

**Abstract.** Forager behavior in three patches of flowering *Cochlospermum vitifolium* (Malvales, Cochlospermaceae) and fruit, flower, seed, and ovule number on trees in six sites were used to test two incipient paradigms and study the role of bee pollinators in tree reproductive success. Anthophorid bees of the genus *Centris* were the most important pollinators. Behavior of both small and large *Centris* species indicated no consistent preference for flowers either in the densest floral arrays or within the stratum containing most flowers in the local flowering population. Flowers 7-12 m in height were never visited more often than flowers  $\leq 4$  m from ground level. However, within groups of 5-33 flowers, *Centris* visited on average at least 50% of the flowers during a foraging bout. Pollinating bees were indiscriminate in selecting inflorescences within floral arrays, but they appeared to maximize the rate of resource harvest once a small group of flowers was entered. The fruit of *Cochlospermum* contained an average seed number equal to 13% of the average ovule number per flower. Seed-set per fruit was no higher among flowers visited more often by pollinators than among flowers visited less frequently. Female competition for pollinators was not detected, but male competition may have occurred at one site where bees preferred flowers that were most abundant in the patch as a whole. Efficient outcrossing of a tree is in direct conflict with the optimal foraging of its pollinators. *Cochlospermum* may manipulate pollinators by (1) presenting small numbers of open flowers, (2) presenting large, conspicuous flowers and no leaves, and (3) providing only pollen concealed in poricidal anthers as a reward. If pollinators rather than the physiological capacity of a tree limited reproductive success, this probably arose from deposition of incompatible pollen on stigmas, rather than intertree competition or low pollinator abundance.

**Key words:** *Centris*; *Cochlospermum vitifolium*; competition; geitonogamy; height preference; optimal foraging; tree pollination; Trigonata; tropical communities.

## INTRODUCTION

Pollinating bees are essential pollen vectors of many tree species in the tropics (Bawa 1974, 1975, Bawa and Opler 1975, Frankie et al. 1976). Although information on the reproductive and population biology of tropical trees is minimal (Bawa 1975, Janzen 1978, Hubbell 1979, Opler et al. 1980), there is strong indication that zoophilous outcrossing predominates and that dispersion of conspecific trees is often clumped. For example, Hubbell (1979) reported clumped dispersion for nearly all tree species within Costa Rican dry forest.

In the same habitat, Frankie et al. (1976) and Opler et al. (1980) observed that bees are the primary pollinators of trees flowering in the dry season (Janzen 1967, Bawa 1975, Heithaus 1979a, Roubik and Michener 1979). Study of bees at natural aggregations of a flowering tree species should reveal patterns of bee and flower behavior that operate in tropical forest. *Cochlospermum vitifolium* (Malvales, Cochlospermaceae) was studied at six sites in Panama and presented a bee-tree system amenable to analysis and hypothesis testing. By studying *Cochlospermum* we focused on two incipient paradigms in the pollination literature and asked the following questions: (1) Do bees prefer flowers presented in large floral displays more than those in small arrays? (Carpenter 1976, Stephenson 1979, Waddington and Holden 1979, Augspurger 1980,

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<sup>2</sup> Present address: Department of Biological Science, University of Puerto Rico, Rio Piedras, Puerto Rico 00931.

Bawa 1980, Morse 1980). (2) Do bees prefer to visit flowers at a particular height? (Levin and Kerster 1973, Frankie 1975, Carpenter 1976, Faulkner 1976, Frankie and Coville 1979, Waddington 1979). We correlate observed foraging patterns with seed-set, ovule number, and flower dispersion within tree patches, then discuss implications of the data in light of foraging theory and the causes of observed tree reproductive success.

METHODS

*The tree and study sites*

*Cochlospermum vitifolium* is not capable of self-fertilization and must be outcrossed to produce fruit (Bawa 1974, D. W. Roubik et al., *personal observation*). The flower is yellow, 10–12 cm wide, and is presented at terminal inflorescences where it is open for 2 d. A single J-shaped style curves down from the flower; the stigma is presented 1–3 cm from the flower surface, slightly below the center of the flower. Numerous poricidally dehiscent stamens (150–200) are positioned in two groups: stamens with short filaments that surround the ovary, and outer stamens that are longer and curve inward at the apex (Croat 1978). Ovule number per flower ranges from 1000 to 2500 ( $\bar{x} = 1765, n = 50$ ). The flower does not produce nectar and in this feature, as well as in size, color, and floral morphology, resembles many *Cassia* (Fabaceae; Salinas and Sánchez 1977). Stamens must be vibrated or buzzed to release pollen (Buchmann and Hurley 1978, Eickwort and Ginsberg 1980). Any size tree from small ones near ground level to those 12 m high, may flower during the dry season (December to March during this study; see also Croat 1978). Fruits develop rapidly and reach 8 cm in length and 4–7 cm in width. Capsules remain on the tree through the dry season, and during this time seeds are dispersed by wind, with apparently no predispersal seed predation. Three sites were selected for observing flower visitors. Three additional sites were used to record fruit and seed-set. All sites were flat, open areas situated 300 m or less from lowland moist forest. Site G was 1.0 km north of Gamboa, Panama Province. Sites F, France Field, and T, near the former Tropical Test Center, were in Colon Province, near the Caribbean coast of central Panama. The three additional sites, denoted GL1–3, were near Gatun Lake in Colon Province. At all sites, individual *Cochlospermum* were in patches 200–600 m in length and 20–100 m in width. We counted 165 trees with fruit at site G, 20 at F, 27 at T, 21 at GL1, 25 at GL2, and 56 at GL3. Almost every tree within these stands held fruit at the end of the study, and many produced fruit by the time the study began (Fig. 1). At no time during the study were other flowering trees or shrubs visible from the study sites. With the possible exception of *Trigona* (Apidae, Meliponinae), which were seen at ground level vegetation, the bees seen at *Coch-*

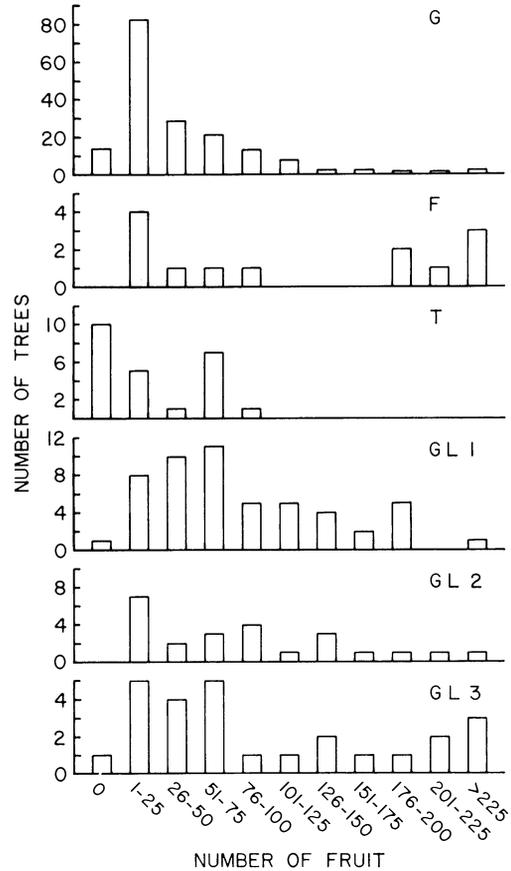


FIG. 1. Total fruit on all *Cochlospermum vitifolium* growing within six patches in Panama. Fruit were counted after the end of the flowering period.

*lospermum* visited no other flowers in the immediate area.

*Observations of flower visitors*

We watched groups of 5–33 flowers for 5-min periods each, on at least 10 trees, then repeated the observation sequence 3 times/d for a total of 30 counts/d. There was almost no visitation to flowers before 0800 and little after 1300. Because of lack of conspicuous floral odor and nectar, the chance of visitation by bats seemed negligible. Flower visitors were observed from 0815 to 1115, although occasional early morning rains necessitated more varied observation periods at sites F and T. We usually collected data during two successive days, followed by a 4-d interval, then repeated this pattern. Observations at site G began on 8 February and ended on 27 February 1980. At site F, visitation data were taken from 19 February until 6 March, and at site T, from 11 February to 9 March. Flowering began earlier in the season at site G, but by the end of the study there were few flowers at any site (Fig. 2). The first individuals to flower did so in December, but peak flowering occurred during

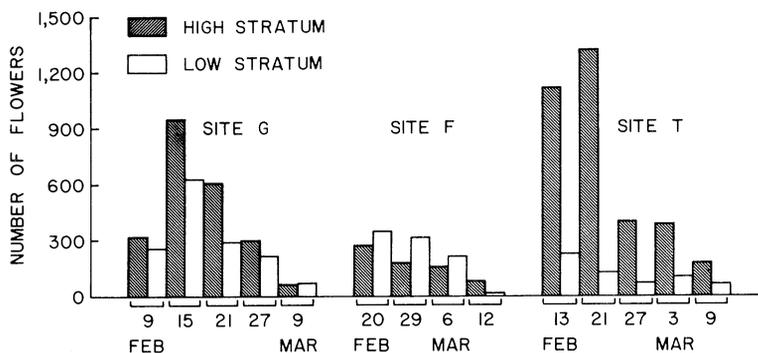


FIG. 2. Total flowers counted in the high ( $\geq 7$  m) and low ( $\leq 4$  m) strata of flowering *Cochlospermum vitifolium* during flower visitor observation periods at three sites.

January and February. In addition, *Cassia alata*, a tree with yellow flowers, flowered during January. Visitors of *Cassia* also visit *Cochlospermum*, and we wished to avoid making observations of pollinator behavior when the bees were likely collecting pollen at more than one tree species.

All records of flower visitors were made for two strata. We designated flowers  $\leq 4$  m from ground level as low and those  $\geq 7$  m as high. The low flowers were generally on small trees not above 7 m in height. High flowers, although often the only flowers on large trees, were sometimes on trees with flowers in the middle stratum. The observations made during 1 d included five trees with low flowers and five with high flowers at sites G and F, and roughly equivalent numbers of observations at each stratum in site T. To quantify flower visitation on a per-flower basis, the number of flowers watched during each 5-min observation was recorded. In addition, we counted the number of flowers on each tree. Every 2nd d of a 2-d observation sequence, we counted the number of flowers and fruit in both strata within the entire study area, which encompassed all the *Cochlospermum* we could see. Visitors at flowers in the high stratum were observed with binoculars. Bees were collected at each site and identified to species. Identification of genera and some species was made with ease in the field, but the collections revealed that several species of fast-flying *Centris* (Anthophoridae) were very similar in size and color. It was therefore not possible to study the behavior of particular *Centris* species, but only of relatively large ( $\geq 15$  mm) and relatively small ( $\leq 11$  mm) species, treated operationally as two forager categories.

#### Measurement of seed-set and pollination

After flowering had terminated, a sample comprising 20% of total fruit was collected from observation trees and from adjacent trees. Additional fruit was harvested at sites GL1–3. Fruit was collected with an extension pruning shears, which facilitated height measure-

ment when fruit was taken. We did not use a random number table to select fruit, but samples were taken from more than one branch. Not all flowers on a branch opened at the same time; thus the fruits contain information on pollinator visits during much of the flowering period. We counted the fruit in all six sites in each of the two strata we delimited, as well as total fruit per tree. Seed-set was determined by opening the capsules and counting seeds within their five locules. The number of seeds within locules differed widely within a capsule; hence subsamples were not used to assess seed-set. The potential seed production of flowers was sampled by counting all the ovules within five low and five high flowers gathered at each of five sites. Flowers for ovule counts were collected in February 1981, and at this time site GL-2 had been cleared. In addition, five fruit were taken from each tree from the same branches on which flowers were collected. Seed-set was determined for the fruit. We wanted to show whether ovule and seed number were correlated and whether ovule number was related to the type of tree (e.g., small tree, low flowers). There was no direct method for determining ovule and seed number from the same flower, but it is likely that adjacent flowers on the same branch had similar ovule number.

To determine whether the small *Trigona* were pollinators, we caged 58 flowers at sites T and F with 1.3-cm (1/2-inch) mesh hardware screen. All other flower visitors were larger than *Trigona* and were excluded from caged inflorescences. We also bagged 10 inflorescences to exclude all visitors.

## RESULTS

### The bees

Principal visitors of flowering *Cochlospermum* were *Centris* and *Xylocopa* (Anthophoridae), *Trigona*, *Eulaema* and *Euglossa* (Apidae, Table 1). *Melipona interrupta triplaridis* (Apidae, Meliponinae) visited flowers occasionally but far less often than the other genera. All but *Trigona* are relatively large bees ( $> 6$

TABLE 1. Total recorded visits by five genera of bees to flowers of *Cochlospermum* censused at three sites in Panama.

Site	Date	Number of flowers observed	Number of recorded flower visits					
			<i>Centris</i> *	<i>Centris</i> †	<i>Trigona</i>	<i>Xylocopa</i>	<i>Euglossa</i>	<i>Eulaema</i>
G	8 February	534	97	106	77	32	1	0
	9 February	296	181	237	61	0	0	0
	14 February	425	121	204	122	4	2	0
	15 February	474	37	41	96	3	6	4
	20 February	507	45	86	122	1	6	0
	21 February	490	70	97	131	14	18	26
	26 February	261	38	177	56	3	7	0
	27 February	257	29	161	35	0	14	8
T	13 February	187	3	13	19	1	1	0
	20 February	114	35	10	41	0	1	0
	21 February	110	29	16	41	9	4	0
	26 February	97	23	20	34	0	8	0
	27 February	68	18	16	20	0	12	0
	2 March	98	8	42	40	0	0	20
	3 March	82	0	55	46	3	6	5
	8 March	85	33	78	45	0	0	2
	9 March	74	25	50	33	0	2	3
F	19 February	314	37	0	134	8	2	0
	20 February	471	34	0	202	0	0	0
	27 February	402	75	9	140	0	0	0
	29 February	280	34	2	144	0	0	0
	5 March	262	18	0	74	0	0	0
	6 March	312	29	2	133	0	0	0

\* Large *Centris*.† Small *Centris*.

mm length) and are buzz pollinators; they vibrate their flight muscles while clinging to stamens and cause poricidally dehiscent pollen to shoot out of the anthers (Buchmann and Hurley 1978, Thorp 1979, Eickwort and Ginsberg 1980). The buzz pollinators commonly visit the same plant species to collect pollen with this specialized technique (Heithaus 1979a, b, Roubik 1979a, b). *Trigona* either gleaned pollen by collecting fallen grains on flower petals or bit through anthers and removed pollen with the proboscis. The first foraging style was seen in *T. (Tetragona) nigra paupera*, *T. (Tetragona) jaty*, and *T. (Partamona) cupira*. Robbers included *T. (Trigona) pallens*, *T. (Trigona) fuscipennis*, and *T. (Trigona) corvina*.

*Trigona* did not visit flowers at the same tempo as the other bees. The relatively large bees *Centris inermis* (14 mm length), *C. fuscata* (14 mm), *C. (Trachina) sp.* (16 mm), *C. trigonoides* (10 mm), *Xylocopa frontalis* (28 mm), *Eulaema nigrita* (20 mm), and *Euglossa imperialis* (14 mm) made very short visits to each flower. For *Centris*, the duration of a visit did not exceed 2 s. In contrast, *Trigona* tended to remain on a flower or hover nearby for several minutes.

#### Height preferences of foragers

The recorded visitation by foragers to low or high flowers was treated as a binomial probability ( $p$ ), and  $p$  was transformed to the arcsine (in radians) of  $\sqrt{p}$  for statistical analysis (Pollard 1977:242). Data on number of visitations  $\cdot$  flower $^{-1}$   $\cdot$  (5 min) $^{-1}$  were pooled for all trees at a site on a given day, and the flower

visits in high and low strata were compared using two-way ANOVA, adding a correction factor for small values. In such tests,  $H_0$  = visitation was random, or flowers in high and low strata received visits in equal number. The analysis was applied to visitation over the entire study period at each site.

A summary of the analysis is presented in Table 2, based on the total visits by forager groups presented in Table 1. Small *Centris*, apparently all of the species *trigonoides*, preferred lower flowers at site G ( $P = .02$ ). No height preference by small *Centris* was seen at site T ( $P = .08$ ), although visits tended to be concentrated in the high stratum. Large *Centris*, which included at least three species in unknown proportions, did not show height preference at sites G and T ( $P = .29$  and  $P = .15$ , respectively), but lower flowers received more visits from the bees at site F ( $P = .01$ ).

*Trigona* showed no height preference at two sites but were more common on higher flowers at site G ( $P = .02$ ). The day-to-day variation in visitation to a stratum by all three forager groups was negligible at all three sites ( $P > .40$ ; Table 2).

#### Forager behavior and the foraging environment

The size of the tree patches (see Methods) was well within the flight range of bees that we observed; the anthophorids and all apids except *Trigona* may readily span distances of several kilometres while foraging (see review by Eickwort and Ginsberg 1980). In this setting, it was possible to assess whether foraging bees

TABLE 2. Two-way ANOVA summary of arcsine-transformed (in radians) probability of flower visitation to *Cochlospermum vitifolium*. The high stratum contained flowers 7–12 m above the ground; the low stratum was  $\leq 4$  m. "Large *Centris*" ( $\geq 15$  mm) comprised at least three bee species, "small *Centris*" ( $\leq 11$  mm) included one species, and *Trigona* at one site comprised at least three species. In the data matrix for each site, columns were flower heights, and rows were the observation dates.

Site	Flower visitor	Transformed mean probability		Flower height		Date		df
		Low stratum	High stratum	F	P	F	P	
G	Small <i>Centris</i>	0.95	0.62	9.75	.02	0.36	.90	1, 7
	Large <i>Centris</i>	0.76	0.84	1.31	.29	0.12	.99	1, 7
	<i>Trigona</i>	0.66	0.88	7.86	.03	0.10	.99	1, 7
F	Large <i>Centris</i>	1.04	0.53	17.96	.01	<0.01	.99	1, 5
	<i>Trigona</i>	0.81	0.77	2.32	.19	1.06	.48	1, 5
T	Small <i>Centris</i>	0.63	0.93	3.97	.08	<0.01	.99	1, 8
	Large <i>Centris</i>	0.62	0.95	2.59	.15	<0.01	.99	1, 8
	<i>Trigona</i>	0.78	0.79	0.03	.86	<0.01	.99	1, 8

learned resource distribution within patches and responded optimally by selecting the most profitable (densest) resource configurations. Again, we do not presume to analyze individual foraging behavior, but the combined foraging preferences of particular genera or size categories. The stratified distribution of total flowers within patches during each census period is shown in Fig. 2. Flowers in the higher stratum predominated at sites G and T. Flowers in the lower stratum were more common at site F. Greater floral abundance at a particular stratum persisted through most of the study at these sites and probably was maintained throughout the flowering period of *Cochlospermum*.

In no instance did *Centris* prefer higher flowers, even though these flowers were most common at sites G and T. However, large *Centris* most often visited low flowers at site F, where lower flowers predominated (Table 2, Fig. 2). *Trigona* were most abundant in the high stratum at site G but were evenly distributed among strata at sites F and T.

A second manner in which bees might select flowers within a patch could be based on the size of the floral display, or total flowers on a tree. Trees held on average  $\leq 25$  flowers at one time, but the range of flower number was considerable (Fig. 3). Some larger bee species were observed in numbers too low to analyze separately (Table 1), and data on visitations by these bees and by *Centris* were combined in a single category. Larger bees showed a clear preference for flowers on trees with the smallest flower number at site T ( $P = .001$ ,  $\chi^2$  test; Table 3). There was no association between flower number and visitation at trees in site G ( $P = .87$ ,  $\chi^2$ ), and an indicated association between greater visitation rate and higher flower number at site F ( $P = .04$ , Fisher's exact test). Tests of association were made by dividing visitation rate and flower number into somewhat arbitrary categories, and different category divisions produce different statistical results. However, such results are potentially misleading only

when expected cell values are very small and probabilities are near the critical (.05) level. Regression analysis did not enhance interpretation of the data. The analysis indicates primarily that foraging behavior of larger bees was not consistent in different patches of *Cochlospermum*. *Trigona*, however, were no more abundant on flowers of trees having many flowers than at trees with few flowers ( $P > .13$ ; Table 4).

#### Fruit and seed-set

The larger bees apparently were efficient and effective pollinators. They spent a short time on individual flowers, landed in the center of the flower, and could contact the stigma while vibrating stamens or when approaching and departing from a flower. Intertree movement occurred frequently. The *Trigona* were inefficient pollinators, hovering by a flower periodically to pack pollen in the corbiculae and spending many minutes on a flower. The robbing *Trigona* often visited flowers in groups of four to eight bees. However, four fruit were produced from 58 caged flowers, and only *Trigona* were seen within the cages. Flowers bagged to exclude all visitors produced no fruit.

Numbers of fruit per tree and seed per fruit were independent of ovule number; ovule number was not associated with tree size, floral stratum, or total flower production on trees. The number of ovules in flowers was not associated with tree size ( $P = .56$ ,  $\chi^2$ ; Table 5). Seed number per fruit was not correlated with ovule number in adjacent flowers on the same branches ( $P = .27$ , Fisher's exact test; Table 5), and ovule number was not associated with the total fruit on individual trees ( $P = .57$ ,  $\chi^2$ ). Trees producing the largest number of fruit did not produce larger numbers of seed per fruit (Table 6), and our limited observations of individual trees during the interval indicated in Fig. 2 showed a positive correlation between total flower and total fruit production ( $P = .008$ , Fisher's exact test). Therefore, the above data indicate that female reproductive success (Cruden 1975), as measured by

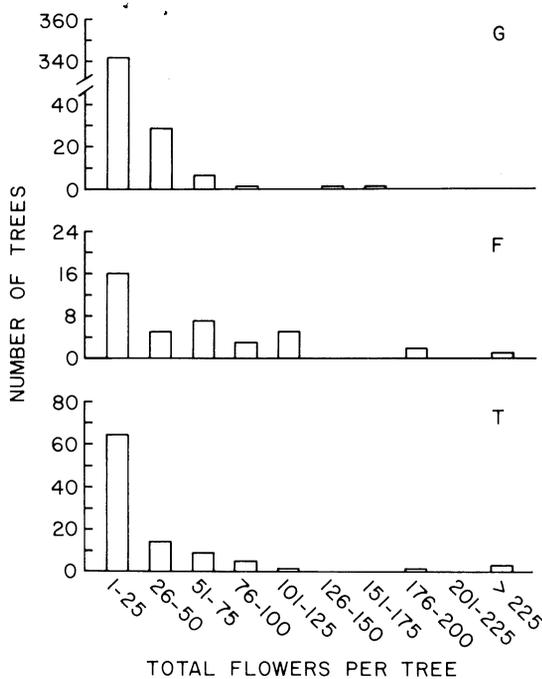


FIG. 3. Total flower number on *Cochlospermum vitifolium* censused for flower visitors at three sites.

the number of seeds in fruit, was not influenced by ovule number, the stratum in which the flowers were produced, the size of the tree, or its total flower production.

No difference in the number of seeds per fruit was found for fruit from high or low strata (Table 7). The data from each pollinator observation site were analyzed separately, but seed-set data from sites GL1-3 were pooled. A nested analysis of variance showed no significant difference in seeds per fruit according to stratum ( $P = .17-.22$ ) at pollinator observation sites.

TABLE 3. Analysis of association between visitation rate by *Centris*, *Xylocopa*, *Eulaema*, and *Euglossa* and the number of flowers on individual *Cochlospermum* at three sites in Panama.

Site	Number of flowers on tree	Visits · flower <sup>-1</sup> · (5 min) <sup>-1</sup>		$\chi^2$	P
		≤0.5	>0.5		
G	5-22	23	23	0.026	.872
	24-182	12	13		
T	5-20	27	19	10.658	.001
	21-227	23	1		
F	6-57	9	2	...*	.038
	62-293	13	16		

\* Fisher's exact test was used in this case because of small sample size.

TABLE 4. Analysis of association between visitation by *Trigona* and the number of flowers on individual *Cochlospermum* at three sites in Panama.

Site	Number of flowers on tree	Visitors · flower <sup>-1</sup> · (5 min) <sup>-1</sup>		$\chi^2$	P
		≤0.2	>0.2		
G	5-22	19	27	0.732	.392
	24-182	12	11		
T	5-20	14	22	2.239	.134
	21-227	13	9		
F	6-57	12	2	...	.194*
	62-293	14	7		

\* Fisher's exact test.

The pooled data from sites GL1-3 showed greater seed production in the higher stratum ( $\bar{x} = 218$ , high;  $\bar{x} = 150$ , low) that approached statistical significance ( $P = .06$ ). Large variance was evident among trees of similar size at each site (variance among subgroups [trees], Table 7).

Distribution of fruit among strata was similar to the distribution of flowers at sites G and T but not at site F (Figs. 2, 4). Higher fruit were far more common at five of six sites (Fig. 4).

DISCUSSION

Pollinator behavior

Bees of the genus *Centris* were the most abundant larger bees visiting *Cochlospermum* and presumably the major pollinators; they efficiently manipulated poricidal anthers to obtain pollen, contacted stigmas, and moved between trees. Flower selection by large ( $\geq 15$  mm) and small ( $\leq 11$  mm) *Centris*, and by larger bees

TABLE 5. Analysis of association between ovule number in flowers and tree size, total fruit production, and seed number in fruit on the same branch. Data were taken from five flowers and five fruit collected on one large tree bearing high flowers and one small tree bearing low flowers of *Cochlospermum vitifolium* at each of five sites (df = 1).

	Number of ovules per flower*		$\chi^2$	P
	<1765	≥1765		
Tree size				
Large (>7 m)	14	16	0.33	.56
Small (<4 m)	11	9		
Fruit total per tree				
<65	12	13	0.32	.57
≥65	14	11		
Mean no. seeds per fruit				
<200	4	1	...	.27†
≥200	2	3		

\*  $\bar{x}$  ovule number = 1765, range 1000-2500.

† Fisher's exact test.

TABLE 6. Fisher's exact tests of association between total fruit on individuals of *Cochlospermum* and seed-set per fruit at six sites in Panama.

Site	$\bar{x}$ seed per fruit per tree	Number of fruit per tree		P
		5-50	55-180	
G	$\leq 200$	11	3	.91
	$> 200$	15	4	
T	5-50	55-105		.17
	$\leq 150$	7	1	
	$> 150$	10	7	
F	5-50	55-320		.50
	$\leq 193$	4	2	
	$> 193$	3	3	
GL1-3	5-50	55-140		.54
	$\leq 150$	3	4	
	$> 150$	7	5	

as a whole (*Centris*, *Eulaema*, *Xylocopa*, *Euglossa*) was not consistent among local populations of *Cochlospermum*. Their behavior did not often conform to a prediction of optimal foraging theory: that bees conduct foraging in such a way as to maximize the rate of resource harvest (Pyke et al. 1977). Bees generally did not prefer flowers in the stratum having the most flowers and did not visit flowers more often on trees presenting many flowers compared to those having few. Total foraging bouts in these flower configurations may have varied with resource display (Roubik 1982), but the number of visits per flower generally did not. *Centris trigonoides* preferred flowers in the richest floral stratum at one site and showed the opposite tendency at another. Large *Centris* species did not preferentially forage in the richest stratum in two sites, but more often visited flowers in the richest stratum at a third site. In none of five height preference analyses made for *Centris* did bees visit higher flowers significantly more often than lower flowers. This finding may be unexpected, considering an experimental study by Frankie and Coville (1979) that showed preference by *Centris* for higher flowers. However, they studied visitation to potted shrubs at 4.5 m compared

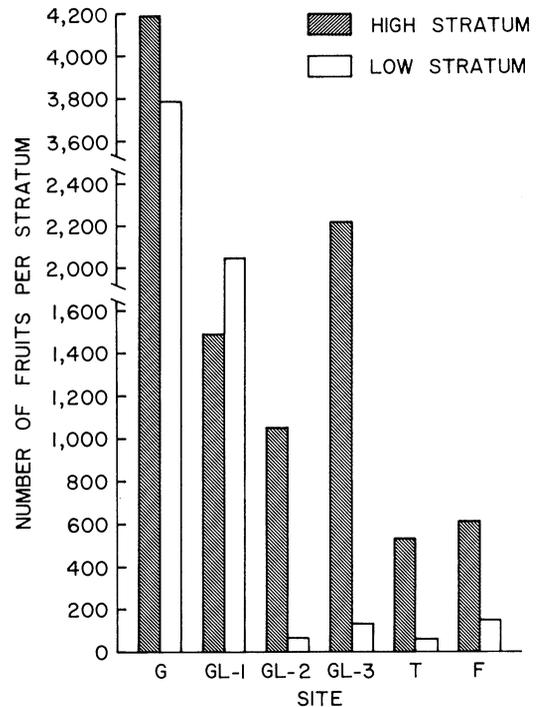


FIG. 4. Total fruit in high ( $\geq 7$  m) and low ( $\leq 4$  m) strata of *Cochlospermum vitifolium* at the end of the flowering period at six sites in Panama.

to visits at  $< 1$ -m height, and these observations are not comparable to natural conditions, which we studied. Selection of trees by larger bees according to total flowers was variable. Each of three possibilities: no preference, preference for small floral arrays, and a greater but statistically marginal preference for large floral arrays, was observed. The observation that inflorescences rather than the combined flowers on a tree constituted a natural unit of attraction to bees is a topic for further study (Stephenson 1979).

Considering the major pollinators of *Cochlospermum* as a whole, the question of what determines flower preference remains open, but the bees apparently responded to individual flowers and inflorescences, rather than to the array in which flowers oc-

TABLE 7. Results of nested analyses of variance of the number of seeds set per fruit in high and low strata of *Cochlospermum* fruit at six sites in Panama. Systematic samples of 20% of total fruit were taken from each tree. Trees included all observation trees at sites G, T, and F; sites GL1-3 were pooled. Nested groups of trees that set fruit at either the high or the low stratum were compared. Statistical methodology was taken from Sokal and Rohlf (1969:274).

Site	Number of trees		Number of fruit		Mean seed-set		Strata		Trees	
	High	Low	High	Low	High	Low	F	P	F*	P
G	14	16	159	114	232	216	1.99	.17	7.23	.001
T	14	9	158	33	175	153	2.04	.17	9.07	.001
F	5	6	134	38	194	156	1.78	.22	2.01	.05
GL1-3	8	8	124	72	218	150	4.12	.06	10.90	.001

\* Among subgroups (trees) within groups (trees with fruit at a particular stratum).

curred. Within the inflorescences we observed, bees seemed to maximize the rate of resource harvest. *Centris* usually visited most of the observation flowers during a single foraging bout ( $\bar{x}$  small *Centris* = 77% of total flowers visited,  $SD = 79\%$ ,  $n = 223$ ;  $\bar{x}$  large *Centris* = 50%,  $SD = 54\%$ ,  $n = 227$ ). Variation about the mean foraging behavior was large, perhaps in part because of species or individual differences within a size category. Behavioral variability among female *Centris* could also arise because of the dispersion of their nests, nectar, and oil flowers (Anderson 1979, Heithaus 1979b, Roubik 1979a, Thorp 1979). Explanation of foraging behavior of any bee at flowers providing only pollen is to some extent precluded by ignorance of other sites bees must visit.

Pollinator movement among flowers was not noticeably influenced by direct interactions among foragers, but robbing by *Trigona* may have damaged stamens to the extent that larger pollinators were deterred (McDade and Kinsman 1980, Roubik 1982). Behavioral interactions involving *Trigona* seemed confined to intrageneric aggression. Individual *T. pallens* and *T. corvina* attacked other *Trigona* on flowers. As pollen gleaners or robbers, *Trigona* appeared opportunistic in the selection of trees and flowers. Height preference was recorded only at one site, and the number of bees on flowers had no relation to the number of flowers on trees at any site (Roubik 1982).

#### *Reproductive success of Cochlospermum*

Was seed-set limited by pollinator visits, and was there significant competition for pollinators? Competition occurs if the reproductive success of one tree diminishes that of another. Our analysis included groups of trees rather than individual trees. Greater visitation to large trees with high flowers, small trees with low flowers, or trees with large or small flower number suggests pollination and pollen donation were more prevalent at flowers of a particular group. Although *Centris* displayed differential visitation to flowers in the above categories at some sites, and it was the most abundant pollinator, this had no effect on seed-set. Preferred trees did not produce more seeds per fruit, although they possibly produced more fruit per flower. Female reproductive success per fruit did not involve competition for pollinators, but male competition is partly implicated by visitation data from one site. Visitation at low flowers was greater at site F, and low flowers were more common than high flowers. Total pollen carried by bees was predominantly that of low flowers. Competition may have occurred between other tree types that were not considered, or between discrete tree patches.

Average seed-set per fruit in combined sites was about 13% of the average ovule number per flower. This fact implies equally that seed production approached a physiological maximum and pollinations were superabundant (Stephenson 1979, Zimmerman

1980), or that incompatible pollen deposited on stigmas greatly limited female reproductive output. *Centris* visited a large proportion of the observation flowers during a foraging bout, and geitonogamy occurred frequently, but detailed study of pollen tube growth within pistils would be necessary to explain the low realized female reproductive success of *Cochlospermum*. If pollinators limited tree reproduction, this may have arisen more from forager behavior at individual trees than from intertree competition or the general abundance of pollinators.

While the seed-set data reflect total visitation during the flowering of *Cochlospermum*, visitation was recorded only during roughly one-half of this period. At least one study (Zimmerman 1980) shows that competition for pollinators may vary during the flowering period of a plant. However, as the visitation rate at all sites did not vary substantially from day to day during 1 mo, we are confident that the visitation patterns can be applied to the entire flowering period.

The reproductive success of an outcrossing tree is in direct conflict with the maximum foraging efficiency of its pollinators. If all pollinators foraged optimally, then outcrossing would be severely limited. Effective outcrossing is in part the result of effective manipulation of bees by trees. Several features of *Cochlospermum* are of particular significance in this regard: (1) 25 or fewer flowers were open at once on most trees; (2) very large, conspicuous flowers were presented, and trees have few or no leaves while flowering, and (3) no nectar is provided, and pollen, like that of buzz-pollinated flowers in general (Thorp 1979), is unusually small and concealed in the anthers. All of the larger bees that visited *Cochlospermum* must collect at least several cubic centimetres of pollen to provision brood cells (D. W. Roubik, *personal observation*, Vinson and Frankie 1977, Roubik and Michener 1979). Bees must visit hundreds of flowers, and they may not perceive the reward received per flower; minute pollen is sprayed on the body, not collected with the legs or received by the mouthparts. Considering the probable ignorance of pollinators regarding the reward obtained from a flower, one simple adaptive strategy would be to visit many flowers and to visit at the maximum possible rate. Once a flower patch has been located, some bees may be relatively indiscriminate in flower selection. Even if pollen available in anthers were perceived, a flower visit would probably be necessary, and pollination could occur. Attractiveness of individual flowers and the small quantity of pollen provided per tree, relative to that needed by the pollinators, appeared to ensure pollination within local populations of *Cochlospermum*.

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