CONTRASTING FORAGING STRATEGIES AND COEXISTENCE OF TWO BEE SPECIES ON A SINGLE RESOURCE[1]

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Abstract. The foraging patterns of two eusocial stingless bees, *Trigona fuscipennis* and *Trigona fulviventris*, were studied on a population of the shrub, *Cassia biflora*, in a tropical dry forest in Costa Rica. *Trigona fuscipennis*, which forages in large groups that monopolize plants, restricted its visits to large, dense clumps of *Cassia*. Visited plants had significantly more flowers than nonvisited plants. *Trigona fulviventris*, which forages as individuals or in small groups, visited more widely spaced or isolated plants. In the isolated plants visited by *T. fulviventris*, there was no significant difference in the number of flowers on visited vs. non-visited plants. In clumps, however, the few plants visited by *T. fulviventris* had significantly fewer flowers than plants not visited. This observation and observations of interspecific aggression suggests that *T. fulviventris* is excluded from the better plants in clumps by *T. fuscipennis*. We believe the observed foraging patterns result from both evolved strategies and displacement due to short-term ecological competition. To explain the results, we hypothesize that two species may stably partition and coexist on a single resource, provided that (1) the resource has a highly variable spatial dispersion pattern, ranging from dense local patches to large regions of thinly spread resource, (2) the thinly spread resource is profitably harvested by only one of the species, (3) the dense patches are controlled by the second species, and (4) the resource is nonmobile such that no mixing of resource occurs between dense and sparse areas. We propose the terms "low- and high-density specialists" to describe such species.

Key words: Bees, stingless; coexistence; Costa Rica; density specialization; foraging strategy; insect, social; resource partitioning; Trigona.

INTRODUCTION

Two species of stingless bees, *Trigona fuscipennis* Friese and *Trigona fulviventris fulviventris* Guérin, foraged for several months in 1972–73 on the pollen of *Cassia biflora* L., a legume shrub of the tropical dry forest life zone (Holdridge 1967), in the Pacific lowlands of Costa Rica.

We undertook a study to determine how the two species utilized the same food resource and whether competition was occurring. Earlier observations (Johnson 1974) suggested that these two species might employ very different foraging strategies, and could achieve the stable partition of a common food resource, provided that the resource was persistent and had a highly variable pattern of spatial dispersion. *Cassia biflora* proved to be an excellent food resource for testing this possibility. The *Cassia* population flowered from late November to late March and exhibited the required variability in pattern of dispersion. *Cassia*, a very important dry season flowering plant in Guanacaste, was a particularly significant food plant for bees in the drought year

1972–73 when fewer alternative flowers bloomed (Johnson 1974).

One colony each of *Trigona fuscipennis* and *Trigona fulviventris* foraged on the *Cassia* population. Both bee species are of equivalent size, come from colonies of approximately equivalent numbers of individuals (Johnson 1974), and employ the same method of pollen extraction, namely chewing open the thick-walled anthers (Wille 1963).

METHODS

The study site is located on the Comelco Ranch in Guanacaste Province, Costa Rica (lat. 10°32′N, long. 85°18′W), about 25 km NW of Cañas. The site (Fig. 1) contains a strip of forest-savanna ecotone where *Cassia*, a second growth species, grows abundantly in patches and as isolated plants.

The study area, 260 m by 160 m, was gridded with stakes at 20-m intervals. Within these quadrats each *Cassia* was numbered on a piece of masking tape attached to the stem, and mapped to the nearest 0.5 m. One nest each of *Trigona fuscipennis* and *T. fulviventris* occurred in the study area; these were mapped. There were two patches of *Cassia*. One was termed the "near patch" as it was closer to both nests, while the other was termed the "far patch."
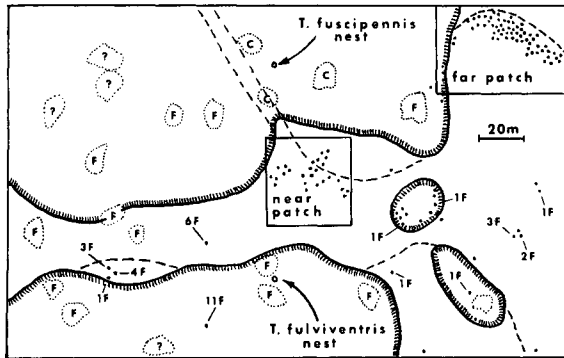
FIG. 1. Map of study site (260 m × 160 m). Hatched lines mark boundaries of forest, and dotted lines mark edges of brush patches. Dots represent individual *Cassia biflora* shrubs. Dotted, irregular circles are outlines of the canopies of *Calycophyllum candidissimum* trees also visited by *Trigona fulviventris* (F) and *T. fuscipennis* (C). Isolated *Cassia* shrubs visited by F or C are marked with the number of bees present. Near and Far patches are expanded in Figs. 3 and 2, respectively. North is toward top of figure.

Counts of bees and open flowers were made for each plant between 1000 and 1100 on three successive days in December 1972. Plants in the near patch were surveyed on the 17th, the widely spaced plants on the 18th, and those in the far patch on the 19th. Thirty-six selected plants were rechecked four more times at 3 to 4-day intervals.

We timed the duration of flower visits and round trip flights for bees individually marked on the thorax with a dot of Testor's paint. The constancy of these bees to particular plants was noted.

We also observed visitation patterns on the simultaneously flowering *Calycophyllum candidissimum* trees (Rubiaceae). Tree crowns near the savanna strip were observed from the 15-m platform of an elevator truck; tree crowns within the forest were observed through binoculars. The *Calycophyllum* were also mapped.

RESULTS

The conviction that all individuals of *T. fuscipennis* and *T. fulviventris* foraging on the *Cassia* came from the nests mapped in Fig. 1 is based on the following:

1) Bees observed leaving a plant with full corbiculae always flew in the direction of one of the nests—the *T. fuscipennis* toward a former *Nasuṭitermes* termite nest 7 m up in the fork of a *Luehea candida* tree (Tiliaceae), and the *T. fulviventris* to an underground nest at the base of a *Lysiloma seemanii* tree (Leguminosae).

2) There were no intraspecific agonistic encounters as would have been in the case if conspecifics
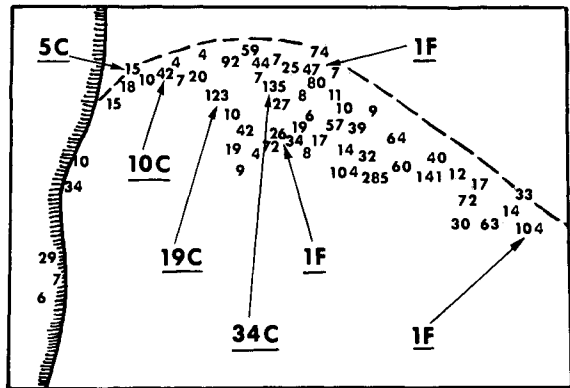

FIG. 2. Far patch insert on study site map of Fig. 1. Dimensions of area are 60 m × 40 m. Numbers refer to number of flowers on each *Cassia* plant, and their positions indicate the positions of the plants. Underlined are the number of *Trigona fuscipennis* (C) or *T. fulviventris* (F) visiting the bush indicated by the arrow.

from different colonies had encountered one another (Johnson 1974).

3) The *Cassia* population was well within the foraging range of the two colonies, but outside or on the fringes of the foraging ranges of the other nearby *T. fuscipennis* and *T. fulviventris* colonies, all of whose locations were known (Johnson 1974).
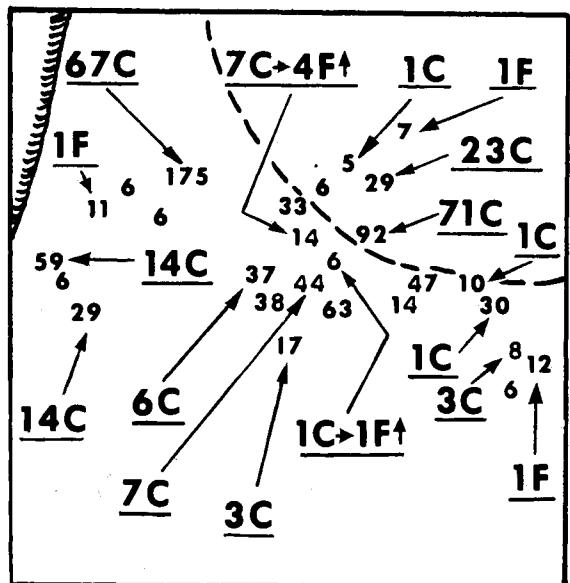

FIG. 3. Near patch insert on the study site map of Fig. 1. The dimensions of this area are 40 m × 40 m. The numbers refer to the number of flowers on each *Cassia*. Underlining has the same notational meaning as in Fig. 2, with two exceptions. On two bushes *Trigona fuscipennis* was observed to displace *T. fulviventris*. Thus, the notation 7C → 4F↑ indicates that seven *T. fuscipennis* arrived in a group and harassed the four *T. fulviventris* foraging on the bush, causing them to leave.

What then, were the contrasting foraging patterns of these two colonies on the *Cassia* population?

Foraging by Trigona fuscipennis

The position of each isolated *Cassia* bush in the study area is shown in Fig. 1. Not a single *T. fuscipennis* was found on these plants on 18 December or subsequently. The *T. fuscipennis* foraged only on the plants in the near and far patches (Fig. 2 and 3), there being no other *Cassia* clumps within reasonable foraging distance, i.e., less than 300 m. The far patch was approximately twice as far from the nest as the near patch (103 vs. 57 m), yet it was visited by less than a third of the total number of *T. fuscipennis* workers foraging on *Cassia* (Table 1). More than 50% of the plants in the near patch were visited, whereas less than 10% were visited in the far patch. The average number of flowers/plant was significantly higher on visited vs. nonvisited bushes, suggesting the bees actively chose those plants within the clump with the most flowers. We found no significant difference between average number of flowers/visited plant in the far vs. near clumps.

Overall, the *T. fuscipennis* were clumped in their distribution on the bushes, i.e., they occurred in groups. The number of *T. fuscipennis* workers visiting a *Cassia* bush increased with increasing numbers of flowers on the bush (Fig. 4). In the near patch the number of workers increased significantly more steeply with an increase in flower number than was the case in the far patch ($p < 0.05$). In both patches the bees devoted more total attention to plants with more flowers, but the increase is a proportional one, not accelerating. Fitting a curvilinear equation with a quadratic term does not significantly increase the proportion of the variance explained by the regression. A visited plant in the far patch had about 44% as many bees as a visited plant with an equal number of flowers in the near patch. How the bees originally chose a *Cassia* bush remains unexplained. Some plants with few flowers were visited by *T. fuscipennis* and some plants with many flowers were not visited by *T. fuscipennis* over the entire 2-wk period of observation (Fig. 2–3). We could discern no difference in quality between the flowers of visited and unvisited plants.
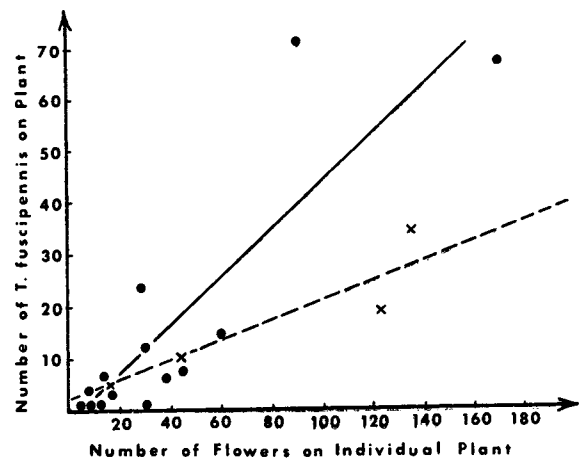

FIG. 4. Graph showing how numbers of *Trigona fuscipennis* visiting a *Cassia* bush increases with number of flowers on visited bush. X = plants in the Far patch; closed circle = plants in the Near patch. Separate least squares regressions have been calculated for the Near and Far *Cassia* patches. Slopes are significantly different from one another and from zero at the $p = 0.5$ level. Lower slope for the Far *Cassia* patch reflects lower total recruitment of bees to that area relative to the Near patch.

Foraging by Trigona fulviventris

There was no significant difference between the mean distances of clumped and isolated plants utilized by *T. fulviventris*, yet only 26% of the *T. fulviventris* workers visiting *Cassia* went to plants in clumps (Table 2). They tended to visit isolated plants even though plants in clumps averaged more flowers/plant (37.5) than isolated plants (24.7). While there was no significant difference in mean number of flowers/ visited and unvisited isolated plants, plants in clumps visited by *T. fulviventris* had significantly fewer flowers than plants not visited.

These patterns raise the possibility that *T. fuscipennis*, which visited only the plants in clumps, and those with the most flowers, partially excluded *T. fulviventris* from these plants and from the patches. Evidence for exclusion is twofold. First, no *T. fulviventris* or Hymenoptera of any kind (except an occasional ant) were ever found on a plant occupied by more than one *T. fuscipennis*. Second, on two bushes in the near clump, *T. fuscipennis* was

TABLE 1. Summary of *Cassia biflora* exploitation by *Trigona fuscipennis*

| | Average nest-plant distance (m) | No. of plants | Total visited | % visited | Average no. of flowers/plant | | Total no. of bees | Flowers/bee[a] |
					Visited	Not visited		
Near patch	57	27	14	51.9	39.6	20.6**	219	2.53
Far patch	103	62	4	6.5	78.8	38.4***	68	4.63

[a] Visited plants only.   ** $p < 0.025$; *** $p < 0.001$.

TABLE 2. Summary of *Cassia biflora* exploitation by *Trigona fulviventris*

	Average nest-plant distance (m)	No. of plants	Total visited	% visited	Average no. of flowers/plant		Total no. of bees	Flowers/bee[a]
					Visited	Not visited		
Clumped Cassia	92	89	9	10.1	26.1	38.8**	12	19.6
Isolated Cassia	80 NS	29	12	41.4	23.2	25.7 NS	35	8.0

[a] Visited plants only. NS = not significant, ** $p < 0.05$.

observed in the act of displacing *T. fulviventris* (Fig. 3). In one case seven *T. fuscipennis* drove off four *T. fulviventris*. One or two *T. fuscipennis* would hover a few millimeters from a pollen-collecting *T. fulviventris* and cause it to fly away. Since two displacements were seen in a total of 3 h of observation of *Cassia* in clumps, it is likely such events occurred relatively frequently, at least in the near patch. A low, continual displacement rate might produce the low visitation rate of *T. fulviventris* on clumped *Cassia*.

Comparison of the patterns

With regard to the spatial aspects of foraging we found visited plants were farther from the nest for *Trigona fulviventris* than for *T. fuscipennis*, but the average distance travelled/bee was no different in the two species (Table 3). The mean number of bees/visited plant was seven times greater for *T. fuscipennis*, but *T. fulviventris* visited more plants. That *T. fulviventris* consistently visited more isolated plants than *T. fuscipennis* is evident from the figures on mean distance to nearest *Cassia* from each plant visited by *T. fuscipennis* and *T. fulviventris*. Plants visited by *T. fulviventris* were an average of 8.1 m from their nearest neighbor, whereas *T. fuscipennis* plants were, on the average, only 1.5 m from their nearest neighbor; the difference was significant ($p < 0.05$).

Figure 5 emphasizes more dramatically the spatial difference in foraging between the two species. Morisita's Index of Dispersion (Morisita 1959), I_δ, was computed for a range of quadrat sizes from 25 m² to 6,400 m² for the *Cassia* population. First

it was computed for all *Cassia* bushes, then only for *Cassia* visited by *T. fuscipennis*, and finally only for *Cassia* visited by *T. fulviventris*. As Morisita has pointed out, how the Index of Dispersion, I_δ, changes with increasing quadrat size reveals a great deal about the dispersion pattern on different scales of observation. Thus, in our case, the line marked with a "2" for all *Cassia* plants indicates overall a highly clumped population dispersion with a mean clump size of about 800 m² and suggests a relatively uniform plant spacing within clumps.

The *Cassia* subpopulations visited by *T. fuscipennis* and *T. fulviventris* have dispersion patterns distinctly different from the *Cassia* population as a whole and from each other. The Dispersion Indices for plants visited by *T. fuscipennis* are significantly higher than for all *Cassia* bushes. This indicates that the *T. fuscipennis* plants are more highly clumped than an equally sized random sample of the population as a whole. In contrast, the *T. fulviventris* plants have lower Indices of Dispersion than *Cassia* bushes at all quadrat sizes, and hence are more uniformly spaced.

Persistence of the patterns

These visitation patterns persisted on the 36 *Cassia* plants selected for periodic observation at various times of day during the next 2 wk. Each bee species continued to occupy the same bushes it originally occupied. The rates of visitation were very constant (Table 4). We computed the mean and the variance of the number of bees/plant over the set of observations. The constancy of the number of bee visitors is indicated by the exceptionally low variance-to-

TABLE 3. Comparison of foraging patterns of *Trigona fulviventris* and *T. fuscipennis* on *Cassia biflora*

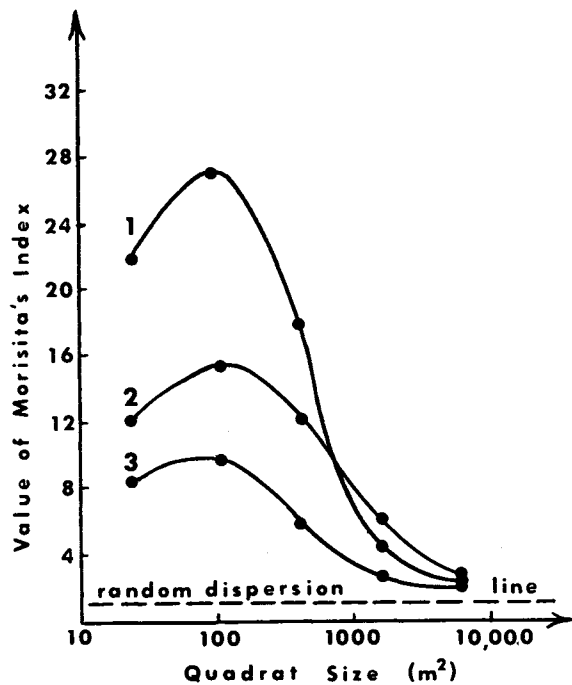|	Average distance to visited plants (m)	Total no. of bees	Average one-way distance traveled/bee (m)	Average no. of bees/visited plant	No. of plants visited	Average distance from visited plant to nearest neighbor (m)
Trigona fulviventris	85.8	47	68.0	2.2	21	8.1
Trigona fuscipennis	65.5**	287	64.9 NS	15.0***	18	1.5

NS = not significant, ** $p < 0.05$, *** $p < 0.001$.

FIG. 5. Clumping in the *Cassia biflora* population. Morisita's Index of Dispersion calculated for quadrat sizes 25, 100, 400, 1600 and 6,400 m². (1) only bushes visited by *Trigona fuscipennis*, (2) all *Cassia* bushes, and (3) only bushes visited by *T. fulviventris*. Dotted line is drawn for $I_\delta = 1.0$.

mean ratio computed for each plant (range: 0.41–1.50). There are no significant differences between average ratios computed for *T. fuscipennis* and *T. fulviventris* plants separately. A low variance-to-mean ratio was also found for bushes not visited by bees in the original observations. In large measure these plants remained unvisited: none was subsequently seen with more than two bees of either species.

We believe the constancy of visitation pattern can be principally attributed to the constancy of individual workers to specific plants. Of five individually marked *T. fulviventris*, four were seen 2, 2, 4, and 4 times respectively on the same plant on different days, but not elsewhere. The fifth bee appeared three times on one plant, and a fourth time on a plant only 4.5 m away. Moreover, the second plant was on a line between the bee's original plant and the nest. The fifth bee was watched continuously between 1200 and 1530 on 28 December. It made two round trip flights to the nest, each time returning to the same plant, where it collected pollen for 85 and 55 min.

Concurrent patterns on Calycophyllum flowers

Observations in other seasons confirm that *Trigona fuscipennis* almost invariably forages in groups; we have also observed this species to arrive in a group at a new resource after discovery of the resource by a "scout." *Trigona fulviventris* on the other hand usually forages in a much more highly dispersed manner (Johnson 1974). These foraging patterns were also observed on *Calycophyllum candidissimum*, which was the only other major food resource visited by either *Trigona* species during the study. *Trigona fuscipennis* visited only the three *Calycophyllum* trees nearest its nest, at distances of 15, 17, and 24 m respectively (Fig. 1). A typical branch was covered with an estimated 22 workers/m² of branch surface. There were virtually no other bees or wasps on this branch, and the few wasps which did attempt to land were aggressively chased away by *T. fuscipennis*.

In contrast, *T. fulviventris* foraged at relatively low densities (2–4 bees/m²) on 13 *Calycophyllum* trees which averaged 75.8 m from the nest. Many other bees and wasps foraged alongside *T. fulviventris*, especially the stingless bees *Trigona capitata zexmeniae* Cockerell (1.2/m²), *T. pectoralis* Dalla Torre (1.0/m²) and *Melipona beecheii* Bennett (< 1.0/m²).

DISCUSSION

The results indicate that *Trigona fuscipennis* forages in groups monopolizing the *Cassia* plants

TABLE 4. Constancy of bee visitation rates over a 2-week observation period on selected *Cassia* plants

		Number of resurveyed plants[a]	Average $s^2 : \bar{x}$
Plants categorized by location	Isolated plants	11	0.805 ± 0.274*
	Near patch	10	0.820 ± 0.301
	Far patch	9	0.816 ± 0.119
Plants categorized by visitors	Originally unvisited	8	0.916 ± 0.207
	Originally *T. fuscipennis*	10	0.838 ± 0.282
	Originally *T. fulviventris*	12	0.800 ± 0.178
Total		30	

* Confidence limits for $p = 0.05$.
[a] Plants never visited were excluded from this calculation.

visited, while *T. fulviventris* forages in lower numbers on more widely dispersed *Cassia*.

These patterns can be explained by two related hypotheses. First, *T. fuscipennis* may be an aggressive, group-foraging species that preempts desirable (clumped) food sources, thereby displacing *T. fulviventris* to less desirable (isolated) food sources. The second hypothesis is that the observed group and solitary foraging patterns may be due, not to short term competitive displacement, but to evolved differences in foraging behavior. We shall present evidence for both hypotheses, then suggest that both are correct. Certainly, the second hypothesis is the evolutionary consequence of long-applied competition of the sort proposed by the first hypothesis, so in the final analysis they cannot be mutually exclusive.

First consider evidence for the competition hypothesis in its purest form. *Trigona fuscipennis* does aggressively displace *T. fulviventris* from *Cassia* in clumps, and from the nature of the observation, such displacements must be relatively frequent. Also we consistently observed that whenever *T. fuscipennis* occupies a *Cassia* (or *Calycophyllum*) no other foraging bees visit that plant. The implication is that, if *T. fuscipennis* is not present, *T. fulviventris* will focus its attention on the *Cassia* patches instead of visiting widely scattered plants. A direct test of this prediction would be to find a site where *T. fuscipennis* is absent but *T. fulviventris* is present, along with a *Cassia* population having all the necessary spatial attributes of clumps and isolated plants, and to observe if *T. fulviventris*, in the absence of competition, concentrates its foraging in clumps of *Cassia*. Unfortunately we did not find such a site. The possibility remains of temporarily closing the *T. fuscipennis* nest (wrapping it in screen) or removing it completely.

There is reason to expect, however, that the removal of *T. fuscipennis* might have little effect on the foraging pattern of *T. fulviventris*, supporting the alternate hypothesis that *T. fulviventris* has a well-evolved foraging strategy. If *T. fulviventris* had chosen to visit the *Cassia* clumps, there were many unoccupied plants it could have visited. Only 6% of all plants in the far patch and 48% of the plants in the near patch were visited by *T. fuscipennis*, leaving many plants, some with a large number of flowers, completely unoccupied. There was no evidence that *T. fuscipennis* was guarding or patrolling these other plants.

On the other hand, *T. fuscipennis* need not be physically present on a food source to deter *T. fulviventris* temporarily. *Trigona fuscipennis* frequently marks food sources with pheromone (Johnson 1974, A. Wille, *personal communication*), a device which aggregates them and helps them locate

the food on a subsequent trip. This pheromone may also deter potential competitors, as suggested by a test of the effect of *T. fuscipennis* pheromone on *T. fulviventris*. When honey-water baits were set up at a site to which *T. fulviventris* had been trained, the *T. fulviventris* normally hovered for 2–5 s a few millimeters from the bait, then landed and fed, and recruited 50–80 bees in 30 min. When baits recently visited and marked by *T. fuscipennis* were transferred to the site, however, the *T. fulviventris* workers flew around them rapidly, landed briefly without feeding, and did not recruit more than 50 bees until 2 h had elapsed.

We would expect *T. fuscipennis* and their pheromone droplets to occur together on *Cassia* plants, since the pheromone has an aggregating function. But the odor of this pheromone might be perceived from nearby bushes in a clump, causing the *T. fulviventris* to shun them and the whole area. Stingless bees, some species of which recruit by means of odor trails (Lindauer and Kerr 1960), can perceive their own pheromone from at least several m (Kerr 1959). Presumably those of other species can be detected from this distance.

The evidence is that *T. fuscipennis* did partially exclude *T. fulviventris* from the *Cassia* clumps, but that at the same time *T. fulviventris* had a strong behavioral tendency to forage in a spatially dispersed manner, as it did on *Calycophyllum* and does on many other flower species (Johnson 1974). Parenthetically we note that *T. fulviventris* is capable of recruiting workers to a source, as it did in the bait experiment described above and probably also in the case of isolated *Cassia* bush No. 5, which had 11 bees and an unusual number of flowers (90) for a *T. fulviventris* bush. The "decision" to forage singly or in small groups is somehow being made. Perhaps the food quality threshold for marking and recruitment is higher for *T. fulviventris* than for *T. fuscipennis*.

If these foraging patterns reflect evolutionary strategies, what are the selective forces which could have shaped them? In an earlier paper (Johnson and Hubbell 1974) we predicted that aggressive species should be large, such as *Trigona silvestriana* Vachal. Here we add that bees which are medium-sized and forage in groups can also use aggressive techniques in resource competition, and that they should likewise specialize on food resources clumped in space and time. This prediction was borne out for *Trigona corvina* Cockerell in the earlier study and also for *T. fuscipennis* in the present work. In the above paper we argue that aggressiveness and monopoly of food resources arose out of intense intraspecific competition for food. Our observation of the uniform intraspecific dispersion of *T. fuscipennis* and

T. silvestriana nests in the forest around the study area also supports this conclusion.

We turn now to the question of competition between *T. fuscipennis* and *T. fulviventris*. In this paper we use the term "interspecific competition" in a somewhat different sense than is customary in ecology. Traditionally the term refers to the negative effect of a population of one species on the growth rate and equilibrium size of a population of another species. In our case, we cannot directly assess the long-term numerical consequences of the short-term interactions we have seen. Other things equal, however, the long-term result of exclusion of *T. fulviventris* by *T. fuscipennis* from shared food resources would seem clear: an increase in the number of *T. fuscipennis* colonies at the expense of the number of *T. fulviventris* colonies. The negative effect of competition would be reduced if *T. fulviventris* took an evolutionary escape route, by foraging on isolated plants.

Foraging on widely spaced plants need not be any more costly energetically than foraging on clumped plants provided that the plants flower for long periods. Such plants can be revisited by plant-constant bees with a minimum of search effort once they have been located.

One could argue that the only reason *T. fulviventris* persisted on *Cassia* at all was because hundreds of *T. fuscipennis* foraged on *Calycophyllum*, leaving some *Cassia* bushes unoccupied. We believe, however, that even if a greater number of *T. fuscipennis* had foraged on *Cassia*, they would not have expanded to visit isolated plants outside the patches. Group foraging appears to be suited for spatially aggregated food resources, which can be effectively guarded by a group of bees against rival colonies. Whereas an isolated bush is also a defensible food source, the food returns/bee, in a group of a size sufficient for defense, would be too low. Of course, this leaves unanswered the question of why *T. fuscipennis* always or nearly always forages in groups, but this is an observed fact. A possible evolutionary explanation is that, over the history of *T. fuscipennis* as a species, clumped, defensible resources have continually and predictably been available.

Trigona fulviventris, whose foraging force tends to be too spread out for effective defense, nevertheless can effectively exploit small, isolated food sources, which do provide ample food for the few workers that forage on them.

In summary, the evidence supports our contention that the observed foraging patterns of these bees result from both evolved strategies and competitive displacement. First, *T. fuscipennis* does seem to forage in groups and avoid isolated plants. In the few cases in which single workers occurred alone on a *Cassia*, the plant was invariably very close to one or more heavily visited plants. This observation suggests that such bees were not foraging alone but were strays from the heavily visited plants.

Second, *T. fuscipennis* selected the plants with the most flowers, which provide food for more bees and are more worth defending. The average number of flowers on isolated plants (24.7) is significantly lower than the number on plants which *T. fuscipennis* selected to visit in the clumps (48.3). The average number of flowers on isolated plants falls to 22.3 if one unusually high value of 90 (plant No. 5) is eliminated from the sample. There may be a threshold number of flowers/plant, below which *T. fuscipennis* is unlikely to visit, and very unlikely to mark and recruit. Most isolated plants fall below this threshold if we accept the contention that the few *T. fuscipennis* workers found on plants in clumps with a low flower number are strays from nearby heavily visited ones, and do not represent recruitment to these particular plants. Isolated shrubs commonly do less well and produce fewer flowers than many of the plants growing in clumps, a pattern which helps tip the balance further in favor of the foraging strategy of *T. fulviventris* on isolated plants. We have also seen this pattern of greater flower production per plant in clumps of other tropical dry forest or second growth shrubs, notably *Cordia currasavica* (Boraginaceae) and *C. inermis*, plants heavily visited by *Trigona* in the wet season.

Finally, *T. fulviventris* seems to be comparatively quick in finding new resources; it takes *T. fulviventris* much less time than *T. fuscipennis* to discover sugar baits (Johnson 1974). This ability to discover new food resources quickly has been seen many times in *T. fulviventris* in the case of natural resources as well, which could be due in part to the high dispersion of the foraging force.

Thus the observed patterns on *Cassia* appear to be the result not only of competition in contemporary time, but also of competition in evolutionary time. Evolved behavior patterns lend each species a food resource "refuge" even when the resource is taxonomically identical for both species.

We label as strategies such evolved behavior patterns and we define strategy below. An adaptation is any heritable morphological, physiological or behavioral trait or collection of traits of an organism assembled by natural selection by virtue of the enhanced reproductive success it gave the organism's ancestors. An adaptive syndrome is a collection of heritable traits whose fitness-enhancing action results from their performance in concert rather than from their individual actions alone. The word strategy has been used in evolutionary biology with at least two valid meanings. One meaning of strategy is
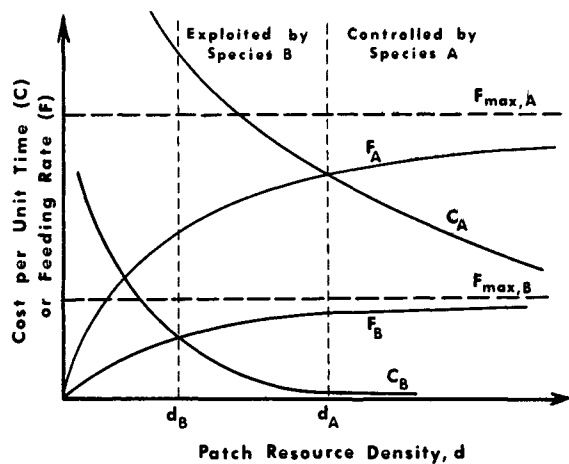
FIG. 6. Hypothetical cost-benefit relationships for a high-density (species A) and a low-density (species B) specialist exploiting a common limiting resource. F_A and F_B are feeding rates, and C_A and C_B the costs of foraging and maintenance per unit time, for species A and B respectively. The resource environment is assumed to be patchy with wide variation in patch resource density. Resource density, d, is measured locally from patch to patch.

an adaptive syndrome of an organism which has a flexible phenotypic expression depending upon the environmental appropriateness of each possible phenotype. An example would be a complex, flexible behavior pattern which changes depending upon the organism's synthesis of current environmental conditions. Some authors have used the word tactic to describe these particular phenotypes as expressed in any given environment, as distinct from the overall strategy of deployment of particular tactics. The second meaning is more appropriate to our usage here, in which strategy refers simply to different adaptive syndromes in different species, as detected by the differing responses of the species to the same or similar environments. The first meaning refers to intraspecific phenotypic flexibility that is adaptive; the second meaning may or may not connote adaptive flexibility, but it does connote differences in adaptation between species faced with the same environment.

HYPOTHESIS

These results suggest to us that a resource with a highly variable local density can be stably partitioned by two species specialized for exploiting at different resource densities. The conditions are that (1) the low density resource is profitably harvested by only one species, (2) the high density resource is controlled by the second species, and (3) there is no net movement through time of resource from dense to sparse regions or vice versa.

We propose that density specialization can evolve when wide spatial variation in limiting resource densities persists over evolutionary time. If, in the evolutionary history of a species, limiting resources tend to be clumped in defensible patches, we might expect a "high-density specialist" to evolve. Species with access to dense patches often have such access only because they can exclude rivals. For solitary animals this ability is often related to large size; in eusocial animals, group aggression becomes a possible competitive mechanism. It is the adaptive syndrome of high-density specialists, however, which makes it unprofitable for them to exploit low-density resources. Large or legion animals have increased maintenance costs and require greater resource density before foraging is profitable.

On the other hand, if, in the evolutionary history of a species, limiting resources tend to occur in small, dispersed parcels, we would expect a "low-density specialist" to develop. A low-density specialist has nothing to gain and much to lose by larger size or group foraging because the amount of resource in each parcel is too small to repay the costs of aggression and large size. Therefore, solitary low-density specialists should be small; eusocial ones should be small and exhibit solitary worker foraging.

Figure 6 graphs the cost-benefit analysis of two hypothetical species. Species A is a large or group-foraging organism that specializes on high-density resource patches. Species B is smaller or forages alone. Resource density d increases along the x-axis. We assume species A and B to have saturating functional responses to resource density (Holling 1966) of the type given by the saturating chemical kinetic equation:

$$F(d) = \text{feeding rate} = (F_{max} \cdot d)/(K + d)$$

where F_{max} is the upper limit on feeding rate at high density, d, and K is the value of d at half-saturation, when $F = F_{max}/2$.

Because species A is larger or forages in groups it has a higher potential maximum feeding rate, F_{max}, than species B. However, species A also has higher maintenance costs per unit time. We assume that these costs, $C_A(d)$ and $C_B(d)$, fall with increasing resource density as the added energy necessary for search diminishes (although these costs need not diminish with increasing resource density for the argument to hold). Neither species profitably exploits resources below the densities at which the feeding rate (F) and cost functions (C) cross. We call these critical densities d_A and d_B for species A and B respectively. A necessary condition for the resource to be stably partitioned is that there exist densities at which B alone can profitably forage.

This condition is met whenever $d_B < d_A$, which

is the same as the requirement that C_A still exceed the value of F for species A at the critical resource density of species B, d_B: $C_A(d)_{d=d_B} > F_{max,A} \cdot d_B / K_A + d_B$, whereas $F_{max,A}$ is the maximum feeding rate for species A, and K_A is the half-saturation parameter for species A.

A second necessary condition for a stable density partition of a single resource is that there be no mixing of resource between low- and high-density patches. If the resource is well-mixed such that patches of dense and sparse resource are continually created and destroyed from random subsets of the entire resource pool, no stabilization is possible. With random mixing and reallocation, competition occurs for the entire resource pool, and eventually the species with the lowest maintenance cost wins. Thus, if the resource is a highly mobile prey or floats in a well-mixed body of water, we would expect purely exploitative competition as opposed to density specialization and aggressive competition.

An exception to this requirement may occur in the case of organisms which have evolved an escape in space or time. An organism can be high-density specialist on a well-mixed resource only if, when resources fall to low levels, it can emigrate to a location with dense resources or go into a resting state to wait for the return of dense resources. For example, many species of phytoplankton grow and divide only when nutrients are concentrated after spring or fall overturn. When concentrations of limiting nutrients fall to low levels in mid-summer, these species commonly settle out and enter a resting state until the next lake overturn. Alternatively, a small fraction of the population may survive in the water column until the next overturn and act as a founder population. The latter possibility has been examined mathematically by Stewart and Levin (1973), who have shown that stability and coexistence are possible on a single resource in a periodic environment in which resource density seasonally alternates between high and low levels.

Although the preceding discussion has concerned one resource, it should be noted that low- and high-density specialists can arise more easily when more than one resource is involved. Whether we suppose many exploitable resources, all of which exhibit wide density variations from place to place, or some of which are always dense and others always sparse, the effect of added resources will always be to increase the long-term predictability and stability of at least some resource at each of a variety of densities. Given that these resources are limiting, specialization of exploiting species for different densities seems highly probable.

We believe that coexistence by density specialization will be found to be common among competing terrestrial herbivores or plant-product specialists, especially among generalized flower-visiting insects. The immobility of terrestrial plants means different density patterns remain relatively fixed and, for this reason, constitute separately exploitable resources. Density specialization can be added to the list provided by Haigh and Smith (1972) of situations in which species can outnumber the limiting resources. Alternatively it can be considered a special case of their category called "self-limited predators" if the term "consumer" is substituted for "predator." This self-limitation arises out of behavioral choice constrained by the adaptive syndrome of the species. The constraints result from an evolutionary branching in adaptations induced by long-term differences in patterns of spatial dispersion of limiting resources.

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