FORAGING STRATEGIES AND THE STRUCTURE OF STINGLESS BEE COMMUNITIES IN COSTA RICA

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SUMMARY

The foraging behavior of *Trigona* (Apidae : Meliponinae) was observed in three habitats in Costa Rica. Eight foraging strategies were recognized in these eusocial bees, several of which could be employed by any given *Trigona* species. These were grouped into solitary foraging strategies and group foraging strategies.

In solitary foraging strategies, each bee makes its decisions to approach particular flowers, resin patches, mud holes, or other attractions independently of the decisions of its sister workers. Four solitary strategies were recognized. In *Avoidance*, a bee chooses not to forage near another bee or group of them, either to collect efficiently from a resource distributed as small units, or to avoid attack. In *Displacement*, a medium or large bee causes the departure of others from a resource by merely arriving or by arriving and behaving aggressively. In *Gleaning*, a small bee arrives at a flower after its peak of attractiveness or after other bees have exploited it, and collects leftovers. In *Insinuation* a small bee nervously but persistently collects from a resource defended by aggressive bees. In group foraging strategies, worker groups assemble at localized resources by means of communication and recruitment. Four group strategies were recognized. In *Scramble* group foraging the only effective competitive trait is the ability to recruit quickly to a locality ; that is, competition at the resource occurs principally by exploitation rather than by interference. In *Bustling* a group is recruited to a spread of resources, and other bees are discouraged from visiting by the hyperactive, «bustling» foraging movements of the recruits. In *Extirpation* a group is rapidly recruited to a resource and rivals are aggressively chased off. In *Opportunism*, a large colony usually forages as solitary individuals, but when an exceptional resource is found by one of the many searchers, they recruit quickly, and collect varying amounts of the resource while it persists, or until extirpators arrive and drive them off.

Illustrations of these foraging behaviors are given. Experiments reported for the first time include : 1/ *Trigona fulviventris* avoided landing on *Cassia biflora* flowers to which a dried, odor-free bee had been pinned. The speed with which the decision was made (seconds of hovering before landing or flying away) was significantly faster when the pinned bee was black (contrasting highly with the yellow flowers) than when it was orange (less contrasting). This suggests that the black color that typifies aggressive species may be an adaptation to permit swift recognition by timid species. 2/ Group foraging *Trigona fuscipennis* marked the *Wissadula* inflorescences they were visiting with visible droplets of mandibular gland pheromone. Incoming bees hovered beside these droplets before landing. When an unmarked, unvisited inflorescence was substituted for one of the marked, visited ones, the bees did not land on it. After these bees had been tricked into marking the unacceptable inflorescence, they landed on it regularly. This suggests that groups of *T. fuscipennis* arise because of mutual attraction to their own marking pheromone.

Stingless bees are generalists, and exhibit broad taxonomic overlap in the resources they visit. Their different foraging strategies, however, allow them to share resources by exploiting them at different times or different spatial densities. Although it is presumed the different foraging strategies evolved in particular resource and competitor environments, it is not known whether all combinations of foraging strategies are compatible and can co-occur in modern bee communities. Several ways of exoloring this question are described.

RESUMEN

Estrategias de forrajeo y estructura de las comunidades de abejas sin aguijón de Costa Rica

El comportamiento de abastecimiento de *Trigona* (Apidae, Meliponinae) fué observado en tres localidades de Costa Rica. En estas abejas sociales, ocho estrategias de forrajeo fueron reconocidas, algunas puden emplearse para cualquier especie de *Trigona*. Hemos distinguido estrategias solitarias y estrategias colectivas de forrajeo. En las estrategias solitarias, cada abeja decide, independientemente de las decisiones tomadas por sus hermanas, si visita ciertas flores, manaderos alimenticios o pegotes de resina en los árboles. En la estrategia de *evitación*, una abeja decide que no forrajea cuando está próxima de otra abeja o grupo de abejas (con motivo de acumular eficientemente una fuente distribuida en cantidades pequeñas, o de no ser atacada). En la estrategia de *desplazamiento*, una abeja de tamaño mediano o grande causa la repartición de otras abejas en la fuente por el mero hecho de su llegada o por su comportamiento agresivo. En la estrategia de *espigueo*, una abeja pequeña visita una flor después de que ésta haya alcanzado su máximo de atracción, o recoge las sobras después de la visita de otras abejas. En la estrategia de *insinuación*, una abeja pequeña recoge, nervosa pero persistentemente, el néctar o polen de una fuente defendida por abejas agresivas.

En las estrategias colectivas de forrajeo, agrupaciones de abejas obreras se forman en los manaderos que han localizado por comunicación y reclutamiento. Quatro estrategias colectivas fueron reconocidas. En la estrategia de *arrebatiña*, la única característica efectiva y de competición es la habilidad de reclutar rapidamente para una localidad ; es decir que la competición en la fuente ocurre más por explotación que por intervención. En la estrategia de *agitatión*, un grupo de abejas se recluta a fuentes más dispersas y las otras se desaniman a visitar la fuente debido al movimiento agitado de las reclutadas. En la de *extirpación*, un grupo es rapidamente reclutado a un manadero y las abejas rivales son perseguidas con agresividad. En la de *oportunismo*, una colonia grande forrajea generalmente como individuos solitarios pero cuando una de las numerosas exploradoras en cuentra una fuente exceptional, se reclutan rapidamente y acumulan hasta que se acabe o que llegan las extirpadoras que las ahuyentan. Ilustraciones de estos comportamiento de forrajeo son dadas. Experimentos reportados por primera vez incluyen : 1/ *Trigona fulviventris* no se pone sobre flores de *Cassia biflora* donde una abeja seca e inodora ha sido pegada. La velocidad con la cual se decide a no posarse (segundos después de permanecer volando suspendidas) es significativamente más rápida cuando la abeja pegada es negra (contrastando con las flores amarillas) que cuando es de color naranjado (menos contraste). Esto sugiere que el color negro, que caracteriza las especies agresivas, es una adaptación que permite el reconocimiento rápido de las últimas por las especies tímidas. 2/ El grupo abastecedor, *Trigona fuscipennis*, marca (con gotas visibles de un olor producido por las glándulas mandibulares) las inflorescencias visitadas del género *Wissadula*. Las abejas que se acercan antes de posarse permanecen volando, suspendidas cerca de estas gotas. Cuando una inflorescencia que ha sido marcada es sustituida por otra que no lo había, las abejas no se ponen, hasta que la marquen de nuevo. Esto sugiere que los grupos de *T. fuscipennis* aparecen gracias a la atracción mutua que tienen para sus olores. Las abejas sin aguijón visitan muchas plantas de diversas clases y manifiestan un ámplio cruce taxonómico en las fuentes alimenticias que frecuentan. Sin embargo, las diferentes estrategias de forrajeo les permiten compartir las fuentes, explotándolas durante momentos distintos o segun las densidades. Aunque se supone que las diferentes estrategias de forrajeo se desarrollan en ambientes con fuentes particulares y de competición, no se sabe si todas las combinaciones de estrategias de forrajeo son compatibles y si podrían ocurrir también en comunidades de abejas modernas. Tres formas de examinar esta cuestión son descritas.

INTRODUCTION

In the eusocial insects natural selection shapes both the behavior of individuals and the emergent colony performance. In foraging, individual actions and group phenomena, mediated by communication and social facilitation, effect a distribution of workers in space and time, with consequences for foraging success. The patterns of worker allocation that are favored by natural selection depend on the dispersion of resource units (calories, for example) in space and time. Resources have a dispersion in and of themselves. In addition, other species or colonies, wherever they are better competitors, remove some kinds of resources from the available pool and leave others. Given diverse, yet limited resources, one would predict that in communities of social insects persisting over evolutionary time there would evolve a degree of complementarity of foraging strategies. I have documented complementarity of foraging strategies of *Trigona* bees (Apidae : Meliponinae) in three habitats in Costa Rica : the tropical dry forest of Guanacaste Province, the premontane wet forest at Turrialba, and the tropical wet forest of the Osa Peninsula. The *Trigona* in these sites have diverse, shared resources, and operate under conditions of at least intermittent food shortage (Johnson, 1974).

In the Costa Rican *Trigona* I studied I distinguished eight types of adaptive foraging strategies. Any given *Trigona* species could exhibit several of the strategies ; expression of the strategies depended on resource conditions, current forager deployment, and the nature of the competition. I will give the identifying features of each strategy, the types of species that use it, and how it works. I will conclude with a discussion of the extent to which one can expect *Trigona* species to be organized into communities of complementary foraging types. The eight strategies are grouped into four types of solitary foraging strategies and four types of group foraging strategies :

Solitary Foraging	Avoidance Displacement Gleaning Insinuation	Group Foraging	Scramble Bustling Extirpation Opportunism

In solitary strategies, each bee makes its decisions to approach particular flowers or resources independently of the decisions of its sister workers ; in group strategies, groups of foragers assemble at resources by means of communication and recruitment. Solitary and group deployment of foragers from a colony are contrasted diagrammatically in Figure 1.

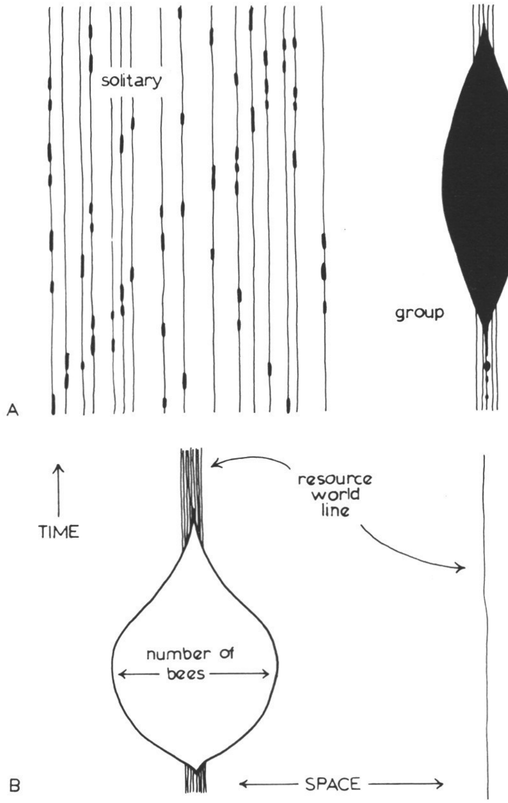

Fig. 1 – Graphical representation of the foraging of eusocial bees. A : Solitary and group foraging in space and time – B : the graphical conventions. Space is represented horizontally, time vertically. A plant resource is drawn as a vertical line or set of lines. The number of adjacent lines per resource indicates the relative richness of the resource in units such as calories, resin volume, or pollen grains. Bees at a resource are superimposed as a shape on the resource world line : width of the shape represents number of bees present at one time.

Fig. 1 – Representación gráfica del forrajeo de abejas eusociales. A : forrajeo solitario y colectivo en espacio y tiempo – B : las convenciones gráficas. Espacio es representado horizontalmente, tiempo verticalmente. El recurso de una planta es representado por una línea recta vertical o un grupo de líneas. El número de líneas adyacentes de cada recurso indica la riqueza relativa de los recursos por unidades como son calorías, volúmen de resina, o granos de polen. Abejas en un recurso son sobreiimpuestas como una figura en la línea «mundial» del recurso ; la anchura de la figura representa el número de abejas presentes en un momento.

SOLITARY FORAGING

Avoidance

In avoidance, a solitary forager chooses not to forage near another bee or group of them (fig. 2A). Why avoid ? Avoidance may improve foraging efficiency. Where the resource is distributed in small packets the sign of another bee on a packet indicates depletion. A suitable response would be to look for unoccupied flowers or resource sites. Avoidance may also prevent attack. Avoidance of this type can occur on a larger or richer resource, which is worth defending aggressively. Table I describes the circumstances under which one would expect to find avoidance as an efficiency mechanism and as an attack prevention device.

Table I – **Environments, in terms of resources and rivals, in which one would expect to find avoidance for efficiency and avoidance for attack prevention.**

Tabla I – **Los ambientes, en términos de recursos y competidores, en que se podía esperar encontrar evitación para el objeto de más eficiencia, y evitación para mejor prevención de ataque.**

	Environment				
	Resource		Bees avoided		
Function of avoidance	*Smaller, poorer*	*Larger, richer*	*From own nest*	*Poorer aggressive competitor*	*Better aggressive competitor*
Efficient foraging	+	–	+	+	+
Prevention of attack	+	++	–	–	+

As an example of avoidance I will report the results of an experiment that tested wheter *Trigona* could visually recognize competitors on flowers. I used *T. fulviventris* flying in to fresh *Cassia biflora* flowers in Guanacaste Province, Costa Rica, February, 1979. Hover time in seconds was recorded, and the subsequent action : land, leave, or touch down (defined as a landing too brief to be recorded on a stopwatch). Bees or models of bees could be pinned to a flower being watched. The bees were pinned specimens at least a year old from which all traces of pheromones and colony odors had presumably evaporated. As an added precaution the specimens were dried for another hour in an oven. The specimens used were of the same size as *T. fulviventris* and co-occured with them in Guanacaste ; they were *T. dorsalis*

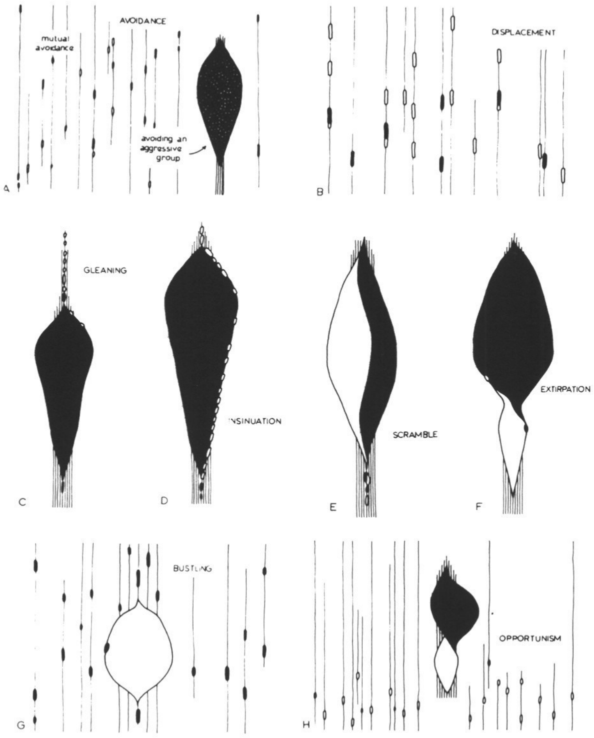

Fig. 2 – Hypothetical examples of the distribution of bees in eight types of foraging – A : AVOIDANCE. Two species of solitary forager (black ; white) avoid one another on the small resources, and both species avoid the aggressive group forager (hatched) on the richer resource – B : DISPLACEMENT. Three displacements are shown, in which an individual of one species (white) is replaced on the vertical track by an individual of another species (black) – C : GLEANING. Gleaners (white) visit a resource abandoned by a group foraging species – D : INSINUATION. Insinuators (white) feed beside aggressive bees (black) – F : EXTIRPATION. An extirpator species (black) chases off a less aggressive species – G : BUSTLING. A species using a bustling strategy (white) visits a patch of resource – H : OPPORTUNISM. An opportunist (white) during solitary foraging finds a rich resource soon after it comes into existence. The opportunist recruits and harvests until the extirpator (black) arrives.

Fig. 2 – Ejemplos hipotéticos de la distribución de abejas en ocho estrategias de forraje – A : EVITACION. Dos especies de abejas solitarias de forraje (negra ; blanca) se evitan mutuamente en los recursos pequeños ; y ambas especies evitan la especie agresiva que forrajea en grupos (rayado) en el recurso más rico – B : DESPLAZAMIENTO. Tres desplazamientos son ilustrados, en los que un individuo de una especie (blanca) es reemplazado en la rastra vertical por un individuo de otra especie (negra) – C : ESPIGUEO. Especies que espigan (blancas) visitan un recurso abandonado por una especie que forrajea en grupos – D : INSINUACION. Especies que insinuan (blancas) forrajean al lado de abejas agresivas (negras) – E : ARREBATINA. Dos especies o colonias reclutan al mismo recurso alimenticio – F : EXTIRPACION. Una especie extirpadora (negra) ahuyenta una especie menos agresiva – G : AGITACION. Una especie empleando una estrategia de agitación visita un área del recurso – H : OPORTUNISMO. Una abeja oportunista (blanca) mientras forrajea en solitario encuentra un recurso rico poco después de que êste aparece. La oportunista recluta y recolecta hasta la llegada de la extirpadora (negra).

(orange) and *T. fuscipennis* (black). The models were orange and black origami bees of equivalent size. The controls were the same flowers in the quarter hour after the pinned object was removed. No flower was used for more than one pinned object. The decision of *T. fulviventris* whether to land or leave was strongly influenced by the treatments (fig. 3). In the control situation *T. fulviventris* landed two out of three time (n = 30). Models reduced to tendency to land ($\chi^2 = 32.7$, $p < .001$) ; in addition, indecision appeared in the form of the brief landings called touch downs. When a flower contained a pinned bee, however, not once in 56 approaches did a *T. fulviventris* land. The distribution of responses differed from that for the controls ($\chi^2 = 111.9$, $p < .0001$) and from that for the models ($\chi^2 = 19.2$, $p < .0001$). These results indicate that *T. fulviventris* avoids *Cassia biflora* flowers that appear to be occupied, and that it can visually discriminate between real bee forms and surrogate bees. Further aspects of this experiment are described in the section on Extirpation.

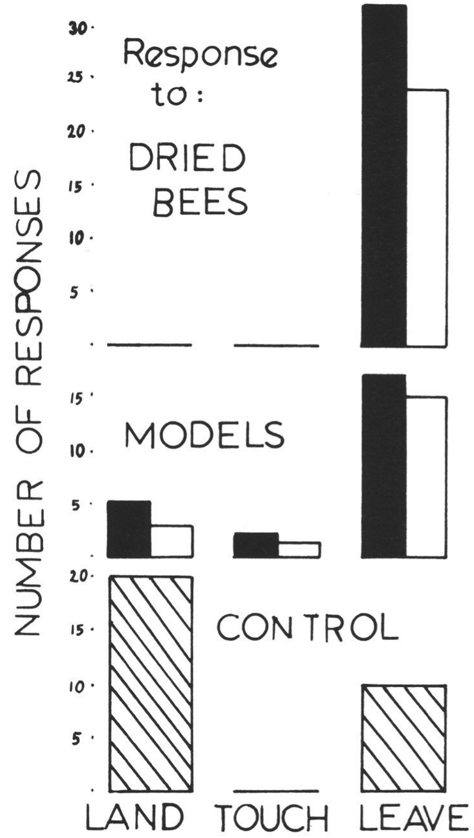

Fig. 3 — Frequency histogram of the responses by foraging *Trigona fulviventris* to control flowers and to flowers with a pinned bee or model. Responses to black bees or models are shown in black, responses to orange bees or models are shown in white, and responses to control flowers are hatched.

Fig. 3 — Una representación gráfica de la frecuencia de como responde *Trigona fulviventris* forrajeando a flores de control y a flores con una abeja prendida o con un lodelo de una abeja. Repuestas a abejas negras o a modelos negros son representados en color negro ; repuestas a abejas anaranjadas o a modelos anaranjados son representados en colo blanco ; y repuestas a flores de control son rayadas.

Generally, we would expect avoidance 1/ where the resource is unlikely to support two bees and where displacement of the first bee by the second is difficult, and 2/ on richer resources where an attempt to land might result in an annoying or damaging attack. We would expect species that commonly exhibit avoidance during foraging to be less aggresive in their physiological make-up, and more vulnerable than their opponents by virtue of smaller body size, weaker, duller mandibles, or other traits. *Trigona dorsalis* is one species that has been identified as an avoider (Johnson, 1974). For species intermediate in aggressive equipment we would expect decisions to avoid or not to avoid to occur after assessment of the rival, and to vary with the nature of the rival. For example, *T. fulviventris*, shown as an avoider, in other situations bites, attacks, or displaces weaker bees.

In summary, one would expect the selective environments favoring avoidance to be small, scattered, slowly-renewing or non-renewing resources, and bigger, sharper, meaner rival species.

Displacement

In displacement, an arriving individual causes the departure of one or more bees on a resource (fig. 2B). Large body size is the most salient charactericitic of a displacing species ; *Trigona capitata* and *Trigona silvestriana*, the largest of the *Trigona* with which I worked, were able to clear a «personal space» around themselves as they foraged. *Trigona capitata* is not only large, it has an unusually large head (for which the species, *capitata*, and its subgenus, Cephalotrigona, are named). The large head presumably enhances its ability to intimidate by cirtue of size, for Kikuchi (1965) reported a dominance hierarchy for flower-visiting insects based on head width. The head of *Trigona silvestriana* is not so large, but solitary foraging individuals will spice their displacement of rivals with a little aggression (Johnson, 1974 ; Hubbell and Johnson, 1978). Aggression may be more of an option for *T. silvestriana* than for *T. capitata* because *T. silvestriana* belongs to a subgenus with more mandibular teeth (Schwarz, 1948).

Examples of displacement, as well as avoidance, could be found in the visits by *Trigona fulviventris* and *T. dorsalis* to *Paspalum notatum* grass inflorescences in Guanacaste Province, Costa Rica, July, 1977. On July 22 I recorded the visitors every minute to 12 blooming plants (fig. 4). These data show four possible cases of interspecific displacement (on plants, H, H, S, T), and imply interspecific avoidance by the rarity of co-occurrence of the two bee species. The arrow points to the only time I recorded both *T. fulviventris* and *T. dorsalis* on the same plant. With the bee densities that morning, the probability of seeing one or fewer *T. fulviventris* co-occurring with *T. dorsalis* is $p < .002$.

Avoidance and displacement were confirmed by behavioral observations on July 21 in an adjacent 1 x 1.4 m plot with 12 blooming *Paspalum notatum*. The observational technique used was sequence sampling (Altmann, 1974).

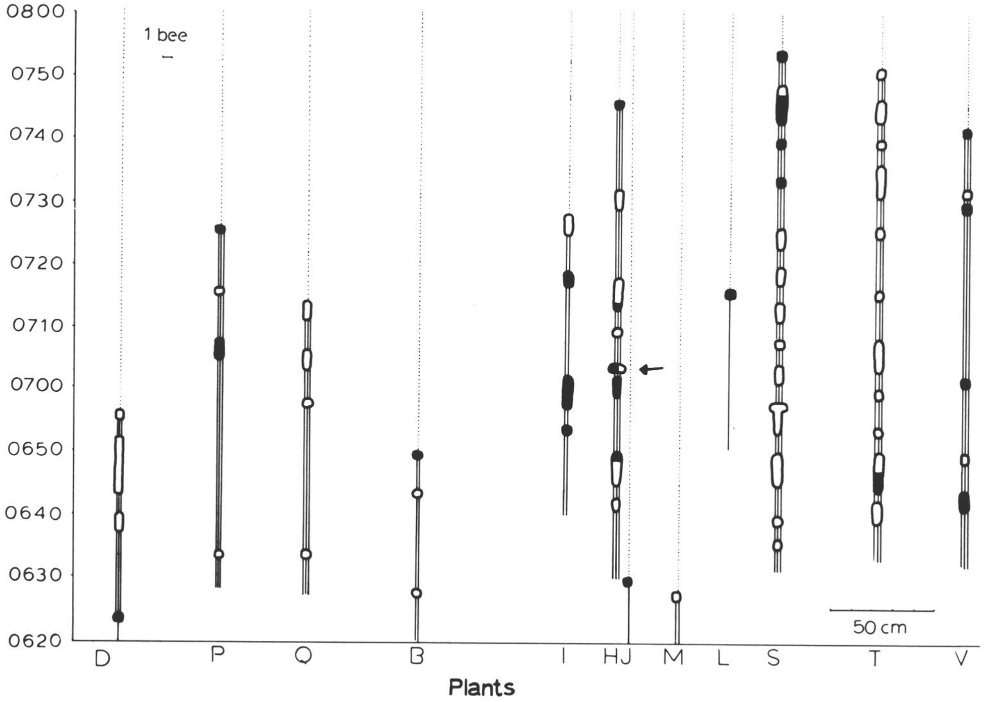

Fig. 4 – Visits by pollen-collecting *Trigona fulviventris* (white) and *T. dorsalis* (black) to 12 blooming grass plants (lettered). Approximate distance between plants is plotted on the abscissa. The vertical track for a plant starts at flower opening ; the number of lines in a track increases with the quality of the plant measured by the number of open flowers.

Fig. 4 – Visitas de *Trigona fulviventris* (blanca) y *T. dorsalis* (negra) a 12 plantas florecendas de hierba (con letras). La distancia aproximada entre las plantas es indicada en la abscisa. La rastra vertical de una planta empieza a la apertura de la flor ; el número de líneas en una rastra aumenta con la calidad de la planta medido por el número de flores abiertas.

A sequence began when an arriving bee hovered beside a bee on a plant, and ended when one or both left. All such interactive sequences involved either avoidance or displacement. An arriving bee was said to avoid if it flew in, hovered, and left, leaving the original bee on the plant. A bee on a plant was said to avoid if it flew away in response to an arriving bee that did not land. A bee on a plant was said to be displaced if it flew away in response to an arriving bee that did land. In the 5 interspecific encounters in which one bee avoided another, *T. dorsalis* always avoided *T. fulviventris*, hence I considered *T. fulviventris* dominant (Table II). In the 7 interspecific encounters in which one bee displaced another, *T. fulviventris* always did the displacing, so again I considered *T. fulviventris* dominant. In this case the displacer, *T. fulviventris*, is the same size as the avoider, *T. dorsalis*. This study accords with years of observation that for whatever reason of internal construction *T. fulviventris* is a more aggressive insect than *T. dorsalis.*

Table II – Interactions of *Trigona fulviventris* (F) and *T. dorsalis* (D) at grass inflorescences. All interactions ended in avoidance or displacement of one bee by another. A binomial test rejected the null hypothesis that F and D are equally likely to win an encounter.

Tabla II – Acciones reciprocas de *Trigona fulviventris* (F) y *T. dorsalis* (D) a inflorescencias de hierba. Todas las acciones reciprocas terminaron en evitación o desplazamiento de una abeja por otra. Una prueba de binómino negó la hipótesis nula que F y D tengan la misma probabilidad de ganar.

	Avoidance		Displacement		Both		
	Loser		Loser		Loser		
Winner	F	D	F	D	F	D	
F	3	5	2	7	5	12	
D	0	2	0	0	0	2	
	p =. 625,		p =.0156,		p =.00049,		two-tailed

The selective resource environments that would favor displacement include resources that can support several visits. Such resources may either have room for about one bee, or be bigger, with sufficiently simple topography that the displacer can easily see rivals on them. The competitor environments favoring displacement are smaller or weaker rivals with poor recruitment capability.

Gleaning

Among solitary foragers, avoidance and displacement result primarily in spatial separation. Gleaning, on the other hand, is a form of temporal avoidance. A gleaner arrives at a flower after its attractiveness has peaked and harvests the leftovers (fig. 2C). For the amount of leftovers to be worth the visit, one would predict the gleaner to be a tiny insect relative to the flower. The bee I have found to be a gleaner is *Trigona buyssoni*, which at 2.5 mm is about as tiny as stingless bees come (Schwarz, 1948). Solitary foragers of *T. buyssoni* collected scattered pollen from *Ardisia revoluta* in Guanacaste, Costa Rica, until at least 1100 hours, even though *Ardisia* flowers peaked in fragrance and attractiveness to bees at 0700 (1.2 bees/inflorescence) and were wilting and largely abandoned by bees at 0900 (0.04 bees/inflorescence).

Wille (1963) used the term «gleaning» in a slightly different sense to describe foraging in *Trigona*. Wille's gleaners were small to medium *Trigona* that visited *Cassia biflora* flowers after the tubular anthers enclosing the pollen had been buzzed or bitten into by larger, stronger bees. These smaller bees than picked up loose pollen grains left on the corolla and anthers. In gleaning in Wille's sense, the priority of larger bees is necessary because it is they that convert the resource into a state that is usable by the smaller bees. Gleaning, in the sense intended here, has the smaller bees arriving later to avoid interference competition from bigger rivals. Since flowers with accessible pollen predominate in the tropics (Wille, 1963), I predict one will find most cases of pollen gleaning to be an adaptive response to interspecific competition. The extent, significance, and dynamics of gleaning, however, remain largely to be demonstrated. Environments favoring the evolution of gleaners would contain ample, clumped resources not always neatly extracted, that attract larger, stronger, solitary or group-foraging competitors.

Insinuation

Wilson (1971) described «insinuator» ants that «... rely on small size... and lack a soldier caste». They do not recruit many workers and «... are usually able to ease their way to the edge of sugar baits through crowds of «extirpator» workers without eliciting aggressive responses».

Like Wilson's ants, *Trigona* insinuators are small and unaggressive and will feed among a crowd of aggressive group foragers (fig. 2D). Insinuator species include *T. latitarsis, T. testaceicornis, T. frontalis, T. buyssoni*, and *T. jaty* (Johnson, 1964 ; Johnson and Hubbell, 1974 ; Hubbell and Johnson, 1978 ; J. Howard, pers. comm.). These species have relatively small colony sizes and recruit poorly. They fly off or back away when threatened, but are persistent and soon land nearby.

If insinuators are small, and few in number because they recruit poorly, but are persistent, the energy and aggressor would expend to keep them at bay could well exceed the calories the aggressor would lose to them if unmolested. The strategy selected for in the aggressor would be to attack only rarely- -just enough to hold down any evolutionary tendencies to exploit the aggressor's resources more fully.

The effectiveness of insinuation can be seen in the relative success of the small, persistent insinuator *T. testaceicornis* and the medium-sized non-insinuating *T. fulviventris* visiting sugarwater baits alongside the large, aggressive *T. silvestriana*. Hubbell and Johnson (1978) monitored a grid of 38 baits for 10 census periods, encompassing an area that contained 4 nests of *T. testaceicornis* and 1 nest each of the other two species. In only 9 cases did

T. fulviventris and *T. silvestriana* co-occur on a bait, and in the majority of these cases, joint occupancy meant just one bee of each species. A pairwise test of association for presence or absence showed negative association ($p < .00001$). In contrast, *T. testaceicornis* insinuated itself onto baits sometimes occupied by more than 20 *T. silvestriana*, and co-occured with them in 70 cases. The association is negative, but much less so ($p < .001$).

A second look at insinuation is provided by three species of *Trigona* visiting a resin source. The bees were collecting from wounded stems of *Macherium kegelii*, a papilionoid legume vine, in Guanacaste Province, Costa Rica, July, 1977. Figure 5 shows the numbers of each species over time sitting on the resource, and hovering above it. At 0741 hours at least 7 aggressive *T. silvestriana* recruits arrived in a group and took over the resin source. *Trigona dorsalis* and *T. frontalis* present in approximately equal numbers in the 10 min before the takeover, responded to the takeover with shorter individual landing times and fewer bees landed per census. The two species

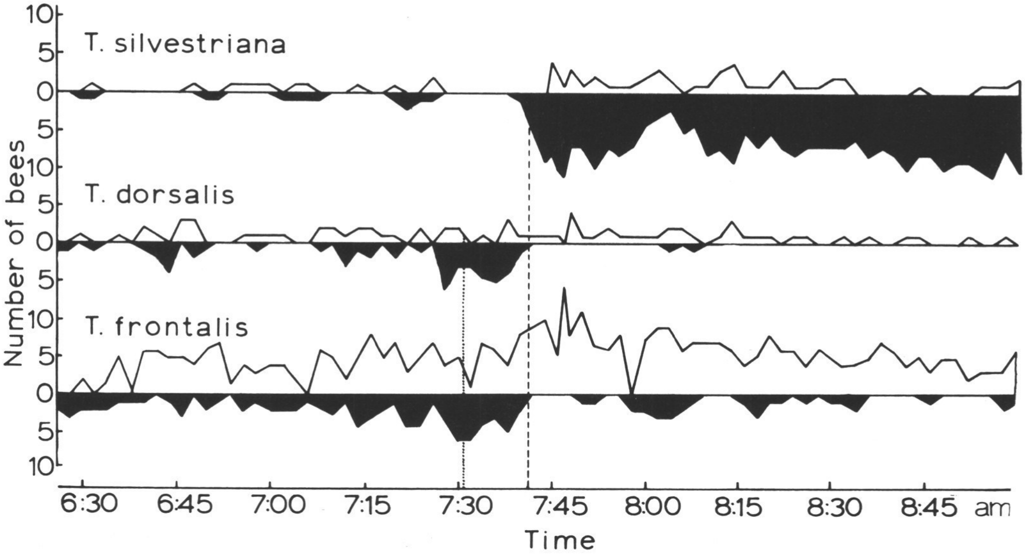

Fig. 5 – Bees at a resin source. Lower graphs (black) show the number of settled bees ; upper graphs (white) show the nomber of bees hovering in a defined zone above the resin. From 0731 to 0741 (between the dotted and dashed lines) approximately equal numbers of *Trigona dorsalis* and *T. frontalis* settled. At 0741 (dashed line) *T. silvestriana* arrived.

Fig. 5 – Abejas en una fuente de resina. Las representaciones gráficas más bajas (negras) muestran el número de abejas asentadas ; las más elevadas (blancas) muestran el número de abejas que se cernan en el aire en una zona definida sobre la resina. De las 0731 a 0741 horas (entre las líneas de puntos o de guiones), approximadamente números iguales de *Trigona dorsalis* y *T. frontalis* se asentaban: A las 0741 horas (linea de guiones), *T. silvestriana* llegó.

differed in their foraging success in the ensuing hour, however. Two *T. dorsalis* landed after the first burst of *T. silvestriana* recruits returned to the nest with their harvest, but no further landings for *T. dorsalis* were recorded in the subsequent hour. The number of hovering *T. dorsalis* dwindled to approximately one. In this way the medium-sized *T. dorsalis* behaved as an avoider. In contrast, the tiny insinuator *T. frontalis* accomplished 14 times as many visits, and was still present at the end of the hour, both hovering over the resin source and collecting from it. Figure 5 shows that while it is more profitable for an insinuator such as *T. frontalis* to have the resource to itself, harvest is still possible in the presence of an extirpator.

GROUP FORAGING

Scramble

Group foraging in stingless bees involves recruitment to particular locations, often by means of pheromones (Kerr, 1969). As with other eusocial insects (von Frisch, 1967 ; Wilson, 1971) the resources to which *Trigona* recruit are rich and ample enough to be worth the efforts of additional bees. In scramble group foraging the only effective competitive trait is the ability to recruit quickly and well to a small region of interest. If a similar colony recruits to the same resource, both scramble for it, neither denying the other access (fig. 2E). In other words, exploitation rather than interference competition is observed (Miller, 1967).

Scrambling foraging was observed in *Trigona testacea* and *T. mexicana* collecting pollen from adjacent *Bactris* inflorescences in Turrialba, Cartago Province, Costa Rica, July 21, 1971 (fig. 6). Through some combination of recruitment or learned experience with the opening time of *Bactris*, the two species built up their numbers and swarmed over the flowers. It was hard to tell if the occasional dislodged bee was attacked or simply jostled ; in any case, neither species prevented the other from exploiting the flowers.

On the following day I set up an analogous situation on the ground in order to observe whether these two medium-sized species attacked one another (interference competition) or whether their attention was directed entirely to the resource (exploitation competition). Randomly selected bees were followed through one feeding visit to a 0.8 M sucrose bait erected near the *Bactris*. Behaviors and their duration were recorded in sequence with a battery-powered event recorder, beginning with «hover» and ending with «fly away». In the 293 seconds that comprised the totaled visits of 8 *T. testacea* and 10 *T. mexicana*, there were 4 acts of interspecific aggression :

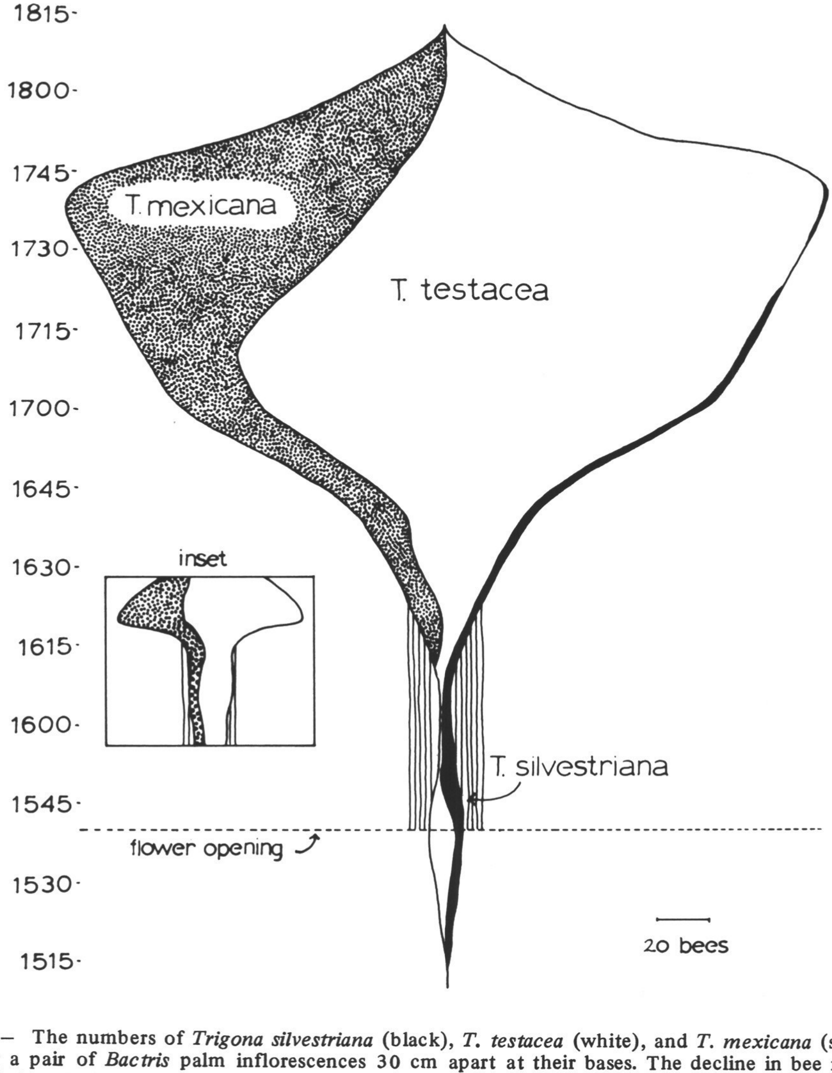

Fig. 6 – The numbers of *Trigona silvestriana* (black), *T. testacea* (white), and *T. mexicana* (stippled) visiting a pair of *Bactris* palm inflorescences 30 cm apart at their bases. The decline in bee numbers coincided with dusk. INSET : visits by *T. testacea* and *T. mexicana* to a sugarwater food dish 20 m from the tree. The inset is drawn to the same scale as the figure, but spans the time from 1255 to 1332 hours.

Fig. 6 – Kis números de *Trigona silvestriana* (negra), *T. testacea* (blanca), y *T. mexicana* (punteada) visitando un par de inflorescencias de la palma *Bactris*, las bases de éstas apartadas 30 cm. La reducción en el número de abejas coincidió con el crepusculo. GRAFICA INTERTADA : visitas de *T. testacea* y *T. mexicana* a uno plato con alimento (solución de azucar en agua) a 20 m del árbol. La representación gráfica insertada es dibujada a la misma escala que la figura, pero abarcando el tiempo desde las 1255 à 1332 horas.

3 threats and 1 attack (i.e., T_1 chased M_1, M_2 opened its mandibles at T_2, M_3 leaned at T_3, and M_4 seized T_4 for 2 seconds). Only in the case of seizure did the aggressor cause departure from the resource. Despite these sporadic incidents both species exploited the resource heavily (fig. 6, inset).

Although the two scramble group foragers did not exclude one another, they did create a situation in which the strategies of other *Trigona* fared poorly. None of a handful of hovering insinuators managed to land between 1700 and 1810. When an inflorescence swarms with 5-6 mm bees, there are few safe corners in which tiny insinuators can land, even briefly. The displacement strategy of *T. silvestriana* was likewise ineffective. At first *T. silvestriana* matched *T. testacea* in numbers (fig. 6), and delivered threat displays to insinuators, wasps, *T. testacea*, and *T. mexicana*, which were acknowledged by flight and other forms of retreat. After 1640, however, such displays went unnoticed in the confusion, and visits by *T. silvestriana* descreased. Although *T. silvestriana* can recruit and be an effective extirpator (Johnson and Hubbell, 1974 ; Johnson, 1981), it is not as «cohesive» in space and time as some group foragers, and thus comes to be competitively outnumbered in certain situations (Johnson, 1974 ; Hubbell and Johnson, 1978). Once *T. silvestriana* is outnumbered by a scrambling mass of bees, there may be the additional difficulty of «tracking» individuals for a biting attack. A filmed study of *T. silvestriana* under varying conditions of competitive crowgind would be instructive.

Scrambling might be expected to evolve in sturdy bees with large colonies in environments with large, rich, but transient resources. Bees preadapted for scramble group foraging would probably not include bees specialized for aggression, which would be so aroused by crowds of rivals that they could not concentrate on simple resource exploitation.

Bustling

Bustling is like scramble in that recruited groups forage on ample resources without attacking other bees. Yet the bustling strategy has certain peculiarities. Since I have found this strategy only in *Trigona pectoralis* Dalla Torre, I will describe some features of the foraging of *T. pectoralis*. Of the species I compared in one patch of tropical dry forest in Guanacaste, Costa Rica, *T. pectoralis* was most often found in large groups (defined as 10 or more) ; about 80 % of the time I saw any, I saw many (Johnson, 1974). A group, however, was not highly localized in space as it would be if scramble group foraging were occuring ; rather, the group was spread out over much of the extent of whatever flower species they were visiting. This suggests that pheromone marking of food sources, if any, may be diffuse. A preliminary analysis of the area extent and caloric dispersion of the subset of floral resources visited by *T. pectoralis* suggests they visit mainly resources that can provide for many bees at once, resources such as *Byrsonima*, a tree, *Cochlospermum*, also a tree, and *Mimosa pudica*, a cesalpinaceous herb which covers large areas with small flowers (Johnson, unpubl.). A *T. pectoralis* colony, moreover, tends to forage as a unit, which results in a lower daily pollen diversity than that of a solitary foraging colony. For example, Klahn (unpubl.) sampled pollen loads every morning for 3 months at colonies of two species, the group forager, *T. pectoralis*, and a predominantly solitary forager, *T. fulviventris*. The pollen diversity for *T. pectoralis* during three morning hours was 3.36 ± 0.24, whereas that of *T. fulviventris* was 7.78 ± 0.40. These differences are significant ($p < .0001$). Additional day-long sampling showed that the 3 to 4 species *T. pectoralis* collected in the morning hours represented the plateau level of diversity for the day, whereas the total daily pollen diversity of *T. fulviventris* was close to 20.

What is interesting about *T. pectoralis* is that whereas it is unaggressive as it forages, at least a third of the time one finds it in monospecific groups (Johnson, 1974), which arise in part because other bees get out of the way of this middle-sized *Trigona*. I speculate this has to do with the way individual *T. pectoralis* move as they forage. An individual forages in a hyperactive manner, stopping only briefly. Such bustling activity may be an adaptation to collect all the tree or patch has to offer during the time available. Because forward movement directed at another bee is a component of threat behavior in other *Trigona*, some movements of *T. pectoralis* may appear to a competitor to be in its direction. As the *T. pectoralis* themselves are accustomed to such activity, it perturbs them little, and several colonies may forage together (Johnson, 1974), a situation not observed for aggressive group foragers.

The proposed bustling strategy (fig. 2G), like scramble group foraging, would be used on a resource that could support many bees. The difference would be that the resource would be spread over a considerable area, and recruitment would be less localized.

Extirpation

Extirpation, to use Wilson's (1971) colorful term, is a group foraging strategy in which bees are recruited massively to a place, and any rivals encountered are chased off (fig. 2F). The localized resource must, of course, be ample enough to supply the aggressive group. In fact, the resources which extirpators frequent are both calorically rich and spatially compact (Johnson, 1974). By means of sugarwater baiting experiments it was determined that both richness and spatial clumping are important to the extirpator strategy.

In an experiment testing the effect of sucrose concentration on the expression of aggression Johson and Hubbell (1974) offered baits of 5 sucrose concentrations in a 5 x 5 array. Three colonies of the extirpator *Trigona corvina* Cockerell fought over the baits. The intensity of fighting, measured by the number of fights and deaths associated with each concentration, increased with molar concentration. This result implies that extirpators are more willing to incur the costs of aggression when the rewards to be won are large.

Johnson (1981) later tested the effects of spatial dispersion of a resource on its defensibility by an extirpator. The baits were hung from clotheslines and could be arranged singly, or pushed together in clumps of ten. The defense of the baits by *T. silvestriana* against *T. corvina* was 20-30 times more successful when the baits were grouped than when they were regularly spaced. Because rich resources are more valuable and more defendable, one could propose that extirpation was selected for in environments containing just such large, rich resources. It also seems reasonable that aggressive group foragers would have physical traits that enhance their aggressive success. Such traits could either evolve in species using aggressive tactics, or could be preadaptations facilitating the evolution of aggressive behavior. Success-enhancing traits of extirpators include medium to large body size, toothy mandibles, black color, and dark wings. Extirpators use these traits in threat displays (raising up on the legs, opening the mandibles, and sticking the wings out), and may follow up the threat with a biting attack (Johnson and Hubbell, 1974 ; Roubik, 1980). Medium to large body size and well-developed mandibular teeth are of obvious importance, and occur in all New World extirpators so far designated. Dark bodies and wings, in turn, may make a displaying bee more conspicuous against a bright background ; black color characterizes the extirpators *T. fuscipennis, T. silvestriana, T. corvina, T. hyalinata branneri*, and *T. amalthea*, but not the orange extirpators *T. pallens pallens* and *T. williana* Schwarz, 1932 ; Wille, 1965 ; Johnson and Hubbell, 1974 ; Hubbell and Johnson, 1978 ; Roubik, 1980 ; Johnson, 1981). Extirpators also recruit quickly to a point in space (fig. 10). Sometimes the first recruits arrive in a well-defined group (Hubbell and Johnson, 1978 ; Roubik, pers. comm.), which makes takeover swifter and surer. To accomodate such recruitment, the colony size of extirpators is large and the entrance is wide.

Recently I tested the hypothesis that black color is an adaptation of aggressive species which renders them more salient to timid species. In the section on Avoidance I described an experiment in which *T. fulviventris* flew to control *Cassia* flowers or to flowers with pinned bees or models. The bees usually chose to land on the control flowers, usually chose to fly away from the flowers with models or live conspecifics, and always chose to fly away from flowers with pinned bees (fig. 3). Figure 7 shows the frequency histograms of the number of seconds of hovering until these decisions were made. Decisions were made quickly in the control situation (x = 1.8 sec) and when a live conspecific was on the flower (x = 1.8 sec). Significantly longer times compared to the controls were required to reach a decision about the model (x = 3.2, $p < .01$, 2-tailed, Mann-Whitney U). The most dramatic contrast, however, was between the pinned orange bees and pinned black bees. Although the decision in both circumstances was invariably to leave, the decision was reached about three times as fast when the pinned bee was black (x = 1.6 sec) than when it was orange (x = 4.4 sec, $p < .001$, 2-tailed, Mann-Whitney U). I interpret this to mean that black, contrasting color permits almost instant recognition of characteristic bee form whereas orange color does not.

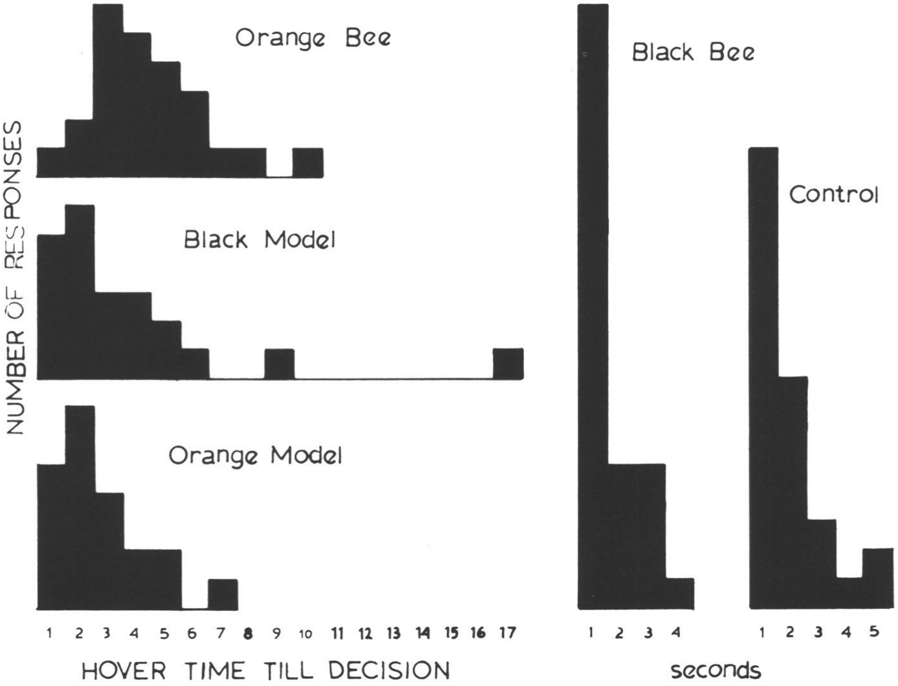

Fig. 7 – Seconds of hovering before decision to land, leave, or touch down was made by *Trigona fulviventris* flying to control *Cassia* flowers, or to flowers containing pinned orange or black bees or bee models. Each square of the frequency histograms represents the hover time of one bee.

Fig. 7 – Segundos de cernerse en el aire antes de la decisión de aterrizar, de marcherse, o deposarse fué hecho por *Trigona fulviventris* volando a flores de *Cassia* de control, o a flores conteniendo abejas prendidas, anaranjadas or negras, o modelos de abejas. Cada cuadrado en las columnas de la frequencias representa el tiempo de cernerse en el aire de una abeja.

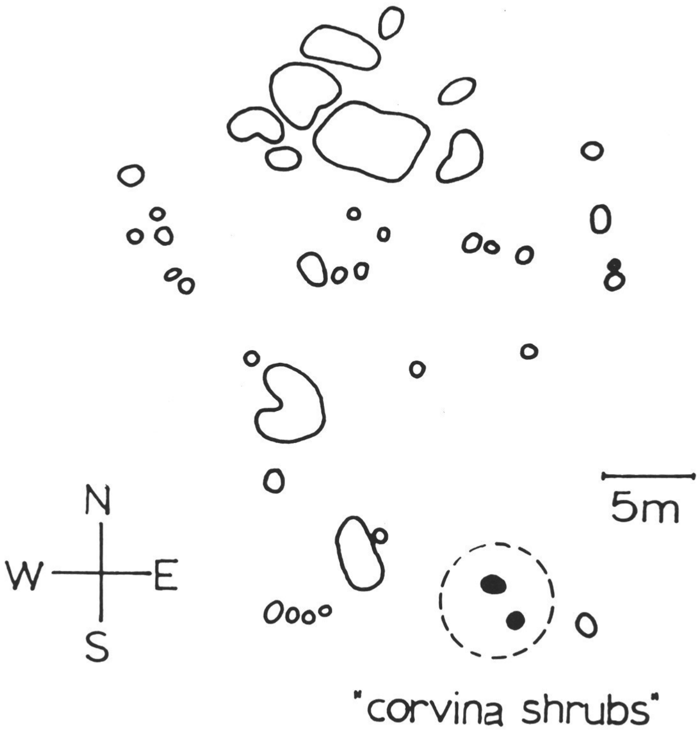

Fig 8 – *Cordia inermis* shrubs on savanna, Guanacaste, Costa Rica. Nineteen of these shrubs had open flowers on August 24 and 25, 1973. In three censuses, 135 *Trigona corvina* were counted, all but one of them on the two shrubs they monopolized (black). On the other 17 flowering shrubs I counted 804 *T. pectoralis, T. fulviventris, T. frontalis*, and *T. testaceicornis*.

Fig. 8 – Arbusto de *Cordia inermis* en sabana, Guanacaste, Costa Rica. Diez y nueve de estos arbustos tuvieron flores abiertas el 24 y 25 agosto, 1973. en 3 censos 135 *Trigona corvina* fueron contadas pero todas menos una de ellas estaban localizadas solamente en dos plantas, las que monopolizaban completamente (negras). En lo demás 17 de los arbustos, conté 804 *T. pectarolis, T. fulviventris, T. frontalis*, y *T. testaceinornis.*

The most extreme extirpators are black, medium-sized species with large colony sizes, namely, *Trigona corvina* and *T. fuscipennis*. These bees cluster in tight monopolistic groups on resources. If the resource is spread out, instead of covering it as the bustling *T. pectoralis* would, the extreme group foragers cluster on one part of it (fig. 8). The basis of such clustering appears to be the strong attraction of these extirpators to their own marking pheromone. Such attraction was shown experimentally in a group of *T. fuscipennis* visiting dried *Wissadula* inflorescences in Guanacaste Province, Costa Rica.

Although these malvaceous forbs were spread over a 150 m^2 area, the *T. fuscipennis* chose to visit only 4 unremarkable adjacent specimens. The bees flew in to the plants with a speed and directness that suggested visual orientation, hovered a few seconds, and landed. They also marked the 4 plants with discernible pheromone droplets from their mandibular glands. It was beside these droplets that incoming bees did their hovering. In a control experiment I counted all bees that hovered and landed on a selected inflorescence during a 15 min period. In all 25 bees hovered of which 21 landed (Table III).

Table III – Response of *Trigona fuscipennis* foragers to *Wissadula* stalks, marked and unmarked with pheromone, at the site of the original, marked stalk.

Tabla III – Repuesta de abejas de *Trigona fuscipennis* a inflorescencias secas de *Wissadula*, marcada o no marcada con perfume, en el sitio de la inflorescencia original.

	#of bees that hovered	#that landed	percent of hoverers that landed
original, marked stalk	25	21	84 %
transplanted, unmarked stalk	17	0	0 %
both stalks, tied together	21	14	67 %
transplanted stalk, now marked	13	9	69 %

Then I cut the stalk and replaced it with an unvisited one of the same length and number of dried flowers. In 15 min 17 hovered and none landed. In each case the bee approached rapidly, as before, began to hover, then suddenly backed up 80 cm or more, flew rapidly up and down the inflorescence, and took off. At least 9 of these bees then flew up and down one of the three adjacent visited inflorescences, damped their amplitude within 4 sec to a stationary hover, landed, and foraged.

Next I took the original inflorescence and tied it to the transplanted inflorescence so that the two were juxtaposed. The droplets had not been replenished since the control experiment. Even so, in the next 15 min 21 bees hovered of which 14 landed on the tied stalks. Some of them visited and marked the transplanted stalk. Finally I removed the original inflorescence. This time the bees did land on the now marked, transplanted inflorescence ; in 15 min 13 hovered of which 9 landed. The hovering time was the usual 2 to 5 sec and the bees did not fly up and down the stalk. I conclude that attraction to their own marking pheromone can explain the tight foraging clusters of extreme group foragers. The small area covered by a dense group of extirpators makes it possible for them to exclude outsiders and monopolize the area they visit. Such tight formations of the medium-sized black bees can be contrasted with the looser groups of the larger *T. silvestriana*, a displacer/

extirpator. Hubbell and Johnson (1978) computed species diversity indices for 114 sugarwater baits set out in the dry forest over two days of census intervals. The least diverse baits were those occupied by the extirpators *T. silvestriana* and *T. fuscipennis*, but the baits of *T. fuscipennis* were considerably less diverse according to Brillouin's index (0 - .1) than those of *T. silvestriana* (.2 - .3).

Environments that would select for extirpation strategies would likely be ones in which there is intense intraspecific competition for successful acquisition of compact but ample resources of sufficient rarity so as to be limiting.

Opportunism

Consideration of the last foraging strategy, opportunism, brings us up against a major drawback of the extirpator strategy. Extirpator bees, normally clumped offensively or defensively in space (Johnson, 1974), are not scattered all over the landscape finding new resources. It is opportunistic species with large colony sizes foraging solitarily most of the time that find good new resources first. In dozens of experiments it has been the aggressive group forager or extirpator that was the last to find new sucrose baits, and the opportunist that was the first (Johnson, 1974 ; Hubbell and Johnson, 1978). An opportunist is a species with many foragers searching independently in the field. When one of them finds an exceptional resource it can quickly recruit, drawing the far-flung net of bees into one spot for harvest. When – or if – an extirpator finally arrives, the opportunist rarely stays to fight. The advantage of the opportunist has been to be early (fig. 2H). I have found one species with this strategy, *Trigona fulviventris*, a normally solitary forager (Johnson and Hubbell, 1975) with up to 2000 bees out in the field at a time (Johnson, unpubl.), capable of swift recruitment to a location (Johnson, 1980).

Figure 9 shows the stages of occupancy of a grid of sugarwater baits visited by the opportunist, *T. fulviventris*, and an extirpator, *T. silvestriana. T. fulviventris* discovered the baits in half an hour, recruited, and spread out from the point of discovery. *T. silvestriana* did not discover the baits for five and a half hours. It then recruited, spread out from its center of discovery, and pushed *T. fulviventris* to the periphery of the grid. As *T. silvestriana* spread from its different discovery point it found baits that had already been found by *T. fulviventris* more frequently than could be explained by chance (a binomial test rejected the null hypothesis that the P values, giving the p of k or more successes in a given census period, are uniformly distributed ; p = .0112). This raises the interesting possibility that *T. silvestriana* may be exploiting the ability of *T. fulviventris* to find new resources readily.

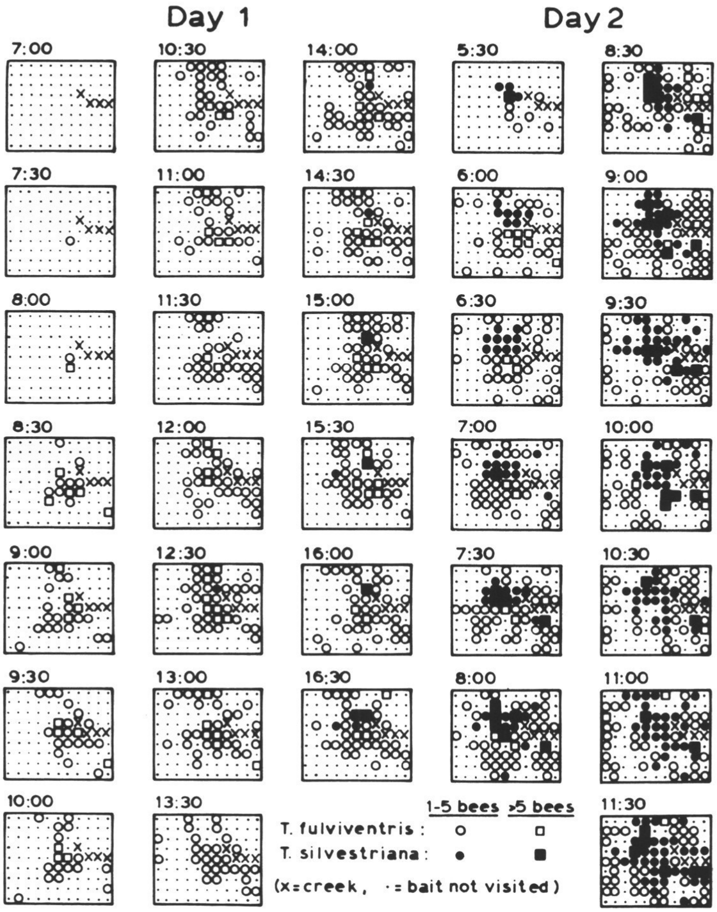

Fig. 9 – Visits by *Trigona fulviventris* and *T. silvestriana* to a 160 x 200 m grid of baits in a tropical dry forest, Guanacaste Province, Costa Rica, July 30-31, 1977.

Fig. 9 – Visitas de *Trigona fulviventris* y *T. silvestriana* a una rejilla de 160 x 200 m con cebos conteniendo un solución de azúcar en agua en un bosque seco tropical, en la Provincia de Guanacaste, Costa Rica, 30-31 julio, 1977.

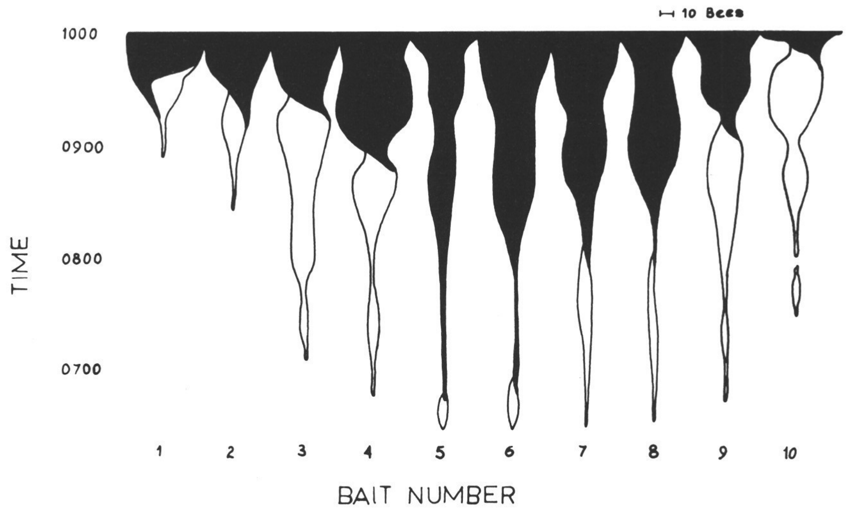

Fig. 10 – Visits by *Trigona fulviventris* (white) and a medium-sized black *Trigona extirpator* (black) to moist sugar baits 10 meters apart in the wet forest of the Osa Peninsula.

Fig. 10 – Visitas de *Trigona fulviventris* (blanca) y una extirpadora negra de tamaño mediano *(Trigona* sp.) (negra) a cebos de azúcar mojados, apartados 10 m en el bosque muy húmedo tropical de la Península de Osa, Costa Rica.

A similar temporal pattern was observed with *Trigona fulviventris* and a different extirpator in a wet forest habitat on the Osa Peninsula, August, 1970 (fig. 10). Of 84 sucrose baits, *T. fulviventris* was the first at 75 of them, and the extirpator was the first at 7 of them. Figure 10 shows one transect of sucrose baits placed 10 m apart. *T. fulviventris* recruited first, followed by the extirpator, who took them over one by one. In this experiment, on baits 4 and 9, *T. fulviventris* fought, but lost badly. Eight years later almost to the day I repeated the experiment at Corcovado, Osa. Again the pattern unfolded. *T. fulviventris* found the line of baits first, and was pushed toward the ends by the later arriving black extirpator. This time, however, I kept elongating the transect by adding new sucrose baits at the ends. On the new baits *T. fulviventris* found a temporary refuge (Johnson, unpubl.). An environment that would select for opportunism would be one with lots of small resources and rare, large, high quality resources of transient availability, transient either because they bloom briefly or because they are taken by a superior, aggressive group foraging competitor.

COMMUNITY STRUCTURE

Stingless bees are foraging generalists, collecting from a variety of plant species (Michener, 1954 ; Heithaus, 1979). This means that different species at a site can show extensive overlap in the plant species they visit (Johnson, 1974). Despite their broad preferences, New World stingless bees are food-limited, at least seasonally or intermittently (Johnson, 1974 ; Roubik, 1980, 1981) ; i.e., if more food were more easily accessible, colonies could reproduce more often. In some cases nest sites probably limit stingless bees, particularly in habitats devoid of the big trees some species require, but Hubbell and Johnson (1977) found no evidence of nest site limitation in a .367 km^2 tropical dry forest site.

If stingless bees species compete chiefly for taxonomically shared food resources, as their use of well-developed interference techniques at food sources suggests, it becomes of interest to know how the resources are partitioned. Since different species of stingless bees have foraging behaviors best suited for resources exhibiting particular dispersions in space and time, it is theoretically possible for competing species to stably partition resources according to dispersion. Johnson and Hubbell (1975), for example, found that an aggressive group foraging *Trigona* and a solitary foraging *Trigona* coexisted on one resource species for several weeks, utilizing clumps and isolated individuals of the plant respectively. The authors presented a graphical model demonstrating the feasibility of what they termed «density specialization». We are now ready to ask whether the complementary of foraging strategies is important enough to structure not only the interplay of particular colonies at resources, but to structure stingless communities themselves. As a null hypothesis one could imagine that community composition arises entirely from historical «accident», in a manner like that proposed by Hubbell (1979) for trees, or MacArthur and Wilson (1967) for island faunas. Bees emigrate at varying rates into a locality from adjacent source areas ; the probability of establishment of a species depends only on saturation of the community. The number of colonies of a species increase or decrease stochastically, and sometimes a species «random walks» to local extinction. Foraging behavior would not affect community structure, because the foraging flexibility of stingless bees (e.g., small, solitary bees can be avoiders, gleaners, or insinuators) would permit coexistence of any bee species with any other.

Alternatively, bee communities, given an equable temperature regime (Darchen, 1973) and a wide range of tree sizes for nesting, could be competitively rather than accidently structured. The probability of persistence of an emigrant into a community would depend on the resource structure and the foraging attributes of its rivals. Competitively important foraging traits could be the ones designated here, such a colony size, body size, aggressivity, and mode of communication, as well as others brought up by Roubik (1980), namely, ability to store food for periods of dearth, and size of foraging range as dictated by flight energetics.

Evidence for competitive structure occurs at least on the scale of a few hundred meters. Hubbell and Johnson (1977) found that the three *Trigona* species in a tropical dry forest that had large colony sizes and could recruit quickly to a precise location were the ones that had uniform spacing of nests, inter- and intraspecifically. Such a pattern could arise if the probability of establishment of a new colony of one of these three species was a function of its distance from existing colonies of these species. The question of whether foraging strategies structure stingless bee communities can be approached in several ways. One is to study the effect of an invading species on the composition it invades. If the relative proportions of the native foraging types are not systematically altered, one could not reject the null hypothesis. Roubik (pers. comm.) has undertaken such a study in Panama, measuring colony growth and reproduction, and foraging patterns of different kinds of stingless bees before and after the predicted arrival of the Africanized honeybee. Another possibility is an island biogeography study. One could record species composition in a tropical dry forest source area and in habitat islands of forest in a savanna «sea», and compare the communities with those predicted by the historical accident model. Finally, one could establish artificial communities on tropical islands uninhabited by stingless bees, beginning with species combinations predicted to be most and least compatible. Success of a species could be more finely monitored if observation hives were used, and results better interpreted if resources were controlled or characterized.

The study of stingless bees, however pursued, should be pursued quickly. Although much remains to be learned about traits of stingless bees and their adaptive significance, the neotropical forests that now support the largest assemblage of eusocial bees in the world are fast disappearing.

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