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FORAGING BEHAVIOR OF COMPETING AFRICANIZED HONEYBEES AND STINGLESS BEES¹

DAVID W. ROUBIK

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panamá

Abstract. The colonizing success and potential influence of immigrant Africanized honeybees in the neotropics depends on their foraging style and competitive ability. Experiments were performed to compare the foraging tactics of this invading species to those of its most abundant competitors, highly social stingless bees of the genera *Melipona* and *Trigona*. In an area containing a rich assemblage of stingless bees in French Guiana, Africanized honeybees were significantly more abundant on honey-water feeders during a high "nectar flow" period than combined stingless bee and wasp species. During the last 15 min of the experiments, when bait was not replenished on feeders, Africanized honeybees abandoned the feeders but native foragers continued to arrive.

None of the stingless bees, including four aggressive *Trigona*, displaced from the feeders the foragers of several (two to seven) colonies of Africanized honeybees. The cost of attacking Africanized honeybees at feeders apparently exceeded the benefit for large, aggressive *Trigona williana* and *T. hyalinata branneri*. These bees abandoned feeders visited by nonaggressive Africanized honeybees. Single, small Africanized honeybee colonies were displaced from feeders by aggressive foragers of *T. pallens pallens* and *T. h. branneri*. In one instance Africanized honeybees shifted almost immediately to a floral resource, while abandonment of the feeders by *T. williana* was not followed by a shift to a natural food source. Reduction of competitive interaction with Africanized honeybees was accomplished by foragers of *T. clavipes* and *T. p. pallens* that partitioned four feeders by visiting only two, leaving the others to Africanized bees. Interspecific displacement was never absolute; a few foragers from a displaced colony always visited the feeders.

Africanized honeybees and *Melipona fulva* foraged nonaggressively both at feeders and flowers, but Africanized bees at feeders exhibited low levels of aggression toward *Melipona* and polybiine wasps on one occasion. Unlike other aggressive *Trigona*, *T. clavipes* was at times unaggressive.

Colonies of *T. h. branneri* and Africanized honeybees, the bees most successful in displacing other species from feeders, were comprised of many more workers than colonies of the other bees. The combined advantages of (1) the ability to communicate the distance and direction of a food source from the nest, (2) large forager size, and (3) large colony size provide Africanized honeybee colonies with a competitive ability superior to that of stingless bees at rich, compact resources.

Key words: Africanized honeybee; *Apis*; colonization; competition; foraging; *Melipona*; stingless bees; *Trigona*; tropical plant-pollinator communities.

INTRODUCTION

When a colonizing species encounters native species at shared resources, competition evokes tactics that evolved in separate communities. In the new context, the value of a particular tactic is immediately altered, and competitive advantage may have little relation to prior competitive success. The proliferation of the Africanized honeybee (a feral hybrid of African and European *Apis mellifera*) in South America (Michener 1975, Taylor 1977) is thought to cause population decline of the highly social stingless bees (Nogueira-Neto 1970 and P. Nogueira-Neto, *personal communication*). This may result from the success of Africanized honeybees in competition for food (Roubik 1978, 1979a). I chose to test the competitive ability of Africanized and stingless bees by observing their interactions at artificial feeders. Behavior at flowers also was observed. Honey-water baits of varying quantity and quality were presented to bees in an undisturbed habitat in French Guiana, South America,

recently colonized by Africanized honeybees. The interactions between native bees and *A. mellifera* during my study were among the first to occur in this region (Taylor 1977).

The foraging tactics of some stingless bees (*Trigona*) include the attack of other foragers (Johnson and Hubbell 1974, 1975, and others). Various workers (Kalmus 1954, Sakagami 1959, Nuñez 1971) have shown that *Apis* are highly aggressive at dish feeders. But this behavior is probably intranidal and not related to foraging. Particularly for such large, highly social bees, the only opportunity for prolonged stationary feeding occurs among the colony stores. Intercolony food transfer (robbing behavior) among Africanized honeybees (Michener 1975), as well as raids of *Apis*, *Melipona*, and *Trigona* nests by cleptobiotic *Lestrimelitta* (Blum et al. 1970, Michener 1974) are among the factors promoting highly developed nest defense systems of the social bees. The design of certain sugar solution feeders seems to cause the release of aggressive behavior never directed at foragers on flowers containing relatively small, scattered resources. Moreover, during preliminary studies with dish feeders I saw intense fighting between *Melipona* and Africanized honey-

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bees, quite unlike their normal foraging style. Therefore, I designed a feeder that more nearly resembled a rich floral resource.

Although physiological, dispersive, and demographic attributes of the Africanized honeybee may allow its spread into areas not previously occupied by honeybees, other factors must be responsible for its persistence and abundance. The stingless bees and Africanized honeybees overlap broadly in nest site and floral preference (Roubik 1979a, b, c). However, Africanized honeybees opportunistically utilize a variety of nest sites not used by other highly social bees, including European honeybees, in the neotropics (Brian 1965, Michener 1974, 1975, Roubik 1979c). If nest sites are not particularly limiting to populations of Africanized honeybees, to what extent is food limiting due to competition with native bees? What effect will the presence of immigrant Africanized honeybees have on the foraging success of native species? It was shown that Africanized honeybees do displace stingless bees from flowers as a consequence of nonaggressive foraging (Roubik 1978).

To understand how they might compete successfully with native neotropical bees for pollen and nectar sources, I manipulated the number of Africanized honeybees having access to feeders and included observations of their interactions with the largest bodied, aggressive local species of *Trigona*. *Melipona fulva*, a bee comparable in size to the Africanized honeybee, and social polybiine wasps also were attracted to the baits. The area in which my study took place contains the richest known assemblage of highly social bees in the world (Roubik 1979a).

METHODS

The experiments were conducted along a 20-km transect of natural habitat ranging inland from coastal forest to savanna and lowland moist forest near Kourou, French Guiana (5°10'N, 52°40'W), during a period of minimum floral abundance. This was at the end of the wet season: May–July 1977. Observations of foraging behavior among bees at flowers were made from July 1976 to August 1977.

Areas selected for the baiting experiments were at forest-savanna edges or near the shore, with known stingless bee colonies in natural situations nearby. When possible, replicate baiting experiments were conducted with one or with several (two to seven) colonies of Africanized honeybees foraging with a different colony of a particular stingless bee. In all but two of 60 experiments, all individuals of each stingless bee species present came from a single nest. The presence of bees from more than one colony of a given species was usually detectable from intraspecific aggression at feeders.

Hives of Africanized honeybees were moved into baiting sites for some experiments. Feral Africanized

honeybee colonies were placed in 6-frame plywood hives measuring 42 × 24 × 22 cm or in standard Langstroth 10-frame plastic hives. The hives contained 6000–20 000 bees when used in the experiments.

Feral colonies of Africanized honeybees foraging at feeders were located in most instances and dissected to determine approximate colony size. Stingless bee nests also were located and opened. The number of bees in feral Africanized honeybee colonies was estimated by comparison to colonies of known forager numbers (the 6-frame plywood hives contained ≈20 000 bees when full). The number of stingless bee adults in natural colonies was estimated from counts of bees in flight by an opened nest and total brood (Roubik 1979c).

The honey-water solutions used as bait were made by diluting honey to 25% or 50% sugar concentration, measured with a pocket refractometer. The solutions were flavored with anise extract to standardize their flavor and maximize their attractiveness, using one drop per litre honey-water. This range of caloric richness nearly spans that of the best floral resources in the neotropics (Ordex 1952) and was expected to incite aggressive foraging behavior. This bait was used because it attracted foragers more readily than sucrose solution and contained nonsugar constituents that comprise floral nectar (Baker 1978).

Each feeder consisted of a piece of plywood 21 × 14 × 1 cm, painted white and covered on one surface with floral-patterned plastic material and a sheet of transparent plastic queen-excluder (obtained from Dadant and Sons). A hand-held sprayer was used to apply honey-water to the surface of the feeder where queen-excluder and plastic material were attached. The queen-excluder material provided many small honey-water reservoirs and resting platforms for foragers, which seemed to promote movement during feeding (Fig. 1). Feeders were hung vertically from vegetation on wire hooks 0.25 to 2.0 m above the ground.

To attract foragers to the feeders, honey-water was first sprayed on vegetation. Four feeders were then placed in the vicinity and sprayed as honey-water on leaves was depleted by foragers. Foragers generally shifted to the feeders at this time. Baiting experiments began at the same site on the following day.

Change in the rate of nectar flow of a floral resource was simulated by varying the amount of bait sprayed on feeders during an experiment. Each experiment lasted 65 min. After an initial application of 6 ml honey-water, it was replenished with sprays directed along the top edge of the feeder. Following the first application of bait, three additional 6-ml applications were made at 5-min intervals. The next three applications, also separated by 5 min, were of 12 ml, and the last three applications were of 6 ml. No additional honey-water was applied during the last 15 min of an experiment. Thus, honey-water was depleted by for-



FIG. 1. A feeder receiving visits from Africanized honeybees, *Melipona fulva* and *Trigona hyalinata branneri*.

agers between 50 and 65 minutes after the beginning of an experiment.

Four feeders were used in each experiment and positioned evenly along a line 8–15 m in length. Counts of the number of each species on the feeders were made every 5 min (immediately before honey-water application for the first 10 counts), providing a total of 13 counts per feeder.

The number of experiments at one site (called a set) ranged from one to 14, depending on the outcome of forager interactions. Data were collected at a baiting site until one species had clearly displaced others from feeders or until species partitioned the four feeders. Agonistic behavior also was noted during each experiment and ranked according to categories described by Johnson and Hubbell (1974). Threat displays were assigned to Level 1 aggression and included the opening of mandibles while facing another forager or spreading of the wings (for *Trigona*) in a "V" position over the body. Hovering face to face with an opponent was also included in this level. Level 2 aggression occurred when there was brief contact as a bee landed on or attempted to bite another forager. At Level 3, aggression was prolonged; several foragers attacked a single bee or an individual closed its mandibles on a rival.

The 50% and 25% sugar baits were used on alternate days, successive when the weather permitted. After each 65-min baiting experiment the feeders were washed thoroughly with water. Feeders were presented at approximately the same time of day and in the same location for each set of experiments. The 60 experiments at nine sites were initiated between 0730 and 1500.

To assess the competitive ability of bee species and depict forager dynamics at the community level, the results of baiting experiments were pooled for analysis. My intention was to show the dynamics of foragers at a limited resource during successive days. Experiments in which native foragers and Africanized honeybees actively recruited to feeders, here defined as the presence of more than two foragers of a species on feeders throughout an experiment, were used to analyze dominance of the feeders by a particular forager group and competitive interactions during such encounters. Experiments in which one species dominated feeders throughout the 65-min period (other species present only sporadically or in low numbers) were used to analyze recruitment dynamics of single species. Such experiments also indicated whether

TABLE 1. Recruitment performance of foragers from single colonies: Fisher's exact test of independence between the appearance of the maximum number of foragers on feeders and the elapsed time during the "nectar flow" period (see text) of a 65-min baiting experiment. A χ^2 test was used to establish whether the number of experiments which showed a maximum number of foragers was equal during the first 20 and the following 30 min of baiting experiments. Thus, no difference in the maxima ($P > .05$) or a higher number in the 1st 20 min ($P < .05$) is entered in the row corresponding to a maximum abundance during the 1st 20 min. Results of Fisher's exact tests for three pairs of species were $P = .03$ for *A. mellifera* and *M. fulva*, $P = .41$ for *T. williana* and *T. h. branneri*, and $P = .61$ for *T. clavipes* and *T. p. pallens*. The sample sizes (number of 65-min baiting experiments) for each species are: *A. mellifera*, 21; *M. fulva*, 9; *T. williana*, 4; *T. h. branneri*, 10; *T. clavipes*, 7; *T. p. pallens*, 13.

Time (min)	Number of experiments in which a maximum abundance of foragers was observed during the indicated time interval					
	<i>Apis mellifera</i>	<i>Melipona fulva</i>	<i>Trigona williana</i>	<i>T. hyalinata branneri</i>	<i>T. clavipes</i>	<i>T. pallens pallens</i>
0–20	13	9	3	5	2	1
20–50	8	0	1	5	5	12

competition for the feeders ceased after one species had displaced another. In addition, the recruitment dynamics of single colonies were analyzed from forager abundance at feeders in combined experiments.

RESULTS

Recruitment

The recruitment performance of foragers from single colonies is summarized in Table 1. The maximum number of foragers counted on the four feeders was compared for two periods during nectar flow: the first 20 min and the next 30 min. The null hypothesis that the maximum number of foragers was the same during the two periods was tested using a chi-square test. The maximum abundance of foragers in combined baiting experiments, according to the chi-square tests, is indicated in Table 1. Further, Fisher's exact test was used to determine whether a colony of a given species recruited rapidly, having the maximum number of its foragers at feeders within the first 20 min of the experiments. Only Africanized honeybees and *Melipona fulva* recruited maximally in a relatively short time ($P = .03$, Fisher's exact test). However, the number of experiments is small for most species, and the analysis is best used to make broad comparisons. For example, *Melipona* and *Apis* appear to recruit the maximum number of nest mates in a short time, whereas *Trigona p. pallens* builds gradually in number.

Foragers of all species appeared when feeders were first replaced in the positions they occupied on the previous day.² These presumably were foragers that had been trained to the feeders. Three workers of *Melipona fulva* recruited 21 nest mates in 5 min to feeders on which no honey-water was yet placed. I watched the first returning foragers enter the nest; a number of foragers issued immediately after their arrival. The bees had been conditioned to visit the feeders and responded to their presence alone. Workers of *T. clavipes* rested in groups of 10–100 bees near vegetation on which feeders previously had been placed, probably anticipating their replacement. One group of ≈ 60 bees appeared daily for 5 d following termination of the experiments at one site, whereas no such group was present before the experiments began.

Although not known to recruit using odor trails, *T. clavipes* often arrived at feeders carrying pungent-smelling resin on their hind legs (corbiculae) which may have promoted nest mate recognition and recruitment. The only species known to recruit with odors was *T. hyalinata branneri* (Kerr et al. 1963). Such odors may also trigger avoidance by other bees (Johnson and Hubbell 1975).

² See National Auxiliary Publications Service document #3729 for 8 pages of supplementary material. For a copy of this document, contact the author or order from ASIS/NAPS, Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, New York 10017 USA.

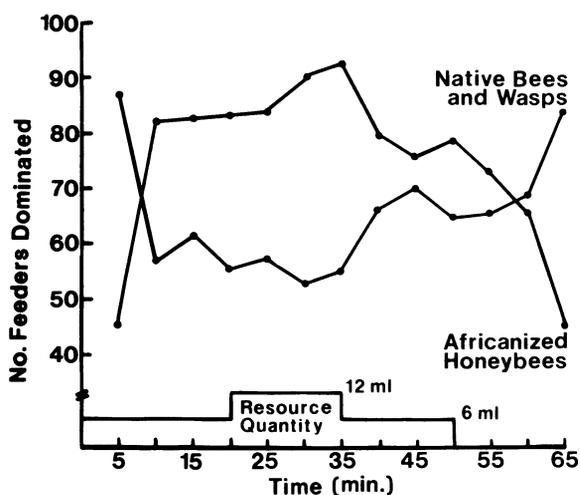


FIG. 2. Dominance of individual feeders (numerical superiority) by Africanized honeybees and combined native social bees and wasps. "Resource Quantity" is the amount of honey-water applied to each feeder at a 5-min interval. The results are from 37 experiments, each incorporating four feeders; 13 counts of foragers were made at each feeder in an experiment.

Although no species exhibited a proportional net increase in forager abundance at feeders as the amount of bait was doubled, the Africanized honeybees were the most abundant foragers on feeders at this time (Fig. 2). Fluctuations in forager visitation rates may have occurred even though not revealed by forager abundance on feeders. Forager turnover rate, although difficult to measure, may have increased when more bait was applied to the feeders.

Aggressive behavior

Africanized honeybees often continued foraging while attacked by aggressive *Trigona* and were not damaged by the bees. *Trigona* climbed on foraging honeybees, biting at the wings or legs. Occasionally Africanized honeybees vibrated their wings while continuing to feed, successfully repelling aggressors. At other times Africanized honeybees were pulled from feeders by hovering *Trigona*. However, Africanized honeybees did not abandon the feeders after such encounters, in one instance even after a *T. williana* worker had become attached by its mandibles to the honeybee. Twice I saw Africanized honeybees on flowers or returning to the nest carrying a dead *T. h. branneri* attached in the same manner.

M. fulva also persistently came to feeders occupied by aggressive *Trigona* but, unlike the honeybees, never tolerated harassment while foraging and usually flew when contacted by aggressive species. Africanized honeybees and *M. fulva* rarely displayed aggression toward other foragers; in one experiment Africanized honeybees attempted to bite *M. fulva* and polybiine wasps on the feeders.

TABLE 2. Levels of aggression displayed by foragers at honey-water feeders and flowers.*

Forager species	Forager species											Relative size†	
	Mf	Am	P	Tw	Tb	Tt	Tp	Tc	To	Tc	Pl		
<i>Melipona fulva</i>	...												192
<i>Apis mellifera</i>	Am1	1-3											135
<i>Polybia</i> sp.	P2	P2	1										125
<i>T. (Trigona) williana</i>	Tw1,2	Tw1-3	Tw2	...									69
<i>T. (Trigona) hyalinata</i> <i>branneri</i>	Tb1,2	Tb1-3	‡	‡	1,2§								60
<i>T. (Partamona) testacea</i>	‡	‡	‡	‡							56
<i>T. (Trigona) p. pallens</i>	Tp1,2	Tp1,2	Tp1,2	Tp3§	Tp1-3	Tp1,2	1§						32
<i>T. (Tetragona) clavipes</i>	Tc1§	Tc1,2§	‡	‡	‡	‡	‡	1,2§					22
<i>T. (Oxytrigona) obscura</i>	...	To1	‡	‡	‡	‡	To1	‡	...				15
<i>T. (Trigona) c. cilipes</i>	Tc1	Tc1,2§	‡	‡	‡	‡	Tp1,2	‡	‡	1§			14
<i>T. (Plebeia) spp.</i>	‡	‡	‡		1

* Initials of the aggressor precede the level of aggression; 1 = threat, 2 = brief attack, 3 = mandibles close on opponent.

† Head width × forewing length × abdomen width in millimetres.

... No aggression.

‡ No co-occurrence.

§ Behavior seen at flowers.

Presence of foragers from more than one colony of Africanized honeybees on the feeders was apparent from fighting among honeybees, two to five jointly attacking a bee presumably from another colony. In addition, Africanized honeybees landed directly on conspecifics on a feeder then foraged with them or attempted to bite or sting. On the other hand, *M. fulva* showed no aggression, although individuals foraging on the same feeders were seen returning to different nests at one site.

The most aggressive bees were *T. williana*, *T. p. pallens*, *T. clavipes*, and *T. h. branneri*. Each displayed all three levels of aggression at 50% and 25% sugar resources. These species often fed with wings held in a "V" position, *T. williana* doing so when it was the only species and colony visiting the feeders. While on the feeders, aggressive *Trigona* turned to face newly arrived foragers of other species with open mandibles, then approached and attempted to bite if Level 1 displays were ineffective in driving away new arrivals. *T. clavipes* was less aggressive than the other aggressive *Trigona* and attacked only sporadically. It displayed Level 1 aggression toward conspecifics from another colony; pairs of bees faced each other while in flight and hovered near the feeders, possibly in a ritualized threat sequence.

Aggressive bees at feeders and flowers were almost exclusively *Trigona* subgenera *Trigona* and *Tetragona* (Table 2). In contrast to other subgenera of the *Trigona*, these bees have toothed mandibles (Schwarz 1948). The largest *Trigona sensu stricto* also were the most consistently aggressive. Three of the *Trigona* were seldom or never aggressive at the feeders. The *Trigona (Plebeia)* species and *T. testacea* were never

aggressive; the former is a minute bee, but the latter is larger than several aggressive species (Table 2). *T. obscura* displayed Level 1 aggression, but infrequently, and did not attack other foragers at feeders.

Polybiine wasps often bit Africanized honeybees and other foragers on the feeders, but generally were not aggressive toward small *Trigona*.

Forager dominance of the feeders

Africanized honeybees and native foragers actively recruited in 22 experiments with 50% sugar solution and in 15 with 25% sugar bait. Native foragers present during these experiments (Table 3) included eight species of *Trigona*, *Melipona fulva*, and polybiine wasps. Several colonies of Africanized honeybees were present in 19 of the experiments, and 18 involved only one small colony (5000–8000 workers). The combined data indicate the type of competition that would result in a variety of settings.

Uncontrolled variables also introduced variation due to feeder discovery rates by bees from single colonies, agonistic behavior, communication and recruitment systems, colony size, forager size, and foraging tempo.

The relative dominance of feeders by Africanized honeybees and combined native foragers is compared in Fig. 2. A forager class was said to "dominate" a feeder if it was numerically superior. Africanized honeybees dominated considerably more feeders than native foragers while foraging on 50% sugar resources (χ^2 , $P < .005$), both for the entire 65-min period and the 50-min period in which bait was replenished (Table 4). At 25% sugar concentration Africanized honeybees dominated significantly more feeders during the 50-

TABLE 3. Native species present with Africanized honeybees on feeders.*

Native species	Total experiments where present	Proportion of experiments with 50% sugar bait	Proportion of experiments with single Africanized bee colony
Polybiine spp.	21	0.57	0.43
<i>Melipona fulva</i>	13	0.62	0.62
<i>Trigona clavipes</i>	12	0.50	0.58
<i>T. hyalinata branneri</i>	12	0.67	0.50
<i>T. p. pallens</i>	10	0.70	0.40
<i>T. williana</i>	7	0.57	0.43
<i>T. (Plebeia) spp.</i>	7	0.57	0.57
<i>T. testacea</i>	3	0.67	1.00
<i>T. obscura</i>	1	1.00	1.00

* In the 37 experiments, 50% or 25% sugar solution was used and single or several colonies of Africanized honeybees.

min nectar flow period (χ^2 , $P < .025$), but their dominance of feeders during the entire 65 min was not significant (χ^2 , $P < .5$). A total of 1832 forager counts was analyzed from 13 counts made at each of four feeders during the 37 experiments. Counts containing equal numbers of two forager classes were not used in the analysis, and in some experiments all four feeders were not visited at each of the 13 observations.

Native foragers dominated the feeders during the first 5 min in 30 of the 37 experiments but were outnumbered by Africanized honeybees within 10 min in 31 experiments (Fig. 2). Near the end of 34 baiting experiments native foragers again became the most abundant group. The general trend for combined experiments with both honey-water solutions was that of lessened foraging by Africanized honeybees and continued visitation by native foragers after the end of the simulated nectar flow. Relatively greater numbers of native foragers at the end of experiments were not a result of aggressive displacement of Africanized honeybees or poor recruitment ability of native foragers.

Displacement and coexistence at feeders

Learned avoidance of either feeders or particular foragers was observed in each instance of displacement. Displacement was never absolute. Foragers from a displaced colony occasionally visited the feeders and appeared to forage successfully. However, the response of the colony to the honey-water baits and initial arrival of bees trained to the feeders declined abruptly. This never occurred at relatively uncontested feeders. The competitive outcome of each set of baiting experiments at the nine sites is given in Fig. 3 and 4. Foragers from a displaced colony never returned in substantial numbers to feeders at a particular site (see footnote 2).

TABLE 4. Chi-square analysis of dominance of feeders by Africanized honeybees and combined native foragers counted at 5-min intervals in 37 experiments.

Forager class	Total counts where feeders were dominated by a class		
	50% sugar bait	25% sugar bait	Total
Africanized honeybees	476† 588	321† 393	797† 981
Native foragers	368† 481	266† 370	634† 851
Chi-square	13.82***† 10.71***	5.15***† 0.69*	18.56***† 9.22***

* $P < 0.5$; ** $P < 0.025$; *** $P < 0.005$; H_0 : Equal numbers of feeders were dominated by competing forager classes.

† The nectar flow period only, the first 50 min of a 65-min experiment; the second figure is for the entire 65 min.

Large colony size was associated with competitive success. The numbers of workers found in natural nests of most species are given in Table 5. The largest stingless bee colonies were those of *T. hyalinata branneri*, having $\approx 60\,000$ workers. Colonies of Africanized *Apis* were comprised of no more than 40 000 workers. Other *Trigona* were from colonies of up to 8 000 workers (*T. clavipes*), and *M. fulva*, like most of its genus, were of colonies having ≈ 600 workers (Roubik 1979c).

Displacement of one species by another usually occurred over 2–5 d (Fig. 3). Nevertheless, when *T. h. branneri* discovered feeders that a small colony (6000 bees) of the Africanized honeybee and *T. p. pallens* were visiting, it displaced both species from all four feeders within 10 min (Fig. 4). A group of ≈ 60 *T. h. branneri* arrived en masse at each feeder, biting and landing on other foragers; all but three of 40 *T. p. pallens* did not skirmish but immediately abandoned the feeders. Rapid discovery of the feeders (this was the first experiment in 15 d at this site) by *T. h. branneri* suggests the bees were foraging nearby. Similar immediate mass recruitment occurred when honey-water was sprayed near bees foraging on ripe fruit, but in other baiting experiments feeders had been presented for several days before *T. h. branneri* arrived in large numbers (Fig. 3). Africanized honeybees displaced this species in an abrupt manner (Fig. 3, site 1) when a large colony (40 000 bees) discovered feeders to which it and a small Africanized honeybee colony had been recruiting. Africanized honeybees nearly covered the feeders, and on the following days no more than eight *T. h. branneri* visited feeders at one time.

Three of the most aggressive stingless bees, *T. clavipes*, *T. h. branneri*, and *T. p. pallens*, foraged successfully with single or multiple colonies of Africanized honeybees. However, although *T. h. branneri* twice displaced a small colony of Africanized honey-

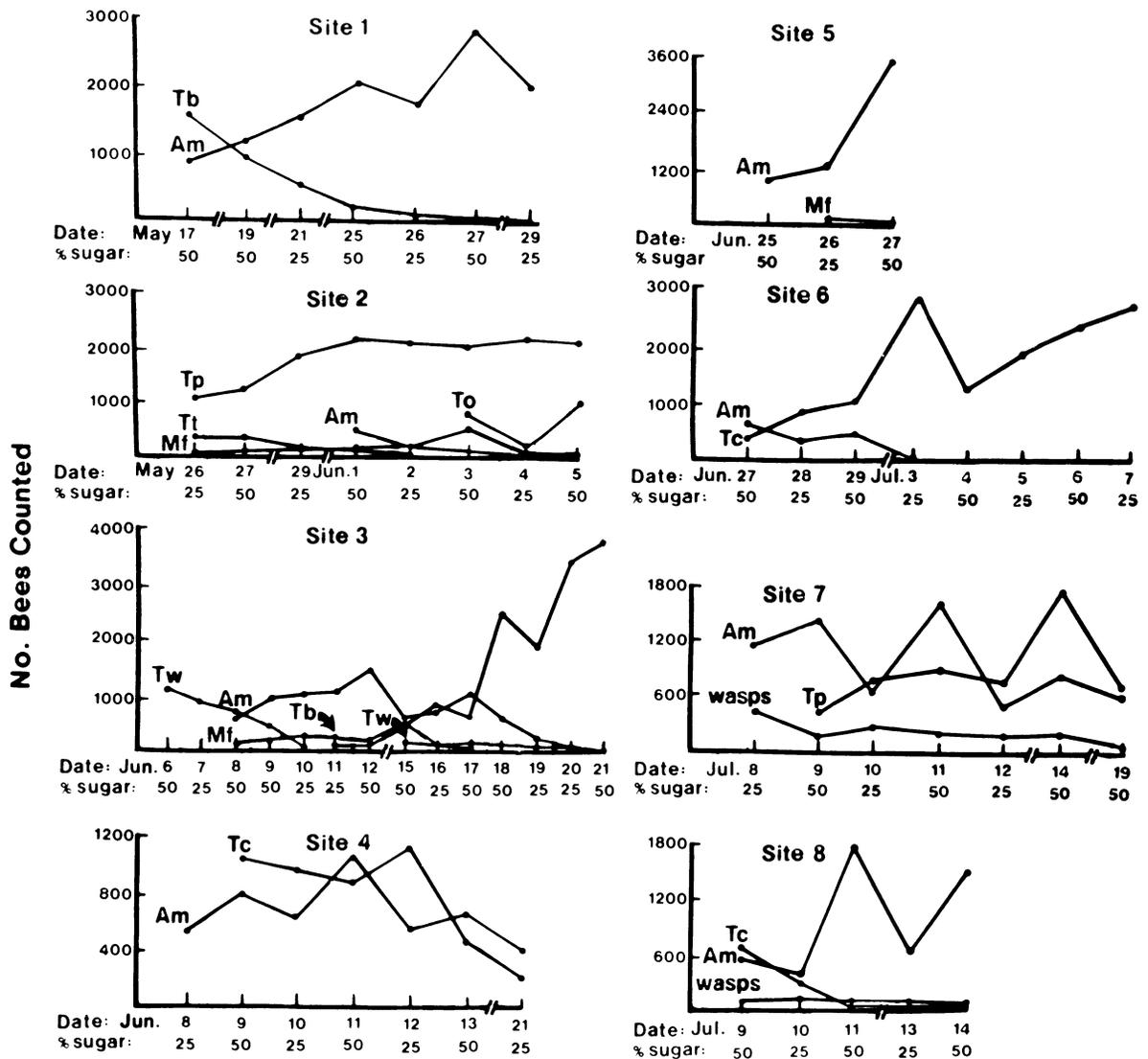


FIG. 3. Numbers of foragers counted on four feeders during 59 experiments at eight sites. The number of Africanized honeybee colonies participating in the experiments were: Site 1, one colony until 21 May, then two colonies; Site 2, one colony; Site 3, two colonies until 12 June, then one colony; Site 4, five colonies; Site 5, seven colonies; Site 6, one colony; Site 7, two colonies; Site 8, one colony. Abbreviations are: Am: *Apis mellifera*; Mf: *Melipona fulva*; Tb: *Trigona hyalinata branneri*; Tp: *T. p. pallens*; Tc: *T. clavipes*; Tw: *T. williana*; To: *T. obscura*; Tt: *T. testacea*.

bees, it did not continue to visit feeders where several colonies or a large colony foraged. *T. clavipes* continued foraging with several Africanized honeybee colonies, monopolizing two of four feeders (Fig. 3, site 4). Conversely, a single large colony of Africanized honeybees displaced two colonies of *T. clavipes* (Fig. 3, site 8). On another occasion a colony of *T. p. pallens* apparently caused a small colony of Africanized honeybees to switch to a floral nectar source. After 5 d in which *T. p. pallens* aggressively dominated all feeders, the Africanized honeybee colony foraged intensively (50 incoming foragers per minute were

counted at the hive entrance) on a floral nectar source (Fig. 3, site 2). In contrast, after 2 d of persistent recruitment and aggression against Africanized honeybees, few *T. williana* returned to feeders (Fig. 3, site 3), and the colony did not switch to another resource. Activity at the nest entrance of *T. williana* was negligible during the baiting experiments following its displacement. In another set of experiments *T. p. pallens* gradually displaced Africanized honeybees from two feeders over a 5-d period but did not dominate more feeders (Fig. 3, site 7). Africanized honeybees and *M. fulva* generally persisted in each others' presence at

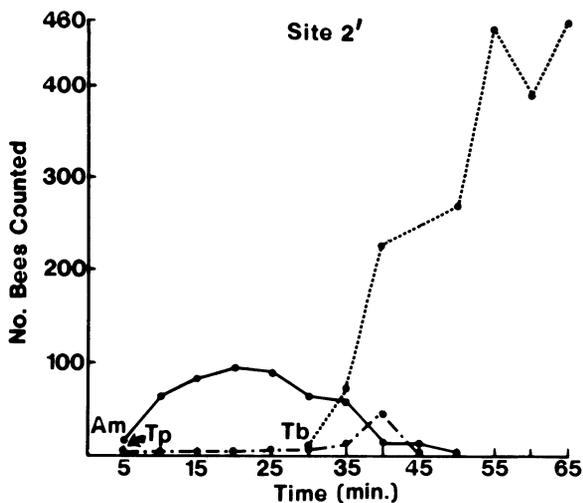


FIG. 4. Numbers of foragers counted on four feeders during a 65-min experiment. The site was the same locality as Site 2, Fig. 3, but different bee colonies were employed. Abbreviations are as in Fig. 3.

feeders, but *M. fulva* was displaced (Fig. 3, site 5) when seven large colonies of Africanized honeybees visited the same feeders.

Although *T. williana* was the largest *Trigona* (Table 2), *T. p. pallens*, *T. clavipes*, and *T. h. branneri* had greater success in foraging with Africanized honeybees. *T. h. branneri* was the most successful stingless bee in displacing other foragers, but it never foraged on the same feeders with *T. clavipes*.

DISCUSSION

Africanized honeybees and *Melipona fulva* were not aggressive toward other species, but Africanized honeybees displaced aggressive *Trigona* from feeders. Parallel experiments with European honeybees and stingless bees in Costa Rica produced similar results (Roubik 1979a); *Apis* and *Melipona* were unaggressive and apparently not harmed by aggressive *Trigona*. *Trigona* should not attack *Melipona*, as they do at flowers, if the cost of attack generally exceeds resultant gain in food (Case and Gilpin 1974); *Melipona* and *Apis* have not evolved aggressive foraging styles also presumably due to cost-benefit aspects of aggression at flowers.

The relatively large body size of *Apis* and *Melipona* may place aggressive foragers at an energetic disadvantage, to the selective disadvantage of the colony. Large body size in these bees is probably related to a relatively large flight range compared to the *Trigona* (Michener 1974, Roubik 1979b). Other factors being equal (e.g., sensitivity to floral odors), this should result in a resource discovery ability greater than that of the *Trigona*. It should also diminish the profitability of defending a resource patch if other, less contested resources are available. In addition, their large size

TABLE 5. Colony sizes of bees foraging at feeders.

Species	Number of workers in colony	Colonies examined
<i>Apis mellifera</i>	5000–40 000	8
<i>Melipona fulva</i>	300–600	8
<i>Trigona p. pallens</i>	1000–5000	3
<i>T. williana</i>	2000–3000	1
<i>T. clavipes</i>	5000–8000	4
<i>T. hyalinata branneri</i>	40 000–60 000	2

and comparatively rapid movement at flowers (D. W. Roubik, *personal observation*) may have interference value. Subtle interference with foraging *Trigona* by *Apis* is, at the colony level, undoubtedly greater than that by *Melipona* because colonies of *A. mellifera* include 10–100 times more workers than those of the *Melipona* (Michener 1974, Roubik 1979c, and Table 5). Their potential for the saturation of feeders or flower patches is therefore greater.

T. williana and *T. hyalinata branneri* continuously attacked foraging *Apis* and eventually abandoned the feeders. In contrast, *T. p. pallens* and *T. clavipes* displayed greater flexibility by partitioning the feeders, which seemed also to lower their rate of attack of *Apis*. Given that conditioned foragers of these species arrived at feeders in large numbers, it can be inferred that *T. williana* and *T. h. branneri* chose to ignore the artificial resource. During the floral dearth period in which the experiments took place, such behavior is best explained as the result of a foraging cost that exceeded the gain. *T. p. pallens* and *T. clavipes* continued feeding with Africanized honeybees by monopolizing two feeders. Since feeders in the same two locations were dominated for several days and the other feeders were seldom visited but were left to *Apis*, these species demonstrated flexibility in their tactics that was not seen in other aggressive *Trigona*. Inflexible aggressiveness may therefore be an inappropriate foraging tactic in contests with the Africanized honeybee. Large, aggressive *Trigona silvestriana* are also unable to displace numerous and persistent competitors from feeders, although they rapidly displace a small number of foragers by threat, attack, and chemical interference (Johnson and Hubbell 1974, Roubik 1979a).

Maximum aggressiveness is likely when both floral resources and colony stores of honey and pollen are in short supply. However, highly social bees that were unaggressive in the dearth period during my study would not be likely to forage aggressively in most circumstances. Accurate characterization of foraging behavior was at times difficult due to the possible influence of intracolony variables on forager behavior. The infrequent occurrence of aggressive foraging by *T. clavipes*, a bee that attacks other bees at flowers (Table 2), may be related to the comparatively large stores

of honey and pollen maintained by this species (Roubik 1979c). Aggressive behavior of some *Trigona* increases with resource richness (Johnson and Hubbell 1974). Among these species aggressiveness is minimal when there is little need for it.

The foraging tactics available to a colony of highly social bees incorporate behavioral, physiological, and structural adaptations. Deployment of the tactics produces competitive ability at resources in a particular community and also determines the success of foraging strategy. Conventional analysis of competitive ability at the population level also considers the projected numbers of competitors, hence the degree of resource saturation. However, a highly social bee colony may effectively saturate a rich, compact resource. Although at present nothing definite can be said of the comparative survival or reproductive rates of Africanized and stingless bee colonies, it is likely that Africanized honeybees will readily establish and defend new nests, and increasingly deprive stingless bees of some of the best food sources. It is questionable, however, that the Africanized honeybees often compete with stingless bees as a whole. Despite the exceptional resources provided at the artificial feeders, only nine of the at least 45 stingless bees species in my study area recruited to the bait.

No highly social bee except *Apis* communicates both the distance and direction of a resource to many nest mates in a short time, without the necessity of providing odor trails or guiding other foragers (von Frisch 1967). Lindauer (1961) demonstrated that trail-laying *Trigona* recruit more nest mates to a feeder placed high above the ground than *A. mellifera*. The abundant visual and olfactory cues provided by flowering trees, however, make inference from such experiments highly suspect. Furthermore, important variables are often neglected in recruitment studies. For example, competition from floral resources, foraging constancy, the number of foragers in a colony, and the colony's pollen or nectar needs influence recruitment rate, conventionally measured as the number of new arrivals at a feeder within a given period. Among the few controlled comparative studies of highly social bee foraging behavior, Nuñez (1974) showed that Africanized honeybees recruit to and discover resources more rapidly than European honeybees in the same tropical habitat. In addition, my data (Table 5) as well as other studies (Nogueira-Neto 1970, Michener 1974, Winston 1978, Roubik 1979c) show that nests of *A. mellifera* contain far more workers than those of the *Melipona* and most *Trigona*. Therefore, colonies of this species have a potentially greater ability to discover and harvest resources.

The results of my study suggest that the persistence of Africanized honeybees and *Melipona* in the presence of aggressive *Trigona* contributes to the competitive ability of the former two genera. However, this study of competition and similar studies incor-

porating artificial feeders present foraging dynamics at an extreme, competition for unusually rewarding resources. In addition, it would be useful to conduct experiments using stingless bee honey and other artificial bait, to determine whether the odor or other qualities of the bait influences foraging behavior.

The relatively large size and recruitment performance of Africanized honeybee colonies permit both rapid exploitation of resources and incidental interference with other foragers. The combined advantages of distance and direction communication, large forager size, and large colony size provide Africanized honeybee colonies with a competitive ability at compact resources that is superior to that of stingless bees. Further, the aggressive foraging style of some *Trigona* does not displace Africanized honeybees from such resources. On the contrary, it leads to displacement of the *Trigona*.

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