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Comparative foraging behavior of *Apis mellifera* and *Trigona corvina* (Hymenoptera: Apidae) on *Baltimora recta* (Compositae)

by

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Abstract: In a short-term study of the foraging behavior of competing bees, European *Apis mellifera* (Apinae) foraged more opportunistically than *Trigona corvina* (Meliponinae). Experimental removal of a large portion of the available *Baltimora recta* (Compositae) which both bees visited caused a 44% increase in *Apis* within adjacent study plots of *Baltimora* and only a 17% increase in *Trigona*. However, analysis of variance showed that the mean number of *Apis* within study plots increased but that of *Trigona* did not during three days following experimental removal of plants. *Apis* visited three flowers in 15.1 seconds, compared to 25.6 seconds for *Trigona*. *Trigona corvina* foraged in groups, and individuals occasionally attacked *Apis*, with no discernible effect. It is suggested that the flexible foraging behavior of *A. mellifera* gives it a competitive advantage compared to *T. corvina* when resources become more scarce.

In natural communities potential competitors often exhibit not only structural divergence (Selander, 1966; Karr and James, 1975; Inouye, 1978) but possess differing foraging behavior as well (MacArthur, 1958; Johnson and Hubbell, 1975; Wolf *et al.*, 1976; Feinsinger and Colwell, 1978). The goal of a foraging bee is perhaps to maximize resource harvest relative to harvest cost. Tactics employed to this end include expenditure for discovery, harvest and occasionally defense of resources. During competition for nectar and pollen, the highly social bees exhibit aggression (some *Trigona*) or forage nonaggressively (many *Trigona, Melipona* and *Apis*) (Johnson and Hubbell, 1974, 1975; Roubik, 1978, 1980).

Competitive differences among native and introduced species are determined by foraging tactics that evolved in separate communities. Native species may therefore display foraging behavior that is ineffective in the presence of introduced competitors. In this study, I induced intense competition for a flowering plant, *Baltimora recta* (Compositae) between resident *Trigona (Trigona) corvina* (Meliponinae) and introduced *Apis mellifera* (Apinae) by removing a large portion of the plants from a patch visited by both bees. The resulting changes in dispersion and foraging behavior of the bees demonstrated their differing competitive ability and foraging tactics.

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MATERIAL AND METHODS

The observations reported here were made near Esparza, Puntarenas Province, Costa Rica (9° N) from July 13 to 16, 1978. The study site was a 2000 m^2 patch of *Baltimora recta* on a hilltop at 208 m elevation. *B. recta* was the only native plant in flower at this location. Eighty-two managed colonies of European *A. mellifera* were 700 m from the study site. Riparian forest was present 100 m to the west and east of the study area.

Eight plots measuring approximately 1.5 x 2.5 m were selected within the study area, and bees foraging in the plots were counted during four successive mornings from 9:00 to 11:00 at 20-minute intervals. In addition, the time spent visiting three flower heads was measured for 50 individuals of both bee species on each day. A successful floral visit, when the forager obtained nectar, was counted as multiple probing of florets by a bee on a flower. Brief visits involving a single probe were not counted. The elapsed foraging time for an individual bee was recorded until it had probed at least two times on each of three flower heads.

On the evening of July 13 and early morning of July 14, approximately 1000 m^2 of *B. recta* were removed from the area surrounding the study plots. The plants were cut near ground level with a machete. Within the study plots, the total flowers were estimated at 6,000, ranging from 500 to 1,200 within plots.

Baltimora recta is a weedy annual that flowers throughout the year (D'Arcy, 1975), and in Puntarenas, primarily between April and August. The plant is very abundant on cleared land grazed by cattle (G. Fuentes, pers. comm.). Since flowering occurs for several weeks, there was little likelihood that floral rewards diminished during the study. Weather conditions were relatively constant and, although the abundance and quality of nectar and pollen may have fluctuated during the experiment, the short duration of the study minimized this possibility.

RESULTS

Visitors of Baltimora: Foragers visiting *Baltimora recta* were almost exclusively *Trigona corvina* and *Apis mellifera,* but *T. angustula (=jaty), T. capitata, T. testaceicornis perilampoides, T. buyssoni,* and possibly *T. cupira* were also seen at flowers. A solitary bee, *Melissodes* sp. (Anthophoridae) and a cantharid beetle also visited *Baltimora.* Bees began to forage for nectar and pollen at 8:15 a.m. Pollen was depleted on flowers by 10:00 a.m. since few foragers were seen carrying pollen loads after this time, but foraging for nectar continued until approximately 2:30 p.m. The humidity was 95% and the temperature near 27 C each day when my observations began.

Numbers of bees within study plots: The number of *A. mellifera* on *B. recta* within the study plots increased after the surrounding plants were experimentally removed ($P<.001$, ANOVA), but the number of *T. corvina* remained stable ($P<1$, ANOVA, Tables 1 and 2). The average number of honeybees in combined plots on July 13 was 70, and on July 14 to 16 the number rose to near 100 (Table 1). The increase in foragers seen on these days was significant ($P<01$, range-STP test, Sokal and Rohlf, 1969). The average number of *T. corvina* in the combined plots ranged from 50 to 61 (Table 2), but there were no significant differences between days ($P > .05$, range-STP test).

TABLE 1

Apis mellifera counted on Baltimora recta

Number of Bees in Combined Plots

Time	July 13	July 14	July 15	July 16
9:00	75	100	106	100
9:20	65	112	103	105
9:40	70	116	94	110
10:00	84	108	100	109
10:20	70	85	81	99
10:40	58	84	95	93
Mean*	70	101	97	103
ANOVA	$p<0.001$	$F=14.045$		

* nearest whole number.

Rates of floral visitation: The average duration of three successful floral visits was relatively constant for *A. mellifera* and increased on one day for *T. corvina* (Table 3). *A. mellifera* foraged at three flowers in 14.3 to 16.1 seconds. *T. corvina* made three visits to flowers in 23.0 to 27.9 seconds. On July 14, the average visitation time by *T. corvina* increased to 27.9 seconds, greater than that observed on July 13 ($P<01$, t-test). The grand means of floral visitation periods of *A. mellifera* and *T. corvina* were 15.1 and 25.6 seconds/3 flowers, respectively ($P<001$, t test).

Aggressive behavior among bees: The number of aggressive acts by *T. corvina* increased after experimental reduction in the number of *B. recta* and the subsequent increase of *A. mellifera* within study plots. One act of intraspecific aggression was seen among *T. corvina* on July 13, but interspecific aggression against *A. mellifera* was seen once on July 14, four times on July 15 and six times on July 16. Hovering *T. corvina* alighted on *Apis* visiting flowers and attempted to bite with the mandibles or flew rapidly at bees in flight. The workers of *A. mellifera* were not aggressive.

DISCUSSION

Depletion of floral resources due either to competitors or floral senescence influences the distribution and activity of foraging European honeybees (Gary *et al.*, 1977). I expected *A. mellifera* and *T. corvina* to become more abundant in plots

of *B. recta* after I removed most of the adjacent flowers. Further, increasing the number of bees within plots was expected to affect the amount of resource available and the foraging behavior of bees (Roubik 1978). These predictions were partially met by *A. mellifera* but scarcely fulfilled by *T. corvina*. It was not surprising that aggression by the latter species appeared to increase in frequency with increasing densities of bees, but total aggressive acts were few.

TABLE 2

Trigona corvina *counted on* Baltimora recta

	Number of Bees in Combined Plots			
Time	July 13	July 14	July 15	July 16
9:00	46	58	68	62
9:20	59	62	65	58
9:40	49	73	57	48
10:00	54	71	54	49
10:20	56	51	51	40
10:40	46	52	56	44
Mean*	52	61	59	50
ANOVA	$0.05 < p < 0.10$		$F = 2.927$	

* nearest whole number

Was *T. corvina* more constant to a smaller foraging territory than honeybee foragers? Although I did not mark bees to determine their foraging area, it appears that *T. corvina* generally did not shift to new foraging areas after I removed flowers near the study plots. In addition to the analysis presented in Tables 2 and 3, the data show that on July 14 the number of *A. mellifera* increased by 44% and that of *T. corvina* by only 17%. Proportionally more *T. corvina* than *A. mellifera* abandoned *B. recta* after flowers were removed. Furthermore, the considerably larger foraging range of *A. mellifera* (Gary *et al.*, 1977) would permit visitation of nearby patches of *B. recta* (ca. 500 m distant), while *T. corvina* would not be likely to reach these flowers (Michener, 1974; Hubbell and Johnson, 1977; Wille, 1976).

Honeybees foraged more rapidly than *Trigona*. The honeybee is somewhat larger than twice the length of *T. corvina* and appeared to more effectively push through the protruding stamens on the disk flowers of *Baltimora* than *T. corvina* both while collecting pollen and probing disk florets for nectar. Honeybees landed near the center of the flower and immediately inserted the proboscis in a disk floret, but *T. corvina* frequently landed on the ray petals.

TABLE 3

Duration, of three floral visits (in seconds) by Apis mellifera *and* Trigona corvina *on* Baltimora recta.

Date	*Apis mellifera*			*Trigona corvina*		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n
July 13	14.8	3.9	50	25.3	8.6	50
July 14	16.2	5.4	50	27.9	7.7	52
July 15	15.2	4.6	51	23.0	8.3	45
July 16	14.4	4.2	52	27.1	9.6	50

Trigona corvina is known to be an aggressive bee and occasionally arrives at resources in a group (Wille, 1965; Johnson, 1974). One group of 15 to 20 bees arrived at *B. recta* at 7:00 a.m. The bees walked on stems and leaves, possibly depositing pheromones on the plant, a practice thought to be common among bees in this subgenus (Michener, 1974). Aggression occurred between workers of *T. corvina* and there were at least four nests within 700 m of the study plots; foraging groups from several colonies were presumably within the study area. Groups of aggressive bees from different nests had possibly partitioned *B. recta* into areas which they dominated and remained constant to. Although no such site constancy was demonstrated, the results of the experiment suggest that aggressive *Trigona* prefer to fight for a foraging territory, rather than search for less contested resources. Other aggressive *Trigona* seem to discover resources slowly (Hubbell and Johnson, 1978; Roubik, 1980). Perhaps the aggressive *Trigona* display an evolutionary trade-off in foraging behavior. They defend resources relatively effectively as a group but are more restricted in foraging movement, and therefore resource discovery ability, due to the cohesiveness of the group. The foraging tactics of *T. corvina* are possibly best suited to resources saturated with other aggressive foragers or with bees that leave readily when attacked. However, aggression by *T. corvina* had no discernible effect on the foraging activity of *A. mellifera,* and honeybees rapidly invaded favorable foraging areas. Moreover, the honeybees continued to visit flowers at the same rate as their density in flower patches increased, suggesting that foraging profitability did not decline. The more flexible foraging behavior of *A. mellifera* indicates that when resources become locally less abundant, honeybees have a competitive advantage over *T. corvina*. The aggressive foraging behavior of *T. corvina* and possible chemical marking of plants have no apparent deterrent effect on foraging honeybees, but more extensive studies are needed to understand the foraging ecology of these abundant pollinators.

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RESUMEN

En un breve estudio experimental del comportamiento competitivo de abejas, se encontró que *Apis mellifera* (Apinae) europea obtenía el alimento más oportunísticamente que *Trigona corvina* (Meliponinae). Eliminación experimental de una gran porción de *Baltimora recta* (Compositae) visitada por ambas abejas causó un aumento de 44% en la presencia de *Apis* dentro de las áreas de estudio adyacentes de *Baltimora* y sólo un aumento de 17% de *Trigona*. Sin embargo, un análisis de variación demostró que la cantidad promedio de *Apis* subió significativamente pero no la de *Trigona* en áreas de estudio durante tres días después de la manipulación experimental. *Apis* visitó tres flores en un promedio de 15,1 segundos, comparado con 25,6 segundos por *Trigona*. *Trigona corvina* obtenía el alimento en grupos y sus individuos ocasionalmente atacaban a *Apis*, sin ningún efecto aparente. El comportamiento flexible de *A. mellifera* sugiere una ventaja competitiva comparada con *T. corvina* cuando escasean los recursos florales.

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