ECOLOGICAL IMPACT OF AFRICANIZED HONEYBEES ON NATIVE NEOTROPICAL POLLINATORS

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SUMMARY

A significant effect of the Africanized honeybee in the Americas is its interaction with resident pollinators. In French Guiana, Africanized honeybees nonaggressively displaced native highly-social bees from floral resources and artifical nectar sources. Compared to native *Melipona* and *Trigona* (Apidae : Meliponinae), Africanized honeybees may succeed in competition for floral resources due to 1) larger colony size ; 2) a more effective recruitment system ; 3) large individual size, and 4) impunity toward aggressive species of *Trigona*.

Experimental community studies in which the density of Africanized honeybee colonies was manipulated show that 10 to 15 colonies of 6,000 to 20,000 honeybees did not affect brood production, resource harvest or worker life spans of *Melipona favosa* or *M. fulva*. However, the experiment incorporated less than one tenth the number of honeybees colonies that might occur normally within foraging range of these social bees. Africanized honeybees were most similar in floral preference to *Melipona*, small anthophorids, megachilids, halictids and *Trigona*. These data are suggestive as to the *type* of bee Africanized honeybees might compete with most often. But without detailed information on the importance of a diet item to reproductive fitness, predictions regarding the population trends of particular bee species due to competition with Africanized honeybees cannot be made with precision.

RESUMEN

Impacto ecológico de las abejas africanizadas sobre polinizadores neotropicales nativos

Un efecto significativo de la abeja africanizada en las américas es su interacción con polinizadores nativos. En Guyana Francesa, abejas africanizadas desplazaron sin agresividad abejas nativas altamente sociales desde recursos florales y alimentadores artificiales. En comparación con *Melipona* y *Trigona* indígenas (Apidae : Meliponinae), abejas africanizadas pueden competir exitosamente debido a 1) mayor tamaño de la colonia ; 2) un sistema de comunicación más eficaz ; 3) gran tamaño individual, y 4) impunidad hacia especies agresivas de *Trigona*.

Estudios experimentales a nivel de la comunidad ecológica, en los cuales se manipuló la densidad de colonias de la abeja africanizada, demostraron que 10 a 15 colonias de 6,000 à 20,000 abejas no afectaron la producción de crías, cosecha de polen y néctar, o duración de vida de obreras de *Melipona favosa* y *M. fulva*. Sin embargo, en los experimentos se empleó menos que una décima parte del número de colonias de abejas africanizadas que normalmente pudieran encontrarse dentro del rango de vuelo de estas abejas sociales. La abeja africanizada fué más similar en su preferencia floral a *Melipona*, anthophoridos pequeños, megachilidos, halíctidos y *Trigona*. Estos datos son informativos en cuanto al *tipo* de abeja con que la abeja africanizada puede competir con más frequencia. Pero sin información detallada sobre la importancia de un alimento en el éxito reproductivo de una especie, no se puede hacer con exactitud predicciones sobre el dinamismo de población que se espera en un polinizador particular debido a competencia con la abeja africanizada.

INTRODUCTION

Colonization of the American tropics by a hybrid of African and European *Apis mellifera*, the Africanized honeybee, has been viewed almost exclusively as a phenomenon influencing the beekeeping industry and public safety. These valid concerns are nevertheless a small subset of total interactions between an invading species and native plants and animals. Given that Africanized honeybees establish nests in many habitats (Brian, 1965 ; Michener, 1975 ; Roubik, 1979a) and reproduce continuously (Otis, this symposium ; Winston, 1979), widespread interactions with native neotropical plants and pollinators are inevitable (Roubik, 1978 ; 1979b, c ; 1980a). In this paper I consider the question of ecological impact on the most numerous and important group of neotropical pollinators : the bees.

My study took place in the lowland forest and savanna of French Guiana, an area that has never possessed feral populations of European honeybees nor been altered extensively by human activity. Africanized honeybees arrived in 1974 and were present at very low density during this study (Taylor, 1977). A unique characteristic of the region is its rich assemblage of highly social bees (Apidae : Meliponinae). In my study area alone there were 51 such species (Roubik, 1980b). In order to predict the course of changes initiated by the invasion of Africanized honeybees in general, I pose the following questions, to be resolved in the remainder of the paper : How does the presence of the Africanized honeybee affect other highly social species through competition for food ? With which groups of bees is the Africanized honeybee most likely to compete ?

METHODS AND MATERIALS

All studies were made on a transect of lowland forest near Kourou, French Guiana (5°N). The area is primarily coastal forest and savanna having white, sandy soil, which is replaced some 14 km inland by continuous forest and red, lateritic soil. The details in methodology for each of my studies have been given elsewhere and thus are referenced in the following descriptions. The studies were initiated in July 1976 and terminated in August 1977. Three experimental studies were made to determine whether Africanized honeybees influenced 1) the abundance of native foragers within patches of flowers ; 2) foraging success of native bees at artificial resources which caused maximum recruitment of highly-social species ; 3) brood production, honey and pollen storage, and worker lifespan in observation hives of meliponines. One descriptive study assessed to what degree Africanized honeybees shared floral resources with native species. The experimental studies were performed with hives of Africanized honeybees that were established by trapping swarms which colonized beewax-lined «swarm boxes» (Taylor and Otis, 1978). Colonies were transferred to standard 10-frame Langstroth hives or 6-frame plywood hives measuring 24 x 22 x 42 cm. I trapped swarms at savanna-forest edges between Cayenne and Sinnamary.

Competition within flower patches. Near four species of ground-level flowers, 2-10 hives of Africanized honeybees were introduced and later removed to determine whether a change in honeybee abundance at flowers caused reciprocal change in the abundance of native foragers (Roubik, 1978 ; 1979b). In study plots contained within larger patches of flowers, I counted the number of foragers of different species at regular intervals beginning at the time of floral anthesis. Behavioral interaction between foragers also were noted.

Competition at artificial baits. Sixty experiments of 65 min duration were performed using 4 feeders on which honey-water of measured quality and quantity was presented. The experiments were made at 9 sites. The largest-bodied local aggressive species of *Trigona, Melipona fulva*, and polybiine wasps, primarily of the genus *Stelopolybia*, were attracted to the baits. In each experiment, the number of foragers of each species was counted on a feeder every 5 min. The experiments continued at a locality until one species had clearly displaced others or species partitioned the feeders and appeared to stably coexist. Honey-water bait of 25 % or 50 % sugar content was used in the experiments, and aggressive interactions between foragers were noted (Roubik, 1979b ; 1980). The studies were made at the end of the wet season, when minimal floral resources were present (see Roubik, in press).

Competition at the level of the colony. Hives of *Melipona fulva* and *Melipona favosa favosa* were maintained at two sites. Feral colonies of the bees were located and transferred intact, with total colony stores of honey and pollen, to specially designed observation hives (Roubik, 1979a, b and in press). At three-day intervals, colony readings were made to determine 1) rate of brood production, 2) colony stores of honey and pollen, and 3) the age of tagged workers. These observations were made for a period of up to six months preceeding the introduction of honeybee hives. Africanized honeybee hives containing 6,000 to 20,000 workers were introduced for one month at each site, while I continued colony readings of the meliponine bees. Ten to 15 colonies of honeybees were used in each experiment. Few or no additional colonies of Africanized honeybees were within the study area. The experimental introduction of honeybees took place at the end of the wet season, in May and June.

Bee and flower associations. Collections of bees at flowers were made at all accessible species of flowering plants near Kourou for a period of 12 months. I tried to collect foragers or record their visitation at particular plant species in several localities and over a period of several days, until no new flower-visiting species were observed. The plants for which data were taken included 53 tree species, 44 shrub species, 24 species of vines and woody lianas, 21 species of sedges and grasses, and 56 additional species of herbaceous plants (Roubik, 1979b, c). Observations were made throughout the day and records were kept of foraging for pollen and/or nectar for each bee.

RESULTS AND DISCUSSION

Experimental studies

Forager abundance on *Borreria* spp. (Rubiaceae), *Mimosa pudica* (Fabaceae), *Rhynchospora globosa* (Cyperaceae) and *Melochia villosa* (Sterculiaceae) during experimental introduction and removal of Africanized honeybee colonies is given in Table I. Only in the experiments with *Melochia* and *Borreria* were there significant changes in the abundance of native foragers that coincided with experimental manipulation of honeybee colonies. At *Borreria*, however, no significant change in the abundance of Africanized honeybees at flowers took place. This experiment was the shortest of the series, and the changes in abundance that were recorded may have been spurious.

Observations were made for two days with the introduced honeybees present and two days in their absence. The change in native forager abundance was not related to the abundance of honeybees. In contrast, at the study plots of *Melochia*, increased abundance of honeybees corresponded with diminished abundance of highly social native bees (*Trigona c. cilipes* and *Melipona fulva*) at flowers. These species were more abundant when honeybee colonies were removed. Competition for floral resources is demontrated by these reciprocal changes. The experiments at *Melochia* lasted 12 days and included two separate 3-day introductions and removals of honeybee colonies. The probability that the reciprocal shifts in abundance were due to chance is 0.012 (probability of an observed increase, decrease, or absence of change in forager abundance = 1/3, therefore two reciprocal changes in forager abundance would occur with a probability of $(1/3^4)$).

Table I – F ratios for mean daily forager number during the presence of and after removal of Africanized honeybee hives. A nested two-level analysis of variance of forager numbers was performed for three forager classes. Nested groups of days were compared in which introduced hives of Africanized honeybees were present or absent. Subgroups within each group were censusing times. Degrees of freedom are : *Mimosa* (1,12), *Rhynchospora* (1,18), *Melochia* (1,8), and *Borreria* (1,12).

Tabla I – La razón F por el promedio del número de pecoreadoras diarias antes y después de remover colmenas de abejas africanizadas. Se realizó un analisis anidado de varianza de dos niveles del número de pecoreadoras para 3 clases de pecoreadoras. Se compararon grupos de días anidados, en los cuales colmenas de abejas africanizadas introducidas estuvieron presentes o ausentes. Los subgrupos dentro de cada grupo representan los tiempos de censaje. Los grados de libertad son : *Mimosa* (1,12), *Rhynchospora* (1,18), *Melochia* (1,8), y *Borreria* (1,12).

	Floral resource			
Forager class	*Mimosa**	*Rhynchospora*	*Melochia*	*Borreria*
Africanized honeybees				
During	9.6	81.5	111.3	371.0
After	0.0	7.5	72.0	365.0
F ratio	25.78^{+}	27.89^{+}	8.11$^{+}_{+}$	0.05
Stingless bees				
During	25.3$^{\beta}$ 32.0$^{\lambda}$	65.6	23.3	124.5
After	19.1$^{\beta}$ 44.5$^{\lambda}$	100.0	61.0	189.5
F ratio	2.10$^{\beta}$	1.08	6.80$^{+}_{+}$	14.5^{+}
Other native foragers				
During			51.8	22.5
After	not present	not present	60.1	59.0
			2.32	11.89^{+}

* Bees per 100 flowers. + P $<$.001. $^{+}_{+}$ P $<$.05. *Mimosa : Melipona fluva* and *M. favosa favosa ; Rhynchospora : Trigona (Tetragona) claviques ; Melochia : M. fulva* and *T. (Trigona) cilipes ; Borreria : M. fulva, M. favosa favosa,* and *T. (Trigona) cilipes ;* β *Melipona fulva ;* λ*Melipona favosa favosa.*

The Africanized honeybees did not interfere aggressively with other foraging insects, thus competition at *Melochia* appears to have been the result of declining food rewards perceived by native bees. The possibility of interference due to odors from the honeybees cannot be excluded as a subtle additional interaction which occurred during the experiments. Despite significant change in the rate of floral visitation by native bees on *Mimosa* after the removal of honeybee colonies, and the large amount of pollen that was collected by the introduced honeybee colonies at *Rhynchospora* (Roubik, 1978), the abundance of native bees did not change at these resources. Competition at these species might have been evident if total colony resource harvest had been measured for the social bees visiting the study plots.

The experiments at artifical feeders are discussed at length in another paper (Roubik, 1980a) and here I present the general results. Combined results from 37 experiments in which Africanized honeybees and native social foragers visited the feeders together are given in Fig. 1. Eighteen of the experiments included a single, small honeybee colony (5,000 - 8,000 workers) and 19 included 2 - 7 colonies. Eight species of *Trigona, Melipona fulva* and several wasp species foraged during these experiments. Honeybees dominated the feeders, particularly when the maximum amount of resource was applied to feeders (Fig. 1). The honeybees were not aggressive toward other species and did not abandon feeders readily when attacked by *Trigona*.

The largest, consistently aggressive *Trigona* eventually abandoned feeders visited by a large colony or several small colonies of Africanized honeybees. These *Trigona* were relatively inflexible in their aggressiveness, and they all but ceased to visit feeders at which they had arrived previously in large numbers. Such behavior is best explained as the result of a foraging cost (constant attack of numerous honeybees) that exceeded the gain (caloric reward of honey-water). Aggressive workers from single colonies of *T. hyalinata branneri* and *T. p. pallens (= T. pallida)* successfully displaced from feeders the honeybees of single, small colonies at two sites. In each instance of interspecific displacement, foragers from a displaced colony occasionally arrived at feeders and foraged successfully, but the response of the colony and the arrival of foragers that had been trained to visit the feeders declined abruptly. This change in response never occurred at relatively uncontested feeders.

Colonies of *T. h. branneri* and Africanized honeybees were far larger than those of the other species. The size of a mature honeybee colony is 10-100 times that known for the *Melipona* and as much as 10 times larger than most *Trigona* colonies (Michener, 1974 ; Roubik, 1979a, 1980a and in press). In addition, no highly social bee except *Apis* is able to recruit many nest mates to a resource in a short time, without the necessity of providing

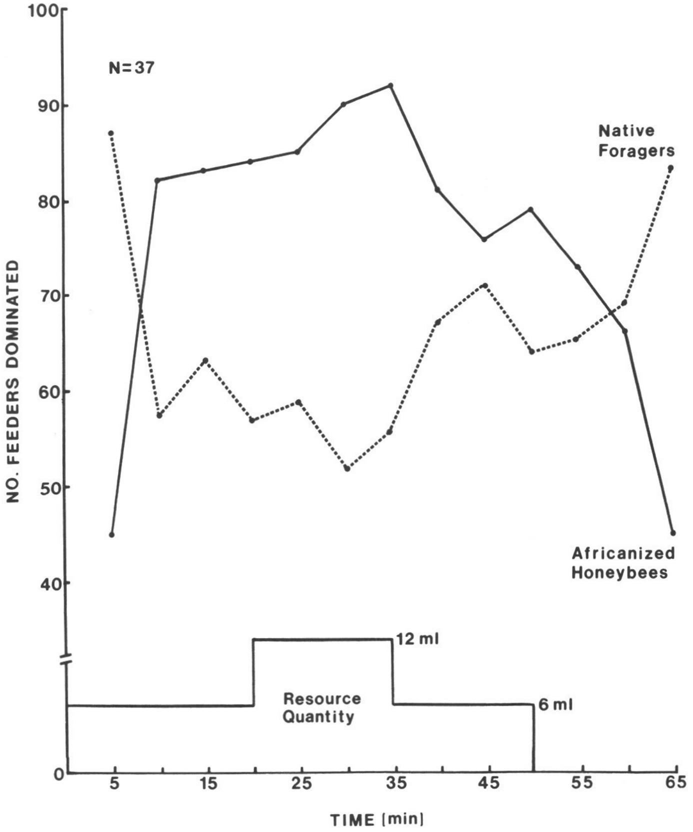

Fig. 1 – Dominance of individual feeders (numerical superiority) by Africanized honeybees or combined native foragers. The data are from 37 experiments, each incorporating 4 feeders ; 13 counts of foragers were made at each feeder in a 65-minute experiment. «Resource Quantity» is the amount of bait applied to a feeder at 5-minute interval.

Fig. 1 – Dominancia (superioridad numérica) de abejas africanizadas o combinación de pecoreadoras nativas sobre alimentadores individuales. Los datos son de 37 experimentos, cada uno incluyendo 4 alimentadores ; se hicieron 13 conteos de pecoreadoras por cada alimentador en un experimento de 65 minutos. «Cantidad de Recurso» es la cantidad de cebo aplicada a cada alimentador a intervalos de 5 minutos.

odor trails or guiding other foragers (Michener, 1974). The relatively large size of *A. mellifera* implies a larger flight range than the *Trigona* and a foraging range comparable to *Melipona* (see Eickwort and Ginsberg, 1980 ; Michener, 1974 ; Roubik, 1979c). The large colony size, more precise recruitment system, particularly for long distances (von Frisch, 1967), and impunity toward aggressive *Trigona* provide Africanized honeybees with a competitive advantage over stingless bees in locating and exploiting rich resources. Other factors being equal (sensitivity to floral odors and response to meteorological conditions, for example), a large colony or multiple colonies of Africanized honeybees should be able to dominate many of the floral resources used by neotropical social bees.

Demonstration of competitive superiority at a particular place or time need not imply that an introduced species will displace another from a geographic area. Particularly for highly social bees which exploit a large proportion of the available flowering plants (Percival, 1974 ; Sakagami, Laroca and Moure, 1967 ; Johnson, 1974 ; Heithaus, 1979 ; Roubik, 1979a, b ; Absy and Kerr, 1977), diminished foraging returns or even total displacement at a resource need not lead to substantial loss at the level of the colony. To test whether probable competition among such generalist foragers affected the functioning of the colony, my introduction-removal experiments were designed to test the null hypothesis that no significant changes occurred in intracolony processes of meliponine bees as a result of the number of Africanized honeybees in close proximity. Acceptance of the null hypothesis does not signify the absence of competition at all levels, but only that intense competition did not accur.

Analysis of data collected as time series presents special statistical problems (Box et al., 1978). One means of circumventing such problems is the technique of repeated-measures ANOVA (Winer, 1971). This method was applied to data from 5 meliponine bee colonies to test for a change in intracolony parameters during three experimental treatments : the absence of honeybee colonies, introduction of honeybee colonies and removal of honeybee colonies. The result are presented in Table II. The statistical model of repeated measures ANOVA predicates independence between subjects (bee colonies) and is applied to analyze the effect of a treatment on subjects that were monitored simultaneously (Winer, 1971). Further, I analized the rate of change of intracolony parameters (the differences between successive readings) rather than the raw data series. No «control» colonies were used in the experiments because a suitable number of colonies in the same stage of their colony cycle (Oster and Wilson, 1978) was not available.

No change in the amount of stored honey, pollen or newly constructed brood cells occurred due to the change in number of introduced Africanized honeybee colonies (Table II). Meliponine worker life spans increased during the period of honeybee introduction, but this was a seasonal trend due to floral scarcity not related to competition with the honeybees (Roubik, 1979b and in press).

The 30-day period in which honeybees were introduced at each site coincided with the end of the wet season and a floral dearth period.

Table II – Results of repeated measures analysis of variance of the rate of change in intracolony parameters that coincided with three experimental treatments of differing honeybee colony density (see text).

Tabla II – Resultados del análisis de varianza de medidas repetidas de velocidad de cambio de los parámetros intracoloniales que coincidieron con tres tratamientos experimentales de diferentes densidades de colonias de abejas melíferas.

Colonies observed (number)	Intracolony variable	Treatment means *			df	F	P
		before	during	after			
M. favosa (2) *M. fulva (1)*	honey	-4.14	-1.61		1,2	2.61	0.25
	pollen	-0.09	0.01		1,2	1.80	0.31
	brood	-0.14	0.10		1,2	0.13	0.76
M. favosa (1) *M. fulva (1)*	honey	-5.30	-2.34	-1.00	2,2	2.81	0.26
	pollen	-0.13	-0.02	0.01	2,2	0.69	0.59
	brood	-0.21	-0.13	-0.13	2,2	0.05	0.97

* Means for honey and pollen are in cm^3 ; brood is expressed in the average number added to the colony per day. The data are presented as rate of change, i.e. differences between successive observations.

The colonies of *Melipona* were experiencing a seasonal decline in brood production and colony stores (Table II). Nevertheless, they brought food to the nest, as did the introduced honeybees (Roubik, 1979b). A lack of intense competition could have been due to the use of different resources during this period. However, of the 75 known floral resources used by *M. fulva* during the year of my study, and the 26 used by *M. favosa*, at least 50 % also were used by honeybees (Roubik, 1979b and in press, see also Table III). It seems that competition may have occurred, but at levels too low to be detected within the nest. Furthermore, the 10-15 colonies of Africanized honeybees used in the experiments were probably the only colonies within the foraging range of the *Melipona*. In a naturally colonized habitat, the density of Africanized honeybee colonies has been estimated at 10 colonies/km^2 to 107 colonies/km^2 (O. Taylor, personal communication and Kerr et al. in Michener, 1975). The foraging range of *Apis mellifera* is at most 14 km (Eickwort and Ginsberg, 1980) and a foraging range of 5 km is common (Gary et al., 1977 ; N.E. Gary, personal communication). The demonstrated foraging range of *Melipona* is at least 2 km (Wille, 1976 ; Roubik, unpublished data). Combining this information, an individual colony of *Melipona* potentially competes with honeybee colonies within a 7 km radius. At Africanized honeybee colony density of 1/km^2, a *Melipona* colony may compete with the foragers of 154 honeybee colonies. Competition is therefore potentially far more intense between Africanized honeybees and native *Melipona* than that which was possible in the present study.

Table III — Floral resource use and diet overlap among Africanized *Apis* and neotropical bees.

Tabla III — Uso de recursos florales y sobreposición de dietas entre *Apis* africanizadas y abejas neotropicales.

Bee genus	*An*	*Ap*	*Aa*	*Ao*	*Bo*	*Cn*	*Cr*	*Ep*	*Eg*	*El*	*Fl*	*Mg*	*Ml*	*Ms*	*Tt*	*Tr*	*Xy*
No. bee species	3	1	12	6	1	25	10	6	25	6	1	14	7	1	18	37	12
No. floral resources	14	75	34	26	20	38	17	11	38	14	12	36	79	15	23	165	63
Diet overlap with *Apis*	.71	1.00	.62	.46	.05	.18	.65	.18	.21	.00	.83	.61	.50	.73	.43	.32	.29

An : *Anthidiinae*
Aa : *Augochlora*
Ao : *Augochloropsis*
Ap : *Apis*
Bo : *Bombus*
Cn : *Centris*
Cr : *Ceratina*
Ep : *Epicharis*
Eg : *Euglossa*
El : *Eulaema*
Fl : *Florilegus*
Mg : *Megachilde*
Ml : *Melipona*
Ms : *Melissodes*
Tt : *Paratetrapedia* + *Tetrapedia*
Tr : *Trigona*
Xy : *Xylocopa*

Resource use

Resource use by coexisting species is a central topic of population and community ecology. The implictions of observed resource partitioning among species are seldom clarified (Schoener, 1974 ; Wiens and Rotenberry, 1979 ; Hutchinson, 1979), but the situation is somewhat more straightforward when a colonizing species is involved. Conventional ecology emphasizes overlap of resource use in space and time and the effect that the rate of food harvest by one species has on the reproductive fitness of other species using the same resource (Hutchinson, 1979). It is often tacitly assumed that the number of diet items held in common between species directly influences the degree to which they compete (Cody, 1974 ; Pianka, 1976 ; Percival, 1974 ; Moldenke, 1975 ; Heithaus, 1979). But this is true only if all diet items are equally important to reproductive fitness. The data presented in Table III should be interpreted accordingly. At the least, they indicate which groups of bees might compete most often with the Africanized honeybee and which would seem not to compete frequently, relaitve to their recorded floral preferences.

With the exception of Africanized *Apis mellifera*, I combined the data on floral preferences of bees of closely-related species. Of the 37 bee genera included in my study (Roubik, 1979b, c), what seem to be adequate or representative data were available only for the 17 genera listed in Table III. A graphic representation of the similarity in resource use among these genera is presented in figure 2, the result of principal component analysis (see Harris, 1975 ; Poole, 1974). A possible shortcoming of the resource data is that only a moderate percentage of the total resources used by bees could be included. Further, the implicit assumption in the analysis is that the species of a particular genus are more similar to congeners in resource use than they are to species of other genera. This assumption may be false in some instances (Heithaus, 1979). However, the data include a broad variety of flowering plants (see Methods and Materials, also Roubik, 1979b, c), and thus may adequately represent this plant-pollinator community. It seems reasonable that closely related species share structural and behavioral attributes that determine which resources they are able to use (Michener, 1979 ; Michener, et al., 1978 ; Inouye, 1978 ; Thorp, 1979). Therefore, the lumping of congeners for the purpose of understanding resource use patterns may be justified. Moreover, the information gathered during one year of observation does not seem to warrant comparative studies of resource use among individual species (see Wiens and Rotenberry, 1979).

The most striking pattern emerging from the data given in Table III and Fig. 2 is that Africanized honeybees share a large proportion of the resources

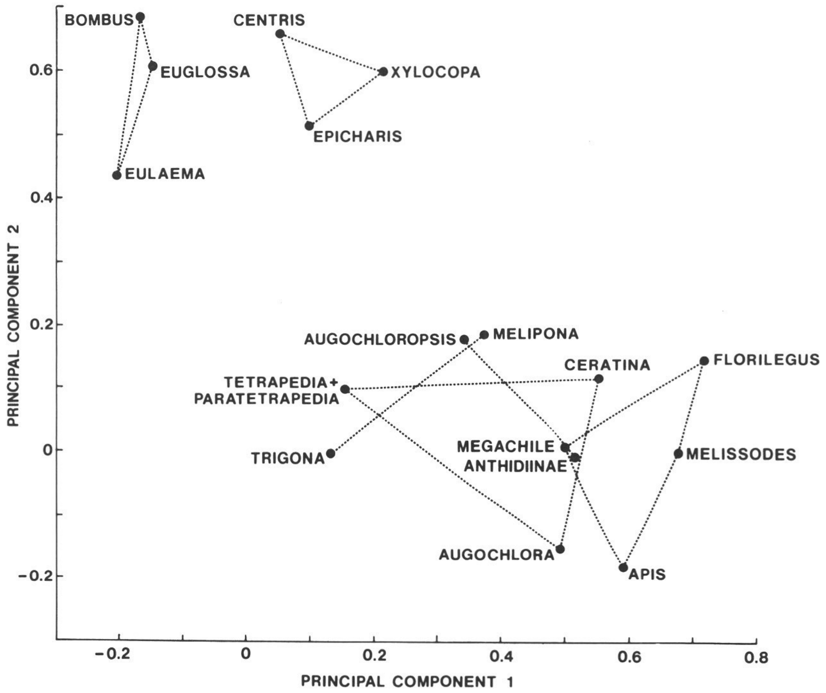

Fig. 2 – Similarity in floral resource use among Africanized honeybees and 17 neotropical bee genera, presented on two axes specified by a principal component analysis. The dashed lines connect genera that clustered together on rotated principal axes which accounted for 51 % of the observed variance in floral preference among bee genera.

Fig. 2 – Similitud en el uso de recursos florales entre abejas africanizadas y 17 géneros de abeja neotropicales, presentados en dos ejes especificados por análisis de componente principal. Las líneas entrecortadas conectan géneros que se agruparon en ejes principales rotados y que explicaron el 51 % de la varianza en preferencia floral entre géneros de abejas.

used by medium-sized to small bees, and not many with the larger bees. Similar associations have been seen among European honeybees and native bees in Costa Rica dry forest (Heithaus, 1979). In French Guiana, bees visiting a species of flower almost always collected nectar and pollen when both were available. Yet it is possible that these resources, although from a single species of flower, may represent different contributions to the fitness of bees. Oligoleictic species, bees that restrict their pollen use to a small number of species, probably sustain greater reproductive loss due to competition for pollen with Africanized honeybees than do other species. The limited available data suggest that many species of small anthophorids and megachilids tend toward oligoleicty in the tropics (Heithaus, 1979 ; Roubik, 1979b, c and Table III), although these species are seldom restricted to one or two species of pollen, as are oligoleictic species in temperate areas (Raw, 1976 ; Michener, 1979). The more generalized flower visitors such as meliponine bees may be less dependent on a small number of resources and thereby less susceptible to competition with generalist honeybees. Even if native species are more efficient at exploiting a particular flower (see Strickler, 1979) than are Africanized honeybees, the sheer numbers of Africanized honeybees arriving at a flower patch from an individual colony plausibly alters their efficiency both through incidental interference (Roubik, 1980a) and depletion of floral rewards. Considering both generalist and specialist bees in the tropics, competition for flowers must be assessed ultimately in terms of reproductive fitness. At present, a crucial question for future research can be phrased : how important is a species of flower to the reproductive fitness of its visitor ? I suggest that this question has not been answered for any tropical apoid.

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