LEARNING TO LIVE WITH AFRICANIZED HONEYBEES[1]

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Prior to 1520 the primary source of honey in "New Spain" and elsewhere in the New World tropics was from the nests of native stingless bees (Meliponinae), whose colonies since remote times were domesticated by the Maya and indigenous people of the Amazon (Brand, 1988; Posey and Camargo, 1985). Even after the introduction from Europe of *Apis mellifera*, the most widely domesticated of all honeybees, stingless bees remained the source of honey in tropical forests, where feral European honeybees were essentially unable to survive and reproduce (Roubik, 1989). Nonetheless, honeybees are primarily tropical insects in their native Old-World habitats. Thus it is no surprize that 34 years ago a tropical variety from Africa, *Apis mellifera scutellata*, was brought to southern Brazil with the intent of improving beekeeping by selective breeding with European honeybees, then widely in use. What followed was remarkable. The African honeybees became feral, interbred with and displaced nearly all colonies of the European races, and most important, colonized all of tropical America. From Tampico to Tegucigalpa, from Petén to Panamá, from Barranquilla to Buenos Aires, we have witnessed the arrival of a new ecotype: the Africanized honeybee. This bee is perfectly capable of sustaining feral populations in cities as well as in rain forests, and it is independent of beekeepers and apiaries (Boreham and Roubik, 1987; Roubik, 1989). It is not "pure" African but nearly so, and its feral populations, numbering in the hundreds of millions of colonies, have established a firm foothold in all the lowland neotropics and up to 2400 m above sea level near the equator (Ruttner, 1988; Lobo *et al.*, 1989; Hall and Maralidharan, 1989; Smith *et al.*, 1989; Roubik, 1989).

Scientific research on honeybees often begins and ends in the apiary. Because Africanized colonies often abandon their hives or sting relentlessly, there has been a tremendous effort to manage irritable bees or replace them with other varieties. In the temperate areas of South America, where there are many European honeybees and also populations of *feral European* bees, the problem has largely taken care of itself. Bees are more docile and more European beginning at the temperate margins of the subtropics, where a reversal to European traits takes place (Ruttner, 1988; Lobo *et al.*, 1989). This scenario might be anticipated for the southern United States and parts of Mexico (Roubik, 1987), where efforts to counter a negative commercial impact of Africanized honeybees currently focus on the multi-billion dollar pollination industry (Levin, 1983; Parker *et al.*, 1987; Taylor, 1988). In the tropics, feral populations of Africanized honeybees are so much larger than those of managed honeybees in hives that manipulation in the apiary can have almost no effect at the population level. The Africanized honeybee is here to stay, but we

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cannot easily predict what its future will be. In addition, fundamental difficulties surround the understanding of Africanized honeybees and their impact. We believe these stem from a general ignorance on the part of beekeepers, scientists and the public on 'wild' honeybees in ecosystems — the systems which contain and regulate the pollination of plants and the ecology of bees (Figs. 1, 2).

An agenda for Africanized honeybee research at an ecosystem level and bee management in Panama was formulated between 1979 and 1982, during the three years preceding arrival of the bees from Colombia. Using this data base and now including up to 11 years of observations, we interpret some of the known ecosystem consequences of the Africanized honeybee invasion, emphasizing impact on human activities. Prior to Africanized honeybee arrival, baseline data were collected on native bee species likely to be affected by the honeybee (Wolda and Roubik, 1986; Roubik and Ackerman, 1987; Roubik, 1988, 1989). Programs were also initiated for the control of apicultural and public health problems in the Republic of Panama and the Panama Canal Area (Boreham and Roubik, 1987). This report gives findings of these continuing studies, compares them to other research conducted in Latin America, and discusses implications of an isolated instance of continuing commercial apiculture with European honey bees on a Panamanian offshore island, where few colonies of the Africanized honeybee arrive.

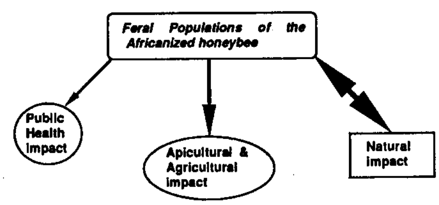

Figure 1. A compartment model showing major environmental impacts of the Africanized honeybee. The width of the arrows between compartments indicates probable strength and persistence of the impact. The double arrow between the feral honeybee populations and natural impact suggests that native plants and animals, over the long run, will have a relatively large impact on the honeybees.

Spread and Growth of the Invading Bee Population

Africanized honeybees were first detected in Panama in early 1982 by a beekeeper in the Darién area who had previously solicited information from DWR about how to recognize these bees. He collected two swarms that arrived near his small apiary in January, the early dry season. Noticing that the bees flew more rapidly, entering hives on the wing rather than walking in from the landing platform, led him to suspect the bees were Africanized. Morphometric analysis of worker bees validated his observation (Roubik, 1982). Two months later an Africanized swarm was collected in Panama City. April of 1982 marked the first confirmed presence of Africanized honeybees in the Canal Area, near the Caribbean coast (Boreham and Roubik, 1987). Additionally, the first sighting of Africanized honeybees in the forest preserve and research facility at Barro Colorado Island, located in central Atlantic Panama in Gatun Lake, occurred in July of 1982. In December of 1982 a few swarms of Africanized honeybees arrived near the town of David, at sea level and 490 km W. of Panama City. In July of 1983 there were honeybee swarms reported in the northwestern coastal town of Bocas del Toro. This area lies on the Caribbean, the lowlands of which receive over twice the annual rainfall of the Pacific coastal area. No honeybees were previously maintained in this part of Panama, therefore the swarms were likely Africanized.

From this chronology, it is apparent that the spread of Africanized honeybees was more rapid in the Pacific area, which is for the most part deforested and relatively dry (1 to 2 m annual precipitation). The spread along the rainier and forested Atlantic area lagged behind by as much as eight months at the western limit of Panama. Arrival on the Pacific island of Taboga, 12 km from the nearest point of the mainland, was confirmed in March of 1983, and numerous reports were made of swarms arriving on ships in the Panama Canal area and in western Atlantic Panama beginning in 1983 (Boreham and Roubik, 1987). Africanized honeybee swarms also arrived on large islands in the Bay of Panama, the nearest of which is 32 km from the Pacific mainland. San José Island, located 68 km from the mainland in the Bay of Panama, received its first Africanized honeybee swarm in May of 1985, when a huge swarm landed in a stack of empty bee hives (2). As emphasized below, the continuation of beekeeping on San José constitutes a case study on the means by which apiculture has been able to adapt to low levels of Africanized honeybee introduction.

The pace of westward swarm movement across Panama was so rapid that nearly the entire country was traversed in a single year. The most reliable data, however, concern the distance of 490 km between Panama City and David, crossed by dispersing swarms in a period of 9 months. The projected dispersal rate from this information is about 650 km annually. Finding Africanized honeybees in Santa Fé, Darién Province during January, a mere two months before colonies appeared in central Panama 250 km farther west, suggests that colonies had existed in the Darién prior to 1982 but were not detected. The eastern half of Panama is very sparsely settled and contained fewer than a dozen apiaries. The environs of Panama City, and the Panama Canal area in particular (Fig. 3), were much more closely surveyed (Boreham and Roubik, 1987 and Reyes, 1984).

Rapid dispersal and rapid detection of Africanized honeybees had at least two unanticipated results in Panama. First, since most beekeeping and managed European honeybee colonies in Panama were concentrated in the westernmost provinces, beekeepers were generally skeptical that a few bees 'over there' in eastern Panama could affect them. When it was determined that the Africanized honeybee had reached western Panama their skepticism increased. The common reasoning appeared to be the following: If the honeybee had already arrived, and beekeeping practices were not in the least altered, then surely all of the negative predictions were false. Second, besides the pronounced seasonal differences in swarm movement (outlined below), a running documentation of the colonization created the impression that the bees were merely passing through. When the frequency of swarm movement diminished, as it inevitably does during the latter half of the wet season (Fig. 4), the belief that the bees had moved on to Costa Rica was reinforced.

General accounts of Africanized honeybees in the Americas are reviewed by Taylor (1985) and need not be repeated here, but a few themes that persisted in Panama deserve mention. Despite the best efforts of newspapers, radio, television, public meetings, and a keen sense of responsibility for public welfare both in Panama and the

Canal Area, myths about the Africanized honeybee held sway over reality for at least the first two years after colonization. Word of mouth seemed to supersede any amount of other information and included notions such as: 1) Africanized honeybees are larger than ordinary honeybees and their venom is sufficiently potent to cause death from a single sting; 2) Africanized honeybees produce more honey than European honeybees, and 3) Africanized honeybees have a "killer instinct" and "swarms" attack without warning. The last point indicates a pan-cultural linguistic problem. The word 'swarm', in the biology of honeybees, refers to a dispersing colony. In nature these are almost completely docile, regardless of origin or genetic variety. The words 'nest' or 'hive' refer to an established colony, which for most honeybees, and particularly those introduced to South America from Africa, can display an explosive defensive behavior that is very rare in swarms (Collins *et al.*, 1982). The specific linguistic problem is that 'swarm' is used by the general public to refer to both swarms and nests, as well as to indicate groups of scout bees that investigate potential nest sites before a swarm actually arrives. Not only does this prevent precise communication about honeybees, it usually leads to the belief that a group of bees expressing no defensive behavior will, even as a nesting colony, continue to display no defensive behavior. Furthermore, since the Africanized honeybee looks very similar to European honeybees, those familiar with the latter see swarms or nests of Africanized honeybees and assume that they are European, particularly if they expected to see much larger "killer-type" honeybees, Such myths were quickly exploited by the local moviehouses. Adding to the confusion of the general public, some beekeepers and newspapers drew attention to themselves by announcing that Africanized honeybees had already existed for years in Panama, or that various large groups of insects (including wasps, flies, moths, grasshoppers and stingless bees) constituted yet more hordes of "killer bees".

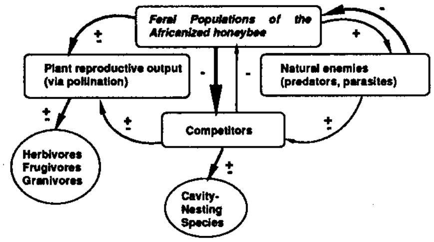

Figure 2. A compartment model of modes by which Africanized honeybees interact with and influence native plants and animals. Omitted from the diagram is food supply to the honeybees of other flower visitors and the long-term effect of their visits on the availability of floral resources. Indirect effects of the honeybees are mediated through flowering plants, competitors, and natural enemies (see text).

Population Change and Control

There is no reason to believe that feral European honeybee populations ever existed in tropical America, thus the contrast with the Africanized honeybee is striking. For example, Villa (1987) shows that even at the upper elevation limits of honeybee distribution in Colombia, between 2000 and 3000 m, there are feral Africanized honeybee colonies and apparently none of European honeybees, despite long-established beekeeping with European bees in this region. Although there have been no rigorous quantitative studies of honeybee colony density in the American tropics (Roubik, 1989), a contrast between highland and lowland sites is evident. In the study of Villa (op. cit.), which took place during the first three years of the Africanized honeybee invasion, 44 colonies were noted in 209 nesting sites that were surveyed during 26 months. In comparison, bee colonies were seven times more numerous at the same phase of colonization in a seven-month study in the lowlands of French Guiana (Roubik, 1980, 1983). In that region a total of 52 colonies was found in 140 nesting sites. Within 50 square km flanking the Panama Canal, 1175 Africanized honeybee colonies were found during the first 48 months of their presence (Boreham and Roubik, 1987). No feral honeybees had been noted in any of these sites prior to arrival of Africanized swarms.

Swarms and nests reported in the Panama Canal Area were removed to ensure the safety of local residents and canal operations; samples of bees from each controlled colony were examined morphometrically Boreham and Roubik, 1987). Similar control measures have been applied in Guyana, Trinidad and Tobago, Mexico, and in many other regions of Latin America, but none has included comparable analysis of bee phenotype and abundance in a fixed sampling area and at consistent sampling intensity. Data from the Panama Canal area show a number of general characteristics that should have broad applicability. First, the movement of swarms is seasonal and highly predictable (Fig. 4). Second, phenotypic change has been gradual, showing decreasing bee size. And third, Africanized honeybee abundance rises to a maximum during the first few years after the colonization and then declines. Our Panama data from March of 1982 to August of 1989 show populations have reached apparent stability with slight decreases in abundance over the past four years, following a rapid decline from the maximum abundance (over 300 colonies per year) seen during the second through fourth years after colonization. Interestingly during both 1987 and 1988 a total of 169 swarms and nests were found within the 50 km² area.

Considering population data on Africanized honeybees from Panama, it is very clear that most reproduction occurs during the first six months of the year from the early dry season through the early part of the rainy season. From 80 to 90% of all swarms and nests were encountered during this time. As can be see in Fig. 4, on the Pacific side of the isthmus there is one pronounced peak, while on the Atlantic side there are two large peaks, one in dry season and one during the first two months of the rainy season in May and June. The abundance of swarms and nests is closely correlated, but a closer examination of swarm abundance is instructive. Swarm number is the combined result of colony reproductive cycles, swarms produced during such cycles, and the emigration or absconding of colonies. The predominant causal factors are evidently food abundance, and to some extent heavy rainfall. Patterns of swarm abundance match the seasonality of floral resources, the most important of which are trees in central Panama (Fig. 5). As Villa (1987) shows in Colombia, colonies often abscond (abandon their nests) after four months of rainy weather and unfavorable foraging. The peak absconding season in Panama observed by DWR occurs during the fourth to sixth months of the rainy season (August to October). Since the rains usually begin in late April and the peak swarming months are January to March, the second highest annual swarm movement (on the Atlantic side usually in June) likely contains a small portion of absconding swarms. The presence of extremely large swarms or "mega swarms", much larger than reproductive swarms, at this time only, is a strong indication that they could be the result of colony 'amalgamation' (Kigatiira, 1988). However, floral resources are renewed at the end of the dry season and beginning of the rainy season, particularly the small trees, shrubs, palms and herbaceous plants (Croat, 1978; Roubik *et al.*, 1984, 1986), Thus while the dry season peak probably results almost exclusively from colony reproduction later wet season swarms are likely to be increasingly composed of absconding colonies. The reproductive cycle of Africanized honeybees had been studied using colonies in hives designed to simulate small nesting cavities (Winston, 1987), and three to four yearly reproductive cycles per colony were extrapolated from this research. The pattern of yearly swarm abundance in Panama does not corroborate the apiary studies (Boreham and Roubik, 1987).

Small numbers of Africanized honeybee colonies seem very likely to disperse over great distances during the early rainy season. It is significan that the first appearance of Africanized honeybee swarms in both the Panama Canal area and the forested island of San José occurred at the onset of the rainy season, and that both swarms were reported to be very large. The amalgamation of small African honeybee swarms into large 'megaswarms' signals the initiation of migratory swarm behavior (Kigatiira 1984, 1988). In central Africa, large megaswarms similar to those noted during May and June in Atlantic Panama (Boreham and Roubik, 1987) are composed of several colonies and their queens. After all but one queen is eliminated from a swarm that may contain over 100,000 workers, the swarms may disperse over 200 km (Kigatiira, 1984, and [3]). In Panama, an abrupt doubling in the proportion of extremely small swarms occurred just at the time of megaswarm appearance in the Atlantic area. In contrast, the proportion of small swarms observed on the Pacific side changed very little and no megaswarms were seen there, compared to 22 sightings in the Caribbean area (Boreham and Roubik, 1987). Larval honeybee queens mature in two weeks and the workers require three, thus at least three weeks must pass before colonies reproduce in response to increased food availability (Winston, 1987). Swarms abundance lagged aproximately one month behind commencement of the dry season flowering. This indicates reproduction in response to recent flowering, rather than emigration to areas where a peak flowering period is beginning. Most swarm movement can be explained as the result of honeybee responses to local resource availability.

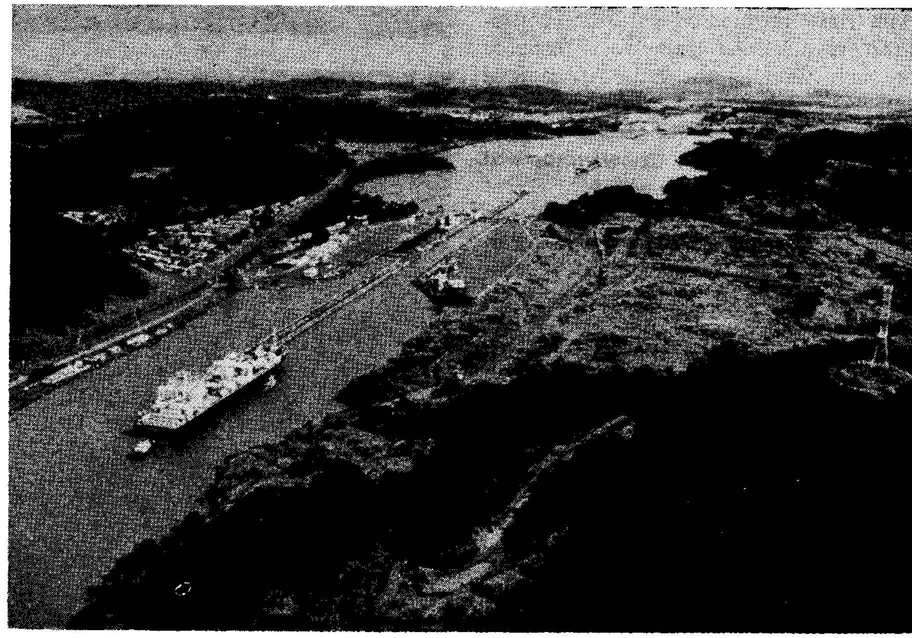

Figure 3a. A view of the Panama Canal Area and its environs in central Panamá, where a large, long-term study has been carried out on the impact of the colonizing Africanized honeybees.

From the first arrival of Africanized honeybees in central Panama, the relatively small morphometric measures characteristic of the Africanized honeybee predominated in the feral population. This was expected because there were no feral honeybees in lowland Panama. Within three years the bees gradually became smaller even when compared with bees from South Africa, where most of the source bees came from. Now Panama bee colonies more closely resemble those of bees from equatorial Africa (Ruttner, 1988; Boreham, and Roubik, 1987). As stated by Michener (1982) the original African honeybee colonies introduced to southern Brazil consisted not of South African bees but also a colony from Tanzania. Most of the Africanized honeybees that arrived in Mexico appear to be descendants of the South African population (Hall and Muralidharan, 1989).

Impact Assessment

Assessing changes in any variable studied over time requires statistical techniques that can separate real deviations from the continuation of past trends. Sound techniques in data collection and analysis are equally important. The potential for an impact from the Africanized honeybee is large, since several classes of organisms interact with the bees throughout the year (Fig. 2). Although the number of Africanized honeybee colonies has declined in Panama, presumably due to predators or other natural enemies, the honeybees are constantly present. As suggested in Fig. 2, both positive and negative effects may result from the honeybees' interaction with particular species of natural enemies, flowering plants, and other organisms. Weedy, annual plants may become more abundant in a short interval due to enhanced pollination by honeybees, but even if this takes place, the abundance of major pollen and nectar sources, the woody perennials, would not be altered by honeybees. The animals that feed on leaves, fruit, and seeds are affected indirectly by Africanized honeybees and their impact on pollination. Other species affected are those that share nesting sites with native species competing with honeybees for food or other resources. At present we are only beginning to understand how closely all of these variables are linked, or whether a balance between them can be expected.

The diagram of Fig. 2 includes the possible negative consequences to European honeybees that may result from augmented parasite or predator pressures. As a new food resource for such animals, the feral Africanized honeybees potentially increase the population of apiary pests. Their impact might be expected to be trivial, compared to the negative influence of direct competition with feral honeybees for mates, food and nest sites. However, preliminary data from Quintana Roo, Yucatán, where a long-term study is being carried out by DWR and R. Villanueva, have clarified some of these issues. After the second year of feral Africanized honeybee presence, apiary colonies of European honeybees are intensely robbed by feral Africanized honeybees. Also, a local vertebrate predator of stingless bee and honeybee colonies, the tayra *Eira barbara* (Roubik, 1989), has shown an alarming increase in its rate of attack on apiaries. We believe this is due to the recent experiences of this omnivore with a new resource (feral honeybee colonies) which has resulted in its predilection for the colonies of *Apis mellifera* and an active pursuit of apiaries. We believe that both tayras and social insects such as army ants and robber bees *(Lestrimelitta)* possibly contributed to the decline of Africanized honeybee populations in Panama, but quantitative data are lacking. Competition between Africanized honeybees and native species of bees and other animals has yet to produce measurable changes in combined bee populations, but several years of field data will be necessary to detect such changes in individual species, if they occur (Roubik, 1978, 1989 and unpublished data). Work in Panama has established that year-to-year changes in native bee abundance are extremely low (Wolda and Roubik, 1986; Roubik and Ackerman, 1987).

Figure 3b. An exposed nest of the Africanized honeybee under the branch of *Enterolobium* (Leguminosae), 22 m above ground level near the Pacific side of the Panama Canal.

Records kept by beekeepers and government officials showed an enormous and abrupt loss in apiculture in Panama caused by the arrival of Africanized honeybees. Cordovez (1987) summarized some figures provided by the Ministry of Agriculture of Panama. A 68% decrease in total honey production occurred between 1983 and 1984. The analysis is, however, complicated by the fact that during 1982-1983 Panama and Central America were greatly affected by the extended dry season caused by El Niño and cessation of the trade winds. In Panama, the dry period caused extended flowering by many plants, which according to beekeepers brought about the highest honey yield seen in Panama. A 60% decrease in honey production was noted in Venezuela within five years of Africanized honeybee arrival (Rinderer, 1985). However, honey production has recovered to prior levels in Venezuela and elsewhere in tropical South America, which may be due to: 1) improved apiary management, 2) the use of feral swarms to stock apiaries, 3) government protection of honey prices and beekeeping, and (4) the extensive harvest of honey from feral Africanized honeybee colonies (summaries in Breed, 1989). Regarding the ecological circumstances surrounding these changes, it is unknown whether the Africanized honeybees have declined or the resources used by honeybees had changed while honey production and beekeeping recovered. Little quantitative information has been compiled on the changes in apiculture in Panama (but see Caron and Gray, in press). During 1982 to 1987, the number of commercial beekeeping enterprises declined from ten to three, and the retail price of honey rose 300%, far outpacing inflation.

Beekeeping was seriously hampered by lack of adequate protective equipment when Africanized honeybees first arrived. A few of the professional beekeepers acquired the needed apiary equipment, but small-scale beekeeping virtually disappeared by 1984 mainly because beekeepers were being severely stung. Apiary locations were changed to prevent stinging of local residents. The complications resulting from relocation of apiaries, or continued apicultural practice (with protective equipment) in the midst of an unprotected public, are many (Michener, 1975; Rinderer, 1985; Taylor, 1988).

The "new apiculture" that has resulted from the arrival of Africanized honeybees has taken several turns. In addition to the crude harvest of honey from feral colonies and the general impossibility of maintaining productive European honeybee colonies in areas surrounded by thousands of feral Africanized bee colonies (Roubik, 1988), this practice has had two other major effects. First, there is no longer beekeeping with European honeybees on the Panamanian mainland. Second, the beekeepers that manage Africanized honeybee colonies maintain less than a few hundred hives. Before Africanization, as in other Latin American countries, prosperous or professional beekeepers commonly operated their business with more than a thousand colonies.

Among local efforts made in the Republic of Panama to diminish losses to the beekeeping industry was the support of a large-scale study of pollen harvests from Africanized honeybees (Roubik *et al.*, 1984). Preserved pollen is sold in supermarkets as well as in health food stores. During a 20-month study from 1982 to 1984, hives were fitted with pollen-collecting traps that continuously sampled the incoming polen carried by foragers. Such collections were made from forested areas in central Panama, and with colonies contributed by beekeepers in central and western Panama. Average pollen yield was approximately 30 g dry weight per day in these colonies, and most pollen was harvested in the mid dry season and early wet season. In addition, Africanized and European colonies in close proximity did not differ in their production of pollen. Pollen-collectors originally designed for European honeybees worked adequately with Africanized honeybees, although increased stinging still complicated pollen harvest.

An additional motive for maintaining pollen traps on honeybee colonies was to gather data on the floral preferences and sources of protein (pollen) used by these bees. Such data are also quantitative, since proportions of different floral types can be estimated from their representation in samples of the pollen pellets brushed from the hind legs of returning foragers and gathered in traps. Microscopic analysis of the pellets, each of which is composed of single pollen species, was carried out to compare them to reference collections representing the local flora (Roubik *et al.*, 1984, 1986, Roubik 1988, 1989). Despite the expected large range in pollen species used by honeybees, surprisingly few accounted for most of the colony diets. In three sites where all common types were identified, and where at least 500 flowering plant species were present (Fig. 5), over half of pollen harvested by the colonies during a year came from fewer than a dozen plant species. The honeybees nonetheless visited the flowers of 200 to 300 plant species during one year at single localities, comparable to the breadth of interaction between European honeybees and flora in Veracruz, Mexico (Villanueva, 1984). Many of the important forage sources were not pollinated by the honeybees, as they often used the residual pollen and nectar from large inflorescences pollinated by other animals or from dioecious species (Roubik, 1988). Palms were a particularly important resource during the rainy season, and bee visits may generally fall into the category of "scavenging" on such flowers (Roubik *et al.*, 1986; Búrquez *et al.*, 1987, and Fig. 6).

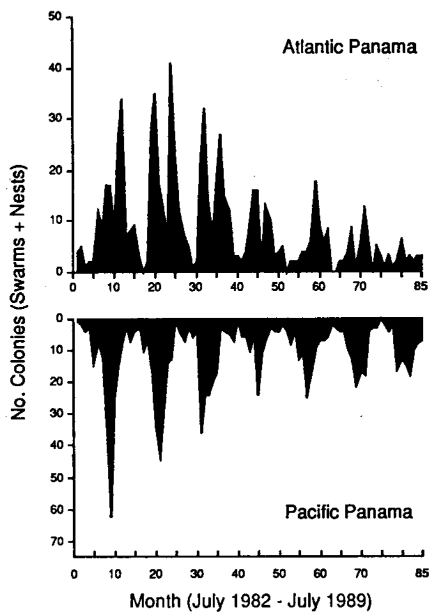

Figure 4. The monthly abundance of Africanized honeybee swarms and nests in the Panama Canal Area (data from the Panama canal Commission).

The stinging behavior of Africanized honeybees in Panama has been evident in the hospitalization of citizens and the deaths of domestic animals. Three verified human deaths occurred because of stinging by Africanized honeybees, and these accidents were all due to feral colonies. One was in the vicinity of Volcán, in Chiriqui Province (1400 m elevation) and two were in central Panama near sea level. The most recent mishap occurred in February 1989. In this instance a large feral colony attacked three fishermen not far from Barro Colorado Island. All were stung repeatedly stung and one drowned in his attempt to swim the 50 m to shore. We previously cited that Panama Canal Commission field crews suffered 35 stinging incidents during 1985 (Boreham and Roubik, 1987); in the three years that followed we have recorded 21, 22 and 16 annual stinging incidents within the PCC work force.

Beekeeping Despite Africanized Honeybees

One beekeeper in Panama continues to maintain 450 European honeybee colonies on San José Island, a large, private island in the Perlas Archipelago. He is currently the largest honey producer in Panama but beekeeping is only one of his business activities. Three key factors enable him to maintain the European honeybees: 1) The queens in all of the apiary colonies are replaced with mated European honeybee queens flown in from the United States once or twice each year; 2) any hives suspected

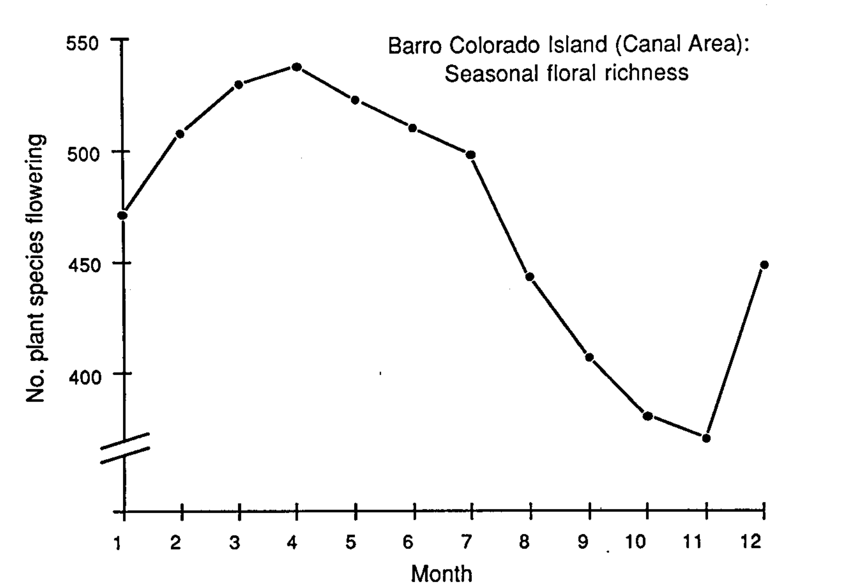

Figure 5. The seasonal abundance of flowering plant species in central Panama, from Croat (1978) *Flora of Barro Colorado Island.*