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Africanized Bees in the U.S.

Africanized honeybees have reached the U.S. from points south. As more of them arrive, they will certainly wreak some havoc but perhaps not the type their "killer bee" nickname would imply

by Thomas E. Rinderer, Benjamin P. Oldroyd and Walter S. Sheppard

The long-anticipated announcement came in October 1990. Africanized honeybees, more popularly known as killer bees (because of sensationalized accounts of their attacks on people and animals), had finally crossed the Mexican border into the U.S. Less than 35 years after members of a honeybee subspecies living in Africa (*Apis mellifera scutellata*) were released outside São Paulo, Brazil, their descendants—the Africanized bees—had migrated as far north as southern Texas. Today the bees occupy a range of about 20 million square kilometers, encompassing much of South America and virtually all of Central America. And their spread continues. They reached Arizona in 1993 and are expected to colonize parts of the southern U.S. before being stopped by climatic limits, probably by the year 2000.

Their arrival in the U.S. raises many questions. How will the newcomers affect public health and the beekeeping industry? Why were African bees brought to the Americas in the first place? What allowed their progeny to be so extraordinarily successful? And, most important, can anything be done to minimize the impact of settlement by Africanized bees in the U.S.? We and others have devoted a great deal of study to this last question. That work, particularly research exploring the genetic makeup of the insects heading for the U.S., offers hope that efforts to control mating between Africanized honeybees and honeybees common in North American apiaries can be of considerable value.

One already obvious effect of the bees' arrival is heightened concern for public safety. Africanized bees typically defend their hives much more vigorously than do honeybee strains in North America. North American honeybees descend from rather gentle subspecies of *A. mellifera* that were imported primarily from Europe, when early settlers found that the New World lacked native honeybees. Compared with the European bees, those with markedly African traits become aroused more readily and are more prone to sting any person or animal they perceive is threatening their nest. They may also attack in larger numbers (occasionally by the thousands) and persist in the attack longer (sometimes for hours).

Such behavior has reportedly caused one human death in the U.S. and perhaps 1,000 in the Western Hemisphere, and it is responsible for many more fatalities among domesticated animals. Fortunately, most nonallergic individuals will survive an attack if they can run away and so limit the number of stings they suffer. Almost all individuals killed by Africanized honeybees have died because they could not flee—either because they had fallen and injured themselves or had otherwise become trapped.

Beyond posing a public health problem, the bees also promise to threaten the livelihood of thousands of commercial beekeepers (apiculturists) and farmers. Amateur and professional beekeepers alike keep their hives outdoors. It is therefore possible that European queen bees will mate with Africanized drones (males) and thereby introduce increased levels of defensiveness and other costly and troublesome traits into apiary colonies.

The queen's mating choices account for the characteristics of a colony because it is she who lays the eggs. Early in life, she mates in flight with perhaps 15 drones from other colonies and then never mates again. When bees are needed in a colony, the queen lays eggs into individual cells. Fertilized eggs usually give rise to worker bees—females that carry chromosomes from each of their parents and are responsible for foraging and guarding the nest. (If the larva emerging from a fertilized egg is fed a special diet, however, it can develop into a queen.) Unfertilized eggs give rise to drones; these males bear a single set of chromosomes (from the mother), and they die after mating.

If beekeepers are unable to control the infusion of undesirable traits produced by mating between European queens and Africanized drones, their profits will shrink, partly because measures will have to be adopted to protect workers and the public from excessive stinging. For instance, apiaries might have to relocate to sparsely populated areas, and everyone handling the bees will have to wear sturdy protective gear. Moreover, the bees tend to abandon hives more readily than do European bees; repopulating hives can be expensive.

Beekeepers could also face a reduction in honey production, which now amounts to about 200 million pounds annually (representing roughly $100 million in sales). Much research suggests that under climatic and ecological conditions that foster the abundant produc-

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AFRICANIZED HONEYBEES have become alert to the presence of an intruder near their hive, as is evident from the raised stance of the bee at the right. Such bees, which look virtually identical to other honeybees, are descendants of a honeybee subspecies (*Apis mellifera scutellata*) that was introduced into South America from Africa in 1956.

tion of honey by European bees, Africanized bees would be less productive.

Meanwhile beekeepers who rent their colonies to farmers for the pollination of such crops as almonds, blueberries, apples and cucumbers would face additional financial losses. Rentals generate an estimated $40 million in fees every year, much of which goes to migratory beekeepers, who truck thousands of colonies to distant sites. Beyond having to exercise particular care to protect the public, beekeepers who maintained many Africanized bees could be prevented from bringing bees into non-Africanized areas.

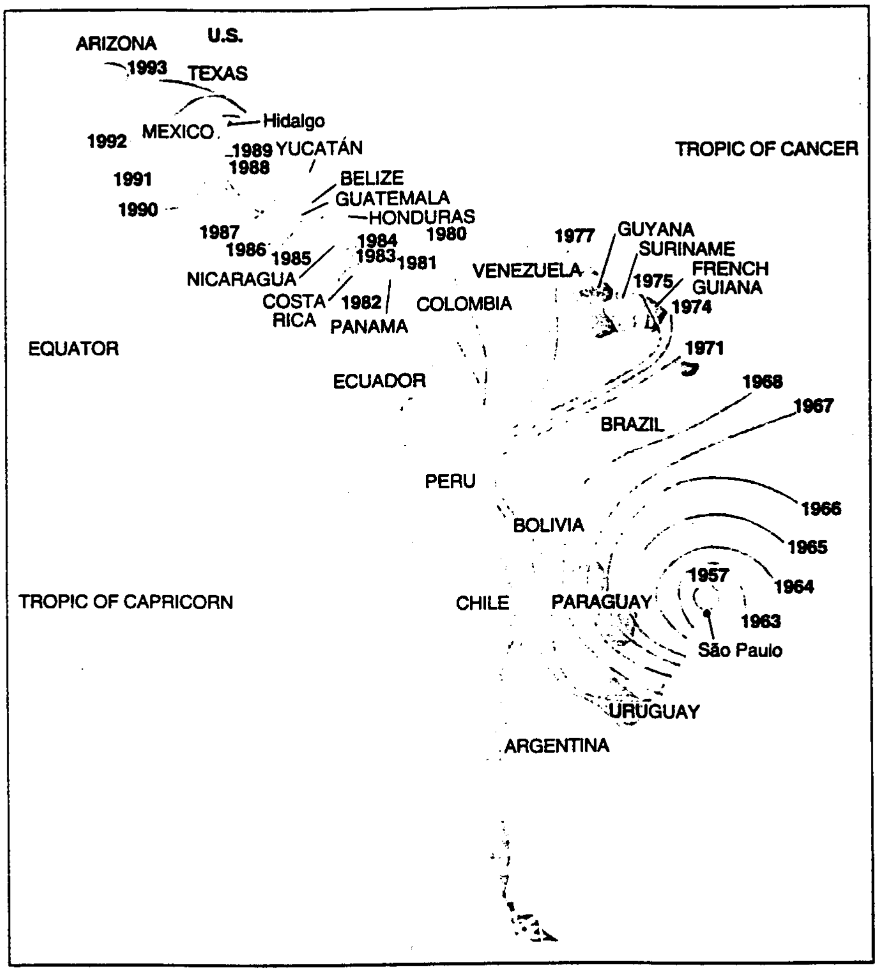
Farmers who rely on pollination services for the production of $10 to $20 billion worth of crops could be hurt even more. Their costs would go up because protection of the public would require them to purchase services from a reduced number of beekeepers whose stocks were known to be European; such beekeepers might have to travel greater distances or might have to charge more because of the expense involved in keeping their apiaries under control and in attaining certification of their success.

Today's concerns are an outgrowth of an unfortunate series of events that began in the mid-1950s, after the government of Brazil decided to shore up that nation's beekeeping industry. At the time, European honeybees formed the basis for a strong beekeeping industry in many places, but not in Brazil. Brazil had only a small apiculture industry, partly because European honeybees were poorly suited to the country's tropical climate. Rarely, if ever, did a colony survive in the wild, and only considerable effort enabled beekeepers to sustain colonies throughout the year.

It is now evident that the poor performance by the European bees was related to their misreading of environmental cues for reproduction. Direct and indirect studies of genetics indicate that European bees, like all subspecies of *A. mellifera,* trace their ancestry to an Asian species that evolved the ability to regulate body temperature and survive in a temperate climate. The bees withstood the cold mainly by clustering together in sheltered nests and eating stores of honey they had collected in warmer seasons. Later they expanded their range to include Asia Minor, Europe and Africa, ultimately forming 20 or more subspecies adapted to particular locales.

In the course of evolution the behavior of the various European subspecies apparently became highly linked to seasonal fluctuations in day length. When hours of daylight begin to increase, heralding the imminent appearance of flowers, European honeybee colonies expand the size of their worker populations. By the time the flowers bloom, many workers are available to forage for pollen and nectar. Nectar, which contains a great deal of sugar, is converted to honey—a prime source of energy.

Linkage of the life cycle to day length works well in temperate regions, but in Brazil day length bears little relation to the availability of pollen and nectar. The rainy periods that are required for abundant production of flowers do not necessarily coincide with periods of extended daylight. Consequently, European colonies can be induced to expand



MIGRATION OF AFRICANIZED HONEYBEES from outside São Paulo, Brazil, to the U.S. was accomplished in less than 35 years. (Red lines indicate the farthest points of detection in the years indicated.) The insects reached the southern tip of Texas on October 15, 1990, and were first spotted in Arizona in 1993.

even when food supplies are too scarce to support large populations.

In 1956 the best solution to Brazil's beekeeping woes seemed to be importation of a honeybee variant more accustomed to tropical living. The government therefore authorized Warwick E. Kerr, then at the University of São Paulo at Piracicaba, to bring *A. m. scutellata* from the highlands of eastern and southern Africa for study. Kerr obtained 170 queens, although only 46 from South Africa and one from Tanzania survived the journey from South Africa to a research apiary in Rio Claro. (Rio Claro lies roughly 100 miles from São Paulo.) He chose individuals that had already mated with African drones and were thus ready to lay the eggs needed to create complete colonies.

In 1957, within months after the African colonies were established, a visitor to the experimental apiary removed screens that had been placed at hive entrances to block queens from leaving. The reasons for the removal are unclear, but before the act was discovered, 26 colonies had abandoned their hives with their queens. For years, those liberated colonies were thought to have been the founders of the entire Africanized population. Recently, however, scientists have learned that soon after the initial release, queens reared from the remaining colonies were distributed to beekeepers in Brazil. The additional releases undoubtedly helped to ensure that enough African insects would be available to establish permanent feral populations of Africanized honeybees in Brazil.

The freed bees and their descendants found Brazil to be a hospitable place, and so they thrived. Compared with European bees, the newer arrivals were better able to take their reproductive cues from variations in the availability of rainfall and flowers and were better equipped to cope with dry seasons. When flowers are abundant, Africanized colonies engage in a process known as reproductive swarming: the queen and a good many hive members split off to establish a new, growing colony. This swarm leaves the remainder of the original colony with a young queen, who repopulates the hive. When floral resources dwindle severely, Africanized bees are likely to abscond—they gather any remaining honey and abandon the hive en masse, to try to find a more hospitable locale. (European bees, in contrast, swarm perhaps once a year and rarely abscond.)

As the Africanized bees flourished in Brazil, they fanned out in all directions, including into areas that previously had no beekeeping. In the 1960s they began to draw an increasing amount of attention, especially for their intense nest defense, and it became clear that they could be very troublesome.

By 1972 the U.S. government began considering the potential impact of the bees on the U.S. A committee organized by the National Academy of Sciences and funded by the U.S. Department of Agriculture found some cause for worry. Although bees in southern Brazil were surely prone to stinging, they were manageable. Areas that supported beekeeping before the release of the African bees continued to do so. But bees in the north—those on a trajectory headed for the U.S.—were unacceptably defensive. Not surprisingly, northern Brazil, which had supported little beekeeping previously, still had little. Consistent with the northern findings, later work indicated Africanized bees that had journeyed north into Venezuela and beyond kept a strong propensity for stinging. They also retained their tendency to swarm and abscond frequently.

In the mid- to late 1980s the U.S. government, with the cooperation of Mexico, decided to try retarding the spread of the bees into the U.S. by establishing a "bee-regulated zone." The final plan called for detecting and killing any swarms that arrived in parts of Mexico the bees would have to traverse in order to reach the U.S. Combined with weather inhospitable to migration, that effort (which proved more difficult to implement than had been hoped) may well have delayed the arrival of the bees for a while. But it was clear they were not going to be stopped altogether.

Interestingly, as anxiety mounted in the U.S., Brazilians found a way to use Africanized bees for the intended purpose: to strengthen their beekeeping industry. Initially many beekeepers abandoned the craft. But the Brazilian government embarked on a campaign to teach potential beekeepers how to cope and to instruct the public about how to avoid the bees and handle attacks. Now a new generation of apiculturists has emerged. Indeed, in some parts of Brazil that were once unable to sustain European honeybees, people earn their livelihood through keeping Africanized bees and harvesting their honey. These individuals maintain reasonable traits in their stocks by destroying queens in the most defensive and least productive colonies.

Unlike Brazil of the 1950s, the U.S. has little to gain from settlement by Africanized bees. And so the bees' entry into Texas and Arizona has added new urgency to the question of whether the introduction of African traits in apiaries and in the wild can be minimized. In theory, two major strategies might be helpful. Certainly, beekeepers could protect their stocks to some extent by practicing "requeening" frequently. The procedure involves inducing colonies to accept substitute queens of a beekeeper's choosing, often purchased from breeders of queens. Beekeepers can thereby ensure that their queens are European and (if so desired) that they have already mated with European drones. Many apiculturists are already adept at requeening. They use it to increase the production of offspring (replacing old, less productive queens with new ones) or to control the genetic makeup, and hence the characteristics, of hive populations.

Another protective strategy, known as drone flooding, calls for maintaining large numbers of European drones in areas where commercially reared queen bees are mated. Even if the areas have been invaded by Africanized émigrés, the vast number of European males would ensure that European queens would mate almost entirely with European drones.

Furthermore, the presence of many European bees would increase the probability that Africanized queens, too, would mate primarily with European drones. If the queens of successive generations then continued to mate with European drones, the gene pool of the bee populations in the affected areas would consist mostly of European DNA. Then the bees would have predominantly European traits. In the end, such gentle hybrids might actually prove to be quite valuable. Some scientists have reported that Africanized bees may be more resistant to acquiring parasites and disease. If these advantages could be harnessed by breeding programs, they might help bees in North America fight off a growing invasion of mites.

Of course, the drone-flooding strategy assumes that honeybees bearing essentially African genes and those bearing essentially European genes can hybridize—that is, mate with each other and produce viable offspring bearing genes and traits from both parents. But can the two groups in fact hybridize? For many years, researchers were unsure of the answer. Some early studies in the 1980s that examined morphology, or physical features, of bees in areas known to have been invaded by the descendants of *A. m. scutellata* seemed to indicate that hybridization was indeed occurring, as did studies of enzymes. But other work disagreed.

Morphological comparisons are much more difficult than they might sound. Even if one examines the extremes—African bees living in Africa and European bees living in Europe—the two groups look alike. But colonies can be distinguished by a statistical procedure called multivariate discriminant analysis. In doing such an analysis, researchers measure many different body parts—among them, the length and width of the wings and leg segments, and the angles at which various veins intersect in the wings. Although the mean scores for African and European samples will not differ significantly on any one measure, combining group means for many measures makes it possible to distinguish overall differences that do exist.

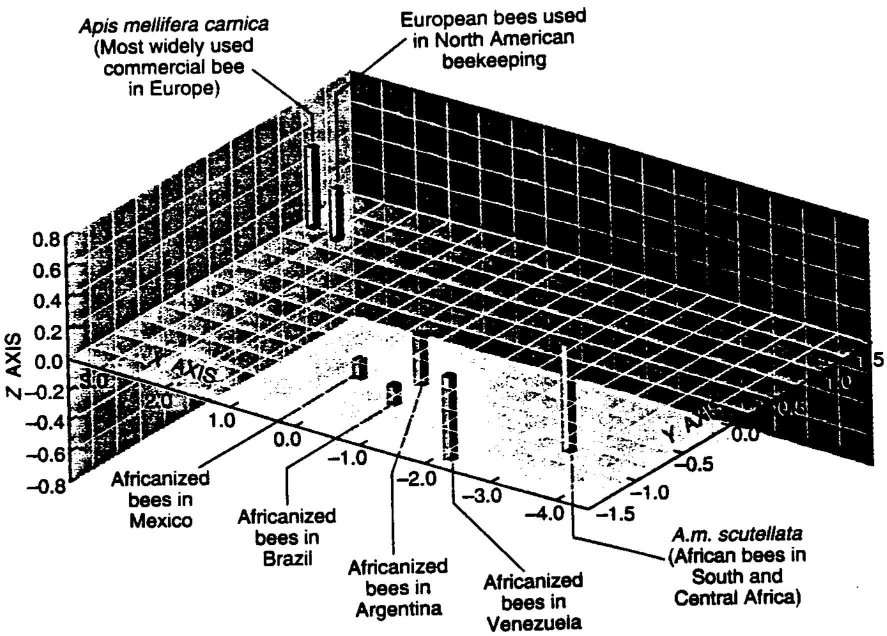
To assess whether the invading bees in Central and South America differed physically from *A. m. scutellata*—which would suggest genetic mixing had taken place—we compared their final scores with those attained for African and European bees. The comparison revealed that feral populations in Mexico, Brazil, Argentina and Venezuela resembled both European and African bees to various degrees, although they were more like the African bees.

Similarly, when we plotted summed measures for three different clusters of traits against one another on three axes, the point representing purely African bees fell far from that representing purely European bees in North America [*see bottom illustration on next page*]. The points representing bees from Mexico, Brazil, Argentina and Venezuela fell in between, roughly a third of the way between those two extremes but closer to the African value. These findings suggested that the populations advancing toward the U.S. were not pure Old World African stock; they were indeed hybrids that had acquired some European genes in their travels.

Other conceivable explanations for the morphological findings existed, though. One was that a founder effect was responsible. Perhaps the relatively few African bees that were originally imported to Brazil happened to carry genes that caused them to look European. In that case, their progeny in the Americas would also physically resemble European bees even in the absence of hybridization. Alternatively, natural selec-

PROTECTIVE CLOTHING is essential for anyone who works around hives of Africanized bees. Compared with the relatively gentle strains of honeybees common in the U.S. (originally imported from Europe), the Africanized bees are more easily aroused. Entire populations of hives can come pouring out in a flash, ready to pursue doggedly and sting any perceived intruder.

MELON PLANTS (*foreground*) are growing close to a residential area in northern California. They are about to be pollinated by European honeybees stowed in nearby boxes. As Africanized bees settle in the U.S., farmers may have more difficulty finding European bees to rent for pollination and may have to pay more for those that are available. For that reason and others, the incursion of Africanized bees into the U.S. could shrink annual profits of beekeepers and farmers.



MEASUREMENTS OF PHYSICAL FEATURES in European, African and Africanized honeybees have been summarized on this three-dimensional plot. The axes represent the collected measures for distinct clusters of traits. One base of each cylinder sits on the floor formed by the *x* and *y* axes. The opposite end of the cylinder (*shaded black*), lying above or below the floor, marks the intersection of *x*, *y* and *z* coordinates; that base represents the overall morphology of the group. The morphology of the Africanized bees (*purple*) is between that of the European (*blue*) and African (*red*) bees—which suggests that the Africanized bees are by-products of mating between European and African bees in the Americas.

tion in the Americas may have favored the survival of African bees that by chance had European-like physical traits.

The attractiveness of these explanations dimmed, however, when the data from multivariate analyses were combined with results from studies that compared enzymes in African and European bees. Jorge A. Lobo and his colleagues at the University of São Paulo at Ribeirão Prêto knew that 98 percent of African bees carry one form, or allele, of a gene specifying the amino acid composition of a particular enzyme: malic acid dehydrogenase. They also knew that this same allele—and therefore the isozyme, or enzyme variant, it encodes—is much rarer in European bees.

When the group surveyed the forms of malic acid dehydrogenase in the bees of Brazil, they deduced that only 70 to 80 percent of the insects harbored the allele common in African bees. Studies of other isozymes yielded a similar pattern. These results led Lobo's group to conclude that at least some Africanized bees are the products of hybridization. It is highly doubtful that both the morphological and the isozyme differences between Africanized and Old World African bees could be the result of happenstance.

Yet the findings favoring hybridization were contradicted by other observations. Notably, bees in the colonized areas seemed to display clearly African traits, namely, intense defensiveness and frequent swarming and absconding. If hybridization was going on, it certainly was not obvious behaviorally. The first direct genetic studies raised similar doubts. They compared mitochondrial DNA in bees from colonized areas with that in European and African bees. Mitochondria, the energy factories of cells, contain small rings of DNA that are distinct from the chromosomal DNA housed in the nucleus. Nuclear DNA directs the emergence of physical and behavioral traits. Mitochondrial DNA provides about a dozen genes required strictly for energy production. Most animal species (including humans) inherit their mitochondria, and thus mitochondrial DNA, exclusively from the mother.

It turns out that African and European bees differ slightly in the sequence of nucleotides (the building blocks of DNA) in their mitochondrial DNA. Hence, by identifying known markers of the variable DNA segments from bees in Africanized areas, investigators were able to trace the maternal lineage of the insects to either Africa or Europe. (The markers used are DNA fragments that form when mitochondrial DNA is cleaved by a restriction enzyme. For example, one fragment generated from African DNA appears as two smaller fragments in European DNA.)

The first published reports found European mitochondrial DNA to be virtually nonexistent in the bees studied. This absence implied that almost none of the sampled bees had descended from European queens. If hybridization had taken place, one would expect to see a greater representation of European mitochondrial DNA.

The results seemed consistent with the possibility that something was preventing hybridization from taking place. Yet it was also possible that the bees in the studies came from tracts that previously supported few feral European bees. In that case, there would be little hybridization because almost no European bees would have been available to interact with incoming African bees.

Determining whether hybridization could in fact occur required investigation of bee colonies from areas known to have been supporting European honeybees when the newcomers arrived. We therefore traveled to Argentina, which lies west of the thin, southernmost part of Brazil and extends much farther south, into a temperate zone. Africanized bees have not become established in the southern half of the country, which supports abundant beekeeping with European strains. But they have established large populations in the northern half, particularly in the topmost quarter of the country, which has never maintained as many European bees.

Julio A. Mazzoli, a graduate student from the University of Buenos Aires, helped us find more than 100 colonies in bridges, trees, electric utility poles, fruit boxes and other enclosed areas favored by honeybees. The collection included representatives from areas extending from the north into the south [*see illustration on this page*]. Back in our laboratories, we evaluated the morphology and the composition of mitochondrial DNA. Our collective results showed decisively that hybridization had taken place. As part of our evidence, we found that a large number of the sampled colonies had physical features intermediate between those of European and African bees. Further, more than a quarter of the colonies either displayed African morphology (reflecting the activity of nuclear genes derived from African ancestors) yet bore European mitochondrial DNA (reflecting the influence of a female European ancestor) or else displayed European morphology yet bore African mitochondrial DNA.

The morphological work yielded another interesting finding: European physical features were more prominent in the southern, temperate regions of the studied territories than in the northern corner, where African morphology predominated. But in a band of fairly temperate territory between those areas, no single cluster of morphological features predominated. This mixture of traits implied that hybridization had occurred extensively in the intervening zone, a conclusion supported by isozyme studies. We found relatively few hybrids outside the transition zone presumably because conditions in the tropical north favor survival of bees having primarily African traits, whereas conditions in the temperate south favor survival of bees having primarily European traits.

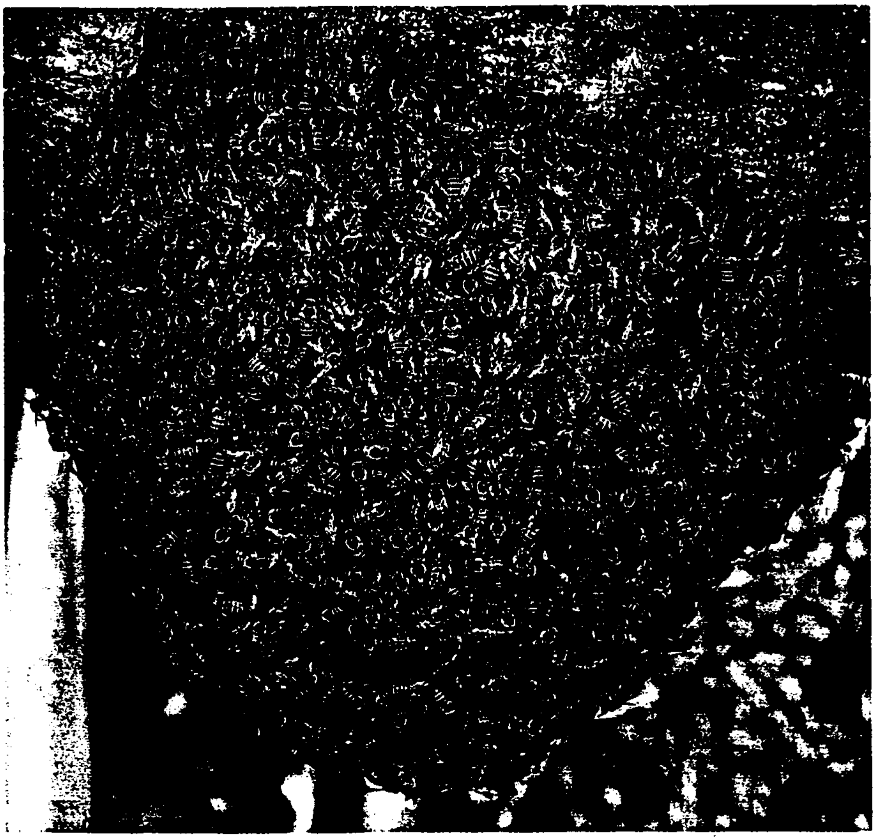
Such selective pressures may lead to a similar pattern in the U.S., where the southernmost regions have a subtropical climate and northern areas are temperate. European-like bees may be less competitive in the Deep South, and African-like bees should be less competitive in the North. In the intervening central regions, there may be a mixture of hybrids whose gentleness and tolerance of cold increase with increasing latitude. It is also possible that hybrids will be abundant in some central areas during the warm seasons but will disappear in the winter.

Because there were few European bees in the tropical regions of Argentina, we could not determine whether the presence of a sufficiently large European population would cause African-like bees to mate with them and produce hybrids that survived and reproduced well in the tropics. We knew only that such behavior was commonplace in temperate areas. If hybridization does not occur readily in the tropics, then the strategy of flooding commercial breeding areas with European bees might prove ineffective in parts of Florida, Texas and other subtropical regions of the U.S.

We sought an answer in the Yucatán Peninsula of Mexico. The peninsula has an ideal combination of a tropical environment and an extensive, long-established population of European honeybees. In fact, the Yucatán has the greatest concentration of commercial honeybee colonies in the world. This was the first massive population of European bees encountered by the expanding populations of Africanized bees as they migrated north from Brazil.

We again collected samples from a large tract. This time we relied on the cooperation of beekeepers, who own most of the bees in the Yucatán. Despite being cared for by humans, the honeybees in the Yucatán are probably the genetic equal of feral bees. Beekeepers obtain them by putting out boxes the insects can colonize. Owners usually make little effort to control the genetic makeup of the hive, other than killing older (less productive) queens and allowing hive members to raise a replacement. An occasional beekeeper will, however, practice requeening with pre-mated European queens.

ARGENTINA can be divided into three zones based on the abundance of Africanized bees. In much of the north (*purple*) the bees are present year-round. In most of the south (*blue*), they are absent. Recent analyses of morphology and mitochondrial DNA in bees from tracts crossing all three areas (*white bars*) indicate that Africanized bees, European bees and a range of hybrids coexist in the intervening transition zone. This finding has helped confirm that mating between Africanized and European bees can yield viable offspring.



CLUSTER OF AFRICANIZED BEES hangs from a tree limb, the insects' temporary home until they can construct a hive in some protected place. Such bees swarm—leave their original hive to establish a new one—as part of the processes by which bee colonies reproduce. Frequent swarming by Africanized bees has contributed to their rapid spread through much of the Americas.

All but a few of our samples came from colonies that had not undergone requeening in the two years since Africanized bees had first been detected on the peninsula. Most of the insects still possessed clearly European morphology, but some possessed mainly African morphology, and many had intermediate morphologies indicative of hybridization. Mitochondrial analyses provided still more evidence of interbreeding: a number of colonies displayed either European morphology and African mitochondrial DNA, or the reverse. Thus, a tropical environment does not appear to pose an unbreachable barrier to hybridization.

The least evidence of African traits appeared in the few colonies that had been requeened. This simple observation implies that requeening—one of the chief tools beekeepers have for controlling the Africanization of their stocks—can certainly be helpful.

Our conclusion that significant hybridization can be achieved in tropical areas has recently been confirmed by Robin F. Moritz of the Technical University of Berlin and Michael S. Meusel of the Bavarian Agricultural Institute for Apiculture in Erlangen, Germany. In a survey of feral Africanized honeybees in Brazil, they found that 17 percent of the colonies had European mitochondrial DNA. The team also mathematically modeled the effects of intensive reproductive swarming by Africanized bees on the composition of bee populations in areas that originally supported only European honeybees. The results show that rapid growth of Africanized bees, combined with the survival advantage they enjoy in tropical environments, could enable Africanized bees to predominate over hybrid or other bees with European traits. So it seems that efforts to foster hybridization in the subtropical areas of the U.S. might require continuous requeening with European bees.

Nevertheless, the potential of Africanized honeybees to hybridize successfully with European honeybees is good news for beekeeping. We anticipate that frequent requeening of commercial colonies and drone flooding in commercial queen-breeding areas would serve to dampen the acquisition of unwanted African traits. We should note, though, that there are dissenters who contend that hybridization efforts will fail to prevent the eventual widespread introduction of dramatic African traits into honeybee populations. These observers hold that Africanized bees will inevitably come to dominate in regions that initially show signs of hybridization. Our evidence does not support that view. We found an abundance of hybrid bees in the transitional zone of Argentina some 20 years after Africanized bees had arrived there.

If we are correct that Africanization of U.S. apiaries can be limited, then it seems that, with care, the practice of transporting bees to crops could be continued safely without leading to the significant establishment of Africanized bee colonies in new territories. Fortunately, there are ways to assess the character of individual colonies, and these methods could be employed to guarantee that colonies moved from place to place are European.

It is inevitable that the incursion of Africanized bees into the U.S. will increase the costs of managing commercial colonies, at least temporarily. It is also likely that some African genes will spread through feral and managed bee colonies. Yet vigilance and coordination by apiculturists have every chance of preserving the European behavior of commercial honeybee stocks, thereby reducing the damaging effects of Africanized insects on beekeeping and allaying the fears of the public.

FURTHER READING

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