

# Africanized Bees: The Africanization Process and Potential Range in the United States

Thomas E. Rinderer

**E**VALUATING the problems likely to be caused by insects not yet in the United States is an unusual enterprise for entomologists. The complexity of the biological world causes such predictions to be wrong at least as often as they are correct, which rarely makes the exercise desirable. But, rarely do we have an opportunity to see a spreading insect population moving toward our borders, as is the case with Africanized bees. The attempt of Taylor (1985) to predict their spread and impact is noteworthy. Only with such attempts can we alert our scientific and agricultural establishments to prepare themselves to mitigate potential problems. However, the predictions of Taylor may have left some *Bulletin* readers with the impression that the impact is most likely to be small and regional, that the Africanization process is fully documented, and that all the important basic research has been finished.

The potential limits of Africanized bees in North America are difficult to predict. Indeed, several considerations, not raised by Taylor, suggest that his predictions based on isotherms are invalid and misleading. African isotherms are probably useless for prediction. The parental stock of Africanized bees, *Apis mellifera scutellata* (Ruttner 1975), has range limits primarily imposed by other African subspecies (Ruttner 1986). It is doubtful that temperature alone defines these subspecies' range boundaries. *A. m. litorea*, found in coastal East Africa, occupies hotter and more humid areas than *A. m. scutellata*. Yet Africanized bees are found in areas in South America, such as the Orinoco delta of Venezuela, that are much more similar to the range of *A. m. litorea* than to the upland savannas of *A. m. scutellata* (personal observation). Because temperature-based predictions are not valid for warmer African isotherm correlates, the validity of cooler isotherm correlates is also questionable. *A. m. scutellata* is bordered on the south by *A. m. capensis*. It is widely held that *A. m. capensis* evolved in the Cape of Good

Hope area of South Africa, primarily in response to extreme local conditions not related to winter (Ruttner 1977, Moritz & Kauhausen 1984, Tribe 1983). Certainly, *A. m. scutellata* can survive winters in this area, because South African government kept them at a mating station on Robben Island in the Cape bay for several years (Fletcher 1978). *A. m. scutellata* survives even more severe winter conditions in the Drakensberg Mountains of southeast South Africa (Fletcher 1978). Probably the majority, and perhaps all, of the limitations on *A. m. scutellata*'s range stem from ecological conditions other than temperature, which have resulted in the evolution of other subspecies.

Isotherms in Argentina are probably equally invalid predictors. Dietz et al. (1985) and Krell et al. (1985) have conducted the most complete study of the distribution and overwintering of Africanized bees in Argentina. They found that Africanized and European honey bees had similar overwintering abilities in a mountain valley in Cordoba. They also found Africanized bees overwintering much further south (39°) than has previously been reported. Several preliminary studies from a project in Colombia (Villa 1985) comparing overwintering abilities showed no fundamental differences between Africanized and European bees. These studies cast serious doubt on the usefulness of invoking temperature as a limiting factor sufficiently important for predictions on other continents. Dietz et al. (1985) suggest that "climatic factors alone are not the only reason for limiting the range and distribution of Africanized bees."

The notion that European bees are perfectly adapted to North America requires rethinking. Because honey bees are not native to the Americas, no European bee can be expected to be highly adapted to North American conditions. This is especially true because commercial movement of bees has probably interfered considerably with any natural selection that may have occurred in North America. Perhaps most importantly, much of our bee stock is derived from an Italian bee, *A. m. ligustica*, a European subspecies that has evolved in a climate more Mediterranean than continental. Yet this stock overwinters reasonably well in northern areas of the United States, espe-

cially with commercial management. The same occurrence might happen with Africanized bees which, after all, show several good indications of having the ability to overwinter.

It is also important to consider commercial activities when predicting the range and rate of movement of Africanized bees in North America. Many beekeepers move bees from state to state, often over long distances. Also, they do not necessarily return the same bees to the same states. Beyond this, many industries transport commodities that could harbor Africanized swarms within them. Probably, commercial traffic of many types will disperse Africanized bees much more rapidly and widely than predictions based on the natural dispersal of swarms suggest.

There is little doubt that Africanized bees can survive and reproduce nearly everywhere in North America from spring to autumn. Also, Africanized queens accompanied by small swarms of workers have a tendency to invade European colonies, especially queenless ones. Commercial honey cropping results in some lost queens (10–20%) (Sugden & Furgala 1982). Thus, late summer or fall honey cropping may result in some Africanized queens overwintering in colonies with European bees. Such overwintering would serve as a source of Africanized queens, drones, and swarms during the following season. These possibilities make Africanization a national rather than a regional problem, regardless of the possible regulations governing the interstate movement of bees predicted by Taylor (1985).

The process of Africanization also requires rethinking. As I understand it, Taylor (1985) and Taylor et al. (in press) invoke two features of reproductive biology to explain Africanization. First, Africanized drones (and by inference, Africanized queens) experience the peak of their mating-flight time somewhat later in the day than European bees. This difference is offered as an explanation (Taylor et al., in press) for the positive assortative mating (partial reproductive isolation) found by Kerr & Bueno (1970). This explanation is understandable. However, the difference is then used to explain why queens from the first very few Africanized swarms to arrive in

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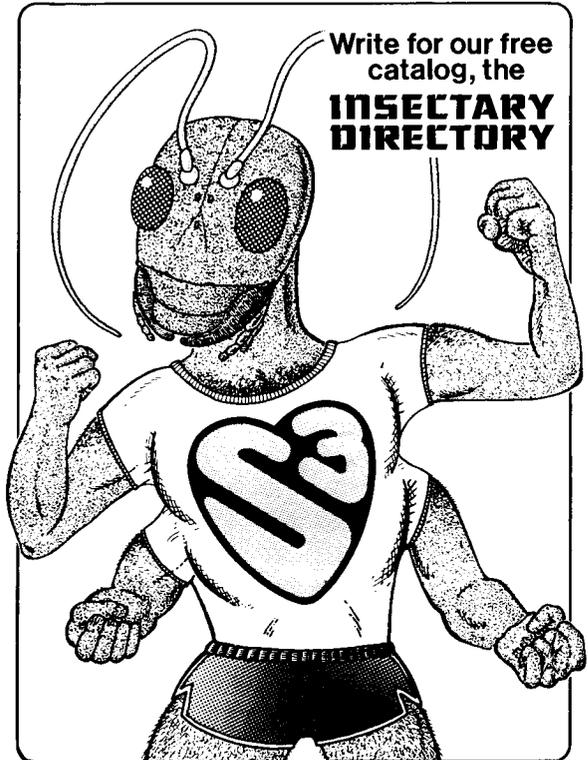
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an area having European colonies do not mate with European drones. The same difference is again invoked to explain why European queens are mating primarily with drones from the Africanized swarms. Second, to enhance their model, Taylor et al. (in press) state that queens fly further than drones on mating flights and cite European literature in support of this contention.

One serious problem with their model is that it is symmetrical. The same conditions that are invoked to explain Africanization, which happens, would work equally well to explain Europeanization, which does not happen. Africanized queens should also be flying further than the drones from their colonies. When they do, they should mate with European drones. Even though average flight times differ, large variance in flight times exists. Whenever Africanized queens are taking mating flights, at least some and usually many European drones are available. Thus, the symmetries of flight times and of longer flights of queens versus drones, present difficulties. When there are comparatively few Africanized colonies, the process should yield Europeanization. When there are comparatively few European colonies, the process should yield Africanization. The commercial density of European colonies in some parts of South America (e.g., near Acarigua, Venezuela, where the U.S. Department of Agriculture has its Africanized bee research field station) was high. This area also supported a feral population of European bees (G. Vogel, personal communication). Nonetheless, the bees in the area quickly became Africanized. Drones from commercial European apiaries and feral colonies had been sufficiently numerous to mate with European queens flying from other European apiaries before Africanization. Yet, they did not Europeanize the few initial Africanized colonies in the region.

Taylor et al. (in press) ignore the early population size differences that are overcome in the Africanization process. They seem to see Africanization resulting from "European apiaries become[ing] islands of drone sources in a sea of African[ized] drones . . ." But their explanation begs the question of where the "sea of African drones" came from during the early phases of Africanization.

A strong possibility is that one or several asymmetrical elements of comparative reproductive biology exist and are the primary causes of Africanization. Three such elements are known. The first (the only one mentioned by Taylor), parasitism by Africanized queens of European colonies has been long understood (Michener 1972). The second, parasitism by Africanized drones of European colonies, was reported in May 1985 (Rinderer et al.). Africanized drones migrate into European colonies in large numbers, whereas Africanized colonies only

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rarely host drones from other colonies. This migration leads to a numerical mating advantage for Africanized bees because it results both in the inhibition of European drone production and enhancement of Africanized drone production. Drone parasitism, in combination with a third factor, differential drone production, resulted in 91.2% of all drones in two apiaries with equal numbers of Africanized and European colonies being Africanized (T. E. Rinderer, unpublished data). These three conditions alone might well account for Africanization.

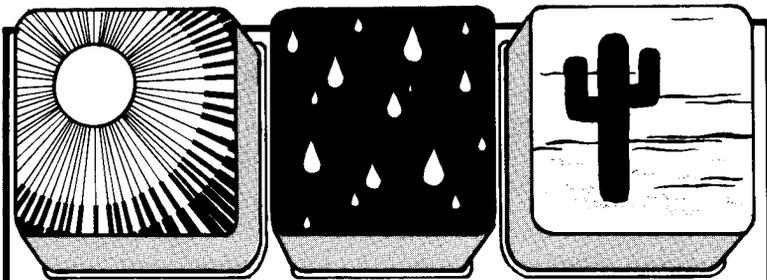
However, a fourth condition, based on observation and hypothesis, may greatly contribute to Africanization and be its major driving force. The first aspect, known from flight-range studies conducted in Europe, is that drones fly farther than queens on mating flights. This is contrary to the interpretation of Taylor et al. (in press) who cite Konopacka (1968), Ruttner & Ruttner

(1972), and Böttcher (1975) to support the idea that queens fly farther. Ruttner & Ruttner (1972) and Böttcher (1975) provide information that might be considered confusing. Ruttner & Ruttner (1972) concluded that queens flew up to 5 km, the average distance being 2 km. In their study, distances flown by queens and drones combined were up to 12 km, with 5–7 km being common (34% of matings). In combining "average" with "common," their data support the inference that because the average queen flew 2 km, and that because the common mating distance was 5–7 km, the drones in their study must have flown 3–5 km, or farther than the queens. Böttcher (1975) inferred that drones came to drone congregation areas from at least 2 km away. He then concluded that queens did not mate in drone congregation areas at or near their hives, and also that most of them did not fly more than 1 km.

The most comprehensive study of the question was conducted by Konopacka (1968, 1970). She used different locations, and a variety of techniques, including counting progeny after matings with drones carrying a body-color mutant and observing flight-experienced drones and queens returning to colonies from various distances and directions. She commented (1970) that "it could be concluded from this [sic] data that, when mating, the drones fly for distances at least as far as 5 km, whereas the mating flight distance of queens does not exceed 1.5 km."

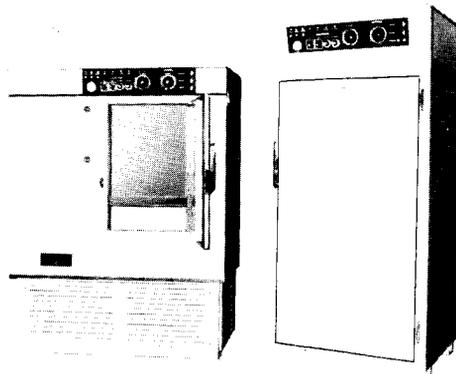
The longer Konopacka report (1970) presents a variety of data which do not always agree precisely with the exact distances mentioned in her conclusions. However, the general trend is that while location-related conditions may alter flight range, drones fly at least twice as far as queens to mate. This can also be inferred from the results of Ruttner & Ruttner (1972) and Böttcher (1975).

It is reasonable that queens would fly shorter distances on mating flights than drones. Honey-bee colonies produce far more drones than queens during their reproductive cycles. By inference, the colony investment in a single queen is higher than the investment in a single drone. Ultimately, the investments in all queens and all drones are probably about equal because



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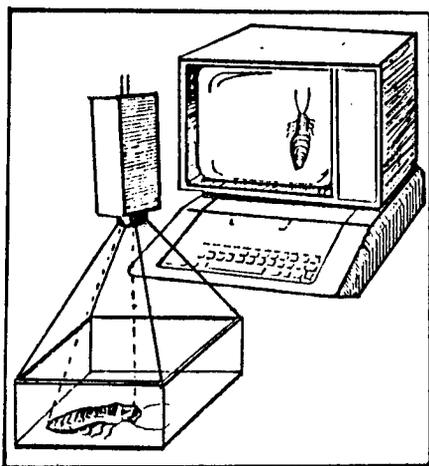


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colonies often add worker bees to the investment in queens in the form of accompanying swarms). If natural selection is at all responsive to differential investments in reproductive insects, then a mating system requiring outcrossing would evolve, which would decrease the risks of mating flights by shortening the flight distance of the sex requiring the higher investment.

The hypothetical part of this fourth asymmetric condition is that perhaps the mating-flight distances of Africanized reproductives are smaller than those of European reproductives. There is some support for this hypothesis. Levenetz (1954) found differences in the mating-flight distances of drones of different European subspecies. Also, the population densities of wild African (Ruttner 1986) and Africanized (Kerr 1973) bees appear to be much higher than those of European bees (Seeley & Morse 1976, Rinderer et al. 1982). It seems reasonable that natural selection would tend to select for longer mating flights where wild colonies were more scattered and shorter mating flights where wild colonies were more common.

The four conditions operating in concert would result in rapid Africanization. Once an Africanized queen enters a colony in an European apiary, she would begin to produce a disproportionately high number of drones through the mechanisms of drone parasitism and differential drone production. Any European queens flying from the apiary would have a tendency not to mate with European drones from the same apiary because the European drones fly farther to mate. However, the flight distance of European queens may well coincide with the flight distance of Africanized drones from the same apiary. This circumstance would produce a very high frequency of matings between European queens and Africanized drones. Africanized queens from the apiary flying still shorter distances could conceivably mate with drones coming in from other sources, perhaps mostly European drones as Africanization is beginning. But, because of the sex-determination system of bees, after mating, Africanized queens would produce Africanized drones, which would again mate in the mating range of European queens from the apiary. European drones from queens that had mated with African-

ized drones would fly far beyond the mating range of Africanized queens in the apiary. The asymmetry of these conditions would lead to rapid Africanization even though only a very few, vastly outnumbered Africanized colonies were in an area.

The advantages of this model are twofold. First, it is consistent with known bee biology. Second, it is asymmetrical and thus can be used to explain how a very few Africanized colonies can cause the overall population to become Africanized in short order. The model of Taylor et al. (in press) is deficient in both of those areas.

Other, more minor problems exist with Taylor's (1985) analysis. First, the bees are more correctly called Africanized than African. The bees from South America differ morphologically (H. V. Daly, personal communication), biochemically (Nunamaker and Wilson 1981, Sylvester 1986) and behaviorally (personal observation) from *A. m. scutellata* in Africa. As an example of published behavioral differences, sometime after being introduced into Brazil, Africanized bees did not always accept Europeanized comb foundation (Wiese 1972), but now always accept such foundation throughout their range. Clearly, some hybridization has taken place. Just as clearly, the characteristics of Africanized bees are more similar to those of African bees. Thus, the continued use of the term Africanized bees is appropriate. Second, there are no confirmed reports of Africanized bees in Mexico to date (6 October 1986). Third, at times I sense that Taylor analyzes Africanized bees as though they were a separate diploid species. He speaks of  $F_2$  generations,  $F_1$  drones, and remarks that the progeny from various crosses are a certain percentage African or European. This terminology is incorrect because bees cannot produce true  $F_2$  generations or  $F_1$  drones, and because the differences between Africanized and European bees are rooted in gene-frequency differences at probably only a few loci. Most genes, those that regulate the fundamental characteristics of honey bees, probably have no allelomorph variation and are common to both subspecies. Also, Africanized bees are populations of honey bees that show various levels of hybridization between subspecies. Populations of Africanized bees fit King's (1968) defini-

tion of a "hybrid swarm" at the subspecific level. That is, these populations contain "a continuous series of morphologically distinct hybrids resulting from hybridization of two [sub]species followed by crossing and backcrossing of subsequent generations." Thus, there is no genetic evidence supporting either the concept of "percentages" of bee types or the hope of an identification system not based on probability of group membership.

Whether my views or the views of Taylor (1985) are more correct is neither an academic issue nor the most important issue. The most important issue is that we require more experimental work. Not all the critical basic research has been accomplished. Although applied research is necessary and being conducted, many basic research questions need to be addressed before meaningful applied research can be fully implemented. The overwintering attributes of Africanized bees require still more study. Certainly, the basic comparative reproductive biology of Africanized and European bees is unfinished. We need a comprehensive understanding of the details of the comparative reproductive biology that produce the Africanization process. It is impossible to provide full recommendations for controlling Africanization until these principles are understood.

Other potential avenues to solutions should not be dismissed. Investigations of *A. m. monticola* in Africa may provide fundamental knowledge critical to the control of Africanization. *A. m. monticola* occupies areas of higher altitude (Mt. Kilimanjaro, Mt. Kenya) than does *A. m. scutellata*. Yet, Africanized bees in South America are commonly found in highland areas (e.g., Santo Domingo, Venezuela) that are similar to areas of Mt. Kenya occupied by *A. m. monticola* (personal observation). We do not know how *A. m. monticola* maintains its subspecies integrity. It is clearly a different subspecies, both morphologically and behaviorally (Ruttner 1986). Indeed, it is extremely gentle (Ruttner 1986; personal observation) and shows signs of commercial usefulness. Research might demonstrate that it would be useful to consider importing stock derived from this bee to the Americas. After all, we are already facing problems caused by stock from one of the worst of the

African subspecies. We might be better able to control Africanization by using stock from the best of the African subspecies. Because it is known to prevent Africanization it might be used either as a barrier or as a stock available for general commercial use.

Basic research, yet to be done, is necessary to determine the desirability of several potential control strategies. Collectively, researchers already studying Africanized and African bees, and perhaps others not yet involved, may learn enough to make recommendations to prevent the disruptions caused by Africanization.

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