Answers to the Puzzling Distribution of Africanized Bees in the United States

"Why Are Those Bees not Moving East of Texas?"

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"Why are they expanding a beekeeping operation since the Africanized honey bee (AHB) is going to be there in the near future?" That was the question that one of us asked in 1985 about a small beekeeping company in Baton Rouge, Louisiana.

This was a logical question since we had seen beekeepers from Argentina to Central America lose or downsize their businesses when confronted with the AHB. Given the knowledge at that time about the AHB range expansion potential and its abilities to withstand cold temperatures, it seemed quite reasonable to think that the AHB would spread east from Texas very quickly. Now, in 2002, it is apparent that the eastward range expansion of the AHB has stalled in Texas. Here, we examine possible causes and implications of the apparent termination of the eastward expansion of the AHB.

The most widely accepted notion about the eventual range of Africanized bees was that winter temperatures would provide limitations to expansion as they seemed to have done in Argentina. This notion generated several prediction maps. The areas predicted to be impacted varied widely, depending on the assumptions. See the contrast between the conservative predictions of Taylor and Spivak (1984), and those presented by Dietz (1992). All predictions had a common point of agreement: areas south of lines following some critical temperature level, which tended to run east and west, were expected to become occupied by the AHB. There was also no disagreement among the predictions that most southern areas in all of the southern tier of states, from California to Florida, were going to be occupied by the AHB.

This predicted distribution of Africanized honey bees has not occurred. Furthermore, there appears to be an unpredicted limitation along a north-south axis in eastern Texas, which does not correspond to winter temperatures. To the west of that line and starting in 1990, Africanized bees have been positively identified in 136 of the 254 counties of Texas, in 7 of the 31 counties of New Mexico, in 9 of the 15 counties of Arizona, in the southernmost county of Nevada and in 9 counties in southern California. More importantly, serious impacts on beekeeping and the public have been experienced almost exclusively in southern Texas and southern Arizona. The lack of advance of the AHB towards coastal Louisiana since 1992 is not an artifact resulting from a lack of effort to find an advance. There has been continuous monitoring of areas to the east of Houston with bait hives by the Texas Apiary Inspection Service and by the Louisiana Department of Agriculture and Forestry. Also, for three consecutive years (1993 to 1995), our laboratory conducted intensive sampling of managed and feral colonies, and trapped swarms in southwestern Louisiana. Even though the AHB had been found 215 miles to the west of our monitoring areas in 1992, only European colonies were found through the three years of sampling.

We have been puzzled for some years about the lack of movement into the vast territory to the east of Houston, which from all known considerations of temperature tolerance, would be prime habitat for the AHB. Recently, we decided to examine potential causes of the limited eastward range expansion of the AHB.

We evaluated the possible roles of a variety of postulated factors in restricting the AHB range expansion. To do this, we needed to find a good measure of Africanization. The intensity of sampling efforts for the AHB in the United States has been variable: Some states have had detection programs using bait hives, others have not. Even within states, sampling has necessarily been constrained by budget and logistics, so that some counties were more intensively sampled than others. Also sampling efforts changed through time, as the AHB moved into new areas, sampling in quarantined counties was reduced, and sampling was intensified 'ahead' of the bees' expected path. We decided to use as the least biased indicator of Africanization, the first documented find in each county that had been reported to the NAPIS (National Association of Plant Industry Services) system. We felt that this approach would be most reliable and unbiased because it would be the least dependent on sampling effort and it would spread possible errors and biases equally over broad geographic areas.

We started a data set that included all counties in Texas, New Mexico, Arizona, Nevada and California that had at least one positive report of the AHB in the NAPIS system. We added to the data set a second category of counties that were AHB-negative and adjacent to or within 100 miles from counties with AHB reports. This second unoccupied group of counties permitted us to look for possible factors that were associated with lack of occupation by the AHB. The final data set with positive and negative finds of AHBs includes all coun-

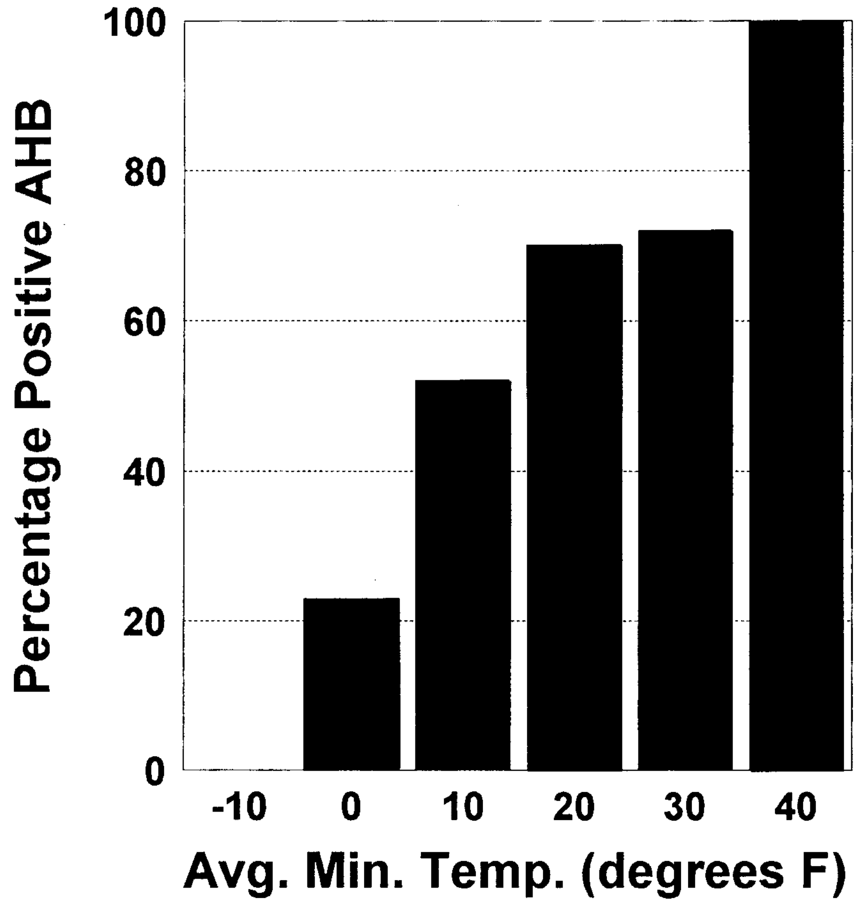


Fig. 1. Percentage of counties with at least one positive AHB find reported, with respect to all counties within the same class of average annual minimum temperature. All counties within 100 miles of a positive occupation were considered as potentially at risk. See text for the number of counties from each state that were considered. The temperatures in the graph indicate the midpoint of the temperature interval.

ties south of Amarillo in Texas. For New Mexico and Nevada, counties north of minimum average temperatures lines of 0°F were not considered because searches for the AHB in those counties had been minimal or nonexistent. All counties in Arizona were included in the data set because the intensity of Africanization in the south has led to more monitoring throughout the state. For California, all counties south of a line from Monterey to Mariposa counties were considered. For each one of the counties we determined an average annual rainfall from maps available at the Oregon Climate Center (**www.wrcc.dri.edu**), an average minimum low temperature from a Plant Hardiness Zone Map (USDA 1990), and an estimated density of fire ants (*Solenopsis invicta*) for each county based on sampling done in 1989 by Porter *et al.* (1991). We then generated three graphs showing the percentage of AHB-positive counties within minimum temperature groups (every 10°F), within average annual rainfall classes (every 10 inches), and within estimated red imported fire ant density groups (0, up to 150, 150-300, and over 300 mounds per acre).

The results were very instructive. Certainly, temperature provides one climatic limitation to AHB range expansion (Fig. 1). Average minimum temperatures of -5° F or less are associated with winter conditions which provide a limit to AHB range expansion. This observation generally agrees with all the predictions that were generated prior to the arrival of the AHB into the United States.

Surprisingly, average annual rainfall appears to place an even more dramatic limitation on AHB range expansion (Fig. 2). Counties with average minimum temperatures above 0° F with an average rainfall of less than 45 inches seem to have reasonably uniform occupations by AHB. However, average rainfall of 45 to 55 inches seems to be associated with very few occupations. No occupations have been observed in the counties with 55 or more average inches of rain, even though their temperature regimes make them likely to be occupied. This lack of observed occupation does not result from lack of opportunity. Most of the uninfested high-rainfall counties have been within 100 miles of infested counties for 6 to 8 years!

Although fire ant densities had a wide range (from 0 to over 300 mounds per acre), we found no clear association between density of fire ants and the presence of AHB (Fig. 3). Indeed, a higher proportion of the counties reported with over 150 fire ant nests per acre had AHB than did counties with no fire ants and counties with less than 150, although the differences are not significant (Fig. 3). We also considered other postulated explanations for the lack of AHB in some areas of east Texas, including changes in natural vegetation and agricultural pesticide use. From our perspective, these two factors would favor occupation of east Texas by AHB over other areas. Because of the transition to forests with larger trees in east Texas, natural nesting sites are probably more available in east Texas than they are in south Texas. A parallel argument can be made regarding agricultural pesticide use. The Rio Grande valley, in both Mexico and Texas, is one of the most intense agricultural regions in North America. Since agricultural pesticide use in the Rio Grande valley has not noticeably restricted the range expansion of the AHB, it is unlikely that agricultural pesticide use elsewhere would do so.

Thus, it appears that a second unforseen limitation to AHB range expansion is annual rainfall, at least in Texas. Certainly, the AHB is found in very high rainfall areas of the tropics, such as the Amazon basin, so rainfall, in and of itself, is not completely limiting. Natural range expansion of the AHB also occurred through the border between Colombia and Panama, one of the highest rainfall areas in the world. However, it is interesting to note that the spread of the AHB through these areas was much slower than the spread through the much drier coastal areas of South America (Taylor, 1985). The numbers of flowering species in tropical wet forest are more evenly distributed through the year than in dry forests (Frankie et al. 1974), and this may explain some of the differences in the AHB movement. In sub-Saharan Africa, the subspecies *A. mellifera scutellata* (the African parental subspecies of the AHB) is restricted to the more arid east and south African regions, while a different subspecies, *A. mellifera adansonii*, is found in the rainier west African zone (Ruttner, 1987). These associations may provide some clues concerning the limits the rains of east Texas impose on AHB range expansion.

East Texas rains are generally evenly spread throughout the year, with minor peaks during summer and winter (Fig. 4), suggesting that a combination of rain distribution and temperature may be more important than just total annual rainfall alone. In east Texas, autumn and winter rains coupled with reduced evaporation, produce ground moisture that does not yield flowers until springtime. In warm

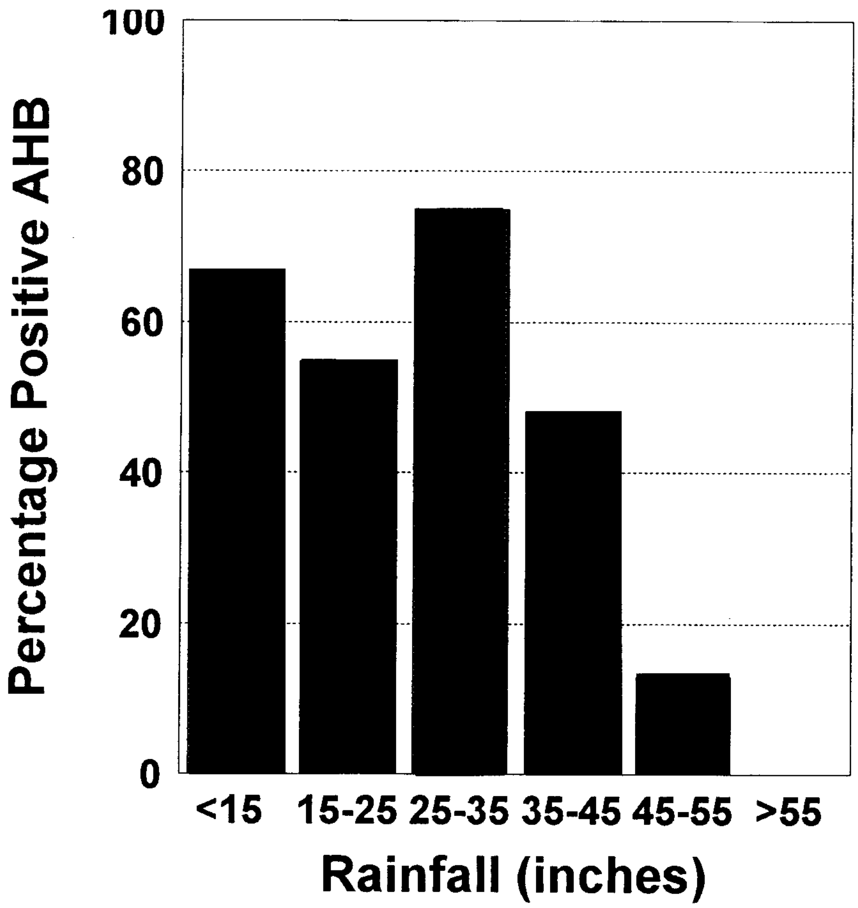
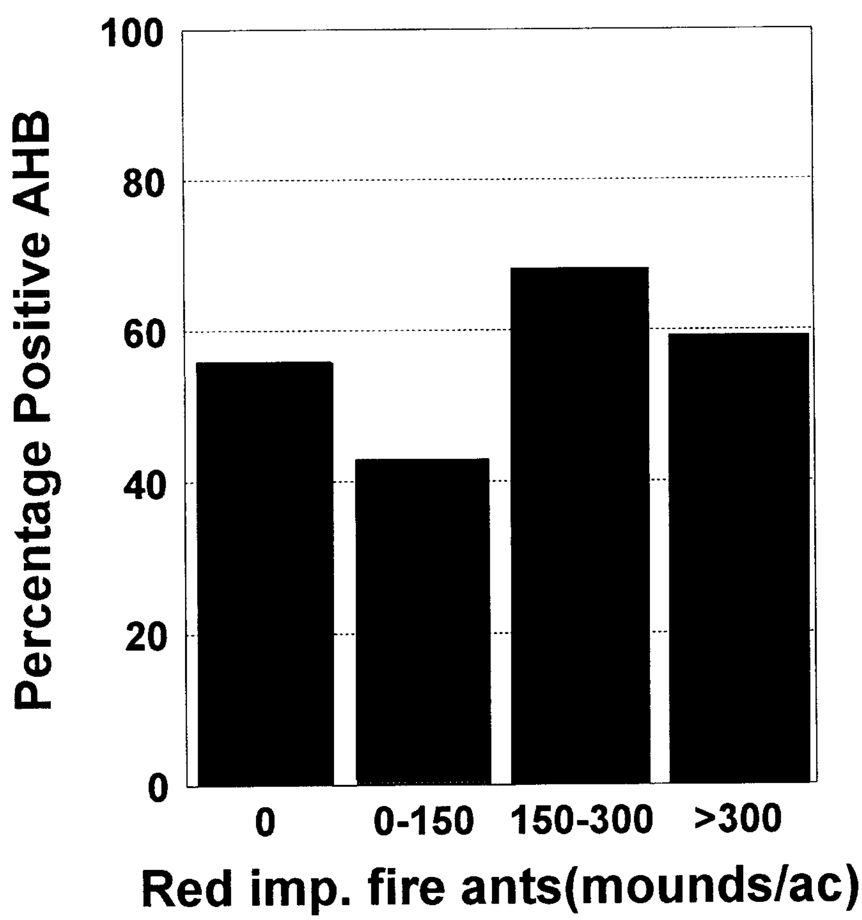


Fig. 2. (Left) Percentage of counties with at least one positive AHB find reported, with respect to all counties within the same average annual rainfall interval. Data set includes all counties considered in Fig. 1.

Fig. 3. (Below) Percentage of counties with at least one positive AHB find reported, and the estimated density of red imported fire ants (*Solenopsis invicta*) based on data collected in 1989 by Porter et al. (1991). The current distribution of fire ants includes more counties to the west and north in Texas than in 1989, but most of those counties were not seriously infested prior to the arrival of the AHB. The data set includes the same counties of Fig. 1 and 2.



arid areas (such as the home range of *A. m. scutellata* in east Africa and the Sonoran desert where the AHB has been very successful) rainfall results in flowers almost immediately. Perhaps the AHB retains a propensity to expand brood nests in response to rain. In arid areas this would lead to better utilization of floral resources (Rinderer, 1988). However, in east Texas, this would tend to lead to colony death since autumn and early winter rains are not quickly followed by flowers.

The higher relative humidity of higher rainfall areas might be contributing to higher *Varroa destructor* infestations, which in turn would negatively impact AHB colony survival and swarming. Perhaps the humidity provided by the 55 annual inches of rain spread throughout the year in east Texas provides conditions that allow *V. destructor* to grow in colonies almost continuously. Relative air humidity below 75% has been shown to produce rapid water loss in adult *V. destructor* (Bruce *et al.* 1997). This could affect such parameters as survival of adult mites on workers or re-infestation of colonies through drifting or robbing honey bees. Reproduction of mites in brood maintained in incubators is reduced at humidities below 40% and at temperatures slightly higher than normal brood temperatures (Le Conte *et al.* 1990). Whether such extreme conditions occur in colonies is unclear. Certainly colonies in dry environments are

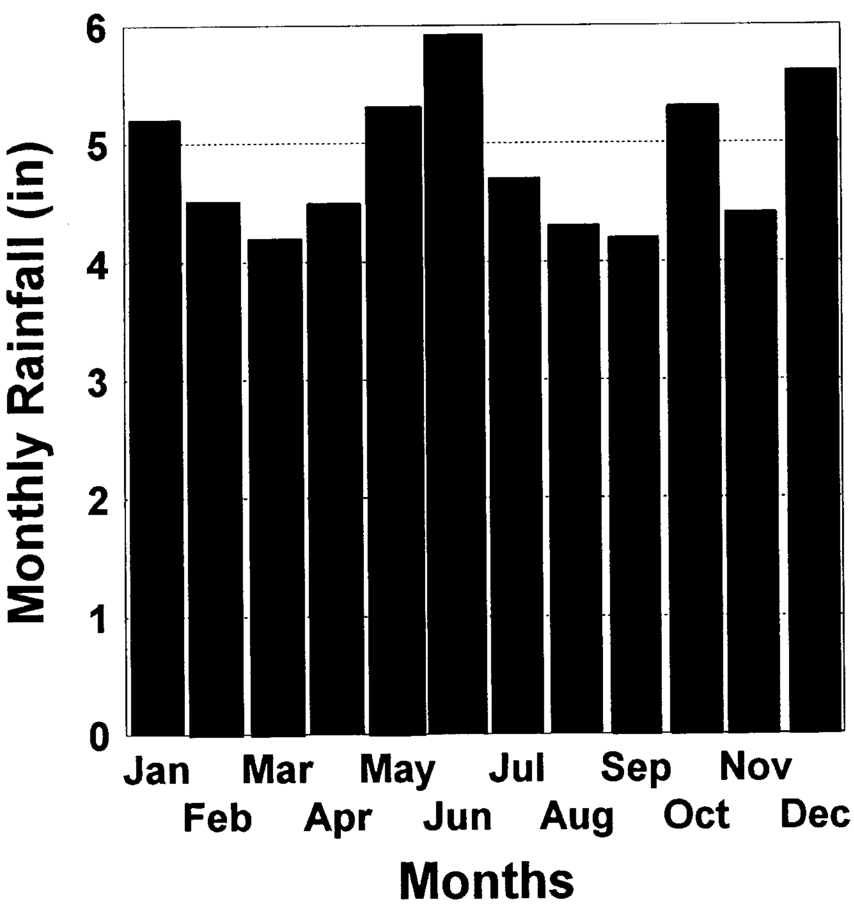


Fig. 4. Average monthly rainfall from stations in 36 counties in east Texas where temperature conditions should have permitted occupation (above the 5°F minimum average temperatures of Fig. 1). They represent most of the unoccupied counties with rainfall above 35 inches shown in Fig. 2.

much more likely to have periods of low air humidity than colonies in environments with high relative humidity, since honey bee colonies lack mechanisms to decrease the water content of air in the hive.

The varroa virulence hypothesis is very compatible with the rainfall 'miscue' hypothesis. Late autumn and early winter brood nest expansion would create an opportunity for *V. destructor* to expand its population in AHB colonies during an unfavorable season for the bees and further damage the colonies.

The addition of rainfall to models for predicting whether or not the AHB will do well in various parts of the country produces a more variegated picture of future AHB distributions. The rain patterns of east Texas extend through much of the Gulf South. Extrapolation suggests that Louisiana, Mississippi, Alabama and northern Florida are unlikely to be troubled by the AHB.

Central and south Florida mostly have annual rainfall averages that exceed 48 inches, but are associated with higher temperature. Hence, the climatic conditions of central and south Florida may be able to support a population of AHB. While a relentless range expansion of AHB from Texas is unlikely to bring AHB to Florida, regulatory vigilance stopping intentional or unintentional shipments of AHB to Florida may be key to keeping Florida free of AHB over the long term.

A few counties in California, which have not yet been found to have AHB, may one day have them because of continued AHB range expansion since they seem to have both favorable temperature and rainfall patterns. However, while all of the United States west coast (including some of the British Columbian coast) falls within the temperature zone, which is favorable for the AHB, the addition of rainfall as a limitation suggests that only southern California provides a favorable habitat.

This analysis is based on rather coarse-grained data. County rather than actual colony locations were used to map the presence of AHB. AHB identifications did not consider varied degrees of hybridization, although both morphometric analysis and modern DNA analyses have the potential to assess degrees of hybridization. Further tests of the hypotheses presented here could productively use such tools. Similarly, presence or absence of positive finds does not give a measure of relative density or impact of the AHB. The AHB has been much more troublesome in the warmer, drier areas of south Texas and Arizona, than in areas it inhabits further north. The AHBs of Texas may be more Africanized in south Texas. Our coarse-grained analysis provides a rough view of the AHB surviving up to, but not beyond, an annual rainfall of 55 inches or more. In reality, levels of Africanization in hybrid honey bees should decrease as rainfall increases eastward across Texas. Owing to the high rainfall in east Texas, a completely and permanently European population should be found in far-eastern Texas or nearby in Louisiana.

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