
THE PROCESSES OF AFRICANIZATION

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The rapid and widespread colonization by Africanized bees of much of South America and all of Central America (Rinderer, 1988) is perhaps the most remarkable biological event of this century. From a reported accidental release of 26 absconding swarms of African bees (*Apis mellifera scutellata*, Ruttner, 1986) in 1956 (Kerr, 1967), the population has grown to many millions of colonies which currently occupy about 20 million square km.

What has enabled the Africanized bee populations to grow so large and to occupy such a large area so quickly? What enables them to occupy such a wide biomic range? What enables them to seemingly displace existing populations of European bees? What are the evolutionary implications for populations of bees in the Americas? The intention of this discussion is to provide an ecological and evolutionary perspective on honey bees which will contribute to our understanding of these questions. Perhaps this perspective will not prove to be correct in all its aspects. Nonetheless, it is consistent with currently known data and provides a framework for a variety of testable hypotheses.

OLD WORLD ORIGINS

In order to appreciate the interactions of Africanized and European bees in the Americas, it is important to understand something of the ecology of the Old World parental stocks. The parental subspecies in Europe and Africa are members of very different ecosystems. Their adaptations to the principal constraining features of these ecosystems are the behavioral and physical antecedents of the genetic revolution now occurring in American honey bee populations.

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The diversity of ecosystems in Africa is tremendous. Predictably, the honey bees of Africa are equally diverse. The darkest, lightest, smallest, largest, most defensive and least defensive Western honey bees are all found in Africa. Ruttner (1986) lists 11 subspecies that collectively display over 70% of the total morphological variation of the species. These subspecies also display large behavioral variation of the species. For example, some of these subspecies abscond so regularly that some authors consider the behavior to be migratory, while other subspecies are not known to abscond at all (Ruttner, 1986).

The parental African subspecies of Africanized bees (*A. m. scutellata*) occupies an arid to semi-arid zone ranging from tropical East Africa to subtropical South Africa. The generally tropical nature of this area leads the casual observer to speculate that since the area is tropical, the bees are only adapted to areas with high temperatures. However, a closer inspection shows that the area is generally composed of highlands which may have cool to cold temperatures, especially at night. One part of the range, the Drakensburg mountains in South Africa, has extended periods of snow cover (Fletcher, 1978). Because of the highland nature of *A. m. scutellata's* range, and because this subspecies does not have a common name, we use the term "Highland bee" when referring to it.

Rather than temperature, the chief climatic feature which appears to limit the Highland bee is rainfall. Rainfall, or more precisely, variability in rainfall, has probably been the primary selective factor in the evolution of the subspecies. The northern extension of the area is considered to have two annual rainy seasons: the "short rains" of October and November, and the "long rains" of March, April and May (Norton-Griffiths *et al.*, 1975). However, the ecological essence of these rains is their unpredictability. They may or may not occur each year; if they occur, they may not occur with strong seasonality or everywhere in the area; and where they occur, their duration and amount is highly varied (Kendrew, 1961; Griffiths, 1972, 1976; Norton-Griffiths *et al.*, 1975).

Similar conditions extend southward. One climatologist (Kendrew, 1961) considers that "most of South Africa except the highest altitudes is arid or semi-arid, the rain being scanty and uncertain in amount and duration." Another (Schulze, 1972) points out that in 11 of the first 60 years of this century, South Africa sustained droughts over large tracts, and writes of a strong unpredictable regional variability in rainfall. This unpredictability is reflected in large fluctuations in South African honey production prior to widespread use of irrigation (Fletcher and Johannsmeier, 1978).

We interpret the distinctive characteristics of the Highland subspecies to be the evolutionary products of the area's unpredictable rains. The vehicle delivering this selection pressure is plant growth and flowering which, in this zone, are completely dependent upon rainfall. Nectar and pollen availabilities are thereby equally dependent upon the unpredictable rains.

Europe

Compared to Africa, Europe is a small continent. Nevertheless, it contains a diversity of ecosystems. There are sufficient differences in ecology and geography to produce five subspecies of honey bees (Ruttner, 1986). Italian bees (*A. m. ligustica*) probably predominate in the ancestry of North American honey bee stocks, and Iberian bees (*A. m. iberica*) probably predominated in the ancestry of South American honey bee stocks prior to their Africanization (Morse *et al.*, 1973; Oertel, 1980). However, all European subspecies have been sources for germplasm introductions to the Americas (Oertel, 1980). Consequently, we are interested in a wide view of European honey bee biology and evolution. Despite diversity, certain generalizations can be made which describe important selection factors for almost all European honey bee populations.

As with Africa, climate is the pivotal selection factor in Europe. Moisture patterns are important, but in almost all of Europe, moisture is coupled with winter periods of varied lengths. Winter clearly promotes the evolution of adaptive honey bee behavior which extends to activities throughout the year. Annual snow melt in spring contributes a reliable annual increase in soil moisture. This predictable moisture, combined with a generally reliable rainfall leads to a dependable, predictable, annual period of plant growth and flowering (Cantu, 1977; Furlan, 1977; Schuepp and Schirmer, 1977). The continent's "rainfall is usually adequate for agriculture, and fluctuations from one growing season to another are rarely excessive" (Bourke, 1984). Thus, in Europe, bees are adapted to climatic regimes which are highlighted by the principle of predictability; predictable winters are followed by predictable periods of plant growth and flowering which are supported by predictable snowmelt and predictable rains.

We interpret the distinctive characteristics of European bees to be evolutionary products of Europe's predictable seasonal cycle. A predictable and sharply varying photoperiod cycle is correlated with European seasonality and has been shown to be an important cue in the regulation of colony population cycles (Morse, 1975; Avitabile, 1978; Kefuss, 1978).

The climatic patterns observed by climatologists in Europe and the highlands of Africa are reflected in apicultural reports of resource availability. Crane (1975) cites several examples of comparatively predictable patterns of nectar and pollen availability in Europe, and Fletcher (1978) and Smith (1951, 1953, 1958, 1960) describe examples of unpredictable patterns for South and East Africa.

CONTRASTS IN HONEY BEE CHARACTERISTICS

Foraging

A variety of studies have led to a model of the regulation of the annual cycle of European honey bee nectar foraging (see Figure 7, Rinderer and Collins, Chapter 12) (Rinderer and Baxter, 1978, 1979, 1980; Rinderer, 1981, 1982a, b, c, 1983; Rinderer and Hagstad, 1984, Rinderer *et al.*, 1984). This model focuses on volatiles from empty comb as the chief regulator of the intensity and efficiency of European honey bee foraging. This seasonably varying regulation is well suited to optimizing the foraging of European honey bees throughout the predictably varying seasonal cycle. A full explanation of the model can be found in Chapter 12.

Several experiments (Rinderer, 1982a, b, c, 1985; Rinderer *et al.*, 1984, 1985a, 1986; Pesante, 1985; Pesante *et al.*, 1987) have led to a model (see Figure 11, Rinderer and Collins, Chapter 12) of Africanized honey bee foraging which stresses a far greater unreliability in nectar and pollen availability. When collecting nectar, Africanized bees are essentially more opportunistic than European bees and behave more like the European bees of autumn. Regardless of season, given the opportunity of a subsistence level of nectar resource availability, Africanized bees will forage, store the resources they collect, and increase their chances of survival. When better resources are available, they will forage, but with less intensity than European bees.

The pollen collection of Africanized bees strongly contrasts with that of European bees. Africanized bees collect more pollen over time, partially because they devote a greater proportion of their foraging cohort to pollen collection (Pesante, 1985; Danka *et al.*, 1987).

Defensive Behavior

The same contrast between resource predictability and resource unpredictability which has led to the evolution of different foraging patterns in European and Highland bees may also underlie some of the differences in defensive behavior between the ecotypes. Interestingly, the foraging regulator, empty comb and its volatiles, also causes changes in the intensity of colony defense (Collins and Rinderer, 1985). More empty comb, which in the natural history of feral bees signals reduced amounts of honey stores, increases the intensity of nest defense by both Africanized and European bees.

The massive defensive responses of Highland bees contrast sharply with the far less intensive responses of European bees (Collins *et al.*, 1982). Certainly, selective pressure from pests and predators is key to the existence of defensive behavior. However, the intensity of the Highland bee's nest defense (Chandler, 1976; Guy, 1976; Nightingale, 1976) and that of its Africanized progeny in the

Americas (Collins *et al.*, 1982) must be primarily rooted elsewhere. A comparison of the honey bee pest and predator complexes of the highlands of Africa and Europe since it was occupied by bees after the last ice-age does not reveal widespread differences (Caron, 1978; De Jong, 1978; Clauss, 1985). Humans have probably been the most efficient and the most abundant honey bee predators in both areas. Beyond humans, similar numbers and kinds of both vertebrate and invertebrate predators of honey bees have existed in Europe and the Highlands of Africa: European brown bears (*Ursus arctos*) are probably equal in destructive ability to ratels (*Mellivora capensis*), and bee wolves (*Phalothus triangulum*) are as notorious as banded bee pirates (*Palarus latifrons*). Perhaps only safari ants (*Anomma spp.*) lack a European equivalent. However, honey bee stinging behavior is not considered an effective defense against ants (De Jong, 1978).

There has likely been a difference in the selective pressures applied by humans in the two areas. In Europe, humans have developed skills in managing perennial colonies of bees for an annual harvest. Where multi-seasonal bee management exists, humans tend to destroy those colonies that sting frequently and to preferentially manage those colonies that sting less. Such artificial selection has probably reduced the overall defensiveness of European bees. In contrast, traditional beekeeping with Highland bees generally involves the periodic trapping of swarms followed by the general destruction of all colonies without regard to their defensiveness during harvest (Smith, 1960; Nightingale, 1976; Kigatiira, 1985). This practice, employed because of the Highland bee's tendency to abscond rather than to establish perennial colonies, is non-selective and cannot be expected to change the general intensity of defensive responses in the honey bee population. Differential human management and selection of bee populations have probably increased fundamental differences between the intensities of the defensive responses of European and Highland bees.

In addition, intensity of nest defense can be viewed as being derived through evolutionary processes which balance the costs and benefits of defense (Seeley, 1985). These costs are not fixed, even for European bees within their seasonal cycle. A notable condition which reduces nest defense is a good immediate availability of harvestable resources (Seeley, 1985), and a notable condition which increases nest defense is the ending of a harvest (Collins *et al.*, 1980). These relationships suggest that part of the balance between the cost and the benefits of defense is measured in the potential for existing bees of the colony to become productive foragers (FIGURE 1). One cost of massive defense is the loss of potential foragers in future harvests. Where harvests in the near future are highly predictable, the costs of losing potential foragers is greater. This increased cost probably accounts for the general reduction of colony defense during nectar flows. It also probably accounts for some of the differences between European bees and Highland bees. The Highland bees, subject to a

Relationship of Resource Predictability and the Intensity of Nest Defense

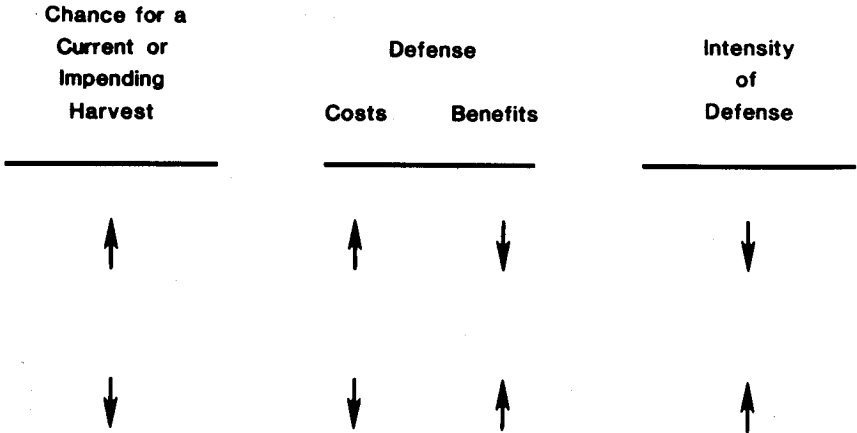


FIGURE 1. Relationship of resource predictability and the intensity of nest defense. ↑= high, ↓= low.

regime of resource unpredictability, harvest resources that are made more valuable by the unpredictability of their replacement.

Through evolutionary time, selective forces should favor bees that conserve collected resources well enough to survive long dearths. Part of this conservation is likely to increase colony defense. The costs of increased defense would be lower, since the potential value of defenders as future foragers is less when the predictability of a future harvest is less (FIGURE 1).

Absconding

A third characteristic difference between European and Highland bees is their tendency to abscond (Ruttner, 1986). European bees rarely abscond. In contrast, Highland bees and their Africanized progeny display the absconding characteristic to a marked degree (Smith, 1960).

Absconding can be organized in two categories. First, swarms which recently have occupied a nest will readily abscond if disturbed. We consider disturbance-induced absconding to be an alternate form of defense; locations that require early active defense often will require frequent active defense. The second category of absconding is resource related. During periods of extended dearth, colonies will often abscond after converting existing food reserves into adult bees. The adaptive value of such absconding is clear in the context of African highland floral resources. Locally unreliable rainfall will cause some large areas to have dearths when nearby areas have abundant pollen and nectar. Absconding in such conditions provides a chance of securing a colony's survival and future reproduction. In Europe, resource related absconding has far less value since European floral resources generally do not have this coarse-grained variability.

Swarming

The patterns of swarming displayed by European and Highland bees also reflect the contrasting patterns of predictable and unpredictable resource availability. Established colonies of European bees can be expected to issue prime swarms one to three times a season (Seeley, 1977; Winston, 1980). An important constraint on this number is the need for both the parent colony and the swarm to harvest sufficient stores during the predictable but time-limited flowering periods to survive the long and also predictable dearth from late summer or autumn to spring. Only very rarely will newly cast swarms themselves produce a swarm during the same season. Thus, European colonies of honey bees generally survive an annual cycle before they reproduce.

In contrast, Highland bees and their Africanized progeny will produce prime swarms up to four times annually (Winston *et al.*, 1981; Otis, 1982) if resources are available. Colonies do not necessarily have ample reserve stores prior to swarming and issued swarms may themselves swarm during the same season (Winston *et al.*, 1981). Apparently, continued swarm production by Africanized bees is dependent upon the continuing availability of resources in the field.

COLONY POPULATION CYCLES

The colony population growth pattern of European honey bees is a remarkable feature of their natural history (FIGURE 2). Often in mid-winter, long before any flowering, colonies begin expanding their brood nests in

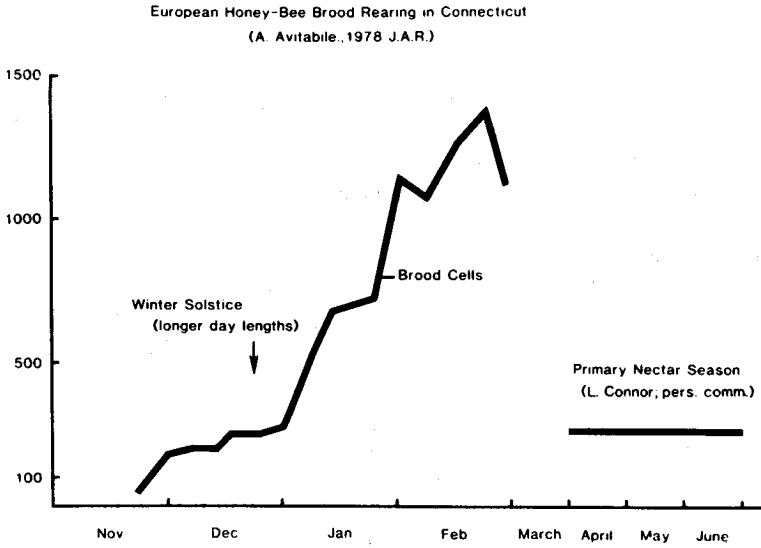


FIGURE 2. European honey bee brood rearing relative to winter solstice in Connecticut.

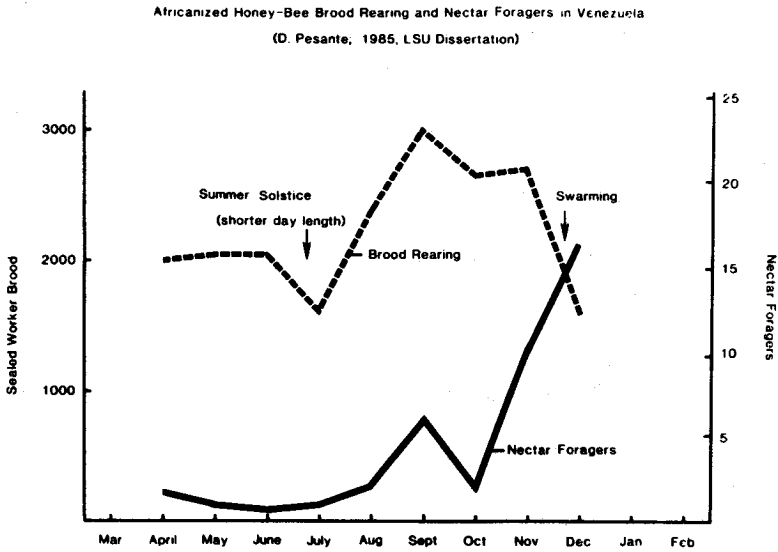


FIGURE 3. Africanized honey bee brood rearing and nectar foragers relative to summer solstice in Venezuela.

response to photoperiod cues (Morse, 1975; Avitabile, 1978; Kefuss, 1978). This early commitment of food resources to the production of large numbers of new colony members is an excellent indication that European bees have evolved in stable, predictable ecosystems. Later in the season, even during the modest nectar flows of autumn, European colonies reduce the intensity of their brood rearing and often discard their reproductive investment in drones. Again, these activities are evolutionarily developed responses to the stability and predictability of European ecosystems.

No data exist on the colony population cycles of Highland bees but good data are available from Africanized bees (Winston *et al.*, 1981; Otis, 1982; Pesante, 1985). Africanized bees develop large colony populations in remarkably short periods. Interestingly, they do so only in response to the immediate existence of harvestable resources (FIGURE 3). During harvests they show a marked preference for pollen in comparison to European bees (Pesante, 1985; Danka *et al.*, 1987). Development of large brood nests and the reduction of brood nests are triggered by the immediate presence or absence of harvestable resources (Pesante, 1985). Rapid expansion is founded on a comparatively high fecundity (Smith, 1958) and shorter individual development times (Smith, 1958; Harbo *et al.*, 1981). Such colony population development events are clearly indicative of bees which have evolved to thrive in unpredictable ecosystems.

Population Densities

There are no exhaustive studies of the sizes of feral honey bee populations from anywhere in the world. However, fragmentary information (Smith, 1953; Kerr, 1971; Seeley and Morse, 1976; Seeley, 1977; Fletcher, 1978; Taber 1979; Rinderer *et al.*, 1981, 1982) from South America, Africa, and North America suggest that in favorable periods, the population densities of European honey bees are far less than those of Highland or Africanized bees. However, personal experience (T.E.R.) in Africa at the end of a widespread drought suggests that, during periods of adversity, the populations of Highland bees can become quite low. A general inference from the scattered data is that European honey bee populations are reasonably stable and that their densities are generally intermediate between the high and low densities of Highland and Africanized populations.

Comparative Demography

Although the characterization of organisms as comparatively "K" or "r-selected" is often imperfect, it still has use in formulating hypotheses and summarizing general comparisons. Honey bees, and especially European honey bees, are considered to be "K-selected" (Seeley, 1978). However, among honey bee subspecies, the Highland bee is, for many characteristics, a comparative "r-

strategist" (MacArthur and Wilson, 1967; Danka *et al.*, 1987). According to Wilson (1975), "r-strategists (1) discover habitat quickly, (2) reproduce rapidly and use up the resources before the habitat disappears, and (3) disperse in search of other new habitats as the existing one becomes inhospitable." The absconding and swarming rates of the Highland bee qualify it well for the label of comparative "r-strategist" within the subspecies of the western honey bee. Demographic theory holds that "r-selected" organisms are adapted to exploiting variable, unpredictable, or ephemeral resources. The food sources of the Highland bee show these characteristics to a marked degree and are a direct consequence of variable and unpredictable rainfall patterns.

The perspective of Africanized bees as "r-selected" is useful for comparisons with European bees and in understanding the broad range of Africanized honey bee adaptability. However, western honey bees generally fit demographic descriptions of "K-selected" species. As such, Africanized bees are well adapted to develop stable populations in conditions of stable resources.

The Adaptability of Honey Bees to Tropical America

The climates of tropical America are highly varied but they generally provide a difficult environment for European honey bees. However, this mismatch is poorly explained by the thought that temperate bees could not possibly be well-adapted to tropical areas. The climates of the American tropics show marked wet and dry seasonal cycles that have a predictability reminiscent of the predictability of the European climates. The natural histories of native social bees in the American tropics are similar in many respects to the natural histories of European honey bees. But the organization of resource predictability that has influenced their evolution is much different. The seasonal rhythm of nectar availability reported for Piracicaba, Brazil differs from the nectar-flow rhythms of Europe (Amaral, 1957) (FIGURE 4). Although Piracicaba is at 22°S latitude, it has its major nectar flow from July to September. Thus, weak photoperiod cues guide European bees to increase the sizes of their brood nests only immediately prior to the nectar flow rather than several months earlier as is the case in Europe. Seasonality in Acarigua, Venezuela has completely opposite photoperiod cues. In Venezuela, at 10°N latitude, resources become available in August or September and are at a peak from November to February. Earlier, in the rainy season of April to August, European bees do so poorly that we used exclusively Africanized bees in our colonies in Venezuela during this period. They conserve resources well in this period, while European bees do not. The extent to which European bees are successful in such areas reflects their limited capacity to adjust to unpredictable resource variation rather than their much stronger capacity to exploit the predictable floral resources of Europe. Other areas of tropical America, as in the Amazon Basin and the Brazilian Highlands, are ecologically different from each other, but are also so different from European

Seasonality of Nectar Availability
at Piracicaba, Brazil
(E. Amaral; 1957 A.B.J.)

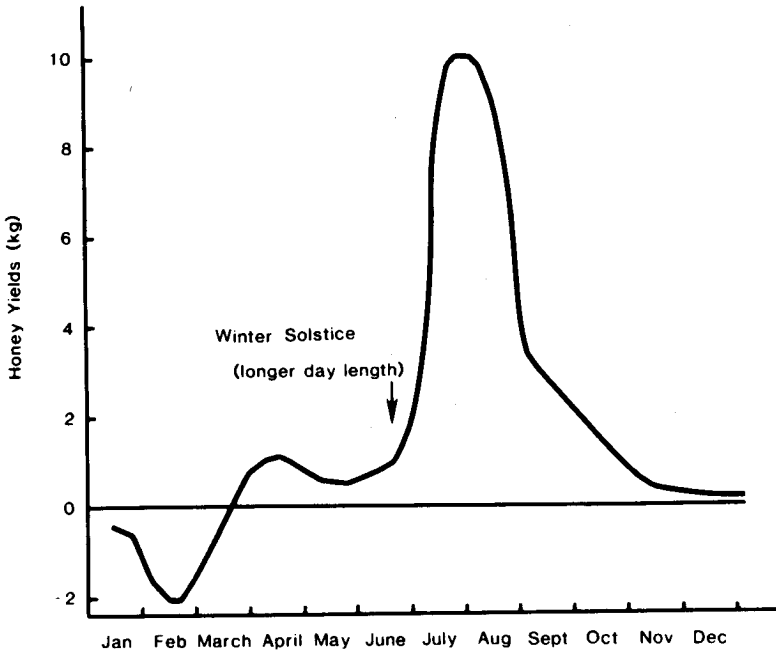


FIGURE 4. Seasonality of nectar availability at Piracicaba, Brazil.

seasonal patterns that they seem to be beyond the range of European honey bee adaptability.

In contrast, Africanized honey bees in the varied and unique ecosystems of tropical America have proved to be highly successful. This success rests, not on general tropical adaptations, but rather on their highly evolved capacity to successfully exploit unpredictable and varied resource conditions. The differing resource periodicities of Piracicaba and Acarigua are both well within the limits of Africanized honey bee adaptability. The unpredictability of the Brazilian highlands is reminiscent of highland Africa and the food resource patterns of Amazonia resemble a poor season in highland Africa. The oddities of the African highland rains have been a foundation for the evolution of adaptive characteristics (foraging, defense, swarming, absconding and colony population development patterns) which have enabled Africanized bees to occupy nearly the entire biomic diversity of tropical America.

THE GENETICAL NATURE OF HONEY BEES IN THE AMERICAS

European Honey Bees

All bees in the Americas are derived from imports. Early importations were probably relatively few in number due to the difficulties of transport by sailing ships. In North America these importations were from northern Europe and were of representatives of *A. m. mellifera*. This was the chief commercial honey bee in North America until the mid 19th century. It was then discovered that bees from Italy, *A. m. ligustica*, were comparatively resistant to the brood disease European foulbrood. A major campaign by the U.S. and Canadian Departments of Agriculture promoted the "Italianization" of commercial apiaries (Oertel, 1980). This effort met with resounding success and in a short time Italian bees were used in the vast majority of commercial enterprises. Most likely, these bees were an admixture of representatives of the two subspecies. The success of this program spurred increased importation of bees from Europe which included bees from a variety of populations, including other subspecies (Morse *et al.*, 1973; Oertel, 1980; Sheppard, 1989). The honey bees of North America are derived from all of these imported honey bees and are now a population of bees which itself has varied sub-populations (H. V. Daly and W. S. Sheppard, pers. comm.).

The European bees of South and Central America are probably derived mostly from the Iberian peninsula as were the European colonists who brought them. The Iberian peninsula contains populations of both *A. m. iberica* and *A. m. mellifera* (Ruttner, 1986; Sheppard, 1989). Representatives of other subspecies have been imported occasionally to South and Central America. However, these importations have been insufficiently large to strongly alter the character of the already existing admixtures of *A. m. iberica* and *A. m. mellifera*.

Africanized Bees

What happened genetically when representatives of the Highland subspecies began colonizing South America is central to understanding the process of Africanization. A morphological comparison by Buco *et al.* (1987) of South American, Africanized and South African (Highland) honey bees helped clarify several features of the process of Africanization.

First, although the samples of Africanized bees which were studied came from west-central Venezuela, their descriptive statistics were nearly identical to the descriptive statistics for samples of Africanized bees studied by Daly and Balling (1978). The Daly and Balling survey of Africanized bees included a larger number of samples from a much larger geographical area. This comparison suggests that the processes of Africanization consistently lead to

similar Africanized bee populations which are maintained for at least several years.

Second, the Africanized bees from South America differed significantly from South African representatives of the Highland subspecies for 19 of the 24 morphometric characteristics analyzed. Africanized bees were consistently larger than Highland bees, although the variances of the two groups were generally similar. The differences found in comparisons of individual characteristics were reflected in a multi-variate discriminant function analysis which completely separated the two populations. The posterior probability of group membership for bees of the Mexican highlands and for Venezuelan Africanized bees for all cases indicated a correct and unambiguous classification when using the derived discriminant function, suggesting the presence of European genes in Africanized populations. A recently completed extensive morphological study involving populations of honey bees from South America, North America, Europe, Africa and Arabia confirms this conclusion (Rinderer *et al.*, unpubl. data) and indicates that about one-third of the morphological characteristics of Africanized populations are derived from European parentage.

Similar evidence comes from a study of honey bees (Lobo *et al.*, 1989) from a transect across the tropics (seven samples) and subtropics (four samples) in Brazil and Uruguay. Lobo *et al.* studied the morphology of forewings in these samples and the frequencies of allelomorphs for several enzyme loci. Both lines of investigation led Lobo *et al.* to conclude that the populations they studied were racial mixtures that differed in the percentages of admixture among these various sampling sites. An increase in the contribution of European parental populations seemed to occur on a North to South cline. Hall (1990) studied populations of feral bees from Mexico and Venezuela using three nuclear DNA probes that detected restriction fragment length polymorphisms of non-repetitive DNA. Although this system of analysis is not yet sufficiently precise to permit the inference of percentages of parentage in hybrid genomes, hybridization was detected in both the Mexican and the Venezuelan Africanized populations.

The conclusion that Africanized bees are a mixture of European and Highland populations contrasts with the conclusions of Hall and Muralidharan (1989) and Smith *et al.* (1989). These investigators reported the frequencies of African and European mitochondria in various samples of bees. Hall and Muralidharan reported that 10 of 10 feral Venezuelan colonies, 19 of 19 feral swarms from Mexico and 3 of 3 feral swarms from Costa Rica all contained African mitochondrial DNA. Smith *et al.* reported that 9 of 10 Brazilian samples, 12 of 12 Venezuelan samples and 38 of 39 Mexican samples contained bees having African mitochondrial DNA. Mitochondrial DNA is only maternally inherited and not subject to sexually derived hybridization as in nuclear DNA. Nonetheless, these authors concluded that European bees have not contributed significantly to the feral Africanized gene pool. However, Page (1989) suggested that given the small presence of European honey bees in

South America prior to Africanization, European mitochondria should be rare if the South American feral population resulted from the expansion of a large and rapidly growing population of African maternal descent. Page's explanation of the data showing low frequency of European mitochondrial DNA in Latin America seems correct. More recently Sheppard (pers. comm.) has found a much higher frequency of European mitochondria in Africanized bees from tropical northern Argentina. Moreover, the bees from that region show a wide range of morphological intergrades.

Thus, the feral bees of South America constitute a population which is genetically quite different from the parental population of Highland bees in South Africa. The most likely explanation for these differences is that Africanized bees in the Americas fit the classic taxonomic definition of a subspecific hybrid swarm (King, 1974) which has resulted from matings with European bees followed by subsequent crossing and back-crossing. The generally intermediate morphometric character of Africanized bees and their hybrids with European bees suggests that a large number of loci are involved in the determination of honey bee morphology (Rinderer *et al.*, 1990). Predictable Mendelian events associated with crossing and then back-crossing between Highland and European bees would produce the Africanized bees measured by Buco *et al.* (1987). Thus, Africanized bees clearly show the influence of both their European and their African parentage.

It is important to understand that Africanized bees are hybrids. The processes of Africanization resist changes in gene frequencies towards the European types and yet there is sufficient mating between Africanized and European bees that extensive measurable hybridization exists throughout the Africanized population. Since Africanized bees only resist cross breeding but are not insulated from it, the processes of Africanization are imperfect. Consequently, (1) hybrid populations form throughout the range of bees in the New World, (2) programs by agencies, groups or individual beekeepers that promote the mitigation of Africanization through hybridization are likely to be successful, and (3) variation derived from hybridization can provide a good basis for the development of quality strains using selection programs throughout the New World.

KNOWN PROCESSES OF AFRICANIZATION

Human Transport

Human transport of Highland bees to Brazil in 1956 was responsible for the start of Africanization. Indeed such transport of bees, either accidental or intentional, remains a major threat to further spread of these bees. There are several reports of Africanized bees being transported on ships into U. S. ports (M. Holmes, pers. comm.). A recent example of an accidental introduction

involved bees presumably accompanying the commercial shipment of other goods into the Bakersfield, California area (Gary *et al.*, 1985). As many as 11 colonies of Africanized bees were found in the area after 24,000 colonies were inspected.

Despite the many undesirable traits of Africanized bees, there is always the threat that these bees could be intentionally introduced into new areas by misinformed people. Some beekeepers want more defensive bees in order to curtail colony theft and vandalism. Others believe that these bees will increase their honey production. Both of these arguments have little foundation. In Venezuela, for example, theft and vandalism of Africanized colonies, usually during the night, occur at a high rate; and honey yields per colony are at least 50% less than they were prior to Africanization (W. Vogel, pers. comm.).

Biological Processes

The biological processes of Africanization may be divided into two main categories. Those involved with the initial spread of Africanized bees into an area, and those involved with reducing the genetic contribution of existing European honey bees to the general bee population.

Africanized honey bees spread into new areas primarily by the movement of absconding swarms. These swarms are generally those that are induced to abscond by resource related conditions. A period of resource unavailability in the field, coupled with reduced stores in a nest induce Highland and Africanized colonies to abscond. Evidence from Kenya (Kigatiira, 1985) suggests that absconding swarms will move along a vector for up to 60-80 km. They make several stops along the way and forage, sometimes for a number of days. Presumably, successful foraging cues such swarms to establish colonies in nearby nesting sites. Once absconding swarms arrive in an area, other characteristics of Africanized bees account for the large scale Africanization of the area and its existing bee populations.

There is a suggestion that mating populations of European bees show certain subtle behavioral changes towards the Africanized type prior to the discovery of Africanized bees within an area (G. Vogel, pers. comm.). Perhaps the reproductive influence through crosses of a few colonies of Africanized bees in an area is more easily observed than the colonies themselves when no special effort is made to find them.

Once in an area, the adaptive characteristics of Africanized bees lead to a rather rapid Africanization of the overall honey bee population. Generally, these traits are r-selected reproductive characteristics. High swarming rates, described earlier, rapidly lead to large feral population of Africanized bees. In and of itself, this comparatively large fecundity is a strong force in the Africanization process and can account in large measure for the Africanization of mixed bee populations (Ruttner, 1986).

Also, social reproductive parasitism has contributed to the success of these bees, and particularly to the general displacement of previously existing populations of honey bees with European origins. Parasitism is widely known among the Apoidea. It ranges from cleptobiosis (food robbing) to cleptoparasitism (typically involving solitary bee species) to true social parasitism, wherein a reproductive female usurps the position of the queen of a parasitized host colony (Wilson, 1971; Michener, 1974). Social parasitism can be facultative or obligate, temporary or permanent, intraspecific or interspecific (Wilson, 1971). Both queens and drones of Africanized honey bees have been observed to parasitize conspecific colonies. Queens engage in temporary facultative parasitism, a phenomenon first described by Wheeler (1904) for ants. A queen which normally is free-living invades a conspecific nest; the parasitism is temporary in that the usurped nest eventually is inhabited only by offspring of the parasite. Such parasitism is regarded evolutionarily as the least specialized form of social parasitism (Taylor, 1939). Drone (male) parasitism has not been reported for other social insects, and does not fit into Taylor's (1939) evolutionary scheme. The behavior is best described as permanent facultative parasitism, since the host queen continues to produce offspring while the colony supports the drone parasites.

Female social reproductive parasitism has long been an activity associated with Africanized bees, but the phenomenon has not been studied on a rigorous experimental basis. Anecdotal reports (Anonymous, 1972; Michener, 1975) typically cite a small cluster of a few to several hundred worker bees, including a mated Africanized queen, landing near the entrance of a hive. Workers from the swarm enter the hive, kill the resident queen, and the parasitizing queen assumes the egg-laying role in the nest. Thus, the usurped colony becomes fully Africanized (i.e., all the bees are Africanized, and no further hybridization with European bees has occurred) after about nine weeks.

Our experience in Venezuela has been that the frequency of queen parasitism increases when colonies are queenless or have failing queens, are small, or have been stressed by manipulation. In one preliminary experiment (unpubl. obs.), queenless colonies of either Africanized or European bees usually accepted both Africanized and European queens when the queens, in small artificial swarms, were placed at the colony entrances. Queenright colonies never accepted foreign queens. European colonies whose queens were confined in cages accepted queens of either type, but similarly prepared Africanized colonies generally did not accept queens of either type.

The sources of parasitizing queens are unknown. It is possible that the small clusters of invading bees are absconding swarms or afterswarms. An observation of parasitism among European bees in Baton Rouge in autumn suggests an absconding swarm as the source. In Africa, migrating swarms of *A. m. scutellata* amalgamate and then cast off extra queens with small groups of

workers (Kigatiira, 1988); if similar swarm mechanics occur in the neotropics, cast queens may also parasitize colonies.

Social reproductive parasitism by queens can contribute to the Africanization process in several ways. Complete Africanization soon occurs when an Africanized queen usurps a European colony. An invaded colony then may contribute to further Africanization through swarms, drones, and additional queens. Recently parasitized colonies may unknowingly be transported to previously uninfested areas; frequent colony inspections and marked European queens are required to observe such occurrences. Africanized queens may be able to overwinter in European colonies in regions with harsh winters, and subsequently contribute to wider Africanization during the spring and summer. In any event, years of reproductive parasitism by Africanized queens may explain why nuclear assays (morphology, isozymes and DNA probes) detect different levels of hybridization for Africanized populations than is detected by mtDNA analysis.

Parasitism by Africanized drones has been the subject of much greater experimental attention than has queen parasitism (Rinderer *et al.*, 1985b, Rinderer *et al.*, 1987). Originally, inspections of an experimental apiary of genetically marked European colonies in Venezuela revealed that the majority of drones in the colonies were Africanized. This observation led to a series of experiments to study the causes and magnitude of this parasitism and its effects on host-colony drone production.

These experiments showed that Africanized drone honey bees migrate into European honey bee colonies in large numbers, but Africanized colonies only rarely host drones from other colonies. This migration leads to a strong reproductive advantage for Africanized bees since it both inhibits European drone production and enhances Africanized drone production.

In addition to social parasitism by drones, Africanized colonies produce and maintain far more drones than do European colonies (Rinderer *et al.*, 1987). The combined effects of drone parasitism and differential production and maintenance resulted in 91% of the total drone population being Africanized in an experiment using two apiaries having equal numbers of Africanized and European colonies.

Such disproportionate numbers of drones would enhance the positive assortive mating tendencies (Kerr and Bueno, 1970) of Africanized bees and impair those of European bees. Over several generations this condition alone would result in substantial Africanization. Maximally, a few Africanized colonies could produce all or nearly all of the drones in a mating area. In this case, substantial Africanization would result in two or three generations.

All of these processes of Africanization are interactive rather than additive. For example, increased numbers of swarms and afterswarms will lead to increased frequencies of queen parasitism. Queen parasitism increases the levels of drone parasitism as does increased numbers of swarms.

An additional hypothesis has been advanced to further explain the Africanization of European apiaries (Taylor, 1985; Taylor and Rowell, 1988; Taylor *et al.*, in press). It is based on the correct observation that Africanized drones experience the peak of their mating flight somewhat later in the day than European drones and the incorrect interpretation of European literature that honey bee queens fly further than do drones from their nests during mating flights (Rinderer, 1986). Mating flight differences may enhance the Africanization process but not in the way suggested by the hypothesis. Mating flight range differences may be asymmetrical for European and Africanized reproductives with queens generally flying shorter distances than drones (Konopacka, 1968, 1970; Ruttner and Ruttner, 1972; Böttcher, 1975). If Africanized reproductives generally fly shorter distances than European reproductives, conditions may be established whereby all European queens mating from an apiary have a high likelihood of mating with Africanized drones flying from the same apiary (Rinderer, 1986). Although there may be numerous other differences between Africanized and European bees that enhance the Africanization process, they probably are all secondary to the important phenomenon of absconding swarms, differential reproductive rates, and social reproductive parasitism. These three categories of biological events are sufficient to account for the observed characteristics of the Africanization process.

CONCLUSION

Natural selection was invoked by Ruttner (1986) to explain the occurrence of Africanized bees in Argentina at 39° South latitude (Dietz *et al.* 1985; Krell *et al.*, 1985). The range and the intensity of the intrusion of Highland honey bee traits into populations of bees in the temperate zones of the Americas will probably depend, in part, upon natural selection. Several questions remain wholly or partially unanswered. In American temperate zones do the populations of European bees, which are themselves hybrid swarms (King, 1974) of varied parentage, already contain highly adapted feral ecotypes as do the populations of Europe? Do the varied American ecosystems provide, on a biome by biome basis, resource availability patterns more tuned to exploitation by Africanized or European honey bees or by some intermediate form? Are adaptive traits in honey bees based upon such a complicated non-additive genetic basis that increased fitness can only occur in rare segregates in hybrid populations? Or, are adaptive traits in honey bees based upon additive genetical underpinnings and simpler non-additive genetical events as is the case with hygienic behavior (Rothenbuhler, 1964)? How much will human activity enhance or retard the development of new ecotypes of bees?

The possibilities exist for natural selection to produce, rather rapidly, new ecotypes of honey bees in the Americas. The ecology of temperate, as well as of tropical America, is rich and varied. In addition, the introduction of Highland

bees and the spread of their Africanized progeny represents an infusion of additional genetic variation. The operation of natural and artificial (i.e., breeding) selection on this expanded genetic variation in the varied American biomes has the potential to produce novel populations of bees very rapidly.

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