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Evolutionary aspects of the Africanization of honey-bee populations in the Americas

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INTRODUCTION

The rapid and widespread colonization by Africanized bees of much of South America and all of Central America (Rinderer 1986) is perhaps the most remarkable biological event of this century. From a reported accidental release of 26 absconding swarms of African (*Apis mellifera scutellata*, Ruttner 1986) bees in 1956 (Kerr 1957), the population has grown to many millions of colonies which currently occupy about 17 million square kilometers.

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. I do not expect that this perspective will prove to be correct in all its aspects. Nonetheless, I offer it with the thoughts that it is consistent with currently known data and that it provides a framework for a variety of testable hypotheses.

An appreciation of the recent changes in the structures of honey-bee populations in the Americas is rooted in an understanding of the ecology and natural history of both African and European bees in their home ranges.

PRINCIPAL SELECTIVE FACTORS IN THE ECOLOGY OF AFRICAN BEES

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. 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 cold (Fletcher 1978). Because of the highland nature of *A. m. scutellata*'s range, and because this subspecies does not have a common name, I will use the term 'Highland bee' for convenience in 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 this subspecies. 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 (Griffiths 1972, 1976, Kendrew 1961, 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.

I interpret the distinctive characteristics of the Highland subspecies to be primarily 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. Because of this, nectar and pollen availabilities are thereby equally dependent upon the unpredictable rains.

PRINCIPAL SELECTIVE FACTORS IN THE ECOLOGY OF EUROPEAN BEES

Although compared to Africa, Europe is a small continent, it nonetheless contains a diversity of ecosystems. There are sufficient differences in ecology and sufficient isolating features to produce 5 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, in broad strokes, describe important selection factors for almost all European honey-bee populations.

Here again, climatic factors are pivotal. And again, moisture patterns are

important. But, in almost all of Europe, they are 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 & Schirmer 1977). In spite of the necessary difficulties of generalization, 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.

I interpret the distinctive characteristics of European bees to be primarily the evolutionary products of Europe's predictable seasonal cycle. Predictable and sharply varying photoperiod cycles are correlated with European seasonality, and have been shown to be an important cue in the regulation of colony population cycles (Avitable 1978, Kefuss 1978, Morse 1975).

CONTRASTS IN HONEY-BEE CHARACTERISTICS

The climatic patterns observed by climatologists for Europe and Highland 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.

Foraging

Prior to studying Africanized bees, I explored the variation in seasonal foraging patterns of European honey bees in North America. A variety of studies have led to a model of the regulation of the annual cycle of European honey-bee nectar foraging (Fig. 1).

The predictable temperate flowering patterns provide a quickly developing major period of resource availability in spring to early summer. During this period, floral resources tend to be both varied and rich. A decline in variety and abundance follows, until by late summer and autumn, only a few, poor-quality nectar sources exist. Occasionally, naturally occurring abundances of resources in autumn do occur (Oertel *et al.* 1980). However, they have probably shaped European honey-bee foraging much less than have the predictable abundances of spring and summer.

Seasonal changes in the concentration and quantity of nectar are paralleled by the amount of empty storage comb in a feral honey-bee nest. The winter use of stored honey followed by the intensified brood rearing of early spring and the consequent food consumption by greater numbers of bees result in a rapid reduction in the amount of stored honey. This causes a concomitant increase in empty comb. During the major nectar flow, the empty comb is utilized for honey storage. Thus, it becomes increasingly less available as the season progresses.

The foraging of European honey bees fluctuates in ways that are most appropriate to the predictable seasonal changes in resource conditions. At the beginning of

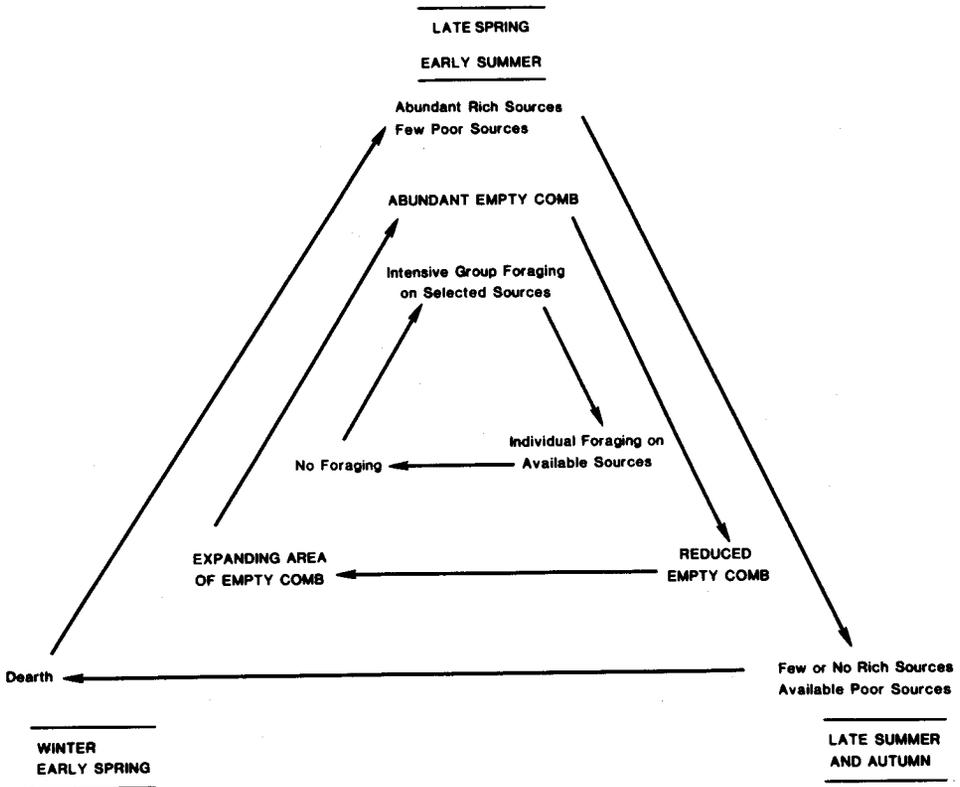


Fig. 1 — A model of the regulation of the annual cycle of European honey-bee nectar foraging.

the major nectar flow, when feral nests have an abundance of empty comb, European bees tend to be more selective of nectar sources and, through the use of increased levels of dance communication, exploit quality sources intensively. Later, when the quality and quantity of nectar sources diminish and feral nests have less empty comb, European bees tend to be less selective of nectar sources and less prone to recruitment dances for all but the highest quality sources.

A collection of experiments (Rinderer 1981, 1982a,b,c, 1983, Rinderer & Baxter 1978, 1979, 1980, Rinderer & Hagstad 1984) demonstrate that different amounts of volatiles emanating from different amounts of empty comb regulate these fluctuating characteristics of foraging. The chief feature in these experiments which demonstrates this regulation is that comb stimulation usual to a specific season causes bees to behave as though they were in that season regardless of the season in which the experiment was conducted.

The adaptive value of seasonally changing nectar foraging patterns in response to comb regulation is clear in the ecological context of European honey bees. Comb volatiles and secondary factors regulating foraging and communication lead to nectar harvesting behavior which is best suited to seasonal conditions that vary predictably.

Describing the contrasting seasonal nectar foraging strategies displayed by European bees sets the stage for understanding the foraging characteristics of Africanized bees. African studies of the foraging characteristics of Highland bees are few (Fletcher 1978, Michener 1975) and have never used comparative experimental designs. However, comparative studies of European and Africanized bees in the Americas do exist (reviewed by Rinderer & Collins 1988). The contrasts found in these studies are probably not widely different from what would be obtained from comparative studies of European and Highland bees in Africa. Several experiments (Pesante 1985, Pesante *et al.* 1987, Rinderer 1985, Rinderer *et al.* 1982, 1984, 1985, 1986) have led to a model (Fig. 2) of Africanized honey-bee foraging which stresses a

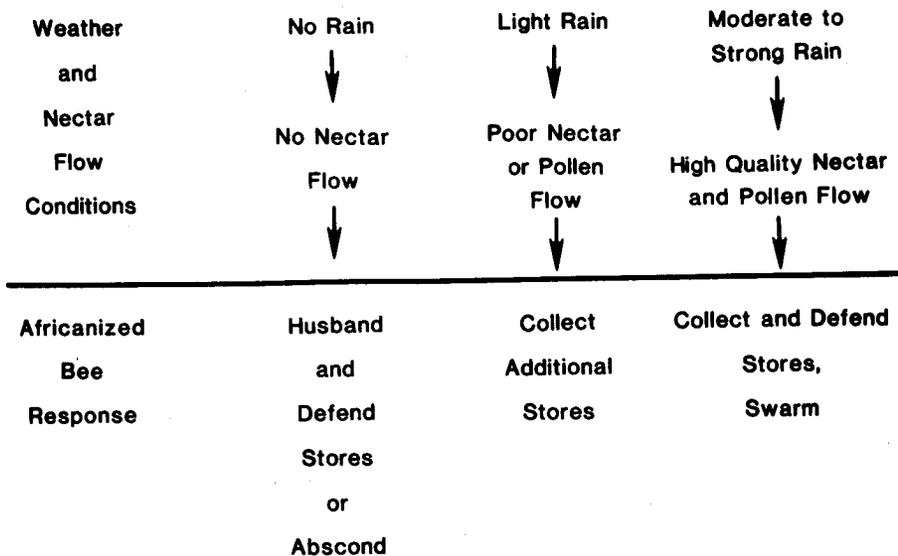


Fig. 2 — A model of Africanized honey-bee foraging.

far greater unreliability of nectar and pollen availability (Rinderer & Collins 1987). 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 resource availability, they 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, partly because they devote a greater proportion of their foraging cohort to pollen collection (Pesante 1985, Danka *et al.* 1987).

The contrast of Africanized bees (cast as individual foragers adapted to glean often poor and always unpredictable resources) and European bees (cast as group

foragers adapted to often rich and generally predictable resources) accommodates a wide variety of sometimes superficially contradictory reports of comparative honey yields (Gonçalves 1975, Kerr *et al.* 1970, Rinderer *et al.* 1985). It is important to emphasize that this contrast is one of degree and not kind. Both geographical types of bee show the capacity, common to all western honey bees, of shifting their foraging from intensive and selective harvesting to gleaning. However, the general tendency of Highland and Africanized bees is to be more successful at the end of the foraging continuum where gleaning is more adaptive. European bees tend to be more successful at the end of the continuum where intense, selective harvesting is more adaptive.

Defensive behavior

The same contrast of resource predictability for European bees in comparison to resource unpredictability for Highland bees which has led to the evolution of different foraging patterns also probably underlies some of the differences in defensive behavior. Interestingly, the foraging regulator, empty comb and its volatiles, also causes changes in the intensity of colony defense (Collins & 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 the 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 Highland Africa and Europe since it was occupied by bees after the last ice age, does not reveal widespread differences (Caron 1978, Clauss 1985, DeJong 1978). 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 (*Philanthus triangulum*) are at least 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 (DeJong 1978).

There has probably been a certain difference in the selective pressures applied by humans in the two areas. In Europe, humans have increasingly developed skills in managing perennial colonies of bees for an annual harvest. Where seasonal bee management exists, probably 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 (Kigatiira 1985, Nightingale 1976, Smith 1960). This practice, employed because of the Highland bees' 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). 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 of the cost and the benefits of defense is measured in the potential for existing bees of the colony to become productive foragers (Fig. 3). One

Relationship of Resource Predictability and the Intensity of Nest Defense

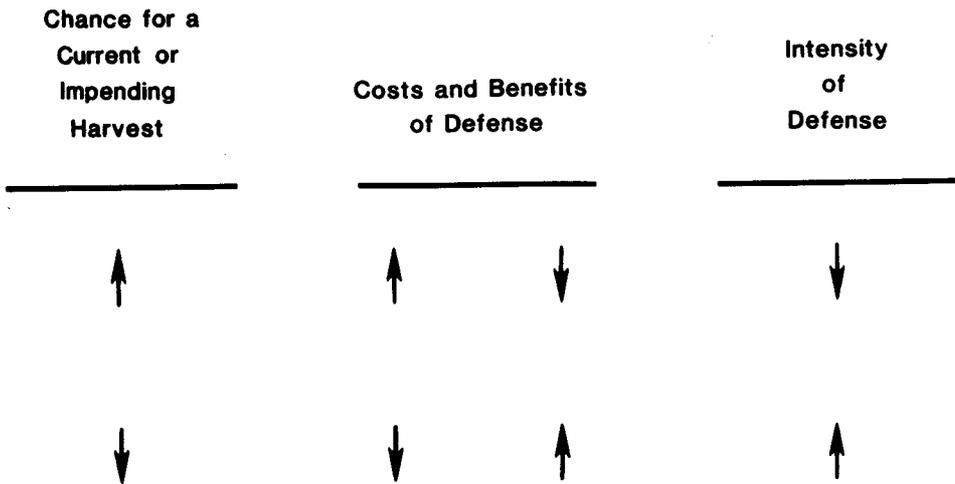


Fig. 3 — A model of honey-bee defensive behavior.

cost of massive defense is the loss of potential foragers in future harvests. Where harvests in the near future are highly predictable, the cost 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 general difference between European bees and Highland bees. The Highland bees, subject as they are to a regime of resource unpredictability, have already harvested 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 be

increased 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.

Abscending

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).

Abscending can be organized into two categories. First, swarms which have recently occupied a nest will readily abscond if disturbed. I consider disturbance-induced absconding to be an alternate form of defense; locations that require early active defense will often 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. Abscending, 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 1 to 3 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 swarms 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 swarm from 6 to 12 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). Generally, continued swarm production by Africanized bees is apparently dependent primarily 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 (Fig. 4). Long before any flowering, and often in mid-winter, colonies begin expanding their brood nests in response to photoperiod cues (Aitavale 1978, Kefuss 1978, Morse 1975). 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

European Honey-Bee Brood Rearing in Connecticut
(A. Avitabile., 1978 J.A.R.)

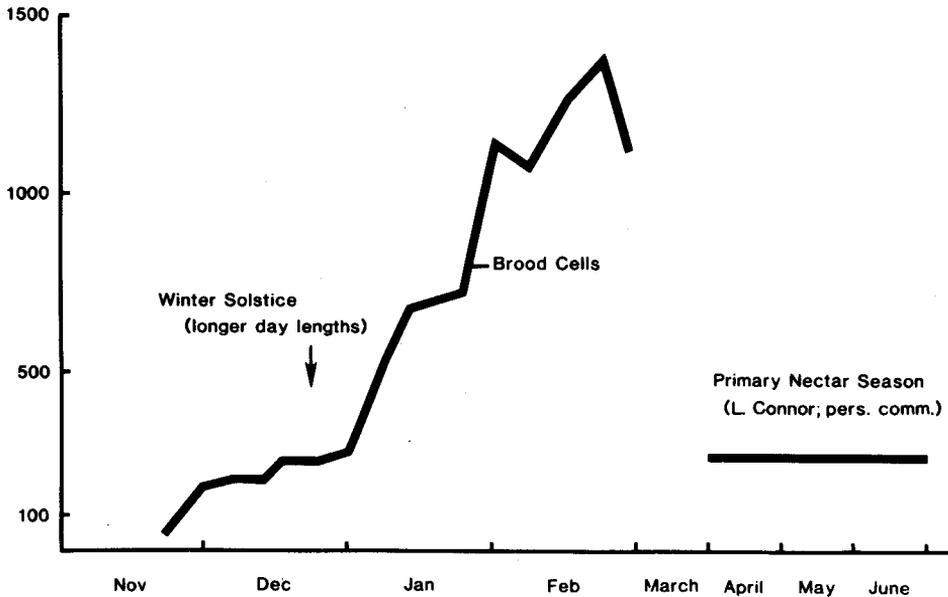


Fig. 4 — An example of the colony population growth patterns of European bees in which photoperiod cues stimulate growth long before the onset of resource availability.

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 (Pesante 1985, Winston *et al.* 1981, Otis 1982). Africanized bees develop large colony populations in remarkably short periods. Interestingly, they do so only in response to the immediate existence of harvestable resources (Fig. 5), and during harvests show a marked preference for pollen in comparison with European bees (Pesante 1985, Danka *et al.* 1987). Development of large broodnests and the reduction of broodnests 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). In my view, 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 (Fletcher 1978, Kerr 1971, Rinderer *et al.* 1981, 1982, Seeley 1977, Seeley & Morse 1976, Smith 1953, Taber 1979) from South America, Africa, and North America suggests that in

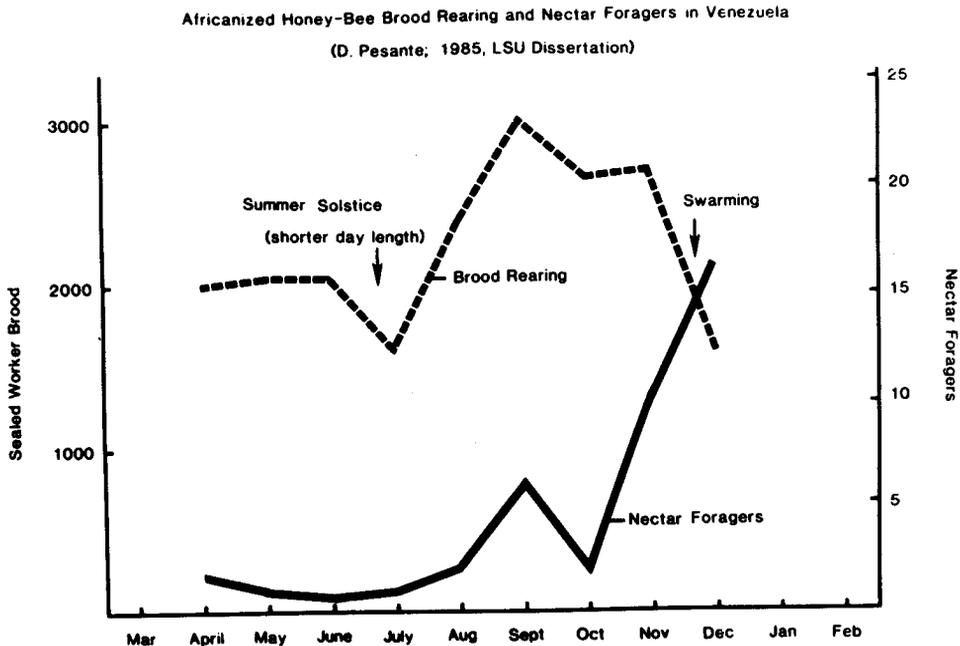


Fig. 5 — An example of the colony population growth patterns of Africanized bees in which resource availability cues development.

favorable periods, the population densities of European honey bees are far less than those of Highland or Africanized bees. However, personal experience in Africa at the end of a widespread drought, suggests to me 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 in some respect, 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 honeybee subspecies, the Highland bee is, for many characteristics, a comparative 'r-strategist' (Danka *et al.* 1987, MacArthur & Wilson 1967). 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 cause it to qualify 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 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 often show strong wet season-dry season 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) (Fig. 6).

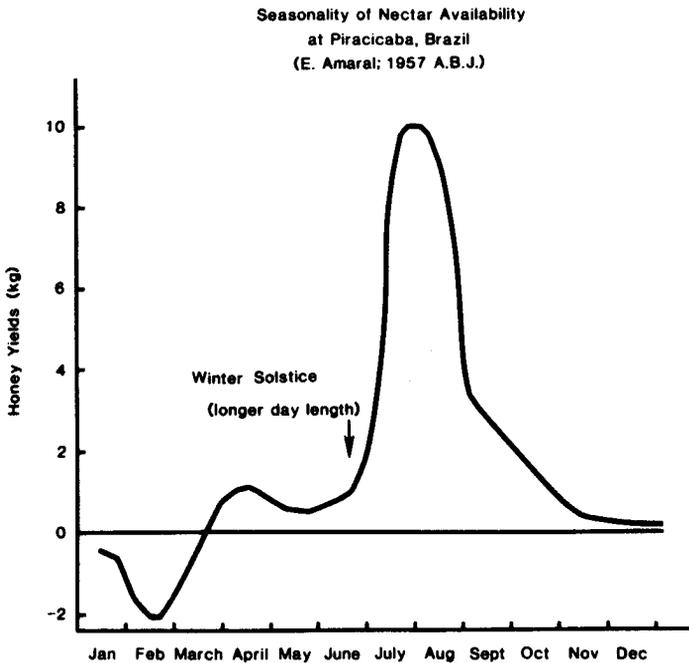


Fig. 6 — An example of South American nectar-flow rhythms.

Although this area 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 Costa Rica (Frankie *et al.* 1974) and near the USDA Africanized Honey Bee Research Laboratory in

Acarigua, Venezuela are completely contradictory to photoperiod cues. In Venezuela, at 10°N latitude, resources become available in August or September and primarily available from November to February. Earlier, in the rainy season of April to August, European bees do so poorly that we have taken to using exclusively Africanized bees in our colonies during this period. They conserve resources well, 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, for example the Amazon Basin and the Brazilian Highlands, although ecologically strongly different from each other, are also so different from European 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 ecologies 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 seemingly 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 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. Also, Africanized bees, although they are more similar to their Highland parents, retain identifiable similarities to their European parents. Morphometrics (Bucó *et al.* 1987, Daly 1988), cuticular hydrocarbon analysis (Carlson & Bolten 1984), and isozyme analysis (Nunamaker & Wilson 1981, Sylvester 1986) all support this view. This measurable influence of European parentage in Africanized populations is probably the consequence of natural selection. Perhaps evolutionary processes are operating on American honey-bee populations in ways that are yielding novel American ecotypes of honey bees reflecting characteristics of both their European- and Highland-parental stocks.

CONCLUSION

Natural selection was invoked by Ruttner (1986) to explain the occurrence of Africanized bees in Argentina at 39°S 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 partly unanswered. In American temperate zones, do the populations of European bees which are themselves hybrid swarms (King 1968) 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 simple 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?

In my view, the possibilities exist for natural selection to produce, rather rapidly, new ecotypes of honey bees in the Americas. The ecologies of temperate, as well as of tropical, America are rich and varied. In addition, the introduction of Highland bees and the spread of their Africanized progeny probably represents an infusion of additional genetic variation. The operation of natural selection on this expanded genetic variation in the varied American biomes will clearly provide us with expanded research opportunities and many future surprises.

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