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## FORAGING BEHAVIOR AND HONEY PRODUCTION

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The indigenous honey bee of the East African dry savanna, *Apis mellifera scutellata* (Ruttner, 1986), was recommended by Smith (1953) as the bee of choice for importation to the tropics of India or the Far East. Although he recognized the "bad tempered" nature of the bee, he considered it to be improvable through selective breeding and "the best of all the honey producers in the tropics." Three years after Smith's evaluation of the Eastern African subspecies appeared, 63 living *A. m. scutellata* queens arrived in a shipment of 133 queens sent to Brazil from primarily South Africa (Kerr, 1957). Forty of these queens survived introduction procedures and produced colonies; 26 of which were considered to be "exceptionally prolific, productive and vigorous" (Kerr, 1957). Breeding plans for these colonies were interrupted when an accident enabled 26 colonies to abscond into a Eucalyptus forest (Kerr, 1967; Gonçalves, 1975).

The intention of this breeding program was to crossbreed the African stock with Italian (*A. m. ligustica*) stock. The crossbred colonies were to serve as a base population in a selection program designed to produce a stock which was both gentle and excellent in honey production (Kerr, 1957). The chief genetic source of productivity was to be the group of imported African queens. *A. m. scutellata* colonies were considered to be "very prolific, better than the Italian in honey production, colony development, and adaptability to climatic conditions, flora and places where colonies are established" (Kerr and Portugal-Araújo, 1958). In part, honey production was thought to be due to the lengths of times in which African bees foraged since "they start work earlier and finish later than

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Italians and black bees, sometimes before sunrise and up to some minutes before nightfall" (Kerr and Portugal-Araújo, 1958).

The view that honey bees of one subspecies invariably will store more honey than the bees of another subspecies is consistent with inaccurate but long held beliefs (or hopes) of beekeepers. Such beliefs tempt beekeepers with the thought that somewhere in the world there exists a bee stock which is vastly superior to the bees in their own apiaries.

Occasionally, action based on such beliefs has resulted in serious errors. Recently, Ukrainian beekeepers forgot that their grandfathers who settled the eastern Primor'e region of Russia near the end of the 19th century took Ukrainian *Apis mellifera* with them (the Primor'e area only had *Apis cerana*). The Ukrainian bees did well there and, due to very large honey crops secured from extensive lime forests, attained sufficient fame that the Latin trinomial *Apis mellifera acervorum* was proposed for them. In the 1960s this special "far Eastern bee" was "introduced" to Siberia, the western part of the Soviet Union and Bulgaria. These returning Ukrainian bees brought with them the parasitic *Varroa jacobsoni* and a resultant large-scale death of colonies (Alpatov, 1976).

The introduction of African bees to the Americas has had equally disruptive results. Although there are some reports from Brazil of increased honey production with Africanized bees, there are many more reports of decreased production, disrupted beekeeping practices and seriously depressed beekeeping industries. In part, these difficulties stem from the colony defense of Africanized bees (Collins *et al.*, 1982). Equally important, the expected production from Africanized bees has not been generally realized. While it is true that Brazilian honey production has increased in the past 30 years (Gonçalves, 1975) this is due to improved agricultural and apicultural practices rather than to Africanized bees (Wiese, 1977). Similar changes in a much smaller developing country with tropical and subtropical climates, Mexico, have caused that nation to increase its honey production several times more than the Brazilian increases (Labougle and Zozaya, 1986). This was accomplished without Africanized bees. Furthermore, where Africanized bees have entered countries with some degree of advanced apiculture, production has dramatically fallen (Rinderer, 1985; Cobey and Locke, 1986; Swezey, 1986).

The biological principles which underlie the disparate reports of Africanized and European honey bee honey production are rooted in the behavioral adaptations of these bees to the differing ecological characteristics of their evolutionary homes. Several behavioral differences relating to foraging and honey production by Africanized and European honey bees may be tested experimentally. How these different behavioral patterns are adaptive becomes clear when they are considered in the context of the floral environment in which they evolved.

In this chapter we will first examine a model of European honey bee foraging and supporting evidence. Using this model as a standard, we will then

examine the comparative foraging and honey production of Africanized and European honey bees. Finally, we will offer an ecologically based interpretation accounting for the differences and provide a model of Africanized honey bee foraging.

## EUROPEAN HONEY BEE FORAGING AND HONEY PRODUCTION

Foraging by European honey bees is highly responsive to seasonally related nectar flow conditions. Von Frisch (1967) experienced difficulties training bees to artificial feeding stations in spring but not in autumn. He attributed these training difficulties to competition from "abundant flowering and a good supply of food." The responses he saw were the result of an elegant regulating system which guides bees to the most productive foraging possible in the various seasons of the year.

The first hint that organized seasonal regulation of foraging occurs in a honey bee colony came from a project in which bees were being bred for increased honey production. Since production records of field colonies contain a substantial environmental variance component, the project involved selecting colonies for breeding based on the performance of a small group of bees from each colony in laboratory cages (FIGURE 1) (Kulinčević *et al.*, 1973). These cages were usually fitted with a small piece of comb and two feeders, one containing 50% (wt/wt) sucrose in water solution and the other containing water. Bees in such cages removed the sucrose solution from its feeder and stored or "hoarded" (Kulinčević and Rothenbuhler, 1973) it in the comb provided. To verify that the differences in the amount of comb in the cages were not a source of experimental variation, cages were fitted with one, two, or three pieces of comb having 47, 94 and 140 sq cm of exposed surface area. Surprisingly, cages with one, two and three pieces of comb had bees hoarding, respectively, 0.11, 0.14 and 0.19 ml of solution/bee/day (FIGURE 2A) (Rinderer and Baxter, 1978). A later experiment showed that increasing the amount of comb up to 280 cm<sup>2</sup> continued to increase rates of hoarding (Rinderer, 1982a).

The principles underlying these experimental designs were then applied to field colonies (Rinderer and Baxter, 1978). Of 20 equal-size field colonies in an apiary experiencing the season's major nectar flow, ten were given empty honey storage combs having 4.06 m<sup>2</sup> of comb surface area (CSA) and ten were given combs having 1.88 m<sup>2</sup> of CSA. After 15 days the colonies with more comb had stored an average of 51 kg of honey and nectar while the colonies that had less comb had stored a smaller average of 36 kg. The storage combs were removed and the colonies were then transported to a new location having an intense nectar flow. There, the CSA treatments were reversed using fresh storage combs: those colonies that had previously received 1.88 m<sup>2</sup> of CSA were given 4.06 m<sup>2</sup> and those that had previously been given 4.06 m<sup>2</sup> were given 1.88 m<sup>2</sup> of CSA. After ten days, the colonies with more CSA had stored an average of



FIGURE 1. A laboratory hoarding cage.

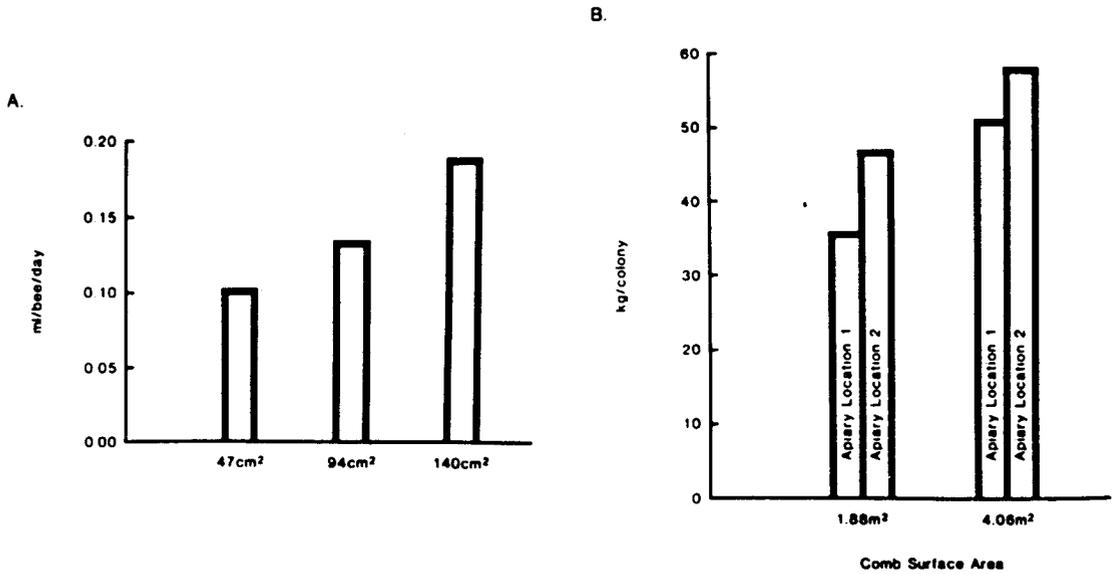


FIGURE 2. (A) Hoarding (ml) of sugar syrup by bees in hoarding cages supplied with three amounts of comb surface area. (B) Honey yields (kg) of colonies in two different apiary locations supplied with two amounts of comb surface area. (From data of Rinderer and Baxter, 1978. Copyright in public domain.)

58 kg of honey and nectar while those with less comb had stored an average of 47 kg. In no case was a colony allowed to fill completely all its storage combs before the experiment ended. Thus, the results of the laboratory experiment were supported by the experiment using field colonies (FIGURE 2B). At least under strong nectar flow conditions, large amounts of CSA resulted in increased nectar gathering by bees and consequently greater honey production.

To test the comb stimulation hypothesis further, an experiment was conducted which was based on the hypothesis that if empty comb does stimulate hoarding behavior, then bees transferred from one level of empty CSA to another would show predictable changes in their hoarding behavior (Rinderer and Baxter, 1979). Bees transferred to greater CSA should increase their hoarding while bees transferred to lesser CSA should decrease their hoarding. In order to accomplish such transfers, bees were first caged for three days with either one piece (47 cm<sup>2</sup>) or three pieces (140 cm<sup>2</sup>) of empty comb. The bees were then transferred to new cages: from cages with three combs to cages with three combs (3-3), from three combs to one comb (3-1) from one comb to three combs (1-3), and from one comb to one comb (1-1). The experiment continued for the following four days.

Before transfer, the bees with three pieces of comb hoarded more sucrose solution than those with one piece (1 piece, mean  $\pm$  SEM = 5.58  $\pm$  0.09; 3 pieces, 7.25  $\pm$  0.11;  $P < 0.01$ ). After transfer, the bees in treatment group 1-3 hoarded 15.0  $\pm$  0.5 ml; more than any other treatment group ( $P < 0.05$ ). Bees in group 3-3 continued a relatively high rate of hoarding (11.7  $\pm$  0.56 ml). The hoarding of group 3-3 was numerically but not statistically higher than that of bees in group 3-1 (9.7  $\pm$  0.45 ml) and it was significantly higher ( $P < 0.05$ ) than that of group 1-1 bees (8.8  $\pm$  0.34 ml). Group 3-1 bees hoarded numerically but not significantly more than group 1-1 bees.

These results were consistent with the comb stimulation hypothesis. The data collected before bees were transferred were similar to comparative data from other experiments: bees with more comb hoarded more sucrose solution or stored more honey. Most importantly, as predicted, the transfer of bees to greater or lesser amounts of comb resulted in a raising or lowering of the hoarding rate.

An unexpected aspect of the results was the suggestion that past experience with comb amounts affects the bees hoarding rate. Bees in group 3-1 tended to hoard more than bees in group 1-1. This indicated that the change to a less intense response, although reasonably rapid, was not immediate. Also, those bees in group 1-3 hoarded more than the comparable controls in group 3-3. This indicated that bees are additionally stimulated by large amounts of empty comb after limited exposure to empty comb.

One of the simplest explanations of these results is that the internal chemistry of bees responds to some type of stimulation from comb. Possibly, the relative abundance of some physiological compound varies with comb availability. An abundance of precursors in the bees might be available to be

changed to a super-normal abundance of a regulating compound in situations similar to those of the 1-3 treatment group. The response of the 3-1 treatment group might be the result of a time lag required for the reduction in the titer of a regulating compound in the haemolymph or nervous system. Explorations of the neurochemistry of bees under various levels of comb stimulation may reveal compounds which are responsible for regulating the intensity of hoarding, foraging, and honey production.

Regardless of precisely how stimulation by comb is internally translated by bees and transformed into the behavioral result of more intensive foraging, the effect of comb on bees is itself known to be mediated chemically. This conclusion was suggested when bees in hoarding cages were only occasionally observed on comb not being used for immediate storage. Seemingly, additional comb had its effect even though bees only infrequently came into direct contact with it.

This hypothesis of chemical stimulation was tested with modified hoarding cages (Rinderer, 1981). The modifications permitted air to be pumped first through a 2 l plexiglass box filled with an experimental material and then into hoarding cages just above the comb. Three experiments were then used to evaluate the effects on hoarding of volatiles from empty comb held at 35°C (the temperature of a colony's brood area) from empty comb held at 5°C and from comb filled with stored honey at 35°C.

Only the volatiles from the warm empty comb increased hoarding rates. Thus, volatiles from empty comb at a temperature similar to that occurring in the brood area of bee nests increased the hoarding of bees. These volatiles were not given off in effective amounts by cold empty comb or warm comb that contained stored honey.

Probably, these volatiles are pheromones incorporated into comb by bees as it is built, repaired and maintained. In an experiment comparing new, light colored comb and older comb which had been used several times for brood rearing, both types of comb increased hoarding to similar levels (Rinderer and Baxter, 1980). Since the stimulatory mechanism of comb is volatile chemicals, the continued ability of older comb to induce increased hoarding likely results from the renewal of its stimulatory properties. Probably, renewal occurs as the bees clean and repair comb.

The performance of bees in hoarding cages is a good, although not a complete, predictor of the foraging and honey storage of bees in the field. Genetic differences between various stocks of bees identified in hoarding experiments were similar to differences discovered in field trials in some but not all cases (Kulincevic and Rothenbuhler, 1973; Kulincevic *et al.*, 1974). Also, hoarding experiments with comb impregnated with 2-heptanone showed that this chemical strongly increased the intensity of hoarding (Rinderer, 1982c). Yet, a similar field trial failed to result in differences between treated and untreated colonies.

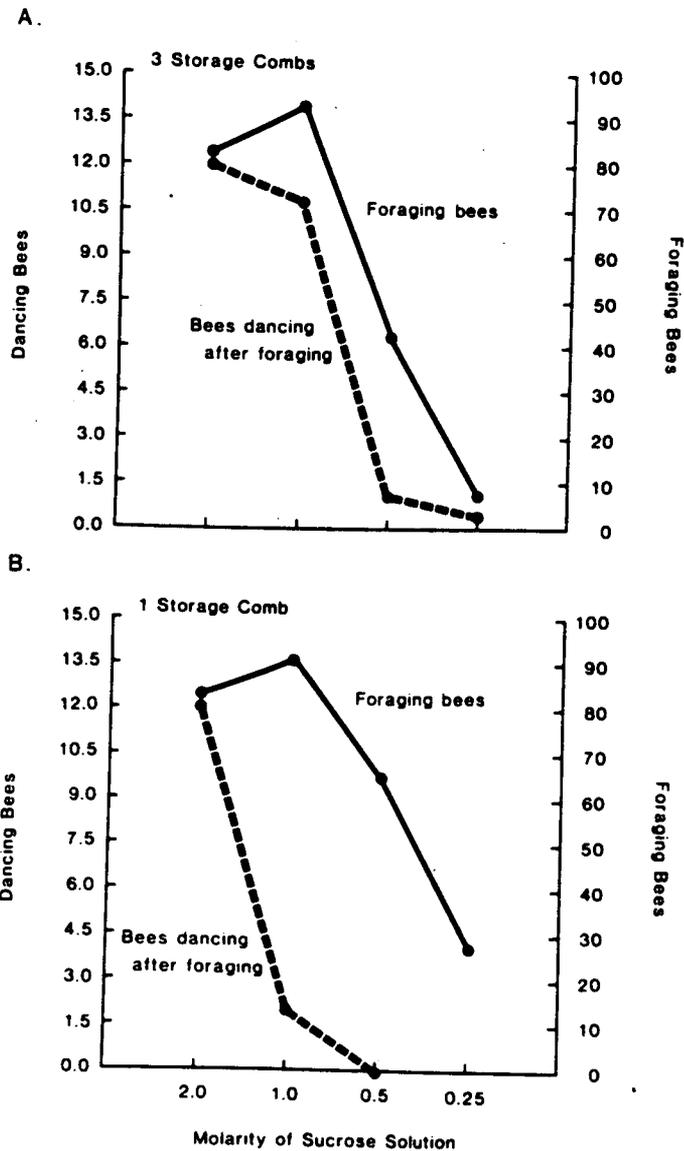
While some effects that were apparent in laboratory experiments were less apparent in field experiments, the opposite was true in experiments using empty comb as a treatment variable. Often the differences found were greater in field experiments. For example, observation hives having three times as much empty comb as control hives stored almost ten times as much honey (Rinderer, 1982b). During this experiment, the recruitment dancing in the colonies reflected the differential honey storage. In colonies with more comb, more bees danced, the dances had greater average durations, and more recruit bees followed individual dances. Consequently, the combined effects of these variables resulted in a two-fold increase in the rate of recruitment.

Further insight into the nature of the influence of additional comb on recruitment dancing was provided by an experiment in which bees were trained to a feeding station (FIGURE 3) (Rinderer, 1982b). Only marked bees which had previously been trained to the feeding stations were permitted to forage at them during the experiment. The experiment using a descending sequence of sucrose solutions (2.0 M, 1.0 M, 0.5 M and 0.25 M) simultaneously at separate feeding stations for observation colonies given one or three empty storage combs.

The data from the experiment were the numbers of bees foraging at the feeding stations and the numbers of bees doing recruitment dances after foraging during equal time periods for each hive type (CSA treatment) and each sucrose concentration. Bees from the two hive types behaved quite differently. Comparatively, bees from hives having three storage combs foraged in significantly reduced numbers at the station when it contained less concentrated food. Yet, if they foraged at all, they had a significantly higher likelihood of doing recruitment dances after collecting sucrose concentrations below 2.0 M. Thus, the stimulation from additional empty comb increased the selectivity of the bees' food choice and also increased their tendency toward recruitment dances and group foraging. Bees that were stimulated by lesser amounts of comb were less selective in food choice, less likely to dance, and more likely to engage in individual foraging; that is, they tended toward gleaning.

Further support for the observation that additional CSA stimulated increased recruitment was supplied by Rinderer and Hagstad (1984). They found, when studying the foragers of field colonies, that increased amounts of CSA resulted in an increase in the proportion of nectar foragers, a decrease in the proportion of pollen foragers and a decrease in the proportion of foragers simultaneously collecting nectar and pollen.

The usefulness of these two contrasting foraging strategies varies through the nectar flow season (Rinderer, 1982b). Honey storage strongly stimulated by empty comb is enhanced during the main nectar secretion period. However, strong stimulation by empty comb impairs honey storage during the poorer quality nectar secretion periods of autumn (FIGURE 4). In such conditions, lesser stimulated bees which forage as individual gleaning bees are more successful. These two foraging strategies, or at least the honey storage pattern



**FIGURE 3.** Numbers of bees which foraged from observation hives having (A) three storage combs or (B) one storage comb, and numbers of bees which danced after foraging on four concentrations of sucrose solution presented at a feeding station in a sequence of descending concentration. (From data of Rinderer, 1982b. Copyright in public domain)

they produce, can derive from conditions other than differential stimulation by empty comb. A curious, previously unpublished result of the experiment shown in FIGURE 4 was a change in the order of colonies when ranked according to the average calories collected by individual foragers (FIGURE 5). These values were estimated for each of six colonies in each of two apiaries throughout the season (levels of CSA were maintained experimentally throughout the season). Initially, in May and June, the ranking of colonies was identical from week to

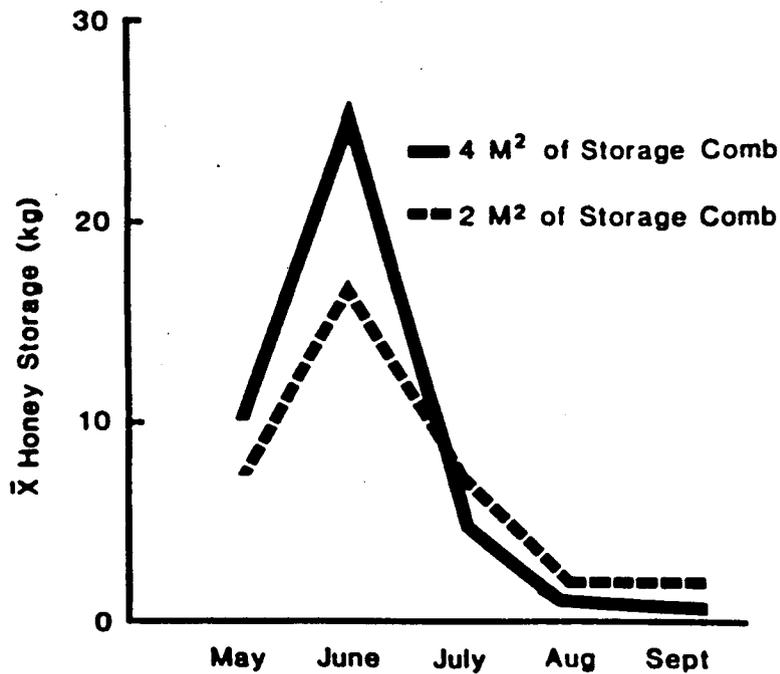


FIGURE 4. Average monthly weight of honey (kg) stored by six colonies with 4 m<sup>2</sup> of storage comb and six colonies with 2 m<sup>2</sup> of storage comb. The colonies were equally divided between two apiaries. (From Rinderer, 1982b. Copyright in public domain.)

CALORIES	JUNE				JULY				AUGUST			
	1	2	3	4	1	2	3	4	1	2	3	4
Most	1	1	1	1	1	1	6	6	6	6	6	6
	2	2	2	2	2	6	1	5	5	5	5	5
	3	3	3	3	6	2	2	1	1	4	4	4
	4	4	4	6	3	3	5	2	4	1	3	3
	5	5	5	5	5	5	4	4	2	3	1	2
Least	6	6	6	4	4	4	3	3	3	2	2	1
Week	1	2	3	4	1	2	3	4	1	2	3	4

FIGURE 5. The seasonal change in ranking, based on the average calories collected by individual foragers from colonies with 4 m<sup>2</sup> of CSA (colonies 1, 2, and 3) and from colonies with 2 m<sup>2</sup> of CSA (colonies 4, 5, and 6). These trends were consistent for the colonies in both apiaries that provided the honey yield data presented in FIGURE 4.

week. The three colonies in each apiary having more CSA had nectar foragers collecting more calories as a group and their rankings were consistent. The three colonies in each apiary having less CSA had nectar foragers collecting fewer calories as a group and their rankings were consistent. As the season progressed, the rankings changed. The ranking of the colonies initially collecting the fewest calories progressively moved higher. At the end of the season, the initial rankings were completely reversed. This phenomenon occurred in identical fashion among the colonies in both apiaries. This remarkable consistency, as well as the inversion of ranks as the season changed, suggested that some stable (probably genetic) component of the individual colonies determined the magnitude of the behavioral response to CSA.

An additional experiment also suggested the involvement of genetic factors. Monthly hive weight records in an apiary of from four to eight colonies given uniform management were recorded by Oertel *et al.* (1980). An analysis of these records permitted an evaluation of the possible influences on honey storage patterns of genetic or very local, stable differences in environment, such as exposure to sunlight (Rinderer, 1982b). From the records of each year, we identified those colonies that stored the most and the least amount of honey during the month in which the apiary stored the most honey. Data on honey storage by this pair of colonies in the first and last months with a nectar flow were then identified. The colonies that stored the least honey during the major nectar flow consistently stored the most during both the early and the later minor flows (FIGURE 6). These patterns of honey storage support the hypothesis that more intense nectar harvesting and selection of primarily highly rewarding nectar sources result in more honey storage during major nectar flows, while less intense harvesting and selection of lower quality nectar sources, i.e. gleaning, result in greater storage during minor flows.

These data were not collected in a way that permitted an unambiguous identification of the source of intercolony variation. Potential genetic sources were confounded with possible, although less likely, environmental sources. Nonetheless, the genetical hypothesis is intriguing, since it would explain why different stocks of bees give different comparative honey yields in different areas. Genetical differences may cause bees to be more or less responsive to stimulation from empty comb and thereby increase the tendency of bees to be either group foragers or individual gleaning foragers. Such genetical variation would permit both artificial and natural processes to select bees best suited to the usual nectar availability of their environment.

## THE ANNUAL CYCLE OF REGULATION OF EUROPEAN HONEY BEE FORAGING

Predictable, seasonal trends in nectar production commonly occur in temperate climates (Crane, 1975; Oertel *et al.*, 1980). In many areas, early

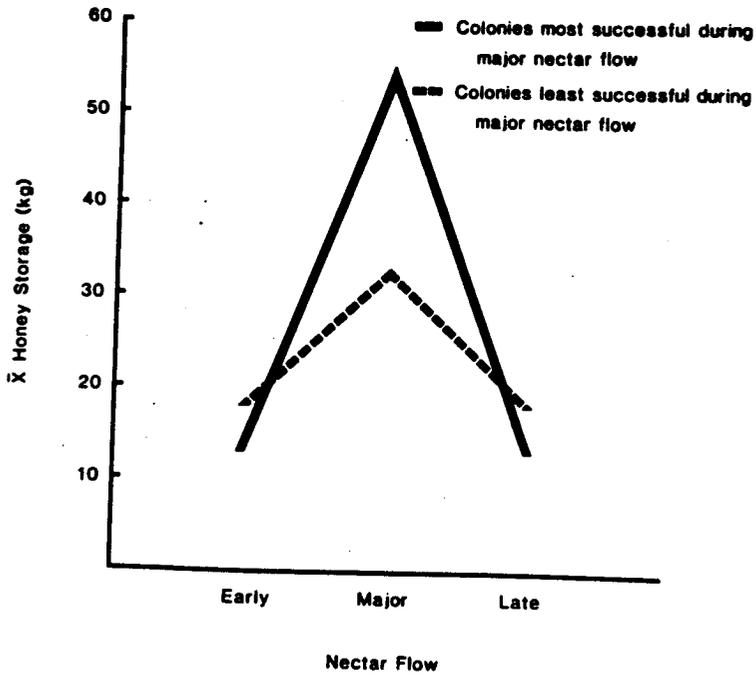


FIGURE 6. Average seasonal weight of honey (kg) stored by colonies with the most and least honey during the major nectar flow during 25 years. (From Rinderer, 1982b. Copyright in public domain.)

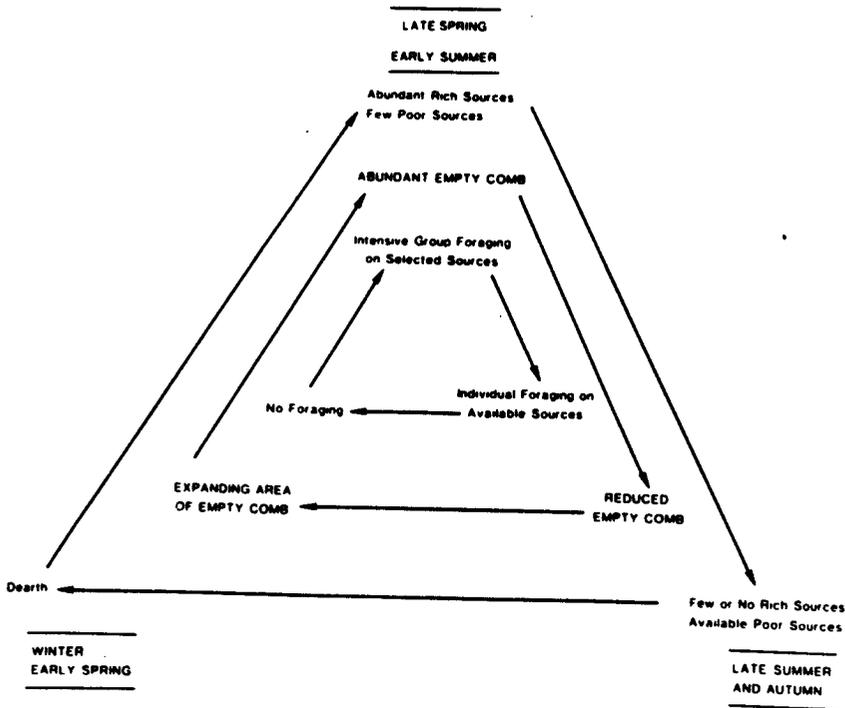


FIGURE 7. A model of the seasonal regulation through the influence of empty comb of European honey bee nectar harvesting and honey production in a temperate climate.

spring nectar sources tend to be both few and poor. This situation changes rapidly, and by late spring to early summer, nectar sources tend to be both varied and rich. A decline in variety and abundance follows, until by late summer, only a few poor quality nectar sources usually exist (FIGURE 7).

These seasonal changes in the quality and quantity of nectar availability are paralleled by the amount of empty storage comb in a feral honey bee nest (FIGURE 7). 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. Consequently, empty comb becomes increasingly less available as the season progresses.

The foraging of honey bees also fluctuates in ways that are most appropriate to the predictable nectar flow conditions of the season (FIGURE 7). The collection of experiments using hoarding cages, observation hives, and field colonies demonstrate that the varying amounts of volatiles emanating from varying amounts of empty comb regulate the fluctuating characteristics of foraging. The chief feature that demonstrates this is that comb stimulation which is usual to a season causes bees to behave as though they were experiencing that season regardless of the season in which the experiment was conducted. In conditions of greater stimulation by comb volatiles, bees tend to be more selective of nectar sources and through the use of increased levels of dance communication exploit quality sources intensively. In conditions of less stimulation by comb volatiles, bees tend to be less selective of nectar sources and less likely to perform recruitment dances for all but the highest quality sources. These conditions hold true, regardless of nectar flow conditions.

The value of comb volatiles as a regulator of foraging resides in its common influence on all the bees in a colony engaged in nectar collection and storage. Scout bees have differing experiences in the field. Thus, the overall nectar flow conditions cannot serve to guide recruitment to only the best nectar sources. Scouts with incomplete experience would dance for the best sources they found as intensively as other scouts would dance for the best available sources. In the same way, the receptivity of house bees to accept nectar loads is insufficient for overall regulation. Bees receiving nectar in the hive also have a limited experience with incoming nectar loads.

Certainly, there are adjustments in foraging and dancing depending upon nectar availability and variety, house-bee receptivity and a host of other extrinsic factors (von Frisch, 1967). Stimulation by empty comb establishes the thresholds for foraging and dancing and probably also house bee receptivity to incoming nectar loads and thereby provides a common reference for the fine-scale adjustment of foraging and communication which is best suited to the colony's needs.

Usually, comb regulation and secondary adjustment of foraging and communication lead to nectar harvesting behavior which is best suited to varying seasonal conditions. In unusual conditions, levels of comb stimulation might be superficially considered inappropriate to nectar flow conditions. A colony with storage combs filled with honey part-way through an unusually strong and prolonged nectar flow might be thought to have a lower nectar harvesting intensity than appropriate. This situation would only serve to increase the number and the probability of the survival of swarms issued by the colony. The parent colony would not suffer a disadvantage, since colonies establish themselves in selected cavity volumes (Seeley and Morse, 1976; Seeley, 1977) that are presumably large enough to hold food reserves capable of supporting the survival of the colony through the season of dearth. Adversity (unusual weather, disease, or predation) may result in a colony having large amounts of empty comb (and low food reserves) at a time before or after the main nectar flow period. Such a colony would be in danger of starvation, and a highly intensive nectar harvesting (and exploitation of only high quality nectar sources) is not inappropriate. Maximal foraging on poor quality nectar sources may not provide sufficient food reserves for survival. However, finding a good quality nectar source (perhaps the honey reserves of a nearby colony), and exploiting it intensely would have a greater chance of ensuring the colony's survival than foraging on poor quality nectar sources.

### **Comparative Nectar Harvesting of European and Africanized Bees**

The experimental pathway to understanding the comparative foraging and honey production of Africanized and European bees rested in comparing representatives of the two groups of bees across varying conditions of forage availability and foraging stimulation. A preliminary experiment compared hoarding by the two groups with standard amounts of comb and comb impregnated with 2-heptanone (Rinderer *et al.*, 1982), since 2-heptanone increased the hoarding rates of European bees (Rinderer, 1982c). Africanized bees hoarded less sucrose regardless of the treatment. The increase in hoarding rate induced by 2-heptanone in Africanized bees was about half the increase in hoarding rate induced in European bees.

These results did not support the conclusion that Africanized bees are superior honey producers in all cases (Kerr, 1967, Kerr *et al.*, 1972; Gonçalves, 1975) since for European bees high hoarding rates correlate well with honey production (Kulinčević and Rothenbuhler, 1973; Kulinčević *et al.*, 1974; Rinderer and Baxter, 1979; Rothenbuhler *et al.*, 1979).

A second, more detailed hoarding experiment (Rinderer *et al.*, 1986) compared Africanized and European honey bee hoarding when the amounts of empty comb were varied. The experiment was modeled after one which showed that for European bees, additional empty comb increased both hoarding intensity

and hoarding efficiency (Rinderer, 1983). Bees in the hoarding cages had access to three identical gravity feeders containing either 20% (wt/wt) sucrose in water solution, 50% sucrose solution or water only. This experimental design, giving bees simultaneous access to different sucrose solutions, permitted estimates of hoarding efficiency. These estimates of reward per unit of work were calculated as total grams of sugar hoarded divided by total grams of solution hoarded, and could range from 0.2 (only 20% solution was hoarded) to 0.5 (only 50% solution was hoarded). Portions of efficiency estimates derived from the hoarding of the 20% solution probably inflate the overall efficiency estimate somewhat, since bees tend to take smaller loads of lower quality food (von Frisch, 1967). This method assumed equal-sized loads. Thus any differences in efficiency were likely to be more extreme than those calculated by this method.

In the comparison of Africanized and European bees, both types of bees increased both their hoarding intensities and their hoarding efficiencies. However, European bees hoarded more with greater efficiency; again suggesting that it might not be valid to extrapolate the observations of superior honey production by Africanized bees to all conditions.

Field experiments that took advantage of various nectar flow conditions indicated that the two types of honey bees respond differently to different nectar flow conditions. In an experiment comparing responses to daily fluctuations in nectar flow conditions (Rinderer *et al.*, 1984), the relative energy content of the nectar loads collected by the two geographical types varied. An important source of this variation was in the volume of nectar collected. Also, European bees generally were more successful in securing a nectar load but their percentage of successful foragers tended to be either high or low. Africanized bees returned more often to their nest without a nectar load but had intermediate as well as high and low percentages of successful foragers. Overall, European colonies had greater number of forages throughout the study.

These differences suggest underlying differences in the use of recruitment and group foraging by the two bee types. Presumably, bees that use increased levels of communication and recruitment and thereby improve their foraging success would be similar to the European bees in this study. Bees with strong tendencies toward group foraging (Johnson and Hubbell, 1975) and that are highly dependent upon communication and recruitment should have either very high or low forager success rates. High rates would occur when there is recruitment and low rates would occur when scouts find only nectar sources lacking sufficient value to stimulate recruitment. Bees showing more reliance on individual foraging would likely have a lower rate of success (mid-range) in conditions favoring group foragers, especially if these sources were scattered and difficult to find. Overall, the result of this experiment suggested that Africanized bees are adapted to nectar resource conditions that are, in most cases, best exploited by gleaning foragers which do not rely strongly on communication. The contrast in the results suggested that European bees are better adapted to

conditions that are best exploited by group foraging which is stimulated by dance communication.

An additional experiment confirmed these conclusions (Rinderer *et al.*, 1985). Comparisons of Africanized and European honey bees were made during two periods of nectar availability. The first period provided relatively intense nectar availability. The dominant nectar secreting plants were widely scattered araguaney trees (*Tabebuia sp.*) Secretion by these scattered trees, primarily at night, provided a rich but patchy source of nectar in the first hours of the morning. In the second nectar flow period, nectar availability was relatively weak. The araguaney trees had nearly finished flowering and they were replaced as a dominant nectar source by fence-row plantings of mataraton trees (*Gliricidia sepium*). These legumes produced nectar primarily during the day until mid-to-late afternoon. Hence, in the second nectar flow period there were many more flowers for a longer period each day, with each flower producing much less nectar. Field colonies were used to study honey yields, nectar-load characteristics, and flight activity including the times of flight initiation and cessation. Colonies in observation hives were used to study dance communication and recruitment of foragers.

The principal theme of the results was that bee-type interacted with nectar flow. This was illustrated by the honey production records (FIGURE 8A). In period 1, European bees clearly produced more honey. In period 2, Africanized bees produced numerically more honey. However, the large variance associated with the honey production of the Africanized bees prevented a determination of whether the Africanized bees produced more or the same amount of honey as European bees. Certainly, they did not produce less. These general trends of interaction appeared in nectar load characteristics of volume, concentration and energy content, and in the daily flight patterns of foraging bees.

The patterns of dance recruitment were especially instructive (FIGURE 8B). These too interacted with nectar flow periods. Similar patterns to those of honey production occurred for the numbers of nectar foragers initiating dancing in a five minute period, the numbers of recruit bees following individual dancing bees, and the duration of individual dances. The product of the first two of these values provided an estimate of the rate of recruitment. During the first nectar flow, European bees recruited much more intensively than did Africanized bees. During the second nectar flow, both types showed reduced recruitment; the European bee reduction in recruitment rate was quite strong and recruitment rates of the two bee types were similar. These results strongly support the hypothesis that the fundamental nectar foraging difference between Africanized and European bees is that Africanized bees are adapted to conditions where an individual gleaning type of foraging is more successful whereas European bees are adapted to conditions where intensive foraging reliant on dance communication is more successful.

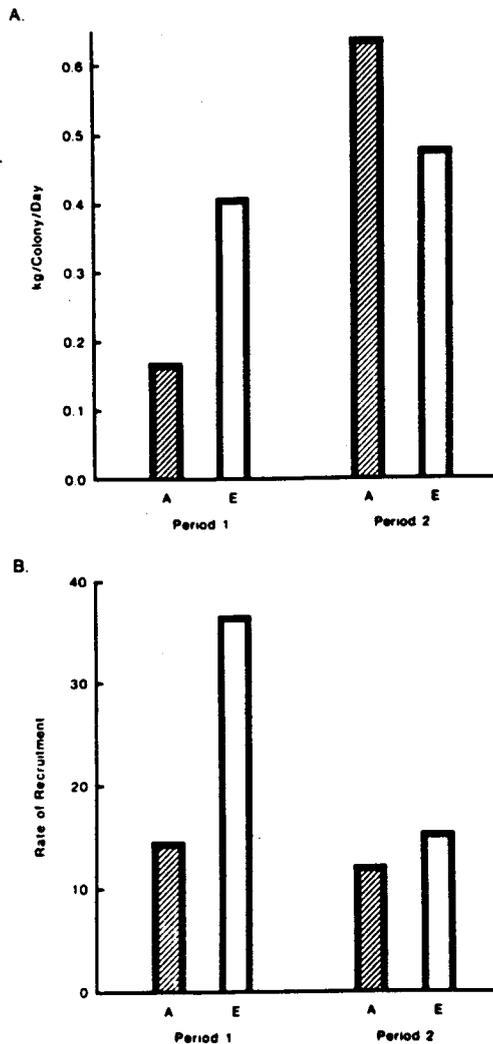


FIGURE 8. (a) Average honey production of ten European (E) and ten Africanized (A) full-sized honey bee colonies during two different nectar flow periods. (b) Average rate of recruitment (numbers of recruited bees/5 minutes) for five Africanized (A) and five European (E) honey bee observation hive colonies during the same two nectar flow periods. (Data from Rinderer *et al.*, 1985. Copyright in public domain.)

Additionally, on each of six days (three for each nectar period) both Africanized and European bees from every colony in the experiment began flying in large numbers before sunrise when illumination measured at colony entrances was 1 lx. The last bees returned to both Africanized and European colonies shortly after sunset when measured illumination was ca. 5 lx. The strict uniformity of flight initiation and cessation of Africanized and European bees in both nectar flow periods strongly suggests that there are no fundamentally important differences in these aspects of foraging behavior. Reported differences (Kerr *et al.*, 1972; Fletcher, 1978) apparently are not sufficiently ubiquitous to

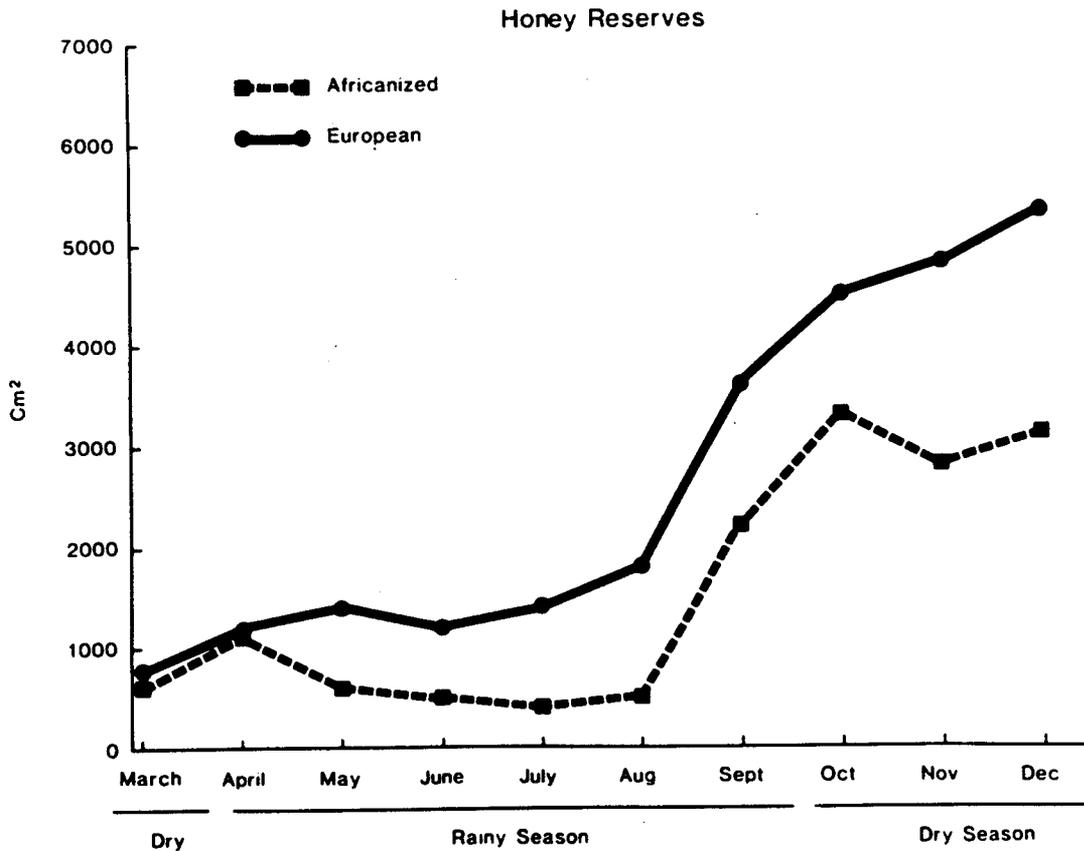


FIGURE 9. The average seasonal accumulation of honey resources by 40 colonies each of Africanized and European honey bees divided equally into two apiaries. (From Pesante, 1985, with permission. Copyright, 1985, by D. Pesante.)

incorporate them into a general model of comparative nectar foraging and honey production.

The results of these shorter term studies were confirmed and extended in a study lasting ten months (Pesante, 1985). He also concluded that "Africanized colonies had lower colony and honey weight gains than European colonies under favorable nectar flow conditions and higher colony honey weight gains than European colonies under poor nectar flow conditions." Across the duration of the study, European bees collected and stored comparatively increasingly greater amounts of honey reserves (FIGURE 9) (Pesante *et al.*, 1987).

Danka *et al.* (1986) studied in detail the apparently greater numbers of foragers from European colonies (Rinderer *et al.*, 1984, 1985). They confirmed the observation and found that the difference was consistent for different sizes of colonies and different nectar flow periods.

Pesante (1985) and then Danka *et al.* (1987) studied the comparative diet selection of Africanized and European bees. Although European colonies had greater overall numbers of foragers, Africanized colonies had greater numbers and higher percentages of pollen foragers throughout the day (FIGURE 10).

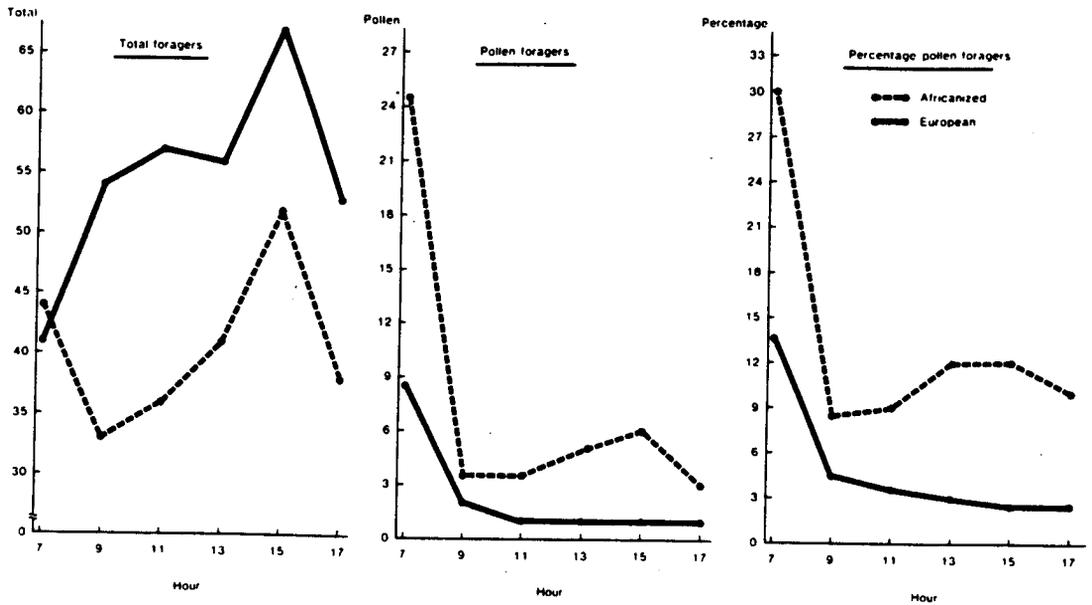


FIGURE 10. Average daily foraging patterns and the proportion of pollen foragers of twelve colonies each of Africanized and European honey bee colonies. (From Danka *et al.*, 1987. Copyright in public domain.)

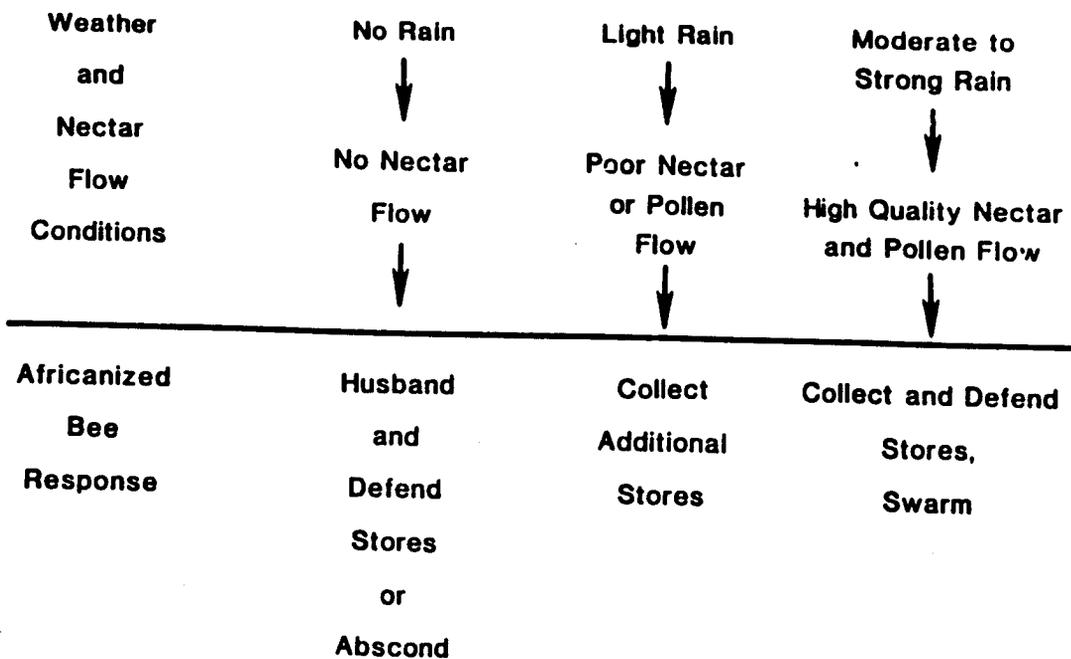


FIGURE 11. A model of the resource dependent nectar harvesting and honey production of Africanized bees. Compare with FIGURE 7.

Africanized pollen foraging resulted in larger stores of pollen in Africanized bee nests in the same experiments in which European nests had larger honey and nectar caches. Additionally, Pesante (1985) found that Africanized bees maintained larger brood nests in conjunction with maintaining larger pollen reserves and smaller honey reserves.

## AFRICANIZED HONEY BEE FORAGING

The differences between Africanized and European honey bee foraging are rooted in the ecological differences in their home range. The chief ecological determinant of foraging in the home range of the parental subspecies of Africanized bees, *A. m. scutellata*, is rainfall. Trewartha (1981) describes a large number of interacting climatic factors which result in "rainfall [which is] modest in amount" and "highly unreliable as well." This unreliability includes amounts, locations and seasonality. Since flowering and nectar flows are dependent upon these unreliable rains, they are also unreliable. "Annual" nectar flows may not occur in specific localities and sometimes in large regions. Where nectar flows do occur they may be quite weak because only light rains have fallen. When they occur, the "annual" onset of nectar flows may vary by as much as two to three months; as does the onset of the "annual" rains.

These three conditions contributing to extreme nectar flow variability have probably been principle selective forces in the evolution of bees in the area. In any event, the behavior of Africanized bees suggests this since their nectar foraging and other aspects of their natural history are well suited to such conditions. Comparative studies (*loc. cit.*) indicate that these bees will tend to forage as gleaners, that is, as individual foragers on whatever nectar is available. They lack the selectivity which would cause them not to forage on a poor flow regardless of stimulation from empty combs. In Eastern and Southern African conditions, foraging on a subsistence flow may insure survival as the onset of a subsequent nectar flow is at least possible.

Brood nest expansion and subsequent swarming by Africanized bees are triggered by nectar and pollen flows (Pesante, 1985), a clear response to flows starting at unpredictable times. Generally, Africanized bees lack significant brood nest expansion prior to the occurrence of nectar and pollen resources. In contrast, European bees begin their annual population growth as early as late December or January, probably using photoperiod as a cue (Kefuss, 1978).

When quality floral resources exist, Africanized bees place more nearly equal energies into the storage of nutritional resources and swarming. Their more intensive pollen foraging (Pesante, 1985; Danka *et al.*, 1987) leads to a reduced potential for honey storage but an increased potential for swarming. Apparently, Africanized bees will continue to swarm at frequent intervals as long as forage is available to support brood rearing (Otis, 1977).

Thus, our model of Africanized honey bee foraging stresses a far greater unreliability of nectar and pollen availability (FIGURE 11). Africanized bees are essentially opportunistic. Given the opportunity of a subsistence flow, they will forage, store the resources they collect, and increase their chances of survival. Later, they will either reproduce on a better flow should it occur, or, given sufficient nutritional stress, abscond. By absconding, they may find an area with a nectar flow because it received some of the scattered unpredictable rain.

The linkage of absconding and colony defense (FIGURE 11) to resource availability helps complete an understanding of Africanized bee foraging. Absconding is a clear response to nectar and pollen flows triggered by rains which are unreliable in immediate locations. Defensive behavior in African bees and their Africanized progeny has probably been shaped by unpredictable and often poor resource availability as much or more than any other selection pressure. Certainly, Africa has a variety of organisms (the most efficient of which are undoubtably humans) which plunder and destroy honey bee nests and colonies. Such predation is essential to the adaptive value of defensive behavior. However, the natural history of bees in Europe also includes predators (humans again being chief among them). Thus, differences in predation are probably not the origin of the strong difference in levels of defensive behavior (Collins *et al.*, 1982) among African, Africanized and European bees. The more likely candidate is resource unpredictability. With predictable floral resources, the response which best contributes to fitness following minor levels of nest plundering may be to recover the losses through intensive foraging rather than to lose potential foragers through defense. Where this is less of a possibility, defensive behavior would presumably be intensified.

Some experimental evidence for this interpretation was provided by Collins and Rinderer (1985). They found that volatiles from empty comb functioned as primers for defensive behavior for both Africanized and European bees. Colonies with more CSA responded faster to moving targets and stung more often than colonies with less CSA. This experimental demonstration of a linkage between foraging and defense shows that colonies which are living in more marginal nutritional conditions are more defensive.

## CONCLUSION

The contrast drawn between Africanized bees cast as individual foragers adapted to often poor and always unpredictable resources, compared to European bees viewed as group foragers adapted to often rich and generally predictable resources, accommodates the wide variety of sometimes superficially contradictory data. It is important to emphasize that this contrast is one of degree and not kind. African bees and their Africanized progeny do have some capacity for group foraging mediated through dance recruitment. Also, their

foraging is regulated, albeit to a lesser degree, by the presence of empty comb in their nests. These characteristics are to be expected. Although keynoted by their unpredictability, the rains of southern and eastern Africa do have a seasonality. The dry season will only have very unusual rain; the wet season will have unreliable rains. European bees have some capacity for reacting to nectar flows best exploited by individual foraging and, to a lesser degree, will be stimulated by resource conditions to forage intensely and even to swarm when confronted by contradictory photoperiod cues. Forage resources in temperate zone areas, although they have greater predictability, also vary from year to year (Oertel *et al.*, 1980). Both geographical types of bees show the capacity, common to all western honey bees, of shifting their foraging from intense selective harvesting to gleaning. However, the general tendency of Africanized bees is to be more successful on the side of the foraging continuum where gleaning is more adaptive. European bees tend to be more successful on side of the continuum where intense selective harvesting is more adaptive.

Because of the interactive nature of bees with their environment, the choice of bee stock by an apiculturalist who has the opportunity to use either Africanized or European bees will vary with local conditions, at least if the economic disadvantages of Africanized bee defensive behavior are discounted. Although Africanized bees are now known to not be superior honey producers due to an extended period of daily foraging, there are conditions where their tendency to be superior gleaning bees will result in better honey yields. Alternatively, in better production areas where intensive nectar harvesting is possible, European bees are the clear commercial choice.

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