Africanized and European Colony Conditions at Different Elevations in Colombia[1]

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ABSTRACT

Africanized and European colonies were moved and tested for a month at different elevations (520, 1350, 1650 and 2450 m above sea level). In most cases, colonies of Africanized bees had a greater increase or a smaller decrease in average total colony weight, adult population, sealed and unsealed brood areas. Weekly changes in these parameters (plus honey/nectar and pollen areas) showed similar trends when measured at the highest elevation during one month. Also, a highland area (2000 to 3000 m) with colonies nesting inside artificial cavities was surveyed over a period of two years; Africanized bees colonized at a low density, while European bees did not colonize new sites even though they had been present in the area for decades. Abundance of colonies increased during months of low rainfall, and decreased during months of high rainfall. Scouting for new nest sites and absconding were observed on different occasions. Africanized colonies appeared to be more mobile than European colonies in subtropical and temperate regions.

INTRODUCTION

HUMAN INTERVENTION has placed honey bees from European temperate climates and from African tropical climates in the Americas. This continental experiment has demonstrated that European bees are capable of forming feral populations in temperate (Seeley 1978) and subtropical climates (Taber 1979), but seldom survive unmanaged in tropical lowlands. Africanized bees, in contrast, have spread through the tropics at rates up to 500 km a year (Taylor 1977). Although exceptions undoubtedly occur, African and Africanized bee colonies are smaller, reproduce more frequently and store less food (Winston et al. 1983), and are composed of smaller bees (Otis 1982, Rinderer et al. 1986), with shorter development periods (Kerr et al. 1972, Fletcher 1978), shorter lifespans (Winston & Katz 1981) and possibly higher energy expenditures during flight (Heinrich 1979) than European bee colonies. These characteristics of Africanized bees could make them less capable of surviving in tropical mountains and temperate climates than European bees. This led to the hypothesis that the performance of Africanized bees would be superior to that of European bees in the lowland tropics, similar at middle elevations and inferior at higher tropical elevations.

In one part of this study, a single group of Africanized and European colonies was moved and tested for one month at each of four different elevations in the Andes of Colombia. In a second part of this study the occupation of artificial cavities by Africanized honey bees in a gradient from 2000 to 3000 m above sea level provided the opportunity to test the hypothesis of an altitudinal barrier to the spread of Africanized bees. Also, the seasonal density of colonies could be recorded to establish the longer term relationship of seasonal conditions with reproductive swarming and absconding.

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MATERIALS AND METHODS

1. Short-term changes in colony conditions

Africanized colonies were formed from swarms or by rearing queens from feral colonies, mating them in an area of intense Africanization and introducing them to nuclei. European colonies were headed by queens introduced from Kansas or reared from a feral colony of *Apis mellifera mellifera* and mated in a plateau area before the arrival of Africanized bees. Morphometric analyses based on fore and hindwing, femur and tibia length (Daly & Balling 1978) and/or comb measurements (Rinderer et al. 1986) confirmed the origins of the locally produced queens. The nuclei and swarms were transferred to Langstroth hives with drawn comb and were allowed to strengthen to 4 to 5 frames with brood and 5 to 6 frames with adult bees.

Nine colonies of each bee type were established at 2450 m. After testing, they were then moved and tested at the other locations (520, 1350 and 1650 m, in that order). Aside from the expected differences in elevation and temperature, the sites differed in cloud cover, rainfall, degree of flowering in the vegetation and therefore availability of nectar and pollen (Table 1). Because the main focus of this short-term comparison was the balance between collection and use of resources at different temperatures, colonies were fed sugar syrup to offset scarcity of forage at some locations. It was assumed that if racial differences in colony conditions did appear they would be due to differential foraging and/or conservation of resources. At any given test site all colonies were fed equally, and they never received more than the equivalent of one kg of sugar in one week.

Before the test at each new site, the colonies were equalized by removing sealed brood frames from the strongest colonies until they matched the weakest one in the apiary (4 to 5 frames with brood and adult bees covering 5 to 6 frames). Colony weights and sealed and unsealed brood areas were measured at the beginning and end of each of the four-week test periods (a five-week period was used at 1650 m). At 2450 m changes in weight, unsealed brood, sealed brood, honey/nectar and pollen areas were measured weekly. Colonies at all sites were weighed between 6:00 and 6:30 a.m. Comb areas were measured with a grid dividing the area of a Langstroth frame into 64 rectangles, each 13.5 $cm.^2$ Adult population was estimated by observing the number of frames covered with bees. Differences between the bee types were compared using two-tailed t tests at the three highest elevations where no previous information showed superiority of either race. The comparisons at the lowland elevation were done with one-tailed t tests to test for superiority of Africanized bees in such areas.

2. Survivorship of feral African colonies at high elevations

A total of 209 concrete electric power poles were examined for occupation by honey bee colonies along 22.2 km of road traversing a slope from 2000 to 3000 m above sea level along the road from Medellín to Santa Fe, Antioquia, Colombia and the service road to the Cerro del Padre Amaya. Most poles have 10 paired holes distributed along their 12 m length which lead to a hollow cylindrical core of circa 250 lt. These artificial nests are readily occupied by single colonies of honey bees at many locations and elevations in Colombia.

The transect was visited 11 times from February 1983 to January 1985 and again in June of 1986. Visits were timed at the end of rainy seasons and of dry seasons to determine periods of minimum and maximum occupation of cavities. No direct assessment of the internal conditions of the colonies could be performed. During the first visits, samples from the 20 colonies existing at the time were collected; ten of the samples were analyzed morphometrically (Daly & Balling 1978). Local farmers were questioned about the dates of occupation of the poles, about stinging problems and about causes for destruction of colonies when there were signs of destruction by humans.

The transect was divided into four 250-m elevational classes to determine if there were altitudinal differences in occupation. The road distance and number of poles within each elevational class were calculated. The number of occupied poles per km of road distance was chosen as a measure of density. Disappearances of colonies were classified into destructions and others. Whenever the disappearance of a colony was matched with signs of fire, entrance plugging or verbal reports of human destruction the disappearance was classified as a destruction. The appearances of colonies were classified into colonizations and recolonizations. Total appearances and disappearances per month were calculated for periods between visits by dividing the changes in occupation observed since the previous visit by the time between the two visits.

RESULTS

1. Short-term changes in colony conditions

The average weekly weight of the Africanized colonies at 2450 m was never below the original average during the period of the test, whereas the average measurements for the European colonies dropped or barely matched the original state (Fig. 1). The principal explanation for these differences in weight appeared to be a greater average increase in the unsealed brood area. The decreases in average nectar/honey and pollen areas were very similar for both groups. The changes in sealed brood areas and adult population showed a greater increase during the early part of the test for the European bees, but the Africanized colonies surpassed the increases in adult population and came close to surpassing the sealed brood increases of the European colonies in the last weeks of the test period.

The monthly changes in colony condition at all sites showed higher performance of the Africanized colonies for all parameters except sealed brood at 2450 m (as stated above) and unsealed brood at 1350 m (Table 2). These two differences were small (compared to those where Africanized colonies were superior) and not statistically significant. Of the 14 comparisons where changes for Africanized colonies were greater than the changes for European colonies, nine were statistically different or suggestive of statistical difference and five were not statistically different. In those comparisons for which European colonies showed average decreases, the Africanized colonies showed increases or values close to 0, except in one case. This special case corresponded to sealed brood area at 1350 m where extremely unfavorable weather conditions and unexpected disruptions in the feeding schedule caused two Africanized

TABLE 1 — Conditions during the one-month tests at the four apiaries where the Africanized and European colonies were moved.

Apiary at Elevation Above Sea Level	520 m	1350 m	1650 m	2450 m
Latitude (N)	6° 32′	6° 03′	6° 10′	6° 09′
Longitude (W)	75° 50′	75° 00′	75° 38′	75° 32′
Max Temperature	36.0 °C	31.0 °C	29.5 °C	26.0 °C
Min Temperature	17.0 °C	16.0 °C	15.4 °C	9.0 °C
Average Mean	25.0 °C	23.7 °C	21.8 °C	16.1 °C
Rainfall	109 mm	581 mm	242 mm	135 mm
Days with Rain	22/28	24/28	25/35	13/28
Sugar Fed (kg)	2.5	1.25	1.5	0

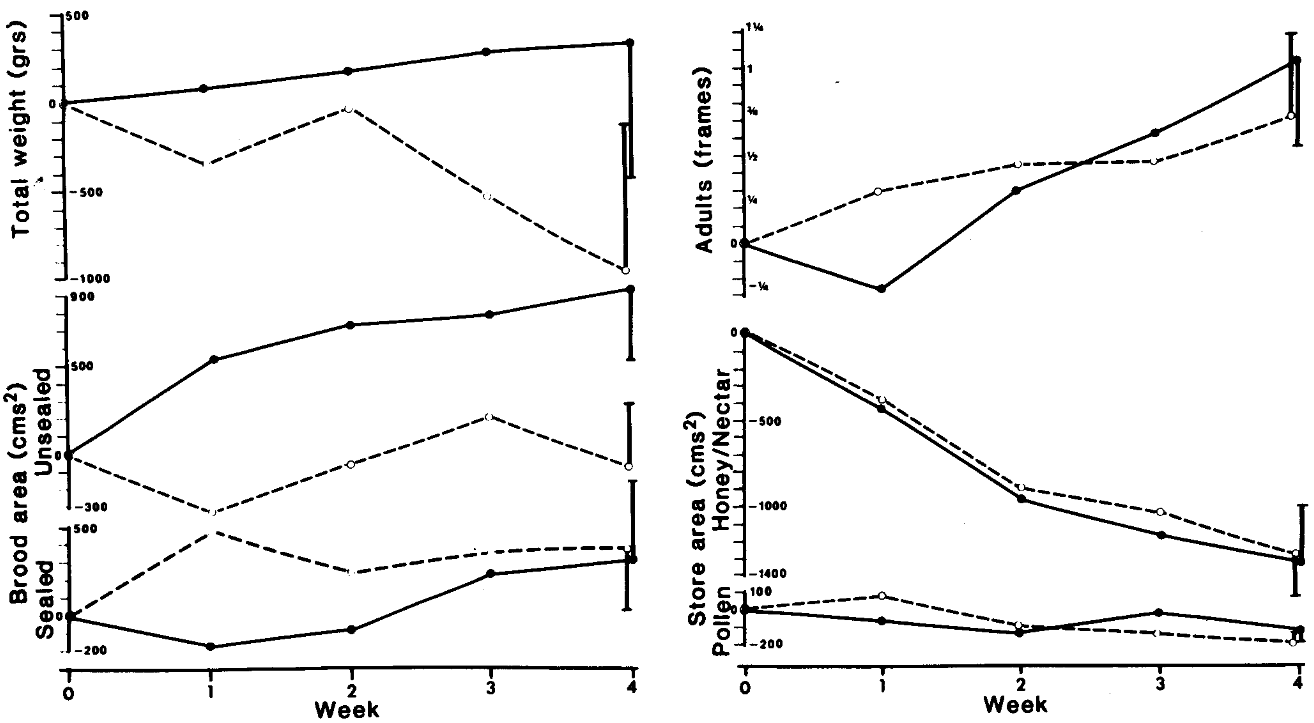

Fig. 1 — Average weekly changes in conditions of nine Africanized (solid circles, solid lines) and nine European colonies (open circles, dashed lines) at 2450 meters above sea level in the Andes of Colombia. Solid bars indicate 1 s.e. for the measurements of week 4.

colonies to abscond and three European colonies to starve.

At 520 m (the only truly tropical site) all changes in measurements of Africanized colonies demonstrated or suggested the superiority of these over European colonies. At higher elevations (and where two-tailed *t*-tests were used) the pattern was not as consistent for all measurements. These results suggest that differences between the two races are greater at lower elevations.

2. Survivorship of feral Africanized colonies at high elevations

The increase in the number of feral colonies in the electric poles in the survey area appeared to be a fairly recent event at the time of the first visit (February 1983). According to local reports, the colonizations had taken place from a few weeks to one year. Only one pole had been occupied by bees before the appearance of Africanized bees in the lowlands of the region (January 1982). A sample from this colony gave an index at the midpoint between the distributions for Africanized and European populations when analyzed morphometrically. The other nine colonies analyzed were clearly Africanized.

The 20 poles between 2750 and 3000 m above sea level were never occupied by bees during the observation period (Fig. 2). At elevations below 2750 m there was no consistent pattern in the proportions of poles occupied with respect to available poles. However, during most of the visits, the number of occupied poles per km was similar for all elevations where colonies were found.

In 1983, a year with normal rainfall, the density of colonies remained fairly constant (Fig. 2). The number of colonies decreased markedly during the period of abnormally high rainfall at the end of 1983 and beginning of 1984. During

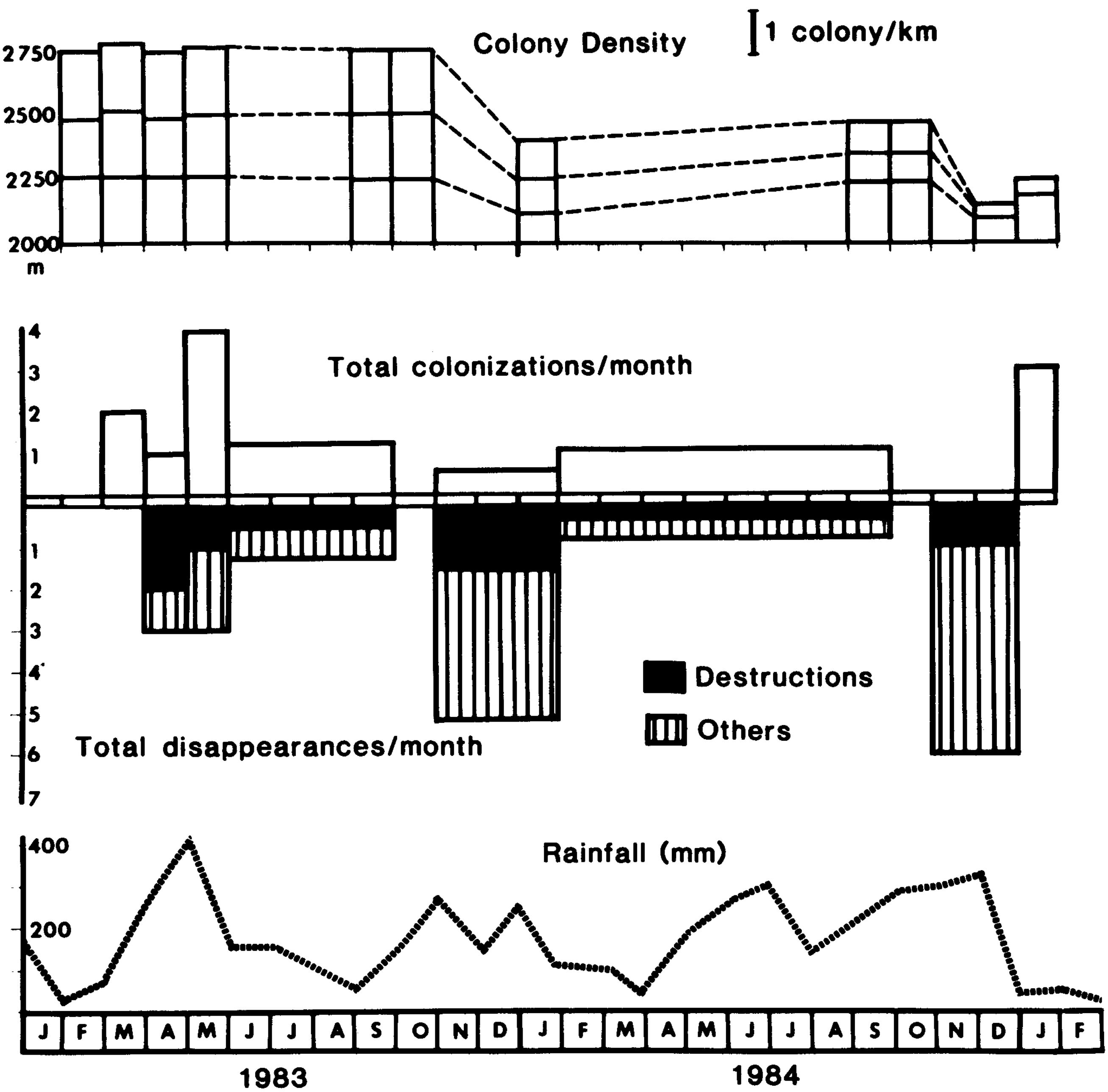

Fig. 2 — Changes in colony density in a gradient with artificial nesting sites from 2000 to 3000 meters above sea level in the Andes of Colombia. The changes in density arose from variable rates of colonization and disappearance. Rainfall, a factor apparently affecting colony density, is indicated.

periods when the rainy season was less than three months long, appearances of colonies closely matched disappearances. Critical periods seemed to appear when the rainy seasons lasted more than 4 months. At the end of such periods disappearances were numerous and colonizations few or nil (November-December of 1983 and 1984). However, the June 1986 survey showed that with the drier years of 1985 and 1986, colony numbers for each elevational class were almost identical to those found in early 1983. Destructions were lower than expected and fairly constant throughout the observations. In spite of the human, animal and vehicle activity around the nests, strong defensive behavior by the bees in the area was not reported. This may explain why there were so few destructions.

The causes for other disappearances were not established with certainty. The colonies, being Africanized, may have absconded rather than died. In August of 1983 a colony at 2450 m was observed in the act of absconding and in January of 1984 a small cluster of bees with a queen was found at 2580 m outside a pole which had been occupied at the time of the previous visit. Colonizing swarms could have had three origins: from absconding in the area, from colony reproduction in the study area and from immigration from other areas. Scouting bees were observed on two previously occupied poles in January of 1984, possibly originating from absconding swarms during that unfavorable season. During a favorable season (January of 1985), six previously occupied poles between 2100 and 2300 m were being scouted and were found to be colonized in June of 1986. Since these observations were made at the lower elevations and very soon after the end of a rainy season, it was assumed that these swarms were migrating from the lowlands. The improvement of colony conditions further into the dry seasons could have permitted colonization by reproductive swarming in the area.

DISCUSSION

The short-term test with colonies at 520 m confirms many reports that the performance of Africanized colonies is superior to that of European colonies in tropical lowlands. The tests at higher elevations (1350, 1650 and 2450 m above sea level) and the periodic survey of a highland area showed that, contrary to what was expected, Africanized colonies maintained a superior condition and colonized in a shorter time at higher densities than European bees which had been in the area for decades. Total weight change due to foraging (obtained by subtracting the amount of sugar fed (Table 1) from the average changes in weight at each test site (Table 2) show that where rainfall was not intense (520, 1650 and 2450 m) the European colonies lost weight while the Africanized colonies maintained a condition above or very close to their original.

Changes in colony condition suggest, however, that the differences between Africanized and European colonies are not as marked at higher elevations. In addition, the survey showed that the density of Africanized colonies at elevations above 2000 m is much lower than densities in tropical lowlands. Assuming that the survey sampled a band only one km wide, the colony densities would fluctuate from 0.7 to 1.5 colonies per km². Such density would be 10 times lower than the one estimated for a tropical dry forest in Venezuela (Taylor 1985) and 100 times lower than one found by Kerr in Brazil (Kerr 1971). The relationship between higher feral colony density and greater differences between the conditions of Africanized and European bees suggests that competition at lowland sites might have an important deleterious effect on European colony performance.

The apparent moderation of the differences between Africanized and European colony conditions with increasing elevation might lead to the idea that at even higher elevations than the ones used, European bees might be superior while Africanized bees reach a climatic barrier. Unless there is a marked change in the behavior or physiology of Africanized bees, it is likely that they can colonize any areas where European bees survive in the tropics. Elevations above 3000 meters in the American tropics present very taxing conditions for any kind of honey bee and to my knowledge there is only

TABLE 2 — Changes in the conditions of European and Africanized colonies after a four-week test period (five weeks at 1650 m) at the different apiaries. (Average changes ± s.e.)

Apiary at	520 m	1350 m	1650 m	2450 m
Number of Colonies	9 E 9 A	6 E 7 A	5 E 7 A	9 E 9 A
Changes in Condition				
Total Weight (kg)	1.60 ±0.328 o 2.41 ±0.334	-0.11 ±0.091 o 0.30 ±0.169	1.67 ±0.187 ns 2.04 ±0.329	-0.95 ±0.266 * 0.35 ±0.422
Unsealed Brood (sq cm)	1310 ±165.5 ** 2136 ±122.3	59 ±115.8 ns 8 ±174.7	222 ±285.5 ns 465 ±183.7	- 57 ±199.8 ** 979 ±210.4
Sealed Brood (sq cm)	964 ±225.5 ** 1854 ±158.2	-279 ± 92.6 ns -187 ±121.9	1080 ±283.2 * 1717 ±352.7	367 ±442.3 ns 312 ±244.8
Adult Bees (frames)	-0.17 ±0.166 o 0.28 ±0.237	-0.92 ±0.153 o -0.14 ±0.373	0.00 ±0.447 ns 0.43 ±0.352	0.72 ±0.354 ns 1.05 ±0.212

ns P value greater than .10
o P value between .10 and .05
* P value between .05 and .01
** P value between .01 and .001

migratory beekeeping at such elevations. The lack of colonizations between 2750 and 3000 m in the survey area probably does not indicate a climatic barrier per se, but is rather explained by a fairly abrupt change to a cloud forest vegetation which even European colonies failed to colonize despite their presence at lower elevations for many years. The 16°C mean higher temperature for the coldest month of the year postulated as coincident with the limit for permanent Africanized bee colonization in Argentina (Taylor & Spivak 1984), does not appear to have predictive value in tropical mountains where normally day and night temperatures differ more than temperatures at different times of the year. Such a line would fall at an equatorial latitude around 3500 meters above sea level, where it is unlikely that any bees could survive permanently.

The conditions of colonies during the tests and the abundance of colonies in the survey area seemed to be closely attuned to rainfall. The survey from 2000 to 3000 m showed appearances and disappearances of colonies throughout the observation period. Disappearances outnumbered appearances at the end of rainy periods and the opposite was true during periods of lower rainfall. The frequency of these appearances and disappearances seems much higher than found for European bees in New York (Seeley 1978) or in Arizona (Taber 1979). The internal conditions of the test colonies were greatly affected by the high rainfall at the 1350 m site (more than 0.5 m in one month) together with a disruption in the sugar syrup feeding schedule, leading to absconding of some Africanized colonies and death of some Europeans. The remaining Africanized colonies exhibited a smaller gain in unsealed brood area and a decrease in sealed brood area which could be explained as a preparation for absconding (Winston 1978). Under situations of lower rainfall (specially at 2450 m) colony conditions did not deteriorate and even improved for some of the Africanized colonies which probably would have swarmed if brood had not been removed prior to the following test. Understanding these rainfall-induced cycles of colony density and strength is basic to enable successful beekeeping with Africanized bees.

Knowledge of the lower density of feral Africanized colonies in tropical highlands coupled with their seasonal decrease in strength and abundance could be useful for control of queen matings in such areas. Such a scheme would require movement of strong colonies with desirable drone populations at the time of minimum feral colony strength and abundance. The higher rainfall during these periods requires feeding of pollen and sugar and could hamper mating flights. The economic success of such an operation would depend on whether a higher demand for queens with low levels of mismatings could offset the costs of migration and feeding.

The data presented here do not permit predictions of the overwintering ability of Africanized colonies since the coldest temperature encountered was probably not less than 7°C and higher temperatures allowed daily flight at all locations. However, preliminary studies have not detected large differences between European and Africanized bees in some of the components involved in overwintering (Krell et al. 1985, Villa 1985). The fairly common belief among beekeepers that Africanized bees are unfit to operate in areas outside truly tropical lowlands needs to be reconsidered. Currently studies are under way to establish with more precision the extent of overwintering abilities in Africanized bees.

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