

“Overwintering” of Africanized, European, and Hybrid Honey Bees (Hymenoptera: Apidae) in the Andes of Venezuela

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ABSTRACT The potential of Africanized honey bees, *Apis mellifera* L., to survive the cold temperatures and confinement of winter was studied at 4,100 m above sea level in the Andes of Venezuela. The first experiment was conducted through the rainy-season “winter” of 1986 using Africanized (A) and European (E) colonies. In 1986, temperature conditions only rarely allowed honey bee flight. Under these conditions, 13 of 14 A colonies died within 18 wk compared with 4 of 15 E colonies. In 1987, European × Africanized (E × A) hybrid colonies were included in a larger experiment with treatments with various initial adult and brood populations. Higher maximum temperatures during this second experiment allowed worker flight almost daily; colonies in one treatment were confined with screens to test the published hypothesis that flight from A colonies during cold weather causes bees to leave their hives and die, causing the colonies to dwindle. All screened A colonies had died by week 10, while screened E and E × A colonies were alive through week 14. In treatments involving free-flying colonies, there were fewer differences between bee types in colony survival, size, brood production, final adult population, or food consumption. E × A colonies had intermediate values for most traits, suggesting that any differences will be reduced with hybridization as Africanized bees expand their range into areas with high-density populations of European bees.

KEY WORDS *Apis mellifera*, overwintering, temperature

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THE NATURAL RANGE expansion in North America of Africanized honey bees (*Apis mellifera* L.) has recently continued into Texas. Although their threat to the general public is minor, their potential to disrupt beekeeping (McDowell 1984) and pollination services (Danka et al. 1987) is great. The extent to which Africanized genes will affect the feral and managed honey-bee population of the United States will largely depend upon the overwintering ability of colonies showing varied levels of Africanization. Hence, clarifying their overwintering ability is useful for predicting their possible negative effects in the United States.

Because of regulatory concerns, overwintering studies with Africanized bees have only been possible in a few temperate countries. Experiments in Poland (Woyke 1973) and in Germany (Villa et al. 1991) demonstrated high mortality for Africanized colonies exposed to winter conditions; Africanized × European hybrids showed improved overwintering capability. In contrast to the results from Europe, experiments in Argentina have led to predictions that Africanized honey bees could potentially overwinter in most of the United States (Dietz et al. 1986).

In addition to trials in temperate countries under winter conditions, high altitudes in tropical countries have provided sites to test the performance of Africanized colonies at low temperatures. Several studies have examined survivorship of Africanized bees along altitudinal transects (500 to 2,800 m above sea level) in Colombia and Costa Rica (Villa 1987, Spivak 1989, Gentry 1991). Contrary to expectations, Africanized colonies outperformed European colonies at these elevations by effectively balancing resource collection with brood production. These earlier studies are not good predictors of colony survivorship through temperate winters: gradients along tropical mountains do not closely simulate latitudinal gradients because of the reduced yearly variation in temperature at any site close to the equator. Rather, each elevational band on tropical mountains presents a uniform thermal environment, which is approximately equivalent to that of a specific time of year in a temperate location, and does not resemble an annual seasonal cycle associated with a specific temperate latitude (Mani 1968).

Above 4,000 m in the tropics, low temperatures cause reduced plant density and productivity, generating a year-round condition analogous to temperate winter (Mani 1968). Homeothermic insects are absent at these highest elevations be-

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Table 1. Tested types, number of colonies of each type, initial colony conditions, duration of the experiment, weight loss, and average survival time in two experiments with colonies of honey bees at 4,100 m above sea level in the Andes Mountains of Venezuela

Exp	Type/Treatment	n	Initial Condition			Length of exp (wk)	Avg wt loss (kg)	Avg survival time (wk)
			Worker population (kg)	Brood area (cm ²)	Hive wt (kg)			
1 (1986)	E A	15	0.5-2.5	0 ^b	22.81	22	4.63	14.00
2 (1987)	E E × A A	30						
	a. Closed	5	2.00	0 ^b	34.07	14	1.90	— ^a
	b. Open	10	2.00	0 ^b	47.25	46	29.06	39.25
	c. Open	10	1.50	302	33.09	45	16.50	21.47
	d. Open	5	1.50	292 ^b	33.86	44	14.98	20.87

^a Five E and five E × A colonies surviving until week 14 were killed to evaluate conditions.

^b Brood was measured every 2 wk for the first 10 wk of the experiment.

cause they probably cannot attain positive energy budgets. Honey bee colonies with homeothermic characteristics similar to those of birds and mammals (Southwick 1983) will experience a year-round negative energy budget under those conditions.

We exposed a total of 120 colonies of Africanized, European, and hybrid bees to these simulated winter conditions (4,100 m above sea level). Initial amounts of adult bees, presence or absence of brood, and screening to prevent flight were experimentally varied. Environmental conditions also impacted flight activity: in the first year temperatures seldom reached flight thresholds; in the second year maximum temperatures permitted flight of all colonies except those that we experimentally confined. The effects of these preplanned and unplanned conditions on colony and worker survival, on brood production, and on the use of honey stores were compared between the three types of bees. These comparisons provide useful indications on the winter survival potential of feral and managed Africanized and hybrid colonies in the United States.

Materials and Methods

Two separate experiments were conducted in 1986 and 1987 at Pico Águila, Mérida, Venezuela, 4,100 m above sea level (8°51'N, 70°50'W). Colonies of each of the three types of bees (Africanized, European, and European × Africanized; abbreviated as E, A, and E × A, respectively) were selected from research apiaries in the lowlands (Acarigua, Portuguesa) at the beginning of each rainy season (May). E colonies were headed by mated commercial queens introduced from the United States, A colonies by mated queens captured from feral lowland swarms, and E × A by European virgins mated in areas having high densities of feral Africanized bees. All colonies had worker populations that were the progeny of the resident queen, and all queens were less than 1 yr old.

Experiment 1: Field Colonies in 1986. Fifteen A and 15 E colonies were formed using only

adult bees in initial amounts of 0.5, 1.0, 1.25, 1.50, 1.75, 2.00, 2.25, and 2.50 kg. Weighed groups of adult workers were shaken into screened cages for transportation to the mountains. These bees were then reintroduced at the highland site into preweighed Langstroth hives with combs produced on European-sized foundation (two to three combs were empty and seven to eight combs were provisioned with honey and pollen). Colonies were checked for cluster size and general condition on nine occasions between their installation on 15 May and the final inspection on 27 October. High precipitation generated daily fog and maintained temperatures during all observation periods below 7°C. At the end of the experiment, surviving colonies were returned to the lowlands for final measurements.

Experiment 2: Field Colonies in 1987. Thirty colonies of each group (A, E, and E × A) were divided among the following four treatments (see Table 1 for comparison with experiment 1): (a) colonies closed, 2.0 kg of workers, no initial brood added, $n = 5$; (b) colonies open, 2.0 kg of workers, no initial brood added, $n = 10$; (c) colonies open, 1.5 kg of workers, initial brood added, $n = 10$; (d) colonies open, 1.5 kg of workers, initial brood added, brood measured during the experiment, $n = 5$.

The broodless colonies in treatments a and b were prepared with 2.0 kg of adult bees and transported on 6 May. Colonies in treatment a differed from those in treatment b in that they were screened; workers could not fly and void feces nor could they forage during the short periods when temperatures exceeded flight thresholds. All free-flying colonies (treatments b, c, and d) were fitted with a simple mesh pollen trap that reduced the amount of incoming pollen.

The colonies having brood, treatments c and d, were formed by adding 1.5 kg of workers to four to five weighed and measured brood combs from the same colony introduced into preweighed hives with five to six combs of honey and pollen. They were transported to the highlands on 13 and 19 May, respectively. The colonies in treat-

ment c differed from the colonies in treatment d in that measurements of brood area were taken in the d group every 2 wk for the first 10 wk.

Observations of colony conditions were made every week for the first 4 wk, biweekly until the tenth week, and, later in the experiment, at longer intervals until the end of the experiment on 24 March 1988. Because all A colonies in treatment a had died by week 12, the conditions of surviving E and E × A colonies were evaluated at week 14 and that part of the experiment was terminated then.

The weather during the 1987 season differed greatly from that of the previous year. The rainy season was greatly delayed and cloud cover and fog were minimal, allowing day temperatures to rise well above flight thresholds (up to 15°C).

Africanized Colony Identities. Using marked E queens and marked A queens, and E daughter queens reared and mated in highly Africanized areas assured that colonies represented E, A and E × A populations. To further clarify the identities of the non-European colonies, workers from all colonies of experiment 2 were sampled on 8 June. Measurements of forewing length of 10 bees from each colony (Rinderer et al. 1987) were followed by 25 computer-assisted morphometric measurements (Daly & Balling 1978, Daly et al. 1982) on all E × A colonies and on A colonies that had intermediate forewing lengths.

Colony Survival and Colony Size. At each inspection, surviving colonies were opened rapidly and the maximum cluster diameter was estimated as the number of combs having clustered bees. Remaining bees were weighed when a colony's population dropped below 200 g of workers, when the colony died, or at the end of each experiment. Total weights of the remaining population and weights of subsamples of 100 bees were used to estimate the final number of workers in colonies.

Worker Mortality and Physiological State. Dead workers were recovered from the bottom of the closed and broodless colonies in experiment 2, treatment a, during each inspection. On week 5, a sample of live workers from those colonies was transported on ice and frozen within 6 h for analysis of protein reserves in heads associated with overwintering (Maurizio 1968). The frozen heads of each of three bees from each colony were oven-dried, weighed, and analyzed for nitrogen content using a Microkjeldahl procedure with spectrophotometric determination of Nessler's reagent.

Brood Production. Brood areas were measured only in colonies of experiment 2, treatment d, because of the possible adverse effects of exposing brood to cold weather. To minimize the effects of cold during brood measurements, the colony and brood were placed in a wooden box with infrared lights over the brood chamber. Because of high queen losses in the hybrid colonies

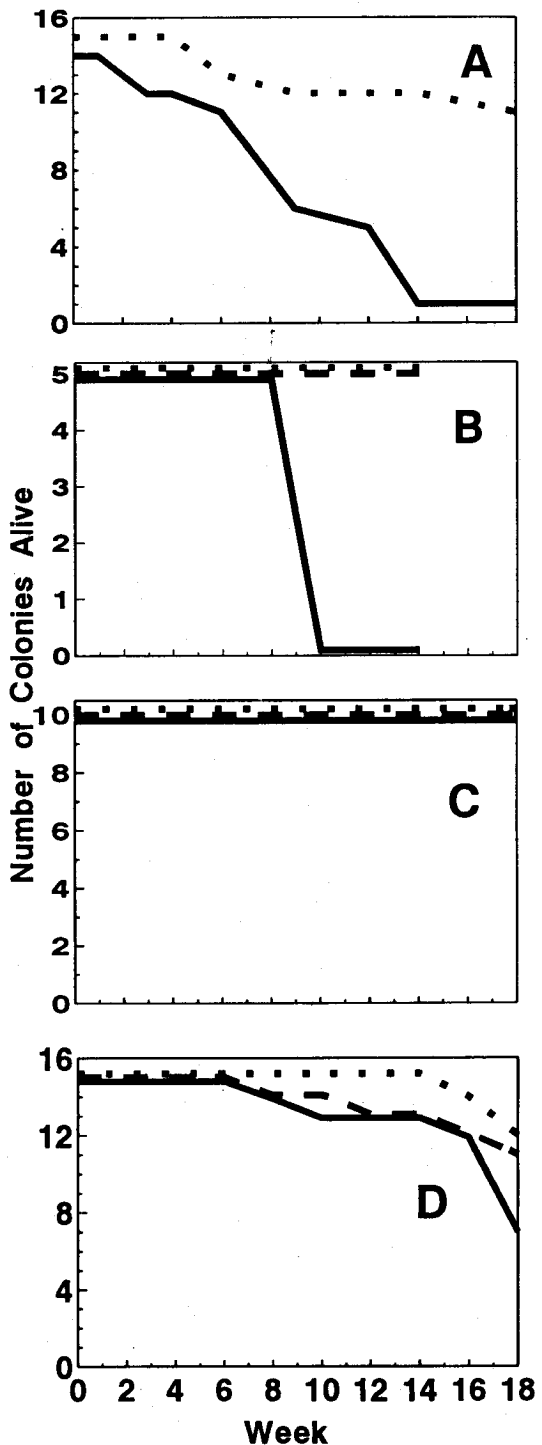


Fig. 1. Number of Africanized (solid lines), European (dotted lines), and E × A (dashed lines) colonies surviving during the first 18 wk. (A) Experiment 1. (B) Experiment 2, treatment a with closed colonies. (C) Experiment 2, treatment b with initially broodless colonies. (D) Experiment 2, treatments c and d with initially broodright colonies.

(probably exacerbated by these manipulations), only the brood areas of the A and E groups were compared.

Food Consumption. Weight loss was calculated for each colony. The weight loss per kilogram of bees per week was calculated by dividing the total weight loss of the hive by the average weight of the worker population (average between initial and final bee weights), and again by the survival time of the colony.

Statistical Analyses. Measurements taken on the same colonies through time (cluster diameter, number of dead bees in treatment a, and brood production in A and E colonies of treatment d) were analyzed with repeated measures analysis of variance (ANOVA) for differences among types (SAS Institute 1989). Total protein and percentage of protein in bee heads at week 5 in treatment a were compared among types by ANOVA (SAS Institute 1989). Estimates of the final number of workers and of rates of weight loss were compared by separate ANOVAs for each treatment, and mean separation among the three types within each treatment was tested by Duncan's multiple range test (SAS Institute 1989).

Results

Africanized Colony Identities. Morphometric measurements on colonies of experiment 2 indicated correspondence with our original grouping. Mean forewing measurements allowed unambiguous identification of 21 of 30 A colonies (range for 21 colony means: 8.57–8.96 mm) (Rinderer et al. 1987). The use of 24 additional characters (Daly & Balling 1978) allowed correct identification of the remaining nine A colonies (range of discriminant scores [D] of 1.968–3.405, with corresponding probabilities of group membership of 0.86–1.00). The 30 E × A colonies had an average D of 1.245 (range, -0.445–2.638), intermediate between the average D for the European and for the Africanized population given by Daly & Balling (1978).

Colony Survival and Colony Size. Survivorship of colonies of the different genetic origins during the first 4 mo (the duration of a winter season) varied considerably between the 2 yr (experiment 1 versus experiment 2) and initial treatments (Table 1; Fig. 1). High mortalities of Africanized colonies were seen during the more winterlike conditions of experiment 1 and in treatment a of experiment 2, where colonies began as broodless colonies and were prevented from flying. In experiment 1, 13 of 14 A colonies had died by week 18, while 10 E colonies had survived to that date. In experiment 2, treatment a, all five A colonies were dead on week 10, while all five E and five E × A colonies had survived to week 14 when they were depopulated for measurements of final size. The differ-

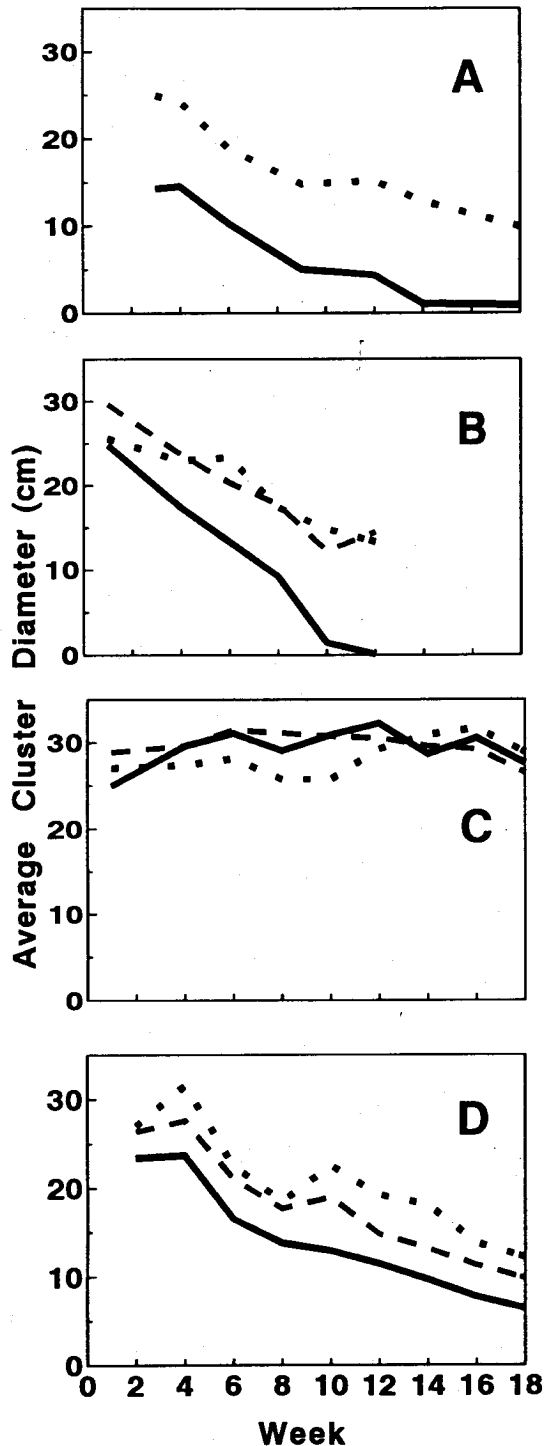


Fig. 2. Average cluster diameter of Africanized (solid lines), European (dotted lines), and E × A (dashed lines) colonies during the first 18 wk. (A) Experiment 1. (B) Experiment 2, treatment a with closed colonies. (C) Experiment 2, treatment b with initially broodless colonies. (D) Experiment 2, treatments c and d with initially broodright colonies. Dead colonies were assigned a cluster diameter of 0.

Table 2. Mean final worker population (number in thousands \pm SE) in colonies of the different types, and ANOVA results on the effect of type within each experiment and treatment at 4,100 m in the Andes of Venezuela

Exp/Treatment	n	Type of colony			F	df	P
		A	E \times A	E			
Exp 1	14, 15	2.5 \pm 0.7		2.2 \pm 0.2	0.19	1, 27	0.668
Exp 2 (all)	30	4.0 \pm 1.2a	5.7 \pm 1.6b	12.2 \pm 2.3b	4.23	2, 78	0.018
Treatment a ^a	5	0.6 \pm 0.3a	3.9 \pm 0.4b	8.9 \pm 1.0c	41.34	2, 12	<0.001
Treatment b	10	7.3 \pm 3.3	8.0 \pm 3.5	19.7 \pm 5.0	2.99	2, 27	0.067
Treatment c	10	3.4 \pm 1.1	6.0 \pm 3.1	12.2 \pm 3.5	2.67	2, 27	0.088
Treatment d	5	2.1 \pm 0.5	1.9 \pm 1.4	0.4 \pm 0.3	1.13	2, 12	0.356

Means within a row followed by the same letter are not significantly different ($P < 0.05$; Duncan's multiple range test [SAS Institute 1989]).

^a Includes bees alive in colonies that were evaluated on week 14.

ences between E and A colony survival were less marked in the free-flying, initially broodright colonies of treatments c and d of experiment 2 and nonexistent in the initially broodless colonies of treatment b.

The death of colonies in the initial period was caused by a rapid decline of worker population. Estimates of colony population (maximum cluster diameter) throughout the course of the two experiments showed curves that paralleled colony mortalities (Fig. 2). In experiment 1, Africanized colonies consistently had smaller clusters ($F = 17.95$; $df = 1, 27$; $P = 0.0002$). In experiment 2, colonies in the broodright treatment c also had significant differences between types ($E = E \times A > A$) ($F = 6.14$; $df = 2, 27$; $P = 0.0063$) and also a significant effect of time ($F = 124.86$; $df = 16, 432$; $P < 0.0001$). In the other free-flying colonies of experiment 2 (treatments b and d) there were no differences between types in cluster diameter ($F = 0.11$; $df = 2, 27$; $P = 0.89$, $F = 2.60$; $df = 2, 12$; $P = 0.11$, respectively). Just as for total colony mortality and cluster size through time, differences between types in final bee numbers were only clearly evident in treatment a, when colonies were depopulated at week 14, and were not significantly different between genotypes in the free-flying treatments of experiment 2 (Table 2).

Worker Mortality and Physiological State. Differences in colony mortality appeared to be linked with differences in worker longevity. In the only treatment where dead workers were recovered (experiment 2, treatment a) at intervals during 8 wk, there were great differences in the number of dead workers between types ($A > E \times A > E$, $F = 12.91$; $df = 2, 12$; $P = 0.001$), an even mortality rate through the time intervals ($F = 2.01$; $df = 5, 60$; $P = 0.09$), and no interaction between type and time ($F = 1.65$; $df = 10, 60$; $P = 0.11$) (Fig. 3). The total amounts of protein in heads were not significantly different among types ($F = 0.55$; $df = 2, 12$; $P = 0.58$). The estimated percentage of protein in the heads of A bees was higher because of significantly smaller heads ($F = 18.07$; $df = 2, 12$; $P < 0.0001$).

Brood Production. In the A colonies, higher worker mortality did not appear to be compensated by increased brood production. In the treatment where sealed brood area was measured during the first 10 wk (experiment 2, treatment d), there was no clear overall difference between E and A colonies ($F = 0.13$; $df = 1, 8$; $P = 0.73$). Brood area decreased significantly with time ($F = 3.14$; $df = 4, 32$; $P = 0.027$), and type and time interacted ($F = 3.12$; $df = 4, 32$; $P = 0.028$).

Food Consumption. The rates of weight loss ranked differently for the three stocks in the different treatments (Table 3) and exhibited some interaction between type and treatment. It is most interesting that in the treatments where colony survivorship diverged to the greatest degree (experiment 1 and treatment a of experiment 2), the Africanized colonies had a lower rate of weight loss. Under those conditions, the rapid death of workers seemed to produce a lower rate of store consumption than that ex-

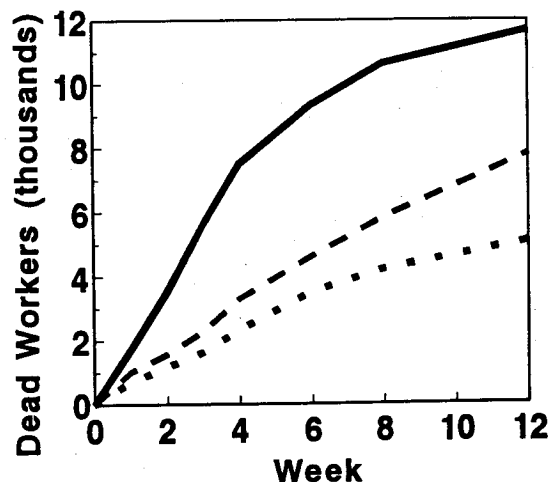


Fig. 3. Cumulative average number of dead workers recovered until week 12 in the closed colonies of Experiment 2, treatment a (Africanized, solid line; European, dotted line; E \times A, dashed line).

Table 3. Mean rates of weight loss (kg wt loss/[avg kg bees*wk] \pm SE) of colonies of the different types, and ANOVA results on the effect of type within each experiment and treatment at 4,100 m in the Andes of Venezuela

Exp/Treatment	n	Type of colony			F	df	P
		A	E \times A	E			
Exp 1	14, 15	0.25 \pm 0.05a		0.41 \pm 0.06b	4.22	1, 27	0.049
Exp 2 (all)	30	0.65 \pm 0.06	0.58 \pm 0.03	0.52 \pm 0.04	1.37	2, 78	0.261
Treatment a	5	0.21 \pm 0.03	0.32 \pm 0.04	0.30 \pm 0.02	3.53	2, 12	0.062
Treatment b	10	0.62 \pm 0.04	0.57 \pm 0.03	0.46 \pm 0.07	2.85	2, 27	0.075
Treatment c	10	0.86 \pm 0.11a	0.67 \pm 0.05ab	0.55 \pm 0.05b	4.55	2, 27	0.019
Treatment d	5	0.74 \pm 0.06	0.65 \pm 0.11	0.80 \pm 0.09	0.65	2, 12	0.540

Means within a row followed by the same letter are not significantly different ($P < 0.05$; Duncan's multiple range test [SAS Institute 1989]).

pected by the calculation of colony size as a mean between initial and final population. For the free-flying treatments of experiment 2, rates of weight loss were only significantly higher in the A colonies than in the E colonies in treatment c.

Discussion

The results of these experiments are very similar to those reported previously from an experiment in Germany (Villa et al. 1991), in which Africanized colonies exhibited higher mortality rates. The different treatments used in the Andean experiments suggest that nest confinement is a possible mechanism to explain the much higher winter mortality of Africanized colonies exposed to true or simulated winters. Conditions of nest confinement lasting 2 mo or more appear to have serious effects on Africanized worker longevity, which leads to high colony mortality. Because the number of consecutive days with normal high temperatures below flight threshold increases with latitude (Southwick et al. 1990), it is reasonable to expect decreased winter survival of Africanized bees as they expand their range northward in the United States.

The possible physiological mechanisms that produce these differences in worker longevity are yet unclear. The shortened longevity of Africanized colonies was clearly not caused by aging associated with depletion of protein stores in the head as has been reported for European bees (Maurizio 1968). Other factors such as physiological problems due to high accumulation of feces or a reduced response in longevity to decreased brood rearing in Africanized workers might be important factors for future research.

Even in treatments where total colony mortalities were similar for the first 18 wk, the mean number of surviving workers at the end of the experiments was marginally lower in the A colonies (treatments b and c of experiment 2). Most Africanized colonies surviving until spring in areas with moderate winters would probably be small. It is still uncertain how these types of bees could deal with these conditions, especially in areas where the onset of flowering is variable.

As in the previous experiment conducted in Germany (Villa et al. 1991), the types did not differ greatly in brood production. The responses of all types were similar in each experiment where brood production was measured. It is interesting that in Germany there was a decrease to no brood rearing, whereas in Venezuela brood rearing continued through the length of the experiment. The fact that brood rearing ceased in Germany (50°N) but only declined in Venezuela (5°N) suggests that the influence of photoperiod upon brood rearing reported for European bees (Kefuss 1978) also occurs in Africanized colonies.

It is probably unrealistic to try to establish an absolute climatic limit to Africanization. The ranges of survival for highly Africanized bees will vary from year to year depending on the intensity and length of winter and on the duration of consecutive days with absolute maximum temperatures below flight threshold. More important, the larger differences between the extreme Africanized and European types disappear with hybridization, and selection could favor colonies with different degrees of Africanized genes in different areas.

The most likely future scenario for the feral honey bee population in the United States predicts a band of high Africanization across the southern states, an Africanized-free band in the northern states, and a band with a high prevalence of hybrid bees between. A recent survey of the feral population in Argentina using mitochondrial DNA and multivariate analysis of morphological characters supports this view (Shepard et al. 1991). Feral population characteristics will exert different degrees of introgressive pressure on the honey bee population maintained by beekeepers. It will be more difficult to continue beekeeping with European bees in the southern United States than in the northern United States.

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