

Overwintering of Africanized, European, and Hybrid Honey Bees in Germany

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ABSTRACT The survival of Africanized honey bees, *Apis mellifera* L., in temperate regions was evaluated in Germany during the 1988-1989 winter. Africanized, local European, and Africanized × European colonies were started by queen introductions on 5 August, and all surviving colonies were depopulated on 21 February. Five of nine Africanized colonies had died by the end of the experiment, whereas all eight European and all five Africanized × European colonies survived. Brood production of the three genotypes declined from 18 August until 13 November with significant differences on two of the seven measurement dates. Brood areas were not different among surviving colonies that had resumed brood production by 21 February. Changes in total colony weights through time were not different. Significant differences were found in the rates of colony weight loss (kilograms total weight/average kilograms of adult bees*time) and in final adult population size. The higher attrition of worker populations and the higher mortality of Africanized colonies suggest a possible reduction of their adverse effect as their range expands northward to temperate areas in the United States. The intermediate values for all characters in the Africanized × European colonies suggest that genes underlying overwintering characters are additive. This additivity will permit different levels of hybridization for different ecological zones, thus complicating predictions about absolute climatic limits.

KEY WORDS Insecta, *Apis mellifera*, hybrids, overwintering

THE GENUS *Apis* provides unique opportunities for studying adaptations by closely related taxa to different ecological conditions. Comparative studies are possible within the original range of species and subspecies as well as in areas where they have been introduced. The relocation for apicultural purposes has brought both tropical (African) and temperate (European) subspecies of *Apis mellifera* L. to the Americas. These introductions provided an opportunity to study whether the bees' prior adaptations to tropical and temperate environments are suitable to new habitats with similar climatic conditions. These fortuitous circumstances permit testing of four possible treatment combinations by matching two major groups of subspecies with two broad sets of environmental conditions.

The first combination, temperate subspecies in temperate environments, has resulted in the successful establishment of European bees as feral populations in North America (e.g., Seeley 1978). The second combination, tropical subspecies in tropical environments, has produced a more dramatic colonization of tropical South America by African-descended honey bees (Taylor 1977). The third combination, temperate bees in tropical areas, has yielded sparsely distributed feral popula-

tions of European bees in tropical America, especially in lowland ecosystems (J.D.V., unpublished data). The fourth combination, tropical bees in temperate regions, has thus far been tested only in Argentina where Africanized bees arrived in the mid 1960s (Kerr et al. 1982). The distribution and density of feral Africanized honey bees in Argentina has not been clearly defined (see Kerr et al. 1982, Dietz et al. 1985).

No studies so far have clearly shown very obvious physiological limits to Africanized honey bee colony overwintering in the New World (Dietz et al. 1986, 1988, 1989; Krell et al. 1985; Villa et al. 1987). Results of these studies are limited by the fact that colonies were not exposed to the lower ranges of "winter" temperatures, or to the full complement of environmental factors associated with winter. Moving established colonies with stores to South American mountains or placing them in cold rooms failed to expose colonies to extreme winter temperatures, short-day photoperiod regimes, and deprivation from foraging for periods longer than 3 mo associated with extreme winters. These tests also failed to encompass the necessary preparation of colonies for winter, where storage of honey and pollen, as well as reduction of brood rearing, are essential to survival.

Another large-scale fortuitous natural experiment will soon begin to test potential climatic limits to Africanized honey bees, given that Africanized bees are starting to move into southern Texas along

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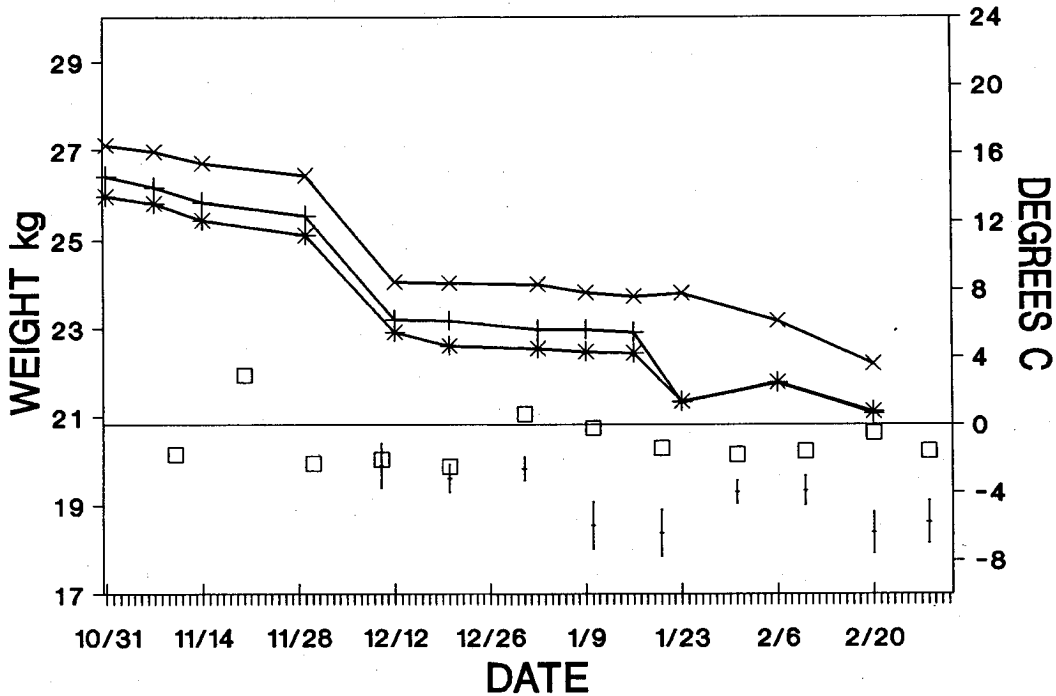


Fig. 1. Average total weights of nine Africanized (+), eight Carniolan (x), and five A x C (*) colonies from 31 October to 21 February. Minimum daily temperatures were averaged by week for the 1988-1989 winter (\square), and for the previous ten winters from 1 December (means \pm SE) (I). Once Africanized colonies died, they were not included in the subsequent calculations of average weights.

the Gulf Coast. The potential economic effect of the northward range expansion of Africanized bees prompted us to test their adaptation to winter in the hopes of providing some useful predictions for the United States and Canada. This was done by relocating Africanized germplasm from tropical America to Germany to submit Africanized colonies to the full complement of fall and winter conditions. Woyke (1973) conducted a similar experiment in Poland and reported on the poor overwintering of colonies with Africanized germplasm. We attempted to answer the following specific questions by comparing Africanized, European, and hybrid colonies: (1) Are there differences in the longevity of colonies during long winter periods? (2) Are there differences in fall and winter brood production between the groups? (3) Are there differences in the rate of consumption of honey stores between the groups?

Materials and Methods

Colonies were established on 5 August 1988 by introducing queens of three different origins together with 1.5-kg packages of local Carniolan workers into hives with three empty combs, six combs of honey, and one comb with pollen. Nine Africanized colonies (A) were headed by queens descended from queens of captured feral swarms in Venezuela. Five hybrid colonies were produced

by Africanized daughter queens which were inseminated with semen from German Carniolan drones (A x C). Eight Carniolan colonies (C) were headed by queens of local stock maintained at the Institute für Bienenkunde, Oberursel, Federal Republic of Germany. All queens were marked and had one set of wings clipped.

All colonies were fitted with entrance queen excluders and moved to an isolated forest 12 km north of the Institut für Bienenkunde. On 5 October, all colonies were moved to the garden of the institute and were fed 2 kg of 50% sucrose syrup. Brood areas of all colonies were measured every 2 wk from 18 August to 13 November. Total colony weights were taken every week, except when prevented by weather, from 21 September until 20 February. On this date, by decision of the administration of the University of Frankfurt, all surviving colonies were killed. All remaining workers were weighed, brood areas were measured, and voucher specimens were stored in the honey-bee collection of the institute.

All brood area measurements and all those weights taken from 31 October to 23 January were compared using analysis of variance (ANOVA) by repeated measures. Weights prior to 31 October were not included in the analysis because populations were not composed primarily of the offspring of the resident queen, and colonies were not undergoing typical winter conditions. Weights be-

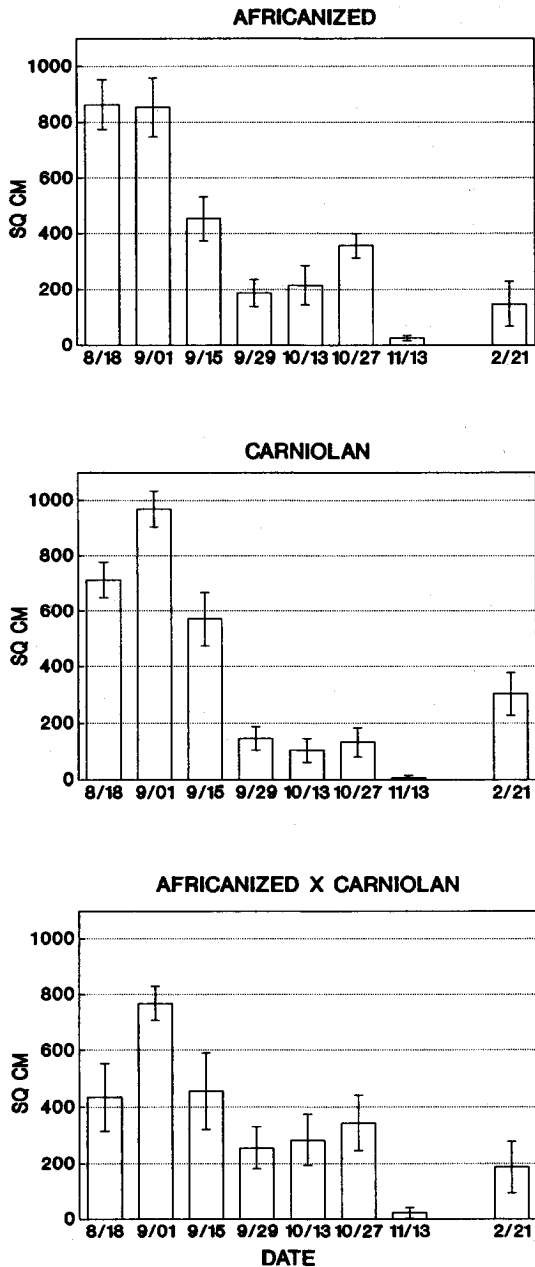


Fig. 2. Average brood areas (\pm SE) of nine Africanized, eight Carniolan, and five A \times C colonies between 18 August and 13 November, and on 21 February. No measurements were taken between 13 November and 21 February.

yond 23 January were not included in this analysis because of the death of some colonies after this date. The rate of weight loss (kilograms stores lost/average bee weight*weeks) was calculated by dividing each colony's weight change between 31 October and the final date by the average population weight and by the number of weeks of survival. The average population weight was calcu-

lated as the average of the initial worker weight (1.5 kg) and the weight of workers at the time of death or at the termination of the experiment (assuming a linear decline in adult population). Final brood areas of all surviving colonies, final worker populations at the time of death or destruction, changes in total colony weight, and rates of weight loss were compared among groups by ANOVA.

Results and Discussion

Five of the nine A colonies but no C or A \times C colonies had died when the experiment was terminated. Two colonies died during the week ending on 19 January, two were observed dead on 24 January, and one died within the week before 15 February. More than 5 kg of honey remained in each of the colonies that died. The experiment was initiated with population sizes and honey stores that, according to our experience, would cause mortality, even in the C colonies. This did not occur because of a warmer than normal winter (see Fig. 1 for a comparison of the average minimum temperatures for the winter of 1988-1989 with the previous 10 winters). During the last 10 winters, winter mortality in the 200 colonies of Carniolan bees maintained by the Institut für Bienenkunde has averaged 10%, whereas winter mortality during the winter of 1988-1989 was only 1%. The death of five of nine Africanized colonies, whereas all other colonies survived until the date of the termination of the experiment, indicates that there may be genotypic differences in overwintering ability.

Brood production was similar in the three groups (Fig. 2). Brood measurements between 18 August and 13 November showed no significant differences among types ($F = 0.67$; $df = 2$; $P = 0.5231$), a highly significant effect of time on brood production ($F = 57.15$; $df = 6$; $P < 0.0001$), and a significant interaction of type with time ($F = 2.82$; $df = 12$; $P = 0.0021$). The interaction between type and time is due to the lower brood areas in the A \times C group on the first date and increases in the 27 October counts in both the A and A \times C groups. Brood areas of the colonies surviving until the end of the experiment did not differ significantly (Table 1). The observations during this experiment do not clarify whether the brood production of A colonies was reduced by such proximal effects as reduced pollen stores or by more ultimate signals such as photoperiod changes. The influence of these factors should be an important component of future experiments.

Final worker population at the time of death or at the end of the experiment differed among the groups (Table 1). It would appear as if the reduction of brood rearing during the autumn in A colonies did not increase the longevity of their workers to the same degree as has been reported for the "winter workers" of temperate European bees (Maurizio 1968). Long periods of decreased or in-

Table 1. Means \pm standard errors and analysis of variance on the effect of type on total weight loss, rate of weight loss, adult worker population at the time of death or depopulation of colonies, and brood area of all colonies surviving until February 20

Variable	Type of colony			F	P
	A (n = 9)	A \times C (n = 5)	C (n = 8)		
Brood area, 21 Feb., cm ^{2a}	148.5a \pm 99.75	186.6a \pm 89.22	301.5a \pm 70.35	0.97	0.40
Final worker pop., kg	0.395a \pm 0.0718	0.596a \pm 0.0963	0.883b \pm 0.0762	10.89	0.0007
Weight loss, kg	5.42a \pm 0.242	5.08a \pm 0.325	4.92a \pm 0.257	1.02	0.38
Rate of weight loss, kg/(kg*week)	0.394a \pm 0.0247	0.284b \pm 0.0331	0.244b \pm 0.0262	9.34	0.0015

Means followed by the same letter are not significantly different at $P = 0.05$ (Duncan's multiple range test).

^a Only the four surviving A colonies were included in this analysis so as not to confound brood area with time of year.

errupted brood production in A colonies could interfere with their ability to overwinter.

Total colony weights between 31 October and 23 January varied with time ($F = 719.61$; $df = 8$; $P < 0.0001$) but not by type ($F = 1.66$; $df = 2$; $P = 0.2159$); also, there was no interaction between type and time ($F = 1.53$; $df = 16$; $P = 0.0974$) (Fig. 1). Weight loss between 31 October and the final date was not different among the groups (Table 1). A faster consumption of stores by Africanized colonies has been proposed as a possible cause for overwintering mortality of Africanized colonies due to a presumed higher metabolic rate (Taylor & Spivak 1984). This experiment did not indicate major differences in metabolic rates between the types. Southwick et al. (1990) found that the metabolic rates of Africanized and European groups at low temperatures are similar in group sizes normally found in colonies, but become very different as group sizes decrease below 500 g.

When store consumption is weighted to average population and to survival time (both of which are different among types), rates of store consumption become significantly different (Table 1). In those years when low accumulation of stores in the fall are followed by long winters, as groups become smaller their slightly higher store consumption rates could be critical to survival of A colonies. However, during average weather conditions, reduction of brood rearing without a sufficient increase in adult longevity might play a larger role in determining colony mortality of Africanized bees during winter periods.

It is impossible to predict precisely the final fate of the colonies if the experiment had continued into the spring. The worker populations of the A colonies at the time of death or depopulation were less than half those in the C or A \times C colonies. Surviving A colonies were thus approaching a critical point in winter survival with worker populations that normally cause mortality of C colonies (N.K., unpublished data). Similar differences in final bee population among types have been observed in experiments in the high Andes of Venezuela (Villa 1986). In the tropics, however, very small Africanized swarms can quickly develop into large colonies once nectar and pollen resources are available, and it is uncertain whether the smaller Africanized colonies in Germany could have sur-

vived during the normally resource-poor period of March and April.

From the results obtained in this experiment, we conclude that some of the adaptations of Africanized honey bees to tropical environments make them less capable of coping with the winters of temperate regions. Viable resource utilization patterns evolved for the tropics, such as high rates of brood production (Pesante 1985), and low adult longevities (Winston & Katz 1981) are inadequate to carry colonies over long periods without resources. Colonies might have enough energy stored in the fall and might be capable of maintaining temperatures within the cluster, but workers might not survive long enough to carry the colony through long winters.

It is important to note that the A \times C colonies had intermediate values for all the characters that were measured. This is an indication that physiological and behavioral characters associated with overwintering are genetically additive, which would allow for a wide range of combinations of overwintering capabilities to develop through natural selection. The lack of association between these additive overwintering characters, and other characters known to be derived from additive genes (honey production, defense), further broadens the possibility of genotypic variance upon which natural selection could operate. Numerous honey bee stock problems could arise with the introduction of Africanized genes into the southern United States honey-bee population. Without adequate mating control, queen breeders in the southern tier of states could inadvertently ship unacceptable genetic stock to the north: bees with European production abilities and Africanized overwintering problems would be as undesirable as the more widely publicized bees with Africanized defensiveness and European overwintering ability.

The ability of Africanized bees to cope with winters is variable. The most likely future scenario for the United States is that the feral density (and therefore the effect) of Africanized bees will vary from areas in the south where the prevailing population has Africanized genes to an extreme in the north where the bulk of the population is European. A similar trend (in this case from north to south) has been found recently in Argentina (W. S. Sheppard, USDA-ARS Bee Research Labora-

tory, Beltsville, Md., personal communication). The final setting of these relative frequencies in North America will depend not only on the average absolute differences in overwintering mortality but also on the genetic variability of the colonizing Africanized population, on the level of introgression of additive genes with the European population, on the yearly variability in the intensity and duration of winters, and on the strength of human response to the undesirable characters of Africanized bees.

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