31 March 1987

JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
60(1), 1987, pp. 4–14

Preliminary Observations on Thermoregulation, Clustering, and Energy Utilization in African and European Honey Bees[1]

JOSÉ D. VILLA,[2] CURTIS GENTRY, AND ORLEY R. TAYLOR, JR.
Department of Entomology, University of Kansas,
Lawrence, Kansas 66045

Honey bees of the African race *Apis mellifera scutellata* evolved under tropical and subtropical conditions, while the different races of European bees evolved under temperate conditions (Ruttner, 1975, 1976). Although Africanized bees have been thought of as hybrids between these two groups of bees, they are more similar to their African ancestors in morphology (Daly and Balling, 1978) and behavior (Fletcher, 1978; Winston et al., 1979; Otis, 1980; Winston et al., 1983). African (Africanized) and European bees have notable differences in morphology, behavior, and physiology of adaptive value to "tropical" and "temperate" environments, respectively (Winston et al., 1983). This concept is clearly substantiated by the failure of European bees over centuries to form noticeable feral populations in the American tropics, contrasting with the dramatic success of African bees in colonizing a vast portion of the continent (Taylor, 1977). On the other hand, European bees form feral populations in temperate regions of America, and African bees have failed to colonize at high densities such areas in Argentina (Taylor, 1977; Kerr et al., 1982).

Some of the comparisons that have been made between European and African bees consider the characteristics of each race in habitats similar to the ones in which each race evolved. Although side-by-side comparisons would be most meaningful, several biologically important trends are discernible from studies of each race in different regions. Individual African bees are smaller (Otis, 1982), develop faster (Kerr et al., 1972; Fletcher, 1978), forage at an earlier age (Winston and Katz, 1982), and have shorter lifespans (Winston and Katz, 1981). These African characteristics promote faster colony growth and rapid arrival at a swarming-age structure (Winston et al., 1980), leading to frequent reproduction by swarming (Otis, 1980), and on the average smaller sizes of colonies with less stores accumulated (Winston et al., 1983). Absconding is the most viable strategy for African colonies encountering periods of regional lack of resources or other unfavorable local conditions, while maximum storage is advantageous for European colonies faced with more predictable and widespread unfavorable winter conditions (Winston et al., 1983). Another adaptation of African bees toward unpredictable tropical daily conditions is a tendency towards "individual foraging" which makes them more successful on scattered low-reward food sources (Rinderer et al., 1984).

The differences encountered so far between African and European honey bees

---

[1] Contribution 1931 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

[2] Present address: Honey Bee Breeding, Genetics & Physiology Research Laboratory, 1157 Ben Hur Road, Baton Rouge, Louisiana 70820.

Accepted for publication 30 October 1985.

encompass many elements of their biology. It is, therefore, not surprising that when indirect evidence for differences in their thermoregulatory abilities and energy utilization have been presented they have been taken as fact. Although the methods utilized and the data collected do not completely warrant his conclusions, Darchen (1973) stated that African bees in Gabon showed less ability to control temperature in their nest than European bees in Israel. Nuñez (1979) found that small groups of caged African bees maintained temperatures similar to those in groups of European bees, but they did so by "running" over the surfaces of the cage instead of clustering. Since smaller African bees maintained thoracic temperatures similar to those of larger European bees under several activities, Heinrich (1979) has predicted that they should have higher metabolic rates to offset a greater rate of heat loss. However, it does not necessarily follow that metabolic rates of clusters would be closely correlated with those of individual bees. In comparing the races it must be determined if groups of African bees have less efficient clustering and if the metabolic rates of clusters of similar mass, surface, or volume are higher than those of European bees.

These suggestions of racial differences in thermoregulation, clustering, and metabolism find further support in the fact that African honey bees have encountered an apparent climatic barrier in Argentina (Taylor, 1977; Kerr et al., 1982; Taylor and Spivak, 1984). If differences in thermoregulation and energy use do exist between the two races, they would fit in well within the other biological trends described. In this paper we report the results of preliminary tests designed to detect such differences.

Materials and Methods

Most of the European bees used in the tests were progeny of marked queens obtained from queen breeders in the southeastern USA. However, two colonies used to measure the energy consumption of units with brood had local European queens reared from a feral colony and mated (prior to the arrival of African bees) at the San Pedro plateau (2600 m above sea level, near Medellín, Colombia) where a feral population of *Apis mellifera mellifera* had existed for decades. The African bees used were descended from queens reared from feral colonies in tropical lowland areas where European bees had never been utilized. These queens were mated at locations with high densities of feral African colonies near Maturín, Venezuela or near Medellín, Colombia. Such isolation was used to obtain colonies that represented feral African bees rather than first or second generation crosses between the two extreme phenotypes or races.

Temperatures

a) Inside colonies at high ambient temperatures (22 to 33.5°C)

Nest temperatures were obtained from an African and a European colony placed under direct sun near Maturín, Monagas, Venezuela during the rainy (dearth) season from June 3 to June 8, 1981. Both colonies had 10 frames of brood and adult populations occupying two Langstroth hive bodies. Six thermistor probes (Yellow Strings Instruments) were located in the same positions in each of the two colonies: two probes between capped brood on frames 5 and 6; one probe within the cluster but not over brood between frames 7 and 8; and one probe on the edge of the cluster between 9 and 10 in the bottom

brood chamber. A fifth probe was placed on the middle of the entrance board and the last between the inner and outer cover. Temperatures were scanned continually for 5 days using a Yellow Springs Instrument Scanning Telethermometer coupled to a Sargent Welch XKR recorder. The maximum and minimum temperatures in the brood area and the minimum temperature inside the colony were obtained for every 2 hour interval and averaged over the period of 5 days.

b) Inside colonies at low ambient temperatures (−2 to 9.4°C)

A single thermistor probe was located in the center of the brood space of an African and a European colony located on a sand dune at 4250 meters above sea level on the Nevado del Ruiz, Colombia. One temperature reading was taken each day (not at the same time), using a Yellow Springs single channel telethermometer, from March 20 until March 26, 1984. On March 24, temperatures were taken every hour from noon until 1800 hours.

c) Inside captive artificial swarms at low ambient temperatures

African (three) and European (three) artificial swarms were prepared by placing a caged queen in the center of several vertical "combs" of plastic queen excluder material attached to the underside of a cover. Two kg of worker bees were shaken from large colonies during the rainy season into a screened Langstroth hive body where they clustered around the queen. Bees had access to a feeder inverted over a hole in the center of the cover. The swarms were exposed to temperatures of approximately 10°C until day 5, about 5°C until day 10, −5°C until day 13 in cold rooms (meat lockers) in Jusepín, Monagas, Venezuela. The temperature and light regimes varied according to the use of the cold rooms for other purposes, but most of the time it was dark and temperatures were close to the thermostatically controlled settings. "Core" temperatures were measured by searching for the highest temperature of the cluster with a Bailey microprobe digital telethermometer.

Clustering behavior

a) In hoarding cages at room temperature

Young bees were obtained from one African and one European colony by introducing a frame with emerging brood into a plastic screen bag and leaving it in an "incubator colony" for 48 hours. One hundred workers were introduced into each of 10 hoarding cages (Kulinčević and Rothenbuhler, 1973) for each race and were supplied with a water feeder and 50% (by weight) sugar syrup. The cages were kept at room temperature, fluctuating from 18 to 28°C. Degree of aggregation was observed at noon of days 2 and 5. The aggregation behavior was classified as "no aggregation" if the group did not appear to have any specific area of aggregation inside the cage; "aggregation on wall" if the bees formed an asymmetrical cluster clinging from the side walls of the cage; and "aggregation on feeder" if the group appeared as a symmetrical cluster hanging from the feeder.

b) In captive artificial swarms at low temperatures

Observations were carried out on the same three African and three European 2 kg swarms inside the cold rooms for which temperature measurements were

taken as described above. Additionally, four African swarms with sizes ranging from 1 to 1.5 kg were prepared in a similar way and kept at 10°C until day 3, 5°C until day 6, and −5°C until day 9.

Energy utilization at low temperatures

a) In broodless colonies

African (two) and European (two) broodless colonies were prepared by shaking 1.5 kg of bees from colonies during the rainy season into boxes with six pre-weighed Langstroth honey frames and then introducing their queen. They were moved to the cold rooms at Jusepín, Monagas, Venezuela, and were kept 2 days at 15°C, 3 days at 10°C, 3 days in which a power failure caused the temperature to rise to 19°C, 4 days at 5°C, and 13 days at −5°C. The colonies were removed after the total of 25 days and the live bees and honey frames were weighed.

b) In colonies with brood

In this test the area of sealed and unsealed brood in each comb was estimated and the individual combs and empty hives were weighed for each of five African and five European colonies of different sizes. After all flight activity had stopped, the colonies were closed, weighed, and transported to 4250 meters above sea level on the Nevado del Ruiz in the Colombian Andes. Temperatures during the test ranged from −2 to 9.4°C. The colonies were opened on the afternoon of day 2 and left at the site until day 10. On day 11 they were transported to the lowlands and on day 12 the same measurements for day 1 were repeated. With these two sets of data the following could be measured for each colony: total weight loss, weight loss of combs, initial and final weight of the adult population and changes in brood area.

Although there was no direct measurement of store consumption to compare metabolic rates during the 11 days, it was possible to estimate these from the above data. Assuming that production of new brood and brood mortality were negligible during that period, the decrease in total brood was used as an estimate of the number of new adults produced during the experiment. This reduction in brood area was converted to weight by assuming there was no effect of the standard cell size in European sized worker combs (3.43 cells/cm^2), in which the brood was reared, on the unengorged weight of African (61.8 mg) and European (92.6 mg) adult workers (Otis, 1982). The weight of new adults was then added to the net change in weight of adults (difference between initial and final weight of adults) so that at final weighing total adult mortality could be estimated. Similarly, the estimated weight of new adults was subtracted from changes in comb weight to estimate changes in stores. Store consumption per colony was scaled to average adult population in order to estimate metabolic rates.

Results

At high ambient temperatures (22 to 33.5°C), the temperatures in an African and a European colony were similar and in general followed similar patterns throughout the day. The average maximum and minimum temperatures registered in the brood nest and between frames 9 and 10 at the edge of the cluster were similar and were influenced to the same degree in each colony by external tem-

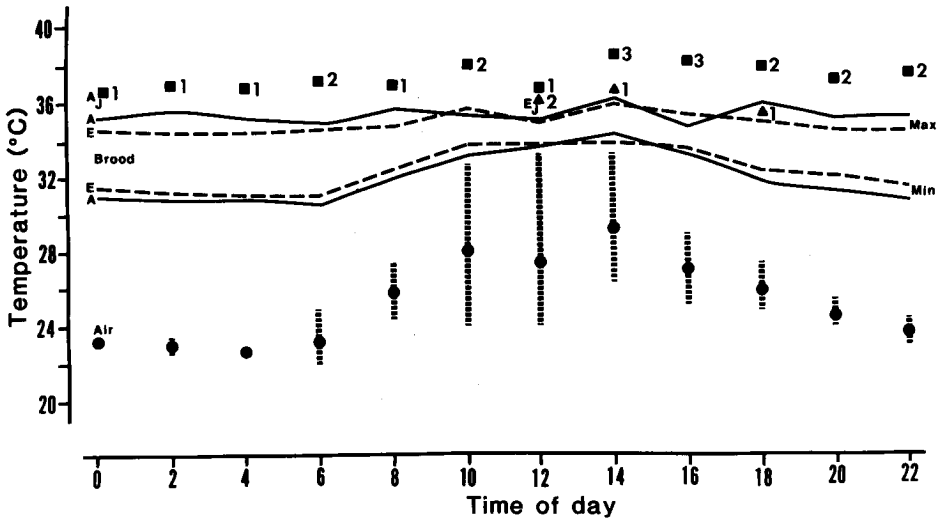

Fig. 1. Average maximum and minimum temperatures in the brood nest of an African (solid line) and a European (dashed line) colony extracted for every 2 hour interval from continuous records of two temperature probes during 6 days. Average air temperature (solid circles) and ranges (dashed bars) are indicated. The average maximum temperatures disregard local "jumps" in temperature which would have given higher values for some periods (African—solid squares, European—solid triangles). The frequency of temperature "jumps" is indicated by numbers beside the symbols.

peratures (Fig. 1). During most of the test period the maximum and minimum temperatures recorded in the brood nest were relatively constant and similar in both colonies (Fig. 2). On certain occasions which could not be related to any external or internal change in the colony, one of the probes in the brood area would show an abrupt rise in local temperature up to 41°C in the European colony and 42°C in the African colony, lasting from 1 to 2 hours. These "jumps" were observed more frequently in the African colony (on 24 occasions) than in the European colony (four occasions) during the 5 days of measurements (Fig. 1). Because the average maximum for the 2 hour interval only considered absolute maximum temperatures in the period, the greater frequency of temperature "jumps" in the African colony creates higher values for the African colony and a more realistic assessment of average maximum temperature is obtained when these "jumps" are disregarded (Fig. 1).

At low ambient temperatures (−2 to 9.4°C), the average "brood temperatures" in an African and a European colony over 6 days were 33.5 and 35.0°C, respectively. During a period from noon until 1800 hours when the ambient maximum was 9.4°C, the recorded temperatures fluctuated from 34 to 35°C in the African and from 35 to 36°C in the European colony.

Core temperatures in captive artificial swarms could not be compared clearly because of marked differences in clustering behavior. The swarms that formed "normal" symmetrical clusters around the feeder and queen were able to maintain a high temperature (Table 1). The swarms that clustered "abnormally" and separated from the feeder had lower temperatures and died earlier. All seven African swarms of sizes from 1 to 2 kg formed asymmetrical clusters, either single clusters on an internal wall of the hive body or several separate clusters. In four cases the

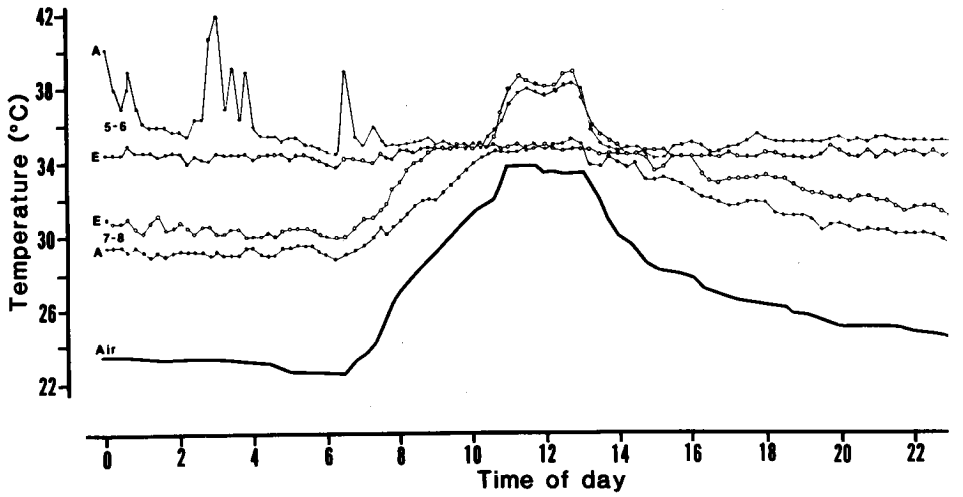

Fig. 2. Continuous record of air temperatures and temperatures between frames 5 and 6 and between frames 7 and 8 in the brood nest of an African (solid circles) and a European (open circles) colony showing typical "jumps" in local temperature in both colonies.

caged African queen was abandoned and died. In three cases the cluster, despite an asymmetrical form, still surrounded the queen which died with the rest of the bees once these were separated from the feeder or subjected to low temperatures. The three European swarms clustered around the queen and only two of them died at −5°C, apparently from being unable to remove syrup from the feeder.

A similar difference in aggregation was also detected in groups of 100 bees kept at "room temperatures" (18 to 28°C). There was a statistically significant difference in the distribution of the types of clustering between the two races on the two observation dates (Table 2).

The four broodless colonies placed in cold rooms for 25 days showed such a wide range in mortality that comparisons between African and European colonies were inconclusive. One African and one European colony had high death rates and low food consumption (Table 3). The other pair had lower death rates and higher food consumption.

Even though the tests of food consumption in colonies with brood lasted only 11 days, there was a wide range in the changes of colony conditions (Table 4). The highest and lowest reductions in estimated brood weight (in European colonies 2 and 5) were matched respectively by the highest and lowest increase in net adult weight, making total adult mortality similar for both colonies (Table 4). Aside from the high total adult mortality of one African colony (number 4) and the low total adult mortality of one European colony (number 2), all net mortalities were similar. Store consumption scaled to average adult population varied much more than total mortalities: African colonies (0.772–1.095 kg) vs. European colonies (0.749–1.018 kg) (Table 4).

Discussion

The African and European colonies at high ambient temperatures showed frequent local "jumps" in temperature up to 42°C. Such 1–2 hour increases above

Table 1. Core temperatures of artificial 2 kg swarms of African and European bees held at different temperatures.

	Race and colony					
	African			European		
Temperature	1	2	3	1	2	3
10°C	22.6, 30.0[a]	34.0	35.0	35.3	35.4	34.2
5°C	[b]	[b]	35.0, 12.3[a]	34.0	34.0	33.1
−5°C			6.0, 4.5[a]	[b]	6.5	[b]

[a] Two core temperatures reported when swarm split into two or more clusters.
[b] Swarm died.

the apparent baseline temperature have not been reported previously. The causes for these increases could not be related to any detectable external or internal condition of the colony. A malfunction of the thermistor probes was discounted after switching to different probes had continued to detect similar "jumps". Rises in local temperature of such a duration could not be caused by individual bees undergoing thermogenesis through muscular activity, since an increase in thoracic temperature normally lasts 1–12 minutes (Esch, 1960; Roth, 1965). It is more probable that the rise in local air temperature was caused by a local burst of group metabolic activity (Kronenberg and Heller, 1982). The African bees might have generated such local temperature "jumps" more frequently than European bees by creating a center of activity around the thermistor probes. It is also possible that at high temperatures and under high humidities evaporative cooling of colonies becomes less efficient, causing local areas in a colony to reach higher temperatures. This could explain in part the broader temperature variability found by Darchen (1973) in African colonies in tropical humid areas of Gabon when compared to European colonies from less humid Israel reported by Lensky (1964a, b).

Any comparison of temperatures in colonies using small numbers of sensors is premature, given that the results are dependent upon the location of sensors in colonies with unknown temperature gradients and relatively high variances (Owens, 1971; Heinrich, 1981). Nevertheless, if African colonies maintain higher average brood temperatures than European colonies at high ambient temperatures, this could explain in part their faster development time (Kerr et al., 1972; Fletcher, 1978), contributing to a reproductive advantage in tropical areas. On the other hand, the African colony at the high elevation site showed lower average brood

Table 2. Clustering behavior of 10 African (AFR) and 10 European (EUR) groups of 100 workers in hoarding cages maintained at room temperatures.

	Date and race			
	November 23		November 27	
Cluster type	AFR	EUR	AFR	EUR
No cluster	2	0	1	1
Cluster wall	8	0	6	0
Cluster feeder	0	10	3	9
	$\chi^2 = 20$	$P < 0.001$	$\chi^2 = 12$	$P < 0.001$

Table 3. Changes in condition of broodless 1.5 kg African (AFR) and European (EUR) colonies after 25 days in cold temperatures.

		Adult population		Store consumption	
		Lost (kg)	Mean (kg)	Total (kg)	Per mean population (kg honey/kg bees)
AFR	Col. 1	0.95	1.00	1.72	1.711
	Col. 2	1.46	0.77	0.70	0.701
EUR	Col. 1	1.03	0.99	1.82	1.888
	Col. 2	1.18	0.91	0.92	0.989

temperature (33.5°C) than the European colony (35°C). If this observation is representative of the response of African bees to colder temperatures, lower nest temperatures could cause slower development of brood, inverting at least this feature of reproduction in favor of European races.

The clustering behaviors of the two races showed marked differences in the tests performed with artificially formed broodless units at room temperatures and in cold rooms. These observations coincide with those of Nuñez (1979). However, all of our observations were made under unnatural conditions: small groups of bees in hoarding cages or captive artificial swarms in cold rooms where periods of light and dark were irregular. African colonies respond to disturbances by "running" over surfaces and it could be that the light conditions of the "clustering tests" promoted such responses. Although no quantitative measurements were taken on the closed broodright colonies maintained in cold rooms or open broodright colonies at high elevations, clustering behavior did not appear to differ between the two races under these more natural conditions. According to Owens (1971), summer colonies with brood placed in cold rooms required over 2 weeks to achieve a stable cluster with isotherms similar to that seen in overwintering colonies. The colonies moved from tropical lowlands to high elevations underwent a similar change in conditions but were not left at the site long enough to observe the formation of a stable "overwintering" cluster.

Table 4. Changes in conditions of broodright African (AFR) and European (EUR) colonies after 10 days in cold temperatures (−2 to 10°C).

	Initial population		Changes in population			Store consumption[a]
Colony	Adult (kg)	Brood (dm^2)	Brood[a] (kg)	Net adult (kg)	Total adult[a] (kg)	kg honey/kg adults
AFR 1	3.55	108	−1.24	−0.25	−1.49	0.866
2	3.70	112	−1.14	−0.18	−1.32	0.980
3	2.30	112	−1.79	+0.65	−1.14	1.095
4	3.79	129	−1.79	−0.68	−2.47	0.775
5	3.39	104	−1.14	+0.17	−0.97	0.871
EUR 1	2.21	104	−1.92	+0.44	−1.48	0.835
2	1.54	52	−0.89	+0.48	−0.41	0.865
3	2.20	104	−2.19	+0.78	−1.41	0.749
4	3.87	104	−1.23	+0.00	−1.21	0.706
5	3.77	91	−0.69	−0.87	−1.56	1.018

[a] For estimation from other direct measurements see Materials and Methods.

There were no statistically significant differences in colony conditions between African and European bees kept 10 days at "cold temperatures" (mean of 4°C). The small differences between the races were confounded by the large variances among colonies. Total mortalities appeared to be fairly similar, but the ranges in consumption of stores related to size were slightly lower for the European colonies. Krell et al. (1985) did not detect significantly different weight changes in overwintering "Africanized" and European colonies in Argentina. Ranges of metabolic rates inferred from the utilization of stores can be compared to those obtained by other authors, assuming that the honey stores consumed had a 20% water content. The ranges in these tests (1.73–2.69 ml O_2/g adults hr) are similar to those measured by Heinrich (1981) for swarms at 5°C (1.8–4.3) and by Southwick (1982) for colonies at 5°C (0.68–2.04), but smaller than those measured by Kronenberg and Heller (1982) in groups of 1500–2500 bees on capped brood at 10°C (8.5–12.8). The ranges also compare favorably with those calculated from some overwintering experiments with European bees: 0.25–1.92 (Corkins, 1930), and 1.39–2.86 (Owens and Farrar, 1967). However, they are higher than the ranges measured by Southwick and Mugaas (1971) over a short period in an overwintering colony (0.2–1.0) and those calculated from data given by Gates (1914) (0.29–0.65) and Milner and Demuth (1921) (0.5) and Free and Simpson (1963) (0.5–1.0). Because of the high variance in metabolic rates it may be necessary to test large numbers of colonies for longer periods under more extreme conditions to demonstrate differences between African and European bees under field conditions.

Assuming that European and African colonies begin the winter with equal stores and that African colonies have slightly higher metabolic rates, they would consume stores at a higher rate and a higher percentage of these colonies would exhaust their stores and starve to death before foraging resumed in the spring. In each race mortality would vary from year to year depending on the stores collected in the previous season and on the duration and intensity of the winter. As winter temperature decreases and winters lengthen with increasing latitude, differential mortality between the races could lead to a decline of African bees such as observed by Kerr et al. (1982) and Dietz (pers. comm.) in Argentina, giving the appearance of a climatic barrier (Taylor, 1977; Kerr et al., 1982; Taylor and Spivak, 1984). The possibility that this "climatic barrier" is an illusion has been raised by Dietz et al. (1985) who have reported "Africanized" bees south of the overwintering zone defined by Kerr et al. (1982) and used by Taylor and Spivak (1984). However, a problem in interpreting the distribution of African-Africanized bees in Argentina is that the morphometric technique (Daly and Balling, 1978) used to identify these bees does not distinguish the extreme feral African bees from first or second generation crosses or other hybrid combinations between these races. In Argentina it is likely that the allopatric "African" populations in the north contain relatively few European characteristics while those further south possess increasing proportions of European traits due to sympatry with European bee populations. More refined technologies to detect the degree of hybridization between African and European bees represented by each colony and more inclusive experiments to control the sources of variance among colonies in field and laboratory tests will be needed to establish adaptive differences between these phenotypes and their intermediates and to assess present and possible future geographic patterns.

Although some generalized predictions concerning climatic limits of African

bees in North America have been made (Taylor, 1977; Taylor and Spivak, 1984), these predictions are based on broad ecological patterns and not on experimental evidence. As such, these are "soft" predictions and detailed observations and experiments are required to determine whether they are realistic. However, even with further study, it seems unlikely that any single factor will be found that determines the overwintering limit of African bees in North America. Rather, a combination of factors, perhaps even a variety of biological factors, which may differ from one ecological zone to another, is likely to be involved. It will be valuable to establish the relative importance of these factors in order to anticipate where and how African bees will interact with feral and managed honey bee colonies. Such anticipations or predictions are necessary for the development of meaningful programs to minimize the impact of African bees on beekeeping and agriculture.

Acknowledgments

Financial support was provided for work in Colombia by Proyecto Abejas Africanas–Colombia (Universidad Nacional de Colombia—International Development Research Centre) and for work in Venezuela by Cooperative Agreement 58-7B30-8-7 (United States Department of Agriculture—University of Kansas). Ricardo Ramirez and Ignacio Villa assisted with data collection and/or fieldwork. Comunidad por los Niños, Parque Nacional de los Nevados (Instituto Nacional de Recursos Naturales–Colombia) and Universidad de Oriente (Venezuela) provided sites for apiary locations. The Ministerio de Agricultura y Cría (Venezuela) permitted use of beekeeping equipment and facilities in Maturín, Venezuela. The USDA-ARS Honey-Bee Breeding, Genetics and Physiology Research Laboratory in Baton Rouge provided facilities for the preparation of the manuscript. Drs. George Byers and Charles D. Michener provided helpful comments on the text.

Literature Cited

Corkins, C. L. 1930. The metabolism of the honeybee colony during winter. Bull. Wyo. Agric. Exp. Sta. 175:1–54.

Daly, H. V., and S. S. Balling. 1978. Identification of Africanized honeybees in the western hemisphere by discriminant analysis. J. Kansas Entomol. Soc. 51:857–869.

Darchen, R. 1973. La thermoregulation et l'écologie de quelques espèces d'abeilles sociales d'Afrique (Apidae, Trigonini et *Apis mellifera* var. *adansonii*). Apidologie 4:341–370.

Dietz, A., R. Krell, and F. A. Eischen. 1985. Preliminary investigation on the distribution of Africanized honey bees in Argentina. Apidologie 16:99–108.

Esch, H. 1960. Über die Körpentemperaturen und den Wärmnehaushalt von *Apis mellifera*. Z. Vergl. Physiol. 43:305–335.

Fletcher, D. J. C. 1978. The African bee, *Apis mellifera adansonii*, in Africa. Ann. Rev. Entomol. 23:151–171.

Free, J. B., and J. Simpson. 1963. The respiratory metabolism of honeybee colonies at low temperatures. Entomol. Exp. Appl. 6:234–238.

Gates, B. N. 1914. The temperature of the bee colony. U.S. Dep. Agr. Bull. 96:1–29.

Heinrich, B. 1979. Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. J. Exp. Biol. 80:217–229.

Heinrich, B. 1981. The mechanisms and energetics of honeybee swarm temperature regulation. J. Exp. Biol. 91:25–55.

Kerr, W. E., S. L. Del Rio, and M. D. Barrionuevo. 1982. The southern limits of the distribution of the Africanized honey bee in South America. Amer. Bee J. 122:196, 198.

Kerr, W. E., L. S. Gonçalves, L. F. Blotta, and H. B. Maciel. 1972. Biologia compararda entre as

abelhas italianas (*Apis mellifera ligustica*), africana (*Apis mellifera adansonii*) e suas hibridas. *In* I Congreso Brasileiro do Apicultura, pp. 51–185. Florianópolis, Brazil.

Krell, R., A. Dietz, and F. A. Eischen. 1985. A preliminary study on winter survival of Africanized and European honey bees in Cordoba, Argentina. Apidologie 16:109–118.

Kronenberg, F., and H. C. Heller. 1982. Colonial thermoregulation in honey bees (*Apis mellifera*). J. Comp. Physiol. 148:65–76.

Kulinčević, J. M., and W. C. Rothenbuhler. 1973. Laboratory and field measurements of hoarding behavior in the honeybee. J. Apic. Res. 12:179–182.

Lensky, Y. 1964a. Les régulations thermiques dans la ruche en été. Ann. Abeille 7:23–45.

Lensky, Y. 1964b. Comportement d'une colonie d'abeilles à des temperatures extremes. J. Insect Physiol. 10:1–12.

Milner, R. D., and G. S. Demuth. 1921. Heat production of honeybees in winter. U.S. Dep. Agr. Bull. 988:1–18.

Nuñez, J. A. 1979. Comparative study of thermoregulation between European and Africanized *Apis mellifera* in Brazil. J. Apic. Res. 18:116–121.

Otis, G. W. 1980. The swarming biology and population dynamics of the Africanized honey bee. Ph.D. Dissertation. University of Kansas, Lawrence, Kansas. 197 pp.

Otis, G. W. 1982. Weights of worker honeybees in swarms. J. Apic. Res. 21:88–92.

Owens, C. D. 1971. The thermology of wintering honey bee colonies. U.S. Dep. Agr. Tech. Bull. 1429:1–34.

Owens, C. D., and C. L. Farrar. 1967. Electric heating of honeybee hives. U.S. Dep. Agr. Tech. Bull. 1377:1–24.

Rinderer, T. E., A. B. Bolten, A. M. Collins, and J. R. Harbo. 1984. Nectar-foraging characteristics of Africanized and European honeybees in the neotropics. J. Apic. Res. 23:70–79.

Roth, M. 1965. La production de chaleur chez *Apis mellifica* L. Ann. Abeille 8:5–77.

Ruttner, F. 1975. Races of bees. *In* The Hive and the Honey Bee, pp. 19–38. Dadant & Sons, Hamilton, IL.

Ruttner, F. 1976. African races of honeybees. *In* Proceedings XXV International Beekeeping Congress, pp. 325–344. Apimondia, Bucarest.

Southwick, E. E. 1982. Metabolic energy of intact honey bee colonies. Comp. Biochem. Physiol. 71A:277–281.

Southwick, E. E., and J. N. Mugaas. 1971. A hypothetical homeotherm: the honeybee hive. Comp. Biochem. Physiol. 40A:935–944.

Taylor, O. R. 1977. The past and possible future spread of Africanized honeybees in the Americas. Bee World 58:19–30.

Taylor, O. R., and M. Spivak. 1984. Climatic limits of tropical African honeybees in the Americas. Bee World 65:38–47.

Winston, M. L., and S. J. Katz. 1981. Longevity of cross-fostered honey bee workers (*Apis mellifera*) of European and Africanized races. Can. J. Zool. 59:1571–1575.

Winston, M. L., and S. J. Katz. 1982. Foraging differences between honeybees of European and Africanized races. Behav. Ecol. Sociobiol. 10:125–129.

Winston, M. L., G. W. Otis, and O. R. Taylor. 1979. Absconding behaviour of the Africanized honeybee in South America. J. Apic. Res. 18:85–94.

Winston, M. L., O. R. Taylor, and G. W. Otis. 1980. Swarming, colony growth patterns and bee management. Amer. Bee J. 120:826–830.

Winston, M. L., O. R. Taylor, and G. W. Otis. 1983. Some differences between temperate European and tropical African and South American honeybees. Bee World 64:12–21.