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AFRICANIZED HONEYBEES IN VENEZUELA: DEFENSIVE BEHAVIOUR

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Introduction

The term Africanized bee refers to the hybrid population of honeybees (Apis mellifera L.) which currently exists in South America. This population resulted from matings between 26 A. m. scutellata queens, imported from South Africa to Brazil in 1956, and the various European commercial varieties that had been imported to Brazil in earlier years. This importation was originally made to improve the quality of honey production by honeybees in Brazil, through the introduction of a genotype adapted to a tropical environment. The imported bees also introduced a genotype that was much more defensive than the European varieties already in use in Brazil.

The rapid spread of Africanized bees through South and Central America poses a threat to the beekeeping industry in the United States. The Bee Breeding and Stock Center Laboratory at Baton Rouge, Louisiana, was directed to carry out research on how to reduce the effects of this bee on the US beekeeping industry. This paper presents the results of part of this research.

Behaviour model

Honeybee defensive behaviour is a complex sequence of actions by a group of honeybees. In order to study such complex behaviour it is first necessary to divide the behavioural sequence into its component parts. We have constructed a model, Fig. 1 (Collins, et al., 1980), to identify units of defensive behaviour which would be subject to genetic analysis and to manipulation by selective breeding. Fig. 1 shows the basic four-step sequence we have proposed, and the stimulus-response pairs within that sequence. The responses can be demonstrated by a wide range of behaviour and can show variation within a particular behaviour.

The first step in the behaviour sequence is alerting. A stimulus from the environment is received by a worker honeybee who then responds in one of three ways: she becomes alert, or she recruits other bees, or she withdraws. An alerted worker has a characteristic posture with her body raised, the abdomen cocked upward, wings extended and sometimes fanning. In this position the mandibles are held open, the antennae are waved, and occasionally the sting may be protracted. The posture is non-directional and reflects a level of excitation that is receptive to a second stimulus from the environment.

A recruiting bee opens her sting chamber with the sting protracted, and runs into the colony. The protracted sting position allows for the release of alarm pheromone which communicates to other bees in the colony; these bees may become alert and possibly recruit more bees. The third possible response, withdrawal or fleeing, may be seen during hive manipulations. Bees not in a physiological state that allows them to engage in defensive behaviour (younger nurse bees) show this response.

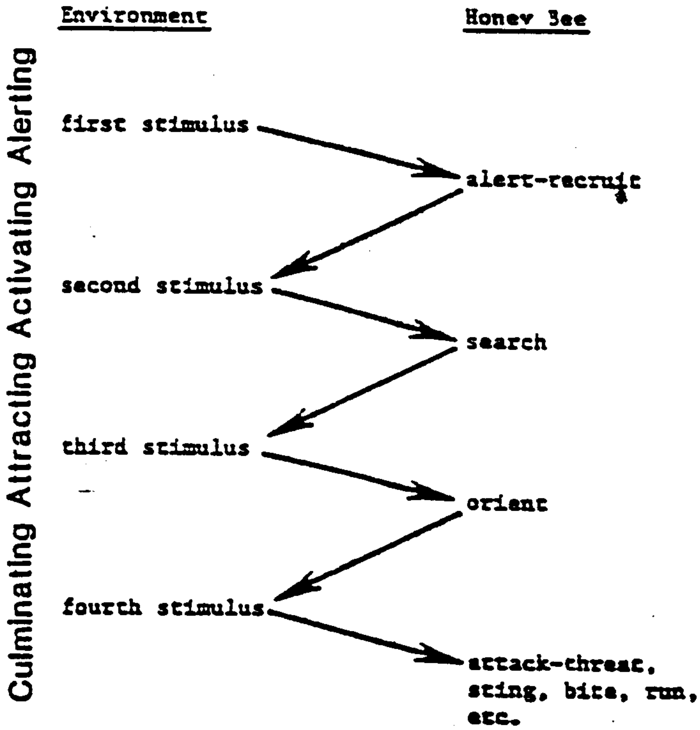

Fig. 1. Honeybee defensive behaviour.

The second step of defensive behaviour is activating, during which a bee will seek the source of the disturbance. Initially the searching behaviour takes place randomly in the area close to the alerted bee. However, in the absence of an appropriate third stimulus this search may continue throughout the colony and beyond the confines of the colony.

During the search phase of defensive behaviour, if an appropriate environmental stimulus (third stimulus) is encountered, the alerted bee will orient (attraction) to that stimulus. Often the same disturbance simultaneously activates and attracts, and the sequence of the behaviour is so rapid that the components may not be distinguished by the observer.

Once the alerted bee has searched and oriented to an appropriate disturbance, the continuation of this disturbance will provide a fourth, culminating stimulus that will elicit attack. Attack can encompass various responses by the worker bee. In threat behaviour, the bee rapidly flies around the source of the fourth stimulus, making a high pitched buzz that is markedly different from that of a foraging bee. This buzzing in itself constitutes a threat that may be sufficient to deter an intruder from disturbing the colony further.

If the bee is on the same surface as the source of the first stimulus, and close to it, her threat behaviour may involve running or walking towards the stimulus, with body thrusts toward this stimulus, and antennae and prothoracic legs waving. Stinging and biting are the most obvious attack behaviour associated with honeybees. In addition the bee may pull hair, or burrow into hair, clothes, fur, or orifices of an intruder. Stinging and possibly biting can release pheromones that serve as the first stimulus to alert other bees, or possibly as a stimulus for orientation of searching bees. Finally, for some bees, running is a defensive option when the integrity of their nest has been severely threatened. Such bees may run away from combs that the beekeeper has manipulated, or they may leave the colony entirely.

Methods for standardized colony evaluation

Having divided the sequence of honeybee defensive behaviour into component parts, it was then necessary to devise a standard measurement procedure to compare defensive behaviour of different types of bees (Collins & Kubasek, 1982). Our standardized test involved presenting a series of stimuli to a colony and measuring the colony's response in several ways. The stimuli presented successively were:

1. A chemical stimulus consisting of a mixture of alarm pheromones associated with the honeybee sting (Blum et al., 1978), diluted in paraffin oil 1:99 (vol/vol).

2. A physical stimulus provided by the propulsion of a glass sphere (weight 18.5 g, diameter 2.3 cm) at the hive directly above the entrance. This physical stimulus provided further arousal to the bees being tested.

3. A visual (as well as a tactile) stimulus: two dark suede leather squares (5 x 5 cm) moved in front of the hive by a mechanical apparatus; they were swung vertically through 20 cm, 120 times per minute, providing a dark, jerkily moving object, with a distinctive leather odour, and a slightly rough texture - all prime stimuli for eliciting stinging (as demonstrated by Free, 1961).

In the standardized test, responses were assessed: by photographing bees at the entrance (from which numbers responding during the defensive behaviour sequence could be counted); by photographing the space in front of the hive (from which counts of flying bees could be made); by recording the times at which bees, responding to the initial chemical stimulus, emerged from the entrance in alerted posture, and the time at which bees responded to the leather squares; and by counting the number of stings embedded in the leather squares.

Experimental results

Comparison of two ecotypes

We used this standardized test of defensive behaviour on 2 ecotype groups: 150 European colonies headed by queens of commercial stocks in Louisiana, USA, and 147 Africanized colonies headed by queens that had free-mated in Venezuela (Collins et al., 1982). Table 1 gives the results; in all assessments of defensive behaviour the Africanized bees were significantly more responsive. They responded about 3 times as fast as the European bees to alarm pheromone, and about 27 times as fast to the leather squares. The number of bees issuing from the colony in response to the disturbance provided by this test was also about twice as great in the Africanized group, at each stage of the test. Finally the number of stings was, on average, 8-10 times as great in the Africanized group.

One other important fact, clearly evident from our results, is that the Africanized population was extremely variable. Colonies that were Africanized could be as non-responsive or gentle as many of the Europeans, but some Africanized colonies were very extreme in their defensiveness, and the values in Table 1 represent an average. However, when a beekeeper is working in an apiary the extremes of this behaviour are his major concern. This variation is very useful because it allows geneticists to select the more manageable bees, and indicates that acceptable stock of Africanized bees could be produced rapidly by genetic selection.

Evaluation of hybrids

Another approach being taken by a few beekeepers in Venezuela is to evaluate a number of types of European stocks or races for their combining ability with Africanized bees. Queens of known European genotypes are being reared and are then allowed to free-mate in an area with Africanized bees. The temperament of the resulting F_1 hybrid colonies is evaluated using our standardized test; Table 2 presents some results. We had 12 European colonies (European queens mated to European drones - 6 Italian and 6 Caucasian), 6 Africanized colonies (swarms caught in the wild, headed by Africanized queens mated in an Africanized area), and 12 F_1 hybrids (6 Italian queens and 6 Carniolan queens, each free-mated in an Africanized area). The results show that the hybrids are clearly intermediate between the two parental types (European and Africanized) for all of the characters. They tend to respond to alarm pheromone almost as slowly as the Europeans do, but their response to the moving target was more like the fast-responding Africanized parent. The number of bees responding was intermediate and so was the number of stings. However 2-3 times the average number of stings from European colonies is a higher level than many beekeepers or their neighbours would tolerate.

Table 1. Results from a standardized test of colony defence using 150 European colonies (US commercial stocks) and 147 Africanized colonies (free-mated in Venezuela).

	response time (s) to:		no. bees responding:				no. stings
	alarm pheromone	moving target	before stimulus	30s after stimulus	60s after stimulus	90s after stimulus	
European	13.1 ±0.5 **	9.2 ±0.5 **	44.2 ±3.5 **	61.1 ±4.9 **	66.6 ±4.0 **	84.3 ±4.4 **	10.4 ±0.9 **
Africanized	5.4 ±0.3	0.3 ±0.1	70.6 ±7.0	121.6 ±6.8	141.7 ±7.8	172.8 ±9.8	85.7 ±2.6

** Paired means are significantly different at P <0.01

Table 2. Results from a standardized test of colony defence using European (6 Italian, 6 Caucasian), Africanized (6) and hybrid (6 Italian x Africanized, 6 Carniolan x Africanized) colonies.

	response time (s) to:		no. bees responding:				no. stings
	alarm pheromone	moving target	before stimulus	30s after stimulus	60s after stimulus	90s after stimulus	
European	10.2	5.6	19.5	33.1	44.5	64.6	30.9
hybrids	8.6	2.2	44.5	49.4	66.5	117.2	76.4
Africanized	3.6	0.8	73.7	89.4	115.5	256.6	143.2

The hybrids in Table 2 were of two types. Considering them separately, we find that the Italian-Africanized hybrid was less responsive in all tests than was the Carniolan-Africanized hybrid. It is thus possible that some specific crosses would be more useful in controlling or modifying defensive behaviour than others. Comparison of our results in Venezuela with results of similar standardized tests in Brazil seems to indicate that the Africanized bee at present in northern South America is more defensive than its counterpart in southern and central South America. A possible explanation for this is that the Africanized bee crossed with a feral population of European bees that existed in Venezuela, probably Apis mellifera mellifera, to produce a hybrid that is extremely aggressive. This particular cross of any bee type to A. m. mellifera, is one that frequently produces defensive bees (Adam, 1984).

Heritability estimates

Another aspect of the genetics of defensive behaviour that we studied was the ability to predict success in a genetic selection programme. For this estimation, an array of inbred honeybee queens (A. mellifera) were mated with single drones from either European (Baton Rouge, Louisiana, USA) or Africanized (Venezuela) honeybee colonies. Worker offspring from these matings were evaluated using the standardized test of defensive behaviour. The heritability (h^2) values calculated for 6 of the tests were variable (Collins et al., 1984). (Heritability is a value lying between 0 and 1 which indicates the quantity or percentage of the variation due to genetic control within the total phenotypic variation.) Time to react to pheromone could not be estimated because of negative variance components in the statistical analysis. The h^2 value for time to react to leather squares was 0.38 ± 0.19; for number of stings h^2 was 0.57 ± 0.24; and for numbers of bees responding before stimulus and 30, 60 and 90 s after stimulus h^2 values were 0.26 ± 0.2, 0.12 ± 0.0, 0.14 ± 0.0 and 0.55 ± 0.0, respectively. These heritability estimates for defensive behaviour were sufficiently high to predict reasonable success in a selection programme for gentler and more productive bees.

Management

I have discussed our genetic approach to dealing with and looking at defensive behaviour. It is also appropriate to consider how management of colonies can be improved or altered. Venezuela had an active beekeeping community when Africanized bees migrated into the country, and there are several ways in which successful beekeepers have adapted to work with these bees. Prior to Africanization a veil, street clothes, and a small smoker were sufficient for working colonies, but now the beekeepers and their helpers must wear a veil, some sort of protective suit usually of heavy cotton, gloves (sometimes rubber gloves), and boots with ties, straps or tape to seal the openings.

Many beekeepers have been asked to move their apiaries because people or livestock in the area were being bothered or were afraid of being stung. Apiaries are now generally much farther away or are shielded, e.g. by a stand of trees. Beekeepers must pay for any animals killed by their bees - an expense not incurred before Africanization. Beekeepers must also spend more time and energy in maintaining good relations with their neighbours; this might include providing information on the importance of honeybees in pollination and giving samples of honey.

Also the management of apiaries has changed. In many areas of Venezuela, hives must be placed on stands for protection from ants. With Africanized colonies, it is frequently necessary to have fewer hives per stand or even to provide a separate stand for each hive. Fewer colonies per apiary help to reduce the level of defensive behaviour and the probability of having neighbours or livestock disturbed. When working a colony, constant smoking is necessary; two people work the colony together, one doing nothing but smoking the bees. (Previously one person could smoke and work the colony alone.) After disturbing the apiary it may be necessary to drive around in the area close to the apiary to escape from the cloud of bees that would otherwise follow the vehicle out of the apiary and towards other people and livestock. Alternatively, colonies are worked at night, particularly when removing honey.

Many beekeepers in Venezuela have given up their beekeeping career. Some have been forced out of business by their neighbours burning or destroying equipment; some do not care for beekeeping any more because of the extreme defensiveness of the Africanized bee and the resulting need to wear protective clothing while working. Many small farmers who used to catch a few swarms to supplement their income no longer do so. The overall result of the migration of the Africanized bee to Venezuela is that there are now very few beekeepers, and they are both very skilled, and very hard working.

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