BEHAVIORAL GENETIC ANALYSIS OF COLONY-DEFENSE BY HONEY BEES*

T.E. RINDERER

Bee Breeding & Stock Center Laboratory,
AR, SEA, USDA, Baton Rouge, Louisiana 70808, U.S.A.

SUMMARY

Defensive behavior in honey bees is a complicated behavioral sequence of actions. The sequence includes four major categories : alerting, activating, attracting, and culminating. Each major category has sub-categories of possible responses. Because of this, complex variation exists among the colonies. Surveys of the defensive behavior of European and Africanized bees showed that in time-limited tests, Africanized bees were ca. 10-fold more defensive than European bees. Measurements of hybrids showed that most genes which intensify defensive behavior are dominant.

RESUMEN

Análisis genético de la conducta defensiva de las colonia de abejas

La conducta defensiva de las abejas es el resultado de una complicada secuencia de actividades interconectadas. Tal secuencia la conforman 4 importantes tipos de actividad : alerta, activación, atracción y culminación, cada una de las cuales esta compuesta por sub-actividades o respuestas posibles que son ampliamente variables entre colonias. Pruebas de conducta defensiva demostraron que, en ensayos de tiempo limitado, las abejas Africanizadas tienen una conducta defensiva diez veces superior a la de las Europeas. Los resultados de las mediciones realizadas en los híbridos, mostraron que la mayoria de los genes responsables del aumento del comportamiento defensivo son dominantes.

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The two scholarly reviews of African- and Africanized-bee literature both give considerable attention to the readiness and capability of these bees to defend their colonies (Fletcher, 1978 ; Michener, 1975). This attention is certainly not unfounded. The sight of a colony of Africanized bees engaged in a massive defensive response commands the undivided attention of an observer, and reports of such events have made vigorous colony defense the best known characteristic of Africanized bees. Since Africanized bees are so capable of defending their colonies, considerable efforts have gone to the study of their defensive behavior. One hope spurring these studies is that modification through selective breeding can help dampen the intensity of this behavior and thereby reduce at least some of the problems caused when a bee population becomes Africanized. However, successful modification of defensive behavior by selective breeding will rest on a reasonable understanding of the genetic elements that regulate this behavior.

Before fruitful genetic experiments themselves can be undertaken, defensive behavior itself must be reasonably well understood. To be most useful, this understanding must include three elements. First, the individual activities which together comprise this complex behavior must be identified. Second, techniques must be devised to measure qualitatively or, as appropriate, measure quantitatively the activities comprising the behavior. Third, sufficient surveys of bee populations must be made to verify that at least some of the component activities as measured by the devised techniques are both adequately consistent in single colonies of bees and also differ between colonies.

The identification of the individual activities comprising colony defensive behavior is not a small task. Even a cursory review of work published on defensive behavior in honey bees reveals that almost every worker in the field has studied a somewhat different aspect. Some researchers have studied the non-stinging alert response to alarm pheromones by bees in field colonies (Boch et al., 1962, 1970 ; Ghent and Gary, 1962 ; Maschwitz, 1964, 1966 ; Shearer and Boch, 1965), and others have studied this same response by bees in small laboratory cages (Collins and Rothenbuhler, 1978). Still others have explored the ability of a variety of stimuli such as color, odor, and movement to elicit stinging by bees (Free, 1961 ; Free and Simpson, 1968 ; Koeniger, 1978). Beyond these basically qualitative studies, several attempts to quantitatively measure non-stinging features of colony defense (Boch and Rothenbuhler, 1974) and also specific aspects of stinging have been made (Gonçalves and Stort, 1978 and Stort, 1970, 1974, 1975a, 1975b, 1975c, 1976). The variety of response measured in these different studies indicates that colony-defensive behavior is a complicated collection of actions. Indeed, when attempting to understand this behavior from a synthesis of published research and personal observation, the paramount emergent conclusion is that the defense behavior of honey bees is extremely diverse and complex.

In an attempt to provide some order to this diversity and complexity, a classification model of defensive behavior has been developed (Collins et al., 1980). This model recognizes two central features of colony defense. First, many actions are clearly temporally sequential. In light of this, the model identifies four discrete sequential steps within the full behavior : alerting, activating, attracting, and culminating. The second central feature of defensive behavior recognized by the model is that at least in the alerting and culminating steps several possible actions may occur which are mutally exclusive, at least temporally. Some bees may, in time, perform all these actions but probably this is not the case for most bees.

The four major steps are reasonably straightforward. In the alerting step a bee may assume a characteristic alert posture (Ghent and Gary, 1962), may recruit other bees by running into the hive with her sting chamber open and her sting protracted (Maschwitz, 1964) or may simply withdraw into the hive. After responding in any of these three ways a bee may then become activated. If activated, a bee seeks the source of disturbance. This search, if the source is not found, may extend to several meters from the hive. In fact, I have observed activated Africanized bees a measured 120 M from their colony. Once an appropriate stimulus source is found a bee orients or is attracted to that stimulus. After having drawn near the source of the disturbance the bee may engage in a culminating response or a sequence of such responses. Among these responses the model identifies threat actions, during which the source of stimuli is not touched. Also identified are burrowing, biting, hair pulling (which is perhaps a variant of biting), and stinging ; all of these actions involve contact with the stimulus source. To this list I add head-bumping. In recent experiences with Africanized bees I observed that on several separate occasions bees in flight repeatedly and forcefully bumped their heads into the stimulus source. In one instance I counted 17 such bumps before the bee finally stung. Lastly, the option of leaving the vicinity of the disturbance is given by the model.

This model supplies an organized classification of the complicated collection of actions which together comprise defensive behavior. It thus permits the development of a system of testing and measurement which is designed to show defensive responses in a clear systematized fashion. Such a measurement system has been developed by staff at my laboratory. Generally, a variety of stimuli are presented to a colony of bees in such a way that the steps in the process of defense can each be observed and measured. Since many responses are momentary, portions of the data are initially recorded on film or videotape.

As yet unpublished experiments evaluating the testing system showed that the data it produces are quite satisfactory. The four major steps of the model were both apparent and measured. Also, repeated tests of the same colony gave essentially the same results. Using this measurement system, surveys have been made of the defensive behavior of approximately 150 colonies of European bees in Louisiana and 150 colonies of Africanized bees in Venezuela. These surveys showed no qualitative but strong quantitative differences between bees in the two populations. At all steps in the defensive process, Africanized bees responded much more quickly to stimuli. For example, when given stimuli appropriate for cueing culmination, Africanized bees responded 33 times more quickly than European bees. Our testing procedure provides an opportunity for bees to sting an object for a period of 30 seconds. Africanized bees stung 8.5 times more than European bees during this period. Generally, when considering the entire test sequence, Africanized bees proved to be ca. 10-fold more defensive than European bees.

These surveys were accompanied by a more closely controlled experiment using small Africanized and European colonies of identical sizes in Venezuela. This comparison revealed differences between European and Africanized bees of similar magnitude and direction to those found in the survey.

As well as providing evidence for the rather obvious conclusion that Africanized bees deserve their reputation as able colony-defenders, the survey also provided two important pieces of information. First, and most importantly, the magnitude of the difference between the defensive responses of populations of Africanized and European bees has been quantitatively documented. Heretofore, such differences have been reported qualitatively or as numerical differences between a few selected colonies. Second, strong differences were not only shown to exist between European and Africanized populations of bees but also between colonies of similar racial origin. These observations strongly support the notion that breeding programs designed to produce less defensive Africanized bees stand a good chance of success.

With a working model of defensive behavior, an adequate system of measurement and the assurance that measurable differences occur between the responses of different colonies of bees, a wide variety of genetic experiments can be conducted. The first and rather obvious experiments are to evaluate the defensive responses of hybrid bees resulting from crosses of colonies that differ strongly. We have done several such experiments both within and between Euronean and Africanized bees. The results of these experiments indicate that F_1 hybrids generally tend to show defensive behavior similar to or, in certain cases, greater than the more defensive parent. Generally, for each step in the sequence of colony defense, these experiments indicate that most genes which intensify defensive behavior are dominant.

Thus Africanized-European hybrids defend their colonies very much like their Africanized parents. Thus far, the results of our experiments suggest that the production of less defensive stocks of bees will be done through careful and rather slow selection programs. There is one notable exception. One specific F_1 hybrid we tested repeatedly followed the general trend of F_1 hybrids for the steps of alerting, activating, and attracting. That is, they were quick to become alert, intensively recruited other bees to defense, and quickly searched out a source of disturbance. However, at that point they went no further. They simply flew near the source of disturbance, but did not sting it nor did they engage in any form of culmination activity. Thus, there is the possibility that, although somewhat rare, important genes exist which tend to strongly reduce the intensity of defensive behavior. The early incorporation of such genes into stocks of bees would speed the progress of selection programs designed to produce tractable bees.

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