Journal of Apicultural Research 19(4): 224–231 (1980)

A MODEL OF HONEYBEE DEFENSIVE BEHAVIOUR*

ANITA M. COLLINS, THOMAS E. RINDERER, KENNETH W. TUCKER, H. ALLEN SYLVESTER AND JAMES J. LACKETT

Bee Breeding and Stock Center Laboratory, AR, SEA, USDA, Baton Rouge, LA 70808, *USA*

Manuscript received for publication 17 *October* 1979

Summary

A model of defensive behaviour by an individual honeybee (*Apis mellifera*) is presented. The behavioural sequence involves four basic steps: alerting, activating, attracting and culminating. The model accommodates both genetic and environmental variation.

Introduction

Interest in honeybee (*Apis mellifera*) stinging behaviour has increased in the last two decades. This interest is, *inter alia*, a response to the importation to Brazil of the antagonistic *A mellifera adansonii* in 1956 (Kerr et al., 1967, 1968) and the subsequent escape, hybridization and spread of this bee (Michener, 1972). Interest has also been spurred on by partial identification of honeybee alarm pheromones: isopentyl acetate from the stings (Boch et al., 1962) and 2-heptanone from the mandibular glands (Boch & Shearer, 1971; Shearer & Boch, 1965).

However, stinging is only one component of the behavioural pattern known as 'colony defence'. Indeed, colony defence is a complicated sequence of actions by many individual bees which may or may not include stinging.

The different approaches to studying colony defence reflect its complexity. A non-stinging alert behaviour, clearly part of colony defence, has been described as a response to isopentyl acetate, 2-heptanone and excised stings (Boch et al., 1962, 1970; Shearer & Boch, 1965; Gary & Ghent, 1962). It has been measured quantitatively at the hive entrance (Boch & Rothenbuhler, 1974), and with bees in small cages in the laboratory (Collins & Rothenbuhler, 1978). Free (1961) and Free and Simpson (1968) investigated the effect of various stimuli, such as colour, odour, and pheromones, on the propensity for bees to sting small cotton balls covered in muslin. Stort (1970, 1974, 1975*a*, 1975*b*, 1975*c*, 1976) and Goncalves and Stort (1978) measured several responses of bees to a leather ball jerked up and down in front of the hive entrance. These included three different measures of stinging, as well as the distance the observer was followed by bees after the test. Boch and Rothenbuhler (1974) assessed the defensive tendency of colonies by blowing human breath at guard bees and by opening colonies. Yet, despite these diverse data, no model for colony defensive behaviour has been proposed.

We constructed a model in an attempt to identify units of defensive behaviour most likely to be subject to genetic analysis and to manipulation by selective breeding. In the process of integrating published research with our personal observations of bee behaviour we were confronted with an array of complexity and diversity. While variation in behaviour is the stock in trade of behaviour geneticists, complex variation requires the clarity of classification before it can be productively investigated with precise experiments. This model is presented as an organization of honeybee defensive behaviour which incorporates known phenotypic variation and identifies those areas of variation where the application of behaviour genetic analysis and selective breeding programmes are most likely to be productive.

---

* In co-operation with Louisiana Agricultural Experiment Station.

Model Considerations

The unit of defence

The basic unit of colony defence is the behaviour of an individual worker bee. It is common in the manipulation of colonies to experience the defensive behaviour of a single bee. Apparently collective defensive episodes can be viewed as an aggregate of individual responses with the activities and pheromone emissions of other members of the colony functioning as stimuli for the individual defending bees. Thus, the model deals with honeybee defence as a major behaviour pattern contained in the behavioural repertoire of a single bee.

The response sequence

Individual honeybees have a wide range of possible defensive responses. Some of these responses are temporally sequential and others are mutually exclusive. The sequential pattern can be classified into four discrete steps: alerting, activating, attracting and culminating (Fig. 1), modified from the ant work of Wallis (1962*a*, 1962*b*), Robertson (1971) and Lofgvist (1976). These steps serve as the fundamental organization of the model.

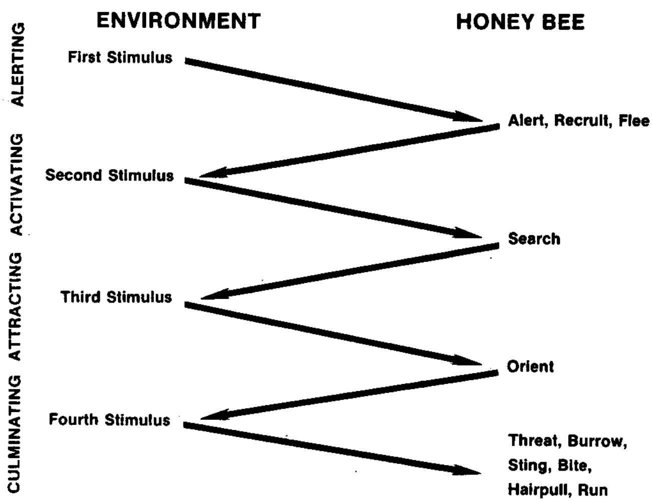

FIG. 1. Basic sequence of honeybee defensive behaviour.

Alerting

The first step in the overall behaviour pattern is alerting. Within this step, three possible responses can be identified: an alert response, a recruiting response, and a withdrawal response.

The characteristic tense posture of an alerted worker has been variously described by Ghent and Gary (1962) and Maschwitz (1964, 1966). A worker raises her body with abdomen cocked upward, and with wings extended and sometimes fanning. In this position the mandibles are held open and the antennae are waved. Sometimes the sting may be protracted. In a group of alert workers, individuals may face in many directions and thereby provide evidence that the response is not directional.

A recruiting bee opens her sting chamber with her sting protracted and runs into the hive (Maschwitz, 1964). Sting protrusion releases alarm pheromone, which in turn stimulates bees in the colony to defensive behaviour. If a recruiting bee has had her sting and its associated pheromones excised, no bees are recruited (Maschwitz, 1964). Possibly a recruiting bee leaves the area disturbed by an intruder and thereby avoids subsequent steps of defensive behaviour. Alternatively, she may encounter her own pheromone emission and, in effect, recruit herself to further defensive activity. Furthermore, a bee recruited by alarm pheromone usually does not recruit other bees (Maschwitz, 1966).

A third possible response within alerting is withdrawal or fleeing. If a stimulus contains directional information, some bees retreat from the stimulus. This is commonly seen during hive manipulations. With further stimulation, however, bees may proceed from withdrawal to other responses.

Activating

The second step of defensive behaviour is activating, during which a bee seeks the source of the disturbance. The searching starts close to the bee if a hive is opened, or near the entrance of an unopened hive. In time, and in the absence of further stimulation, activated bees may engage in searching several metres or more from the hive.

Attracting

When a searching bee encounters an appropriate stimulus, she orients (or is attracted) to that stimulus. Often the same disturbance simultaneously activates and attracts, and a sequence of the effects is so rapid that it goes unnoticed by an observer. However, the discrete nature of the two responses is apparent when two spatially separate stimuli occur, or when a complex stimulus is presented and is then quickly removed to a remote location.

Culminating

In this step various responses are possible. Only one response can occur at a time, but a bee may sequentially display two or more of the following responses: threat, burrow, sting, bite, hairpull, run.

In threat behaviour, the bee rapidly flies around the culminating stimulus. This flying is accompanied by a high-pitched sounding buzz that differs markedly from that of a foraging bee. If a stimulus is close to a bee and on the same surface, threat behaviour involves running or walking towards the stimulus source, making body thrusts towards the source, with antennae and prothoracic legs waving.

For some bees, running is a defensive option when the integrity of their nest place has been disrupted. These bees run away from combs that are being manipulated and go to undisturbed combs or even leave the nest.

Stinging, biting and hair pulling, and burrowing into hair, clothes or fur, are well known to experienced beekeepers. Stinging, and perhaps biting, can release pheromones that serve as stimuli for other bees.

Associated stimuli

In Fig. 1 the terms first, second, third, and fourth stimulus represent any of a number of possible cues from the environment that might function as stimuli. A particular cue might function as a stimulus in any or all of these steps, but some cues may be specific to a particular step. Table 1 is a list of cues believed to be stimuli for each step of defensive behaviour, compiled from beekeeping experiences. In any step stimuli can be summed. They can be cumulative in action; several different cues from the environment can serve in combination as a stimulus for one step. Simple stimuli can be cumulative over time; subliminal repetition of the same stimulus can cause a response.

Variation

Two sorts of variation in colony defensive behaviour are commonly observed in the field. One is a difference from bee to bee or colony to colony under similar conditions; the other is a difference in the response of the same colony under different conditions. Genetic and environmental variation are to be expected in both cases, genetic variation being predominant in the first and environmental variation predominant in the second. Evidence for genetic differences in colony defensive behaviour has been provided by Boch and Rothenbuhler (1974), Collins and Rothenbuhler (1978), and Goncalves and Stort (1978). Some environmental conditions that may possibly cause variation are listed in Table 2. These and the stimuli listed in Table 1 cover all the factors that, in beekeeping literature, are suggested as making stinging more or less likely. Environmental conditions that may have direct effects are those that operate *during* defensive behaviour; those that may have indirect effects influence the bee before the onset of a defensive response.

All the variation occurs within the four basic steps. For example, one bee may be induced to alert behaviour and no further, by a stimulus that takes another bee quickly through all steps to culminating. Also, on a single occasion few if any bees display all the behavioural options in those steps having options.

TABLE 1. Stimuli known or believed to elicit defensive behaviour in the honeybee.
0 — probably *not* a stimulus for this step
? — may be a stimulus for this step
X — probably *is* a stimulus for this step

Stimulus	*Alerting*	*Activating*	*Attracting*	*Culminating*
Motion	?	?	X	?
Colour contrasts	X	?	X	?
Shape	?	?	X	?
Texture of substrate	0	0	0	X
Vibration of substrate	X	?	0	?
Mechanical stimulation of bee	X	X	X	X
Harassing bees	?	?	?	?
Scent:				
colony	0	0	?	X
mammalian:				
breath, CO_2	X	?	X	0
sweat, fur	?	?	?	X
Pheromones				
2-heptanone (mandibular gland)	X	X	?	?
isopentyl acetate (sting)	X	X	?	0
other components (sting)	X	X	?	?
whole sting	X	X	?	?

The Model

We have employed a hydraulic model to organize the relationships and variations of the defensive behaviour pattern. Fig. 2 represents the defensive pattern of a single hypothetical bee that would display all the known behavioural options. Simple changes made in Fig. 2 would give models for bees that have somewhat different defensive behaviour patterns.

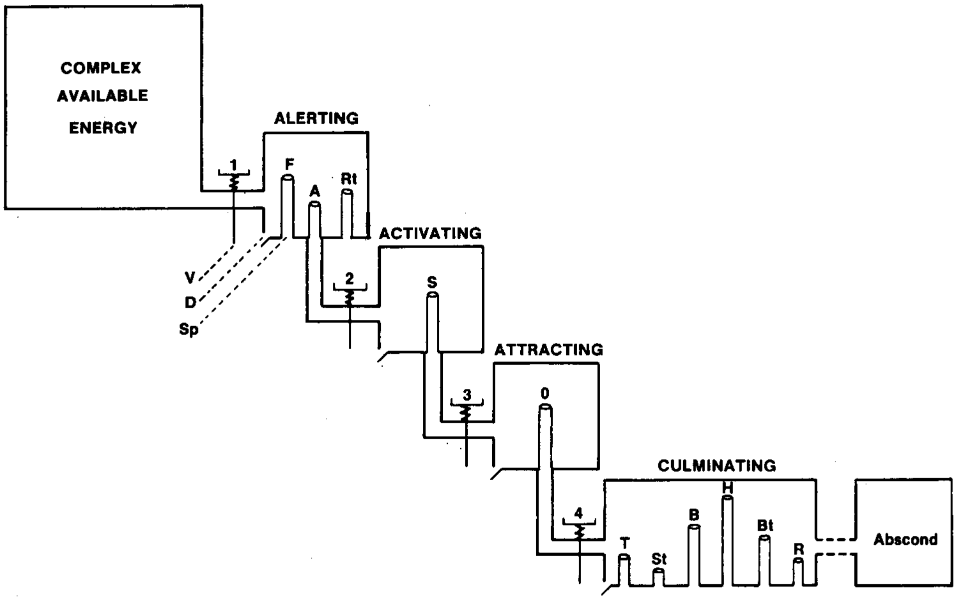

FIG. 2. Detailed epigenetic model of honeybee defensive behaviour.
Explanation in text. V — value, D — drain, Sp — standpipe, F — flee, A — alert, Rt — recruit, S — search, O — orient, T — threat, St — sting, B — burrow, H — hairpull, Bt — bite, R — run, 1 — first stimulus, 2 — second stimulus, 3 — third stimulus, 4 — fourth stimulus.

Complex available energy

This model, inspired by the motivational-hydraulic model of Lorenz (1950), uses the flow of a fluid through a series of reservoirs. The fluid, or complex available energy (CAE), represents the amount of energy a single bee would use in defensive behaviour. The position of the CAE in the system indicates the current activity of the bee. Greater amounts of CAE would result in greater flow rates through the system, which would give an increased intensity of response throughout the entire behavioural pattern.

Reservoirs

The model contains several reservoirs. The first is the bee's reserve of CAE; its amount is a major variable between individual bees. The next four represent the four steps of defensive behaviour: alerting, activating, attracting and culminating. Letters within each reservoir indicate the options for the expression of the defensive behaviour at that step on the sequence.

The last reservoir represents absconding, an event in which the queen and the adult bees abandon the hive or nest. Repeated disturbance of a colony, with the resultant stimulation of defensive behaviour, at times results in absconding. We have put the absconding reservoir in the model to indicate its connection with defensive behaviour. The connection is represented by dotted lines because its precise nature is still unclear. However, this response has been reported as part of the colony defence of an ant, *Pheidole dentata* (Wilson, 1976).

TABLE 2. Environmental conditions that may possibly affect defensive behaviour in the honeybee. Entries under the heading *Direct* do not necessarily relate to entries in the same line under *Indirect*.

Direct	*Indirect*
Age	Age distribution in colony
Agricultural and industrial chemicals	Agricultural and industrial chemicals
Atmospheric electrical potentials	Brood-rearing activities
Barometric pressure	Comb-building activities
Geomagnetic field	Crowding:
Humidity	in one colony
	no. colonies per unit area
Light:	Disease:
sun *vs* shade	adult
day *vs* night	brood
photoperiod	
	Nectar flow
Nutritional level:	
current stores	Nest destruction:
sources	by moth (other than stimulus)
	by mouse, fungus, etc.
Temperature:	
variable regime	Nutritional level:
hot	developmental
cold	current stores
	sources
	Pollen availability
	Queenlessness
	Robbing
	Water availability

Valves

Spring-loaded valves control the flow of CAE between reservoirs. The valves are connected to pans that collect cues appropriate as stimuli for the next response.

Differences in perception of stimuli by different bees are of major importance. To accommodate these differences, various model representations would have springs of different strengths controlling the valves. Relatively low perception of stimulus would be analogous to slightly depressed (opened) valves, as a consequence of stronger springs. Relatively high perception of the same stimulus would be analagous to strongly depressed (opened) valves, as a consequence of weaker springs. Variation of spring strength would be inversely related to the flow rate of CAE, the feature of the model that relates to intensity of response.

Standpipes

Within the reservoirs are standpipes that represent features of defensive behaviour. Each possible response in those steps with alternative possibilities may or may not be available to a particular bee. This would be indicated by the presence or absence of specific standpipes within each reservoir in different model representations. A bee's age, genotype or physiological condition will determine what response she will make. For example, a very young bee is not normally involved in colony defence and has low levels of alarm pheromone, so her only option in the alerting step may be to flee.

If various responses are available, only one is performed at any one time. In the model, the last standpipe that CAE has begun to flow through indicates the current behaviour. The CAE flows through the lowest standpipe in a reservoir first, indicating that that response is occurring. If the flow of CAE is strong enough, CAE builds up within the reservoir until it reaches the next higher standpipe, and the next response is expressed.

Behavioural sequence may differ for alerting and culminating. In other words, if several responses are possible in a particular situation, their sequence may differ from bee to bee. This may arise from differences between bees in their thresholds for each response. Difference in sequence is a major variation between different genetic stocks of bees and is quite likely to be strongly influenced by genotype. This complexity can be accommodated by changing the relative standpipe heights within the reservoirs for different model representations.

Variation in response threshold levels between different bees is distinct from variation in their perception of stimuli. It is possible that a bee may perceive a stimulus but, because it has not reached her response threshold, she does not respond to it. Response threshold is represented in the model by absolute standpipe height. Models representing different genotypes can have different absolute standpipe heights, yet similar relative standpipe heights for the same responses. Then the sequences of responses will be the same, but more or less CAE will be necesssary for any response. Differences in both absolute and relative standpipe height would represent different sequences of responses with different thresholds.

Drains

If behaviour is not expressed because the stimulus results in excitation below the threshold required for response, the energy of excitation would be gradually dissipated. This is accommodated in the model by the presence of drains in all the reservoirs. If the flow of CAE allowed through the valve does not reach standpipe height before the stimulus ceases, no response is seen.

Drains also account for two time-related observations. Bees that have been recently aroused to defensive behaviour respond very quickly when subsequently stimulated. In the model, CAE would not have been entirely drained from the reservoirs and, in effect, thresholds would be lowered. However, if more time has passed between two subsequent arousals, the two occurrences are similar. In this instance the CAE would have completely drained from the reservoirs, and the thresholds would have been returned to their original state. Differences in size of drains would be featured in different model representations, to account for different periods required by different bees to return to their least activated state.

Discussion

The model presented deals with a complex behaviour pattern known to vary in a number of ways. This variation is a consequence of intricate interactions within and between the environment and the genotype that have occurred during the history of the colony and of its individual members, as well as during the actual defensive event. As such, our view is an epigenetic conceptualization of behaviour intended to emphasize and organize variation known to exist in a behaviour pattern of a species. Although some of the subunits of the model—for example, the act of stinging—may be viewed as fixed action patterns, there is a variation associated even with them. Intensity of response, the magnitude of stimulus necessary to elicit response, and the influence of prior response events, are variable characteristics identified by the model.

In all likelihood, other complex behaviour patterns expressed by honeybees and other animals could be organized in models similar to this one. The use of such models should encourage the study of variation in behaviour and in the epigenetic events which underlie that variation.

References

BOCH, R.; ROTHENBUHLER, W. C. (1974) Defensive behaviour and production of alarm pheromone in the honeybee. *J. apic Res.* 13: 217-221

BOCH, R.; SHEARER, D. A. (1971) Chemical releasers of alarm behaviour in the honeybee, *Apis mellifera. J. Insect Physiol.* 17: 2277-2285

BOCH, R.; SHEARER, D. A.; PETRASOVITS, A. (1970) Efficacies of two alarm substances of the honeybee. *J. Insect Physiol.* 16: 17-24

BOCH, R.; SHEARER, D. A.; STONE, B. C. (1962) Identification of iso-amyl-acetate as an active component in the sting pheromone of the honeybee. *Nature* 195: 1018-1020

COLLINS, A. M.; ROTHENBUHLER, W. C. (1978) Laboratory test of the response to an alarm chemical, isopentyl acetate, by *Apis mellifera. Ann. ent. Soc. Am.* 71: 906-909

FREE, J. B. (1961) The stimuli releasing the stinging response of honeybees. *Anim. Behav.* 9(3/4): 193-196

FREE, J. B.; SIMPSON, J. (1968) The alerting pheromones of the honeybees. *Z. vergl. Physiol.* 61: 361-365

GHENT, R. L.; GARY, N. E. (1962) A chemical alarm releaser in honeybee stings (*Apis mellifera* L.). *Psyche* 69: 1-6

GONCALVES, L. S.; STORT, A. C. (1978) Honeybee improvement through behavioural genetics *A. Rev. Ent.* 31: 197-213

KERR, W. E. (1968) Solucao e criar uma raca nova. *Apicultor* 1: 7-10

KERR, W. E.; GONCALVES, L.; BUENO, D. (1967) Biological and genetical information of *Apis mellifera adansonii. Proc. XXI int. apic. Congr.*: 14-17

LOFGVIST, J. (1976) Formic acid and saturated hydrocarbons as alarm pheromones for the ant *Formica rufa. J. Insect Physiol.* 22: 1331-1346

LORENZ, K. Z. (1950) The comparative method of studying innate behavior patterns. *Symp. Soc. exp. Biol.* 4: 221-268

MASCHWITZ, U. W. (1964) Gefahrenalarmstoffe und Gefahrenalarmierung bei sozialen Hymenopteren. *Z. vergl. Physiol.* 47: 596-655

———(1966) Alarm substances and alarm behaviour in social insects. *Vitams Horm.* 24: 267-290

MICHENER, C. D. (chairman) (1972) Report of the committee on the African honeybee. *Springfield, VA: Natn. tech. Inf. Serv.*

ROBERTSON, P. L. (1971) Pheromones involved in aggressive behavior in the ant, *Myrmecia gulosa. J. Insect Physiol.* 17: 691-715

SHEARER, D. A.; BOCH, R. (1965) 2-Heptanone in the mandibular gland secretion of the honeybee. *Nature* 206: 530

STORT, A. C. (1970) Methodologia para o estuda da genetica da aggressividade de *Apis mellifera. I° Congr bras. Apic.*: 36-51

———(1974) Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. I. Some tests to measure aggressiveness. *J. apic Res.* 13: 33-38

———(1975*a*) Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. IV. Number of stings in the gloves of the observer. *Behav. Genet.* 5: 269-274

———(1975*b*) Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. V. Number of stings in the leather ball. *J. Kans. ent. Soc.* 48: 381-387

———(1975*c*) Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. II. Time at which the first sting reached the leather ball. *J. apic Res.* 14: 171-175

———(1976) Genetic study of aggressiveness of two subspecies of *Apis mellifera* in Brazil. III Time taken for the colony to become aggressive. *Cienc. Cult.* 28: 1182-1185

WALLIS, D. I. (1962*a*) Behaviour patterns of the ant *Formica pusca. Anim. Behav.* 10: 105-111

———(1962*b*) Aggressive behaviour of the ant *Formica pusca. Anim. Behav.* 10: 262-267

WILSON, E. O. (1976) The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 1: 63-81