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Nocturnal defensive responses of Africanized and European honey bees to the greater wax moth (*Galleria mellonella* L.)

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Abstract. Colonies of honey bees (*Apis mellifera* L.) in Brazil, the United States and Venezuela were presented with adult greater wax moths (*Galleria mellonella* L.) at their hive entrances. Africanized colonies were quicker, more persistent, and more intense in their attacks than were European colonies. Both races attacked female moths in preference to males. Although colony size did not appear to be related to defensiveness, attack data were correlated with the numbers of bees guarding the entrance. Africanized colonies had significantly more guard bees. During successive trials, both races attacked the moths in significantly shorter times. These findings may help explain the unexpectedly low population levels of *G. mellonella* in some areas of South America.

The greater wax moth (*Galleria mellonella* L.) maintains a scavenger–parasitical (ectosymbiotic; Wilson 1971) relationship with its primary hosts, the honey bees, i.e. *Apis mellifera, A. cerana, A. dorsata* and *A. florea* (Singh 1962). Larvae tunnel through the honeycombs, consuming the beeswax and stored food materials. The late instar larvae are somewhat resistant to the efforts of bees to be rid of them by virtue of their silk webbing (Fletcher 1976), their comparatively high tolerance to bee venom (Rhoads & Yurkiewicz 1978), and their tough cuticle (Nielsen & Brister 1979). Bees often resort to the simple expedient of dragging larvae out of the nest. Strong colonies usually rid themselves of most larvae (Langstroth 1853), while weak colonies often die or abscond (Fletcher 1976). Fully developed larvae (prepupae) seek out protected locations within the bee nest and spin their cocoons. The adult moths emerge within the nest, and generally exit from the nest at dusk. In contrast to more typical lepidopteran behaviour, males take up a 'calling' position and release a two-component pheromone that is very attractive to females (Röller et al. 1968; Leyrer & Monroe 1973; Finn & Payne 1977). The adaptive value of this sex-role reversal is not understood. Further, males emit short pulses of high frequency sound which may be involved in attracting females (Spangler 1984). Mated females return to the colonies at night and lay eggs both in and outside the nest. Females gain entrance to nests of *A. mellifera* by slowly approaching the guard bees, resting quietly for a time and then running quickly into the entrance (Nielsen & Brister 1977). Bees do not seem to notice the moths until they come very close or actually touch them. Bees then appear actively to seek the moths but have difficulty catching them. Females generally leave the colonies before dawn the next morning (Nielsen & Brister 1977).

This moth is thought to be Asian in origin (Paddock 1926; Morse 1975), though it has been spread worldwide by the movement of *A. mellifera* colonies. Its range is probably limited by extended cold periods and high elevations (Paddock 1930). It is particularly troublesome to beekeepers in the southern parts of the United States, where the longer frost-free growing season permits several generations of moths to develop. Consequently, it was with some surprise that the African Bee Committee (Michener 1972) noted that, in certain areas of Brazil, honey bee colonies showed little wax moth damage. During a recent visit to areas near the cities of Ribeirão Preto, São Paulo and Curitiba, Parana we observed similar low levels of infestation. This is unexpected as conditions seem favourable, i.e. there are substantial numbers of bee colonies and a tropical or subtropical climate.

The high level of defensiveness of Africanized bees, which have recently colonized this area, has been well documented using tests that measure defensive behaviour toward large animal or mammalian type stimuli (Michener 1972; Stort 1974, 1975a, b, c, 1976; Collins & Kubasek 1982; Collins et al. 1982). The present study was designed to test whether Africanized and European bees differ in their response to the greater wax moth, one of their principal insect ectosymbionts.

MATERIALS AND METHODS

Experiment 1

Ten colonies of Italian honey bees (*A. mellifera liguista* sp.) were tested in Georgia, U.S.A. Four colonies were located near Athens (latitude 33° 56′ N, longitude 81° 21′ W) and six on Sapelo Island (latitude 31° 23′ N, longitude 81° 16′ W). Queens of these colonies were descended from stock reared in Georgia. All observations were made during a 2-week period on colonies which were in equipment of Langstroth dimensions (Langstroth 1853; Dadant 1975).

Adult moths were obtained from recently established cultures started from wild stock, as described by Eischen et al. (1984). Newly emerged virgin male and female (0–24 h) and old male moths (20–21 days) were prepared by freezing. Moths were thawed and pinned on no. 3 black insect pins to a height of 8 mm. Additionally, a small label indicating age and sex was attached. As a control, the tip of a cotton swab (Q-tip) measuring 1·5 cm (chosen for its neutrality) was prepared in a similar fashion.

Forty-eight hours before observation, a false landing board (12 × 36 cm) was placed in front of the colonies at the same height as the colony landing board. (This observational area was designed to minimize disturbance to the colonies but proved unnecessary and was not used in subsequent experiments.) Observations began 1·5 h after sunset.

After pinning the moths to the false landing board, 6 cm apart and 8 cm from the colony entrance, the numbers of bees attacking the moths and control were observed every 15 s during a 10-min period. A flashlight fitted with a red filter was used to provide illumination every 15 s for counting attacking bees. Bees did not appear to be affected by the light. At the end of 10 min the moths were removed. When more than 7–8 bees were attacking a particular moth, it became difficult to make precise counts; numbers were estimated in such cases. Temperatures averaged 26 ± 3°C ($\bar{X} \pm$ SE) during the two trials which were performed on successive nights. A few days following the tests, colonies were examined and quantities of brood estimated. Estimates were made in frame-equivalents, i.e. a honeycomb measuring 20 × 43 cm. Colonies found to be queenless were excluded from the test.

Experiment 2

Eight colonies of Africanized bees (representative of the naturally occurring population descended from European stock and *A. mellifera scutallata*; formerly *adansonii*: Ruttner 1981) were tested at the Universidade de São Paulo located near Ribeirão Preto, Brazil (latitude 21 10′ S, longitude 47° 48′ W). Procedures were similar to those used in experiment 1. Two trials were performed 48 h apart. Bees from these colonies were determined as being Africanized by morphometric analysis (Daly & Balling 1978). Colonies were located on stands (pedestals) 40 cm high. Entrances measured 1·7 × 11 cm. The moths and the control were gently pinned into the landing board 4 cm from the entrance. Treatments consisted of a young male, a young female, and a control. Temperatures averaged 23 ± 3°C.

Experiment 3

Nine colonies each of Africanized and European honey bees were tested at the Universidad Centro Occidental Agricultural Research Station near Sarare in the province of Lara, Venezuela (latitude 9° 34′N, longitude, 69° 11′W). Colonies of Africanized and European bees shared common stands 40 cm high. Africanized alternated with European colonies and the two faced opposite directions. Approximately 30 cm separated the colonies.

Moths were obtained locally by incubating prepupae from the nest of a dead honey bee colony. Fully cocooned pupae were isolated in small paper cups (20 ml). Upon emergence, adults were sexed and frozen.

Observations were alternately made on Africanized and European colonies. About 1 min before testing, during trials 2–4, the number of bees at the entrance were counted or estimated if more than 25 were present. Colonies were tested between 2100 and 0130 hours by pinning the moths on the landing board centred in front of the entrance at a distance of 4 cm. The sequence of colonies tested was reversed on alternate trials. Four trials were conducted 48 h apart. Temperatures during observations averaged 21 ± 2°C. The experimental design was nested, and the data evaluated with ANOVA and Duncan's multiple range test.

All three experiments were conducted according to a split-plot design. The whole-plot factors for experiment 1 consisted of the nested effects for location, trial and colonies, with the sub-plot factors being moth sex and control. Additionally, since analysis of variance indicated that bee responses at the two locations were not different, analyses were performed on pooled data. Experiment 2 was basically the same design, except that it was conducted at only one location. The whole-plot factors for experiment 3 consisted of the nested effects of race, trial and colonies, with the sub-plot factors being moth sex and control. Duncan's multiple range test was utilized for mean separations in all three experiments.

RESULTS

In general, the responses of both races of bees initially consisted of investigating the moth. This usually involved touching it with the antennae and/or tongue. After touching the moth, the bee usually backed away, and then groomed its antennae or tongue. This was often followed by a return to the moth and repetition of the sequence. Sometimes the response involved running about the entrance in an apparently agitated state, and occasionally bees turned themselves over and spun about in an erratic manner. Eventually, bees began to pull, bite and sting the moth. These responses were counted as attacks. Multiple attacks were frequent, and often the moths were mobbed by as many as 30 bees. Though the moths in these cases were destroyed, bees continued to attack whatever remnants remained. Bees appeared to sting the moths, but their stings did not become embedded and could be retracted.

Bees also investigated the control, often walking over it. Genuine attacks on controls were never observed, but if a bee climbed onto one, this behaviour was counted as an 'attack'. The time to first attack on controls is underestimated, as the bees frequently failed to attack during the 10-min period. Such colonies received a score of 600 s even though they had not attacked.

Experiment 1

European bees in Georgia, U.S.A.

Bees began attacking moths within 2–3 min (Table I). Initial attack time was not different for either sex. Young moths were attacked more quickly than controls ($P<0{\cdot}05$), but not significantly more quickly than old males. Bees were also more persistent in their attacks on young females than on old males ($P<0{\cdot}05$). On average, young

Table I. Honey bee response to adult greater wax moth*

Treatment	N†	Time to 1st attack (s) $\bar{X}\pm$SE	Persistence of attack‡ $\bar{X}\pm$SE	Total no. attacks $\bar{X}\pm$SE
European bees in Georgia, U.S.A.				
Young female	20	120·0 ± 47·1a§	72·4 ± 8·5a	201·2 ± 47·0a
Young male	20	159·8 ± 44·5a	67·7 ± 8·8ab	129·9 ± 35·8ab
Old male	20	186·8 ± 49·8ab	55·3 ± 8·8b	92·8 ± 32·3b
Control	20	272·2 ± 59·7b	24·6 ± 7·2c	20·1 ± 8·1c
Africanized bees in Sao Paulo, Brazil				
Young female	15	119·0 ± 54·9a	80·9 ± 9·5a	397·7 ± 93·3a
Young male	15	179·0 ± 61·9ab	51·2 ± 10·9b	170·3 ± 81·1b
Control	15	213·0 ± 69·0b	50·0 ± 11·7b	201·1 ± 75·2b

* Observed during a 10-min exposure.

† Ten colonies of European and eight colonies of Africanized bees were tested on two nights.

‡ Persistence equals percentage of observations containing attacks, when measured from the time of first attack.

§ Means followed by the same letter within a column do not differ significantly at the 0·05% level as determined by Duncan's multiple range test.

females received more attacks (201·2) than young males (129·9) or old males (92·8) ($P < 0{\cdot}05$). That is, females received significantly more attacks than old males ($P < 0{\cdot}05$), but not significantly more than young males.

The quantity of brood was positively correlated with the number of attacks on old males ($r = 0{\cdot}90$, $P < 0{\cdot}01$), but not the number of attacks on young males or females. Colony size averaged $4{\cdot}0 \pm 1{\cdot}2$ frames of brood.

Experiment 2

Africanized bees in Sao Paulo, Brazil

Bees began to attack moths within 2–3 min, and initial attack times on males and females were not significantly different (Table I). Colonies were more persistent (measured as percentage of observations containing attacks) in their attacks on females (80·9%) than on either males (51·2%, $P < 0{\cdot}05$) or on controls. The persistence of attacks on males and controls was about the same. Females received an average of 397 attacks, which was significantly greater than the 170 attacks on males ($P < 0{\cdot}05$) or the 201 attacks on controls ($P < 0{\cdot}05$). Colony size averaged $4{\cdot}6 \pm 0{\cdot}7$ frames of brood. Colony size did not correlate with attack data.

Experiment 3

Africanized and European bees in Lara, Venezuela

Table II shows that Africanized bees attacked all treatments sooner than the European bees ($P < 0{\cdot}05$). Africanized bees began attacking after 2 min, while European bees did not attack until 4 min had elapsed. In their initial attack, neither race of bees differentiated between the male and female moths. Africanized colonies were more persistent than European ones in their attacks on all treatments ($P < 0{\cdot}01$). In Africanized colonies, the average percentage of observations containing attacks was 78·9% for male and 73·9% for female moths. European colonies averaged 66·9% and 45·9% for females and males respectively. That is, European colonies attacked females more persistently than they attacked males ($P < 0{\cdot}05$), but Africanized colonies did not. However, both Africanized and European bees attacked females more often than males ($P < 0{\cdot}05$). Additionally, Africanized bees attacked all treatments more often than European bees ($P < 0{\cdot}05$).

An average of $55{\cdot}5 \pm 17{\cdot}4$ bees were counted on the entrances of Africanized colonies (Table III). In contrast, European colonies had only $9{\cdot}5 \pm 2{\cdot}5$ bees on average at their entrances ($P < 0{\cdot}05$). Additionally, examinations of the colonies revealed that the size of Africanized and European colonies were not significantly different (Table III).

A number of significant correlations were found among colony size, number of bees at the entrance, and attack measurements (Table III). A positive correlation between brood quantity and the number of bees at the entrance was found for European bees ($r = 0{\cdot}73$, $P < 0{\cdot}05$), but not for Africanized bees. Negative correlations between guard number and time to first attack existed for European colonies ($r = -0{\cdot}39$, $P < 0{\cdot}05$ and $r = -0{\cdot}49$, $P < 0{\cdot}01$, for males and females, respectively), but not for Africanized colonies. A positive correlation was also found between the number of bees guarding European colonies and the persistence of attack on male moths ($r = 0{\cdot}67$, $P < 0{\cdot}01$).

Table II. Africanized and European honey bee responses to adult greater wax moths in Lara, Venezuela*

Treatment	*N*†	Time (s) to first attack ($\bar{X} \pm$ SE) Africanized	Time (s) to first attack ($\bar{X} \pm$ SE) European	Persistence of attacks ($\bar{X} \pm$ SE) Africanized	Persistence of attacks ($\bar{X} \pm$ SE) European	Total no. of attacks ($\bar{X} \pm$ SE) Africanized	Total no. of attacks ($\bar{X} \pm$ SE) European
Young female	36	141·2 ± 36·1a§	223·8 ± 34·5a	78·9 ± 6·1a	66·9 ± 7·2a	146·5 ± 16·2a	116·1 ± 22·6a
Young male	36	125·4 ± 33·8a	244·2 ± 37·0a	73·9 ± 6·3ab	45·9 ± 6·6b	95·5 ± 11·4b	42·8 ± 8·7b
Control	36	314·6 ± 42·5b	506·2 ± 30·7b	12·1 ± 2·9bc	4·3 ± 2·8c	5·6 ± 1·5c	0·7 ± 0·3c

* Observed during a 10-min exposure.

† Nine colonies of both Africanized and European bees were tested on four nights.

‡ Persistence equals percentage of observations containing attacks when measured from the time of first attack.

§ Means followed by the same letter within each column do not differ significantly at the 0·05% level as determined by Duncan's multiple range test.

Table III. Colony size and numbers of bees at their entrances (guards) correlated with defensive responses to the greater wax moth (GWM) in experiment 3

	Africanized colonies	European colonies
Colony size		
Mean no. ± SE guard bees†	55·5 ± 17·4a‡	9·5 ± 2·5b
Mean no. ± SE frames of brood ($N=8$)	3·4 ± 0·4a	2·9 ± 0·3a
Mean no. ± SE frames of bees ($N=8$)	4·4 ± 0·3a	4·7 ± 0·6a
Correlation (r) between no. guards and:		
Frames of brood ($N=8$)	0·48	0·73*
Frames of bees ($N=8$)	0·41	0·61
First attack time, male GWM	−0·18	−0·39*
First attack time, female GWM	−0·22	−0·49**
Attack persistence, male GWM	0·27	0·67**
Attack persistence, female GWM	0·21	0·38
Total attacks, male GWM	0·47*	0·75**
Total attacks, female GWM	0·37	0·79**

† Unless indicated otherwise, $N=25$ for Africanized colonies and 27 for European colonies.

‡Means within a row followed by the same letter do not differ significantly at the 0·05% level as determined by Duncan's multiple range test.

* $P<0\cdot05$; ** $P<0\cdot01$.

Positive correlations between numbers of guard bees and attacks were found for Africanized colonies and male moths ($r=0\cdot47$, $P<0\cdot05$), European bees and male moths ($r=0\cdot75$, $P<0\cdot01$), and European colonies and female moths ($r=0\cdot79$, $P<0\cdot01$). Although the above correlations suggest that colony size may be related to colony defensiveness in some way, no significant correlations were found between quantities of brood or bees and number of attacks.

Figure 1 shows that during successive trials, colonies of both races significantly decreased the time to their first attack ($P<0\cdot05$). Africanized attack times were always quicker, and their overall decrease in time to first attack greater ($P<0\cdot05$).

DISCUSSION

Africanized honey bee colonies were quicker, more persistent and more intense in their attacks on adult *G. mellonella* than were European bees. These results are consistent with the well known daytime defensiveness of these bees. This defensiveness may explain, in part, the relative scarcity of *G. mellonella* infestations observed in some parts of South America. However, it is not known if defensiveness against mammalian stimuli is a reliable indicator of defensiveness against this ectoparasite. Historically, the Dark bee (*A. mellifera mellifera*) was reputed to be quite defensive, but also susceptible to *G. mellonella*. The latter trait apparently was one of the reasons apiculturists in North America replaced them with Italian honey bees, a race known for its gentleness (Langstroth 1853; Rothenbuhler et al. 1968).

The defensive actions of the two races were not qualitatively different. With the exception of flying, attacks appeared similar to daytime attacks. The most striking quantitive difference was the number of bees guarding the nest entrance. In colonies of about equal size, Africanized bees had five times as many guards, on average. Defensive behaviour of European bees correlated strongly with the number of guards. This was not the case for Africanized bees. However, this difference may be an artefact of test procedures. The 10-min observation period with 15-s recordings was chosen for convenience and may not have detected important variations for the Africanized colonies. In any case, it seems reasonable to suppose that the greater the number of guards, the higher the probability of detecting and attacking an intruder. This seems especially applicable for the nocturnal intrusions by *G.*

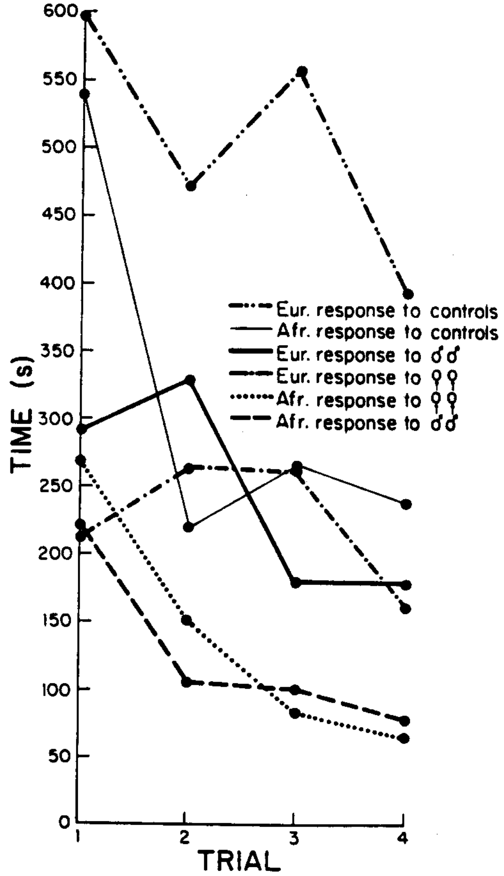

Figure 1. Time to first attack by Africanized and European honey bees in Lara, Venezuela. Four trials were conducted on nine colonies of each race. Forty-eight h separated trials.

mellonella, as bees apparently detect them only at short ranges.

A greater number of guard bees is only one facet of the overall defensiveness of colonies. Kerr et al. (1974) found positive correlations between quantity of 2-heptanone and defensive behaviour. Their data also suggest that workers from Africanized colonies contain higher concentrations of 2-heptanone in their mandibular glands than do Italian bees. Collins (1982) found that Africanized bees are more intense and persistent in their response to a mixture of compounds that have been identified as being associated with the sting (Blum et al. 1978). Our data, as well as those of Collins et al. (1982), suggest that Africanized colonies respond more quickly than European colonies. Taken together, the above findings suggest that colonies with large numbers of guard bees are more likely to detect potential intruders. Should these bees also have greater amounts of alarm pheromones to release, as well as a more intense reaction to them, then the overall colony response is likely to be rather quick and intense.

The decreasing times to first attack observed over the four Venezuelan trials suggest that either the bees were in a greater state of arousal as a result of the previous trials, or that they associated the presence of the moths with some cue (either from the moth or inadvertently supplied while administering the test). The fact that the number of bees on the landing boards for both Africanized and European colonies did not significantly increase, suggests that colonies were not in a higher state of arousal as a result of prior testing. Additionally, Africanized bees showed the greatest decline in response time, which is consistent with previously observed elevated defensiveness of these bees.

It seems reasonable for both races of bees preferentially to attack female moths, since they represent an imminent threat. Although females were attacked more frequently, they were not attacked more quickly than males. Apparently females are distinguished only at close range. It is not known what cues bees use to detect wax moths. The wing span and body length of females is, on average, about 10% larger than males (Vohringer 1934). Their larger size apparently did not help the bees detect them, as the time to first attack was similar for both sexes. The increased surface area presented by females could have influenced attack behaviour subsequent to detection. However, this relatively small difference in size may not account for the 1·5–2·7-fold increase in attacks on females.

In general, correlations between colony size and defensive responses were not found. Similar findings were reported for the daytime defence response to mammalian-like stimuli (Michener 1972; Boch & Rothenbuhler 1974; Rothenbuhler 1974). Collins & Kubasek (1982) also indicated that population size was unimportant. If detection and threat of intrusion are not closely related to colony size, and if any given potential intruder requires some minimum number of defenders to repel it, then it may be adaptive for smaller colonies to commit a proportionally higher number of workers to guarding and defending the nest. This would tend to weaken correlations between colony size and defensiveness.

The defensiveness of honey bees has probably been shaped by the size, destructiveness, tactics, frequency, etc. of intruders (see Seeley et al. 1982). The selective importance of small invertebrates such as *G. mellonella* is unknown. However, their prevalence in some areas suggests that frequent encounters must occur.

Regardless of origin, the heightened nocturnal defensiveness of Africanized bees appears to be adaptive when confronted with *G. mellonella*. Their quickness and persistence of attack may help explain the scarcity of this ectosymbiont in some areas of Brazil.

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