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Efficacy of the Ventral Abdominal Secretion of the Cockroach *Eurycotis floridana* (Blattaria: Blattidae) as a Defense Allomone

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In assays investigating the abdominal sternal secretion of the cockroach Eurycotis floridana*, it was determined that the secretion provides an effective deterrent against potential predators. Analysis of grooming patterns of* Peromyscus leucopus *mice revealed significant increases in mouth grooming and loss of coordination following exposure to* E. floridana *secretion. Mouse–cockroach interactions also changed following exposure of the mouse to the spray, as the mouse incited fewer interactions and more frequently struck with its forepaws than with its mouth.* Monomorium *sp. and* Camponotus *sp. ants also were repelled by the secretion, and* Periplaneta americana *were significantly irritated by the application of* E. floridana *secretion. The secretion is able to deter without physical contact, presumably via noxious volatiles.* Eurycotis floridana *is capable of accurately aiming the discharge as well as ejecting it several times the length of its body. It also was found that* E. floridana *exhibits autotoxic responses following contact with the secretion of conspecifics.*

KEY WORDS: *Eurycotis floridana*; defense allomone; (*E*)-2-hexenal; *Peromyscus leucopus*; *Monomorium*; *Camponotus*; *Periplaneta americana*.

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INTRODUCTION

Eurycotis floridana is a large, flightless cockroach ranging from the southeastern United States to the Caribbean (Hebard, 1917; Brenner and Pierce, 1991) and is usually found in or near wood piles as well as under ground cover around buildings (Brenner, 1988). It has a large abdominal secretory gland which opens at the midline between the sixth and the seventh sternites and is functional only in adults. Individuals have been reported capable of ejecting the gland's secretion a distance of several centimeters (Roth *et al.*, 1956) to approximately 1 m (Eisner *et al.*, 1959). The secretion is biphasic, consisting predominantly of a very complex organic phase, of which *E*-(2)-hexenal is the primary component, and an aqueous phase present in small quantities (Farine *et al.*, 1997).

(*E*)-2-Hexenal has been found in glandular secretions of a number of insect species and functions in various semiochemical roles including aggregation and alarm pheromones and defense allomones (Blum, 1981). Although Farine *et al.* (1997) demonstrated that (*E*)-2-hexenal may serve as an alarm component in the secretion of *E. floridana*, the primary fuction is thought to be defensive. Eisner *et al.* (1959) documented the fact that the spray acted as a deterrent to some arthropod and vertebrate predators, but little detail was given. In this paper, we extend the findings of Eisner *et al.* (1959) and demonstrate quantitatively that the secretion of *E. floridana* is an effective deterrent to both vertebrate and arthropod predators.

Natural predators of *E. floridana* are undocumented (Roth and Willis, 1960) and therefore cannot be assayed directly, though the cockroach likely suffers both invertebrate and vertebrate attacks. Being a dominant taxon with many aggressive, omnivorous species, ants rank among the most common invertebrate predators (Blum, 1965; Waterhouse and Wallbank, 1967) and are known to attack cockroaches (Blum, 1965). Several taxa of predacious ants are common in habitats occupied by *E. floridana* (e.g., *Solenopsis* spp., *Iridiomyrmex* spp., and *Camponotus* spp.) (Roth and Willis, 1960). It is therefore probable that ants have been instrumental in the evolution of defensive allomones in *E. floridana*. Rodents are also likely predators based on the geographic range and diet of several groups (Roth and Willis, 1960; Whitaker, 1963; Wolff *et al.*, 1985; Parmenter and MacMahon, 1988). Vertebrate and invertebrate predators were assayed for behavioral changes following exposure to the secretion of *E. floridana* to determine the efficacy of the secretion as a deterrent. Further, the ability of the cockroach to aim its secretion was determined. *Eurycotis floridana* was also tested for autosensitivity to the secretion to understand better the role of the secretion in intraspecific interactions.

MATERIALS AND METHODS

Experimental Animals

Eurycotis floridana were maintained in laboratory colonies and provided water and food ad libitum except during experimentation. Individuals were not sexed, as there is no sex-based differences in body size (∼40 mm), gland size (Stay, 1957), chemical composition of the secretion (Farine *et al.*, 1997), or behaviors such as movement pattern, duration, and rate (personal observation). All individuals used were naive with respect to experimental predators.

Peromyscus leucopus (Rodentia: Muridae) were obtained from a naive colony at the College Landing Biological Laboratory, College of William and Mary, and maintained on a 16:8 (L:D)-h photoperiod at a temperature of approximately 25°C. Water was provided ad libitum at all times except during the actual assay and rat chow (Agway Prolab Rat/Mouse/Hamster 3000, Syracuse, NY) was provided ad libitum, except as follows. To provide experience in attacking and feeding on live insects, rat chow was withheld and large *Acheta domestica* (Orthoptera: Gryllidae) crickets provided as food for the 2 nights prior to experimentation. Ten crickets were provided on the first night and four on the night immediately prior to the assay. Since the dry weight of 10 crickets represents approximately 25% of the normal daily food intake of an adult *P. leucopus* (Heideman, personal communication), the mice should have been in a state of hunger during experimentation.

Monomorium pharaonis (Hymenoptera: Formicidae) ants were collected from foraging columns in Millington Hall on the campus of the College of William and Mary immediately prior to use in assays. *Camponotus* sp. (Hymenoptera: Formicidae) ants were collected from foraging parties in Williamsburg, VA, and used in assays within 2 h. Adult *Periplaneta americana* (Blattaria: Blattidae) were collected from Millington Hall and maintained on water and Purina Cat Chow until use.

Experimental Setup

Peromyscus *Assays*

The arena for mouse assays consisted of a clear Plexiglas terrarium (17 cm wide × 31 cm long × 17 cm high) with a clear Plexiglas lid. To prevent cockroaches from escaping, the walls were coated to a height of 7 cm with Fluon (DuPont), a liquid that dries to a low friction surface. The arena floor was lined with litmus blue paper (WLS65285-C; VWR, USA), which turns pink upon reaction with secretion. Trials were performed under red light during the dark cycle and recorded on videotape for later analysis. Statistical analyses were performed using SPSS 8.0 for Windows (SPSS Inc., 1998).

For each trial, a mouse was transferred to the arena and allowed a 5-min acclimation period. Its activities were then videotaped for 10 min to determine its baseline behavioral patterns in the novel environment. A single *E. floridana* was then introduced into the arena and cockroach and mouse behaviors and interactions were recorded for 10 min. Each mouse was tested only once to limit the study to the behaviors of naive mice (i.e., no previous experience with *E. floridana*). Each *E. floridana* was also naive to ensure novel responses in each of the 20 trials performed.

Based on previous studies (e.g., Dell'Omo and Alleva, 1994; Petruzzi *et al.*, 1995) as well as our own observations, mouse grooming frequency and patterns were considered diagnostic of the behavioral state of the mouse. Grooming behavior was recorded in the following three categories: head grooming, mouth grooming (where the mouth–snout region specifically was vigorously washed with the forepaws), and body grooming (any other body part). In addition, initiation time and duration of each behavioral category were noted. Unusual movement behaviors, including rolling and changes in walking patterns (e.g., listing to one side, disoriented running patterns, and spastic movements), were recorded and grouped together as disorientation. Pilot studies revealed that head and body grooming, presumably displacement behaviors, were the most common forms of grooming behavior in the novel environment and that mouth grooming was typically observed only after oral contact with an unusual substance (e.g., feces or secretion). As head and body grooming were common in the absence of the cockroach, they were considered control behaviors, and mouth grooming and disorientation were considered experimental behaviors. Mice spent the majority of time in exploratory and resting behaviors, but these behaviors were not recorded since they did not differ substantially between treatments.

Data from only 15 of the 20 trials could be utilized since there were no secretion events in five trials. Data were divided into five temporal classes based on the presence of the cockroach and any secretion event. The "preroach" class was the 10-min control period before the introduction of the cockroach, the "prespray" class occurred between the introduction of the cockroach and the first spray event, the "prehit" class was the period following an initial discharge that did not visibly contact the mouse, the "hit" class was the 60-s period immediately following a discharge that visibly hit the mouse, and the "posthit" class was any period greater than 60 s following a discharge that hit the mouse.

The total time (T_t) in each temporal class and length of time each behavior was exhibited in that temporal class (T_b) were determined for each mouse. This yielded the proportion of time spent per behavior type relative to the total time ($pT_b = T_b/T_t$) within each temporal class. Sample sizes vary between temporal classes for several reasons. Two trials lacked a hit to the mouse, resulting in a sample size of 13 for the hit and posthit temporal classes. In eight trials, the first spray event hit the mouse, eliminating the prehit class from those trials. In one trial, the cockroach sprayed the mouse immediately upon being placed in the arena, resulting in the absence of the prehit temporal class. Changes in pT_b between and within temporal classes were analyzed by one-way ANOVA, and post hoc multiple comparisons were performed using the Games–Howell post hoc test (Sokal and Rohlf, 1995) due to heteroscedasticity of data.

Time of contact, initiator of contact (mouse or cockroach), and location of mouse contact on the cockroach's body were analyzed relative to the four latter temporal classes described above. The interval between contacts was analyzed by ANOVA, and post hoc multiple comparisons were performed by the Games–Howell test due to heteroscedasticity of data. Initiator of contact and induction of discharge relative to contact location were analyzed by likelihood-ratio tests of independence. Type of contact (snout or forepaw) across temporal classes was analyzed by chi-square tests of independence with Sidák's adjusted critical values for multiple comparisons (Rohlf, 1995; Sokal and Rohlf, 1995).

Ant Repellency Assays

To determine if the secretion is an olfactory deterrent to invertebrates, an ant repellancy assay was performed using methods similar to those of Jefson *et al.* (1983) and Peschke and Eisner (1987). A circular glass finger bowl ($r = 43$ mm) served as the testing arena, and the walls were coated with Fluon to prevent ants from escaping. A small drop of honey was placed in the center of the arena as an attractant and approximately 15 *M. pharaonis* ants were introduced. Ants were allowed 5 to 7 min to acclimate, a sufficient amount of time to find the honey and begin feeding but not to feed to repletion. Assayed substances were presented to ants via vertical capillary tubes (Fisher 02-668-68; bore diameter, 1.1–1.2 mm) suspended from a zip-line such that the substance, contained in the bottom of the tube, was 2 mm above the honey. Prior to each replication ($n = 8$), the position of each tube was verified to ensure uniform presentation between and within trials. After the acclimation period, three presentations were made, each for 30 s and separated by 2 min: (1) an empty tube, (2) 10 μl of distilled water, and (3) 10 μl of freshly collected *E. floridana* secretion. Trials were videotaped and analyzed to determine the number of ants feeding at the honey at the beginning of a presentation and the proportion feeding at 5-s intervals for 30 s. Data were analyzed by ANOVA.

To determine whether the secretion functions as a contact deterrent to potential invertebrate predators, an adult *E. floridana* was placed in an arena with 10–12 *Camponotus* ants. Ants sprayed with ventral abdominal gland secretion were observed for changes in behavior. Observations were made on six replicates.

In addition, water and secretion were applied serially to the bodies of 15 *Camponotus* ants by camel-hair brush. A single *Camponotus* ant was placed in a test arena and allowed a 2-min acclimation period, and distilled water was applied to its dorsal surface. Behavioral observations were made for 30 s. After a 2-min recovery period, freshly obtained *E. floridana* secretion was applied to the same ant and observations were made for 30 s. Behaviors similar to those reported by Blum (1965) to be indicative of discomfort in ants (chaotic running, splaying of legs, rubbing of the abdomen and thorax on the substrate, and frequent working of the mandibles) were scored as positive reactions. Data were analyzed by likelihood-ratio tests of independence.

Cockroach Topical Irritancy Assay

A modification of the assays of Eisner *et al.* (1976) and Peschke and Eisner (1987) was used to determine the ability of the secretion to function as a topical irritant. When an irritant is topically applied to a cockroach leg, the leg is brought forward to the mouthparts for preening (Eisner, 1961). Fifteen each of adult American cockroaches, *P. americana*, adult *E. floridana*, and juvenile *E. floridana* were decapitated by razor blade to reduce ambulatory behaviors, and the wounds immediately sealed with dental wax. A 90-min recovery period was provided prior to experimentation.

Each trial consisted of application of distilled water to both of the middle pair of legs followed by a 30-s observation period (control), a 5-min interval, and application of freshly obtained *E. floridana* secretion to the same pair of legs followed by a 30-s observation period (treatment). Compounds were applied using camel-hair brushes. A positive reaction was scored if either leg was brought forward in a preening-like motion within the observation period. Data were analyzed by likelihood-ratio tests of independence.

Spray Accuracy and Distance Assay

Thirty-two secretion events from 12 trials were videotaped and analyzed to determine the ability of *E. floridana* to aim its secretion accurately in relation to stimuli. Angular measurements were made relative to the midline of the abdominal tergites. The abdominal terminus was utilized as the spray origin, as the gland opening is proximal to it and opens between the sixth and the seventh sternites. The most frequently observed mode of contact incited by the mouse was with its nose, so the nose was considered an accurate indicator of contact angle. The mean angle of secretion coverage was determined from the two widest secretion markings registered on the litmus paper. This is a conservative estimate of accuracy, as the area of spray coverage is usually wide and the cockroach is able to bend and rotate its abdomen.

Five secretion observations were discarded because the cockroach was attempting to climb the chamber wall when discharge occurred. In such cases the cockroach was unable to leave the floor due to the Fluon layer, thereby preventing it from spraying behind itself when vertical. Analyses of the relationship between the angle of incidence and the spray angle were performed with Spearman's coefficient of rank correlation (Sokal and Rohlf, 1995), as data were nonnormal.

Spray distance was measured in 32 secretion events, however, 23 of the spray events were discarded, as either the cockroach was vertically oriented as it attempted to climb the tank wall or the secretion hit the wall or the mouse. Therefore only nine secretion events were considered to be indicative of the distance attainable. All measurements of distance originated at the abdominal terminus and extended to the farthest visible mark on the litmus paper.

RESULTS

Mouse Assays

Mouse grooming behaviors varied significantly across temporal classes (Table I, Fig. 1). Head grooming varied with the presence of *E. floridana* and the secretion, but not significantly. Body grooming decreased significantly with the presence of the roach and the secretion. The two recorded behaviors hypothesized to be indicative of discomfort, disorientation and mouth grooming, occurred significantly more frequently following release of secretion, particularly after an accurate discharge (i.e., hit and posthit classes). Proportions of recorded behaviors also varied within temporal class. The majority of time within temporal classes was not classified, as it consisted of ambulatory, exploratory, and resting behaviors that did not vary in type or magnitude between temporal classes. No significant alterations in behavior were observed in the preroach and prespray periods, and no disorientation was observed. No significant differences were observed during the prehit temporal class, though this could represent a Type II error due to

Table I. Mean Percentage of Time Exhibiting Behaviors in Each Temporal Class[a]

Behavior	Preroach (15)		Prespray (14)		Prehit (7)		Hit (13)		Posthit (13)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Head grooming	$2.911^{a;\dagger}$	0.006	$0.288^{a;\dagger}$	0.002	$0.993^{a;\dagger}$	0.005	$0.299^{a;\dagger}$	0.002	$1.998^{a;\dagger}$	0.012
Body grooming	$3.744^{a;\dagger}$	0.012	$0.042^{b;\dagger}$	0.000	$5.762^{a,b;\dagger}$	0.044	$1.160^{b;\dagger}$	0.007	$2.615^{a,b;\dagger}$	0.011
Mouth grooming	$1.067^{a;\dagger,\S}$	0.005	$0.895^{a;\dagger}$	0.005	$3.918^{a,b;\dagger}$	0.021	$24.160^{c;\S}$	0.034	$8.869^{b;\S}$	0.017
Disorientation	$0.000^{a;\S}$	0.000	$0.000^{a;\dagger}$	0.000	$0.211^{a;\dagger}$	0.002	$19.140^{b;\S}$	0.048	$1.807^{a;\dagger}$	0.010
Other[b]	92.28		98.78		89.10		53.20		84.70	

[a] Numbers in parentheses after the temporal class heading represent sample sizes. Means in the same row with different superscript letters are significantly different at $\alpha = 0.05$; means in the same column with different superscript symbols are significantly different at $\alpha = 0.05$.

[b] The percentage of time per temporal class exhibiting nonrecorded behaviors.

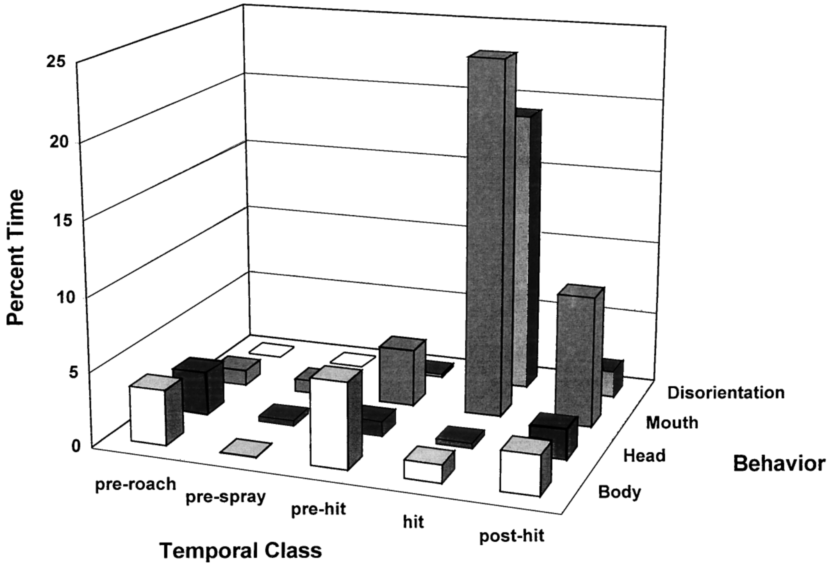

Fig. 1. Percentage of time *Peromyscus* mice exhibited recorded behavioral activities per temporal classes (bars represent means).

small sample size ($n = 7$). Disorientation was observed for the first time during the prehit temporal class and is probably attributable to aerosol contact with sensitive membranes. Highly significant differences were observed during the hit and posthit temporal classes, with disorientation and mouth grooming occurring most frequently.

The mean interval between contacts within temporal classes increased progressively with the presence of the secretion, particularly following accurate spray events (Fig. 2A) (prespray mean = 5.69, SE = 0.58, $n = 108$; prehit mean = 11.09, SE = 1.21, $n = 112$; hit mean = 14.00, SE = 2.71, $n = 60$; posthit mean = 19.49, SE = 2.47, $n = 237$). Differences were significant ($N = 517$; df = 3, $P < 0.005$) and the Games–Howell post hoc test revealed three homogeneous subsets ($\alpha = 0.05$): (1) prespray, (2) prehit and hit, and (3) hit and posthit. A linear regression indicates that decreases in contact frequency were not due primarily to the progression of time during the assay, as only 5% of the variation was explained by the passage of time (data not shown).

The proportion of forepaw slaps at cockroaches (prespray, 11 of 122; prehit, 7 of 112; hit, 10 of 61; posthit, 55 of 237) increased significantly following secretion events ($P < 0.005$) (Fig. 2B). Comparisons using Sidák's adjusted critical value ($\chi^2_{0.05,6,3} = 11.693$) revealed that the posthit temporal

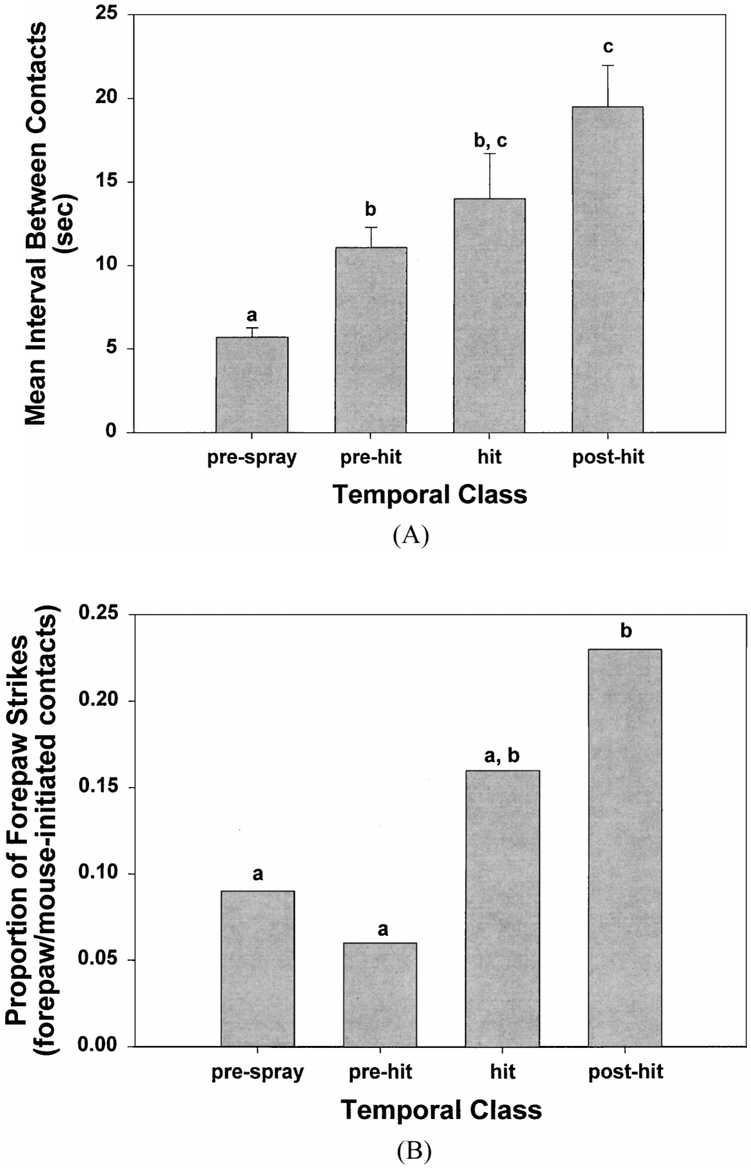

Fig. 2. *Peromyscus* mice behaviors relative to *Eurcyotis floridana* secretion presence. (A) Mean interval between mouse–cockroach contacts relative to secretion presence and liquid-phase contact. Bars with the same letter do not differ significantly at $\alpha = 0.05$ (bars represent standard errors). (B) Proportion of forepaw strikes by mouse versus total number of mouse-initiated contacts. Bars with the same letter do not differ significantly at $\alpha = 0.05$.

class differed significantly from the prespray ($G_{\mathrm{H}} = 11.903$) and the prehit ($G_{\mathrm{H}} = 17.368$) classes.

Although there was a small reduction in the proportion of mouse-initiated contacts over time (prespray, 106 of 122; prehit, 99 of 112; hit, 50 of 61; posthit, 187 of 237), it was not significant ($P = 0.09$). There was an overall reduction in contact rate, as the mouse often appeared to avoid contact with the cockroach following secretion events.

The location of contact significantly affected the likelihood of a spray event ($N = 532$; $P < 0.005$). Contacts with the posterior of *E. floridana* resulted in a spray event in 17.6% of cases ($n = 148$), versus only 0.83% ($n = 120$), 0.00% ($n = 141$), and 4.06% ($n = 123$) of head, thorax, and lateral abdominal contacts, respectively.

Invertebrate Assays

In all olfactory repellency tests, the number of feeding ants remained unchanged by placement of an empty capillary tube above the honey. An object moving and positioned overhead can therefore be ruled out as a stimulus inducing departure from the honey. Since an ANOVA revealed no significant change in the proportion of ants at the honey between intervals after presentation of either water ($P = 0.980$) or secretion ($P = 0.958$) (Fig. 3),

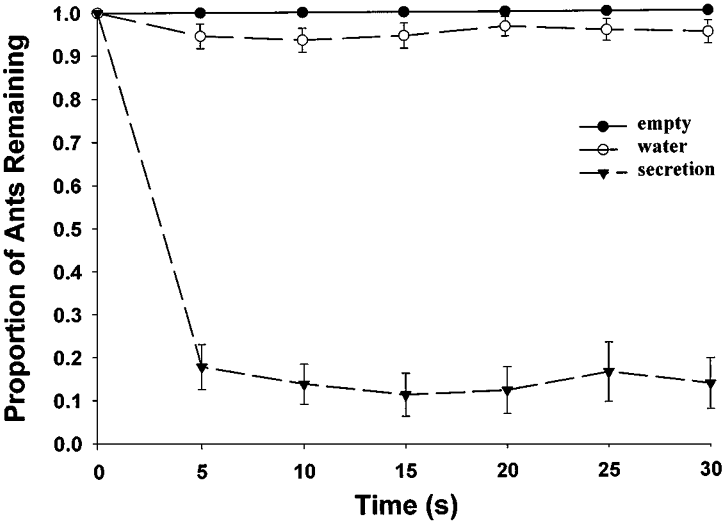

Fig. 3. Proportion of *Monomorium pharaonis* remaining at honey at 5-s intervals following capillary tube presentation of blank, water, and *Eurycotis floridana* secretion (bars represent standard errors).

data for the six time intervals of each replicate were averaged to provide a single value for further analysis. A *t* test revealed a highly significant difference ($P < 0.0005$) between the proportion of ants feeding after presentation of water (mean $= 0.950$, SE $= 0.0211$; $n = 8$) and that feeding after presentation of *E. floridana* secretion (mean $= 0.141$, SE $= 0.0444$; $n = 8$).

All six replicates of the *E. floridana–Camponotus* sp. antagonism assay resulted in a spray event by *E. floridana*. Ants visibly contacted by the secretion withdrew from the cockroach and moved in chaotic patterns, dragging their abdomens and frequently swiping their heads against the substrate in an apparent attempt to remove the secretion. Several minutes typically passed before any ants again approached the cockroach, though the duration varied widely. When secretion was directly applied to ants by brush, 14 of 15 *Camponotus* sp. reacted positively, whereas none reacted positively to the application of water ($P < 0.0005$). Behavioral changes were discernible by 2 s after application and persisted for at least 1 min in 12 of the positive replicates and longer than 2 min in 6.

Application of *E. floridana* secretion to the legs of *P. americana* resulted in a positive response in all 15 replicates, in comparison to zero responses to distilled water ($P < 0.0005$). Both legs reacted positively in all applications of *E. floridana* secretion. Adult *E. floridana* were irritated by conspecific secretion (15 of 15 positive to secretion, 2 of 15 positive to water; $P < 0.0005$). However, only one leg reacted to water application and the reaction occurred more than 5 s after application, whereas all positive responses to secretion involved both legs and occurred by 2 s after application. The secretion also irritated *E. floridana* nymphs (15 of 15 positive to secretion and 1 of 15 positive to water; $P < 0.0005$).

Accuracy Assay

The mean angle of coverage was highly correlated with the angle of contact incidence ($n = 27$; Spearman's $r = 0.706$, $P < 0.005$), indicating that *E. floridana* is capable of significant accuracy. Mice were visibly contacted by the liquid phase of the secretion 19 times in 27 observations. Also, in the mouse-presentation assay described above, 25 of 44 spray events visibly contacted the mouse in the face–head region. The maximum spray distance observed was 21.0 cm, and the mean distance 14.2 cm (SE, 12.35 cm).

DISCUSSION

Although actual predators of *E. floridana* are unknown, the dietary habits and range overlap of *Peromyscus* spp. (Whitaker, 1963; Wolff *et al.*,

1985) and predatory *Camponotus* sp. ants (Arke *et al.*, 1995; Klotz *et al.*, 1999), as well as other rodents and ants in that area, make the predators used in these assays viable models. The secretion appears to be an effective deterrent of both vertebrates and invertebrates. Our quantitative vertebrate data support the conclusions of Eisner *et al.* (1959) that the secretion is an effective deterrent of vertebrate predators. Predator disorientation and discomfort provide the cockroach with ample time and opportunity to escape in natural situations. Additionally, in longer duration pilot assays, of 1 h, several mice eventually consumed cockroaches. However, each observed consumption resulted in emesis by the mouse, a behavior that could reinforce the effects of the secretion in vertebrate predators. Our ant repellency results mimic those of the *Monomorium* repellency tests utilized by Jefson *et al.* (1983) and Peschke and Eisner (1987) to show efficacy of glandular secretions of the beetles *Creophilus maxillosus* and *Blaps mucronata*, respectively, on insect predators. In all cases glandular secretions proved to be highly effective repellents of ants. Also, *E. floridana* secretion appears to be a general arthropod deterrent, and it is predicted that is should be effective against a wide range of insect predators. The complexity of the secretion may increase the affected insect range by overloading general sensory systems (Blum, 1978) or by expanding the range of receptors that may be affected.

Efficacy of the secretion is increased by the attainable spray distance as well as spray accuracy. Although the spray distance of 21 cm that we observed is closer to the "several cm" distance reported by Roth *et al.* (1956) than it is to the yard (91.5 cm) reported by Eisner *et al.* (1959), it is still superior to reliance on a passive contact defense. The ability to spray and contact antagonists accurately from a distance is a beneficial property when confronted with vertebrates and swarms of ants, and in the latter case the large angle of coverage would be highly adaptive. Also, lack of contact by the liquid phase of the secretion does not preclude the secretion's efficacy. The volatile components of the secretion are aversive, without need for contact by the liquid, as demonstrated by changes in *P. leucopus* behavior during the prehit temporal class and by avoidance behavior in the *M. pharaonis* trials.

That *E. floridana* reacts to the secretion may be problematic since it is unlikely that an individual can spray the secretion without self-contact, and, as shown in our study, this could result in autotoxic effects. Farine *et al.* (1994), however, have reported the presence of secretion on the epicuticle surrounding the duct opening of unprovoked adults, thereby indicating that individuals are capable of withstanding the secretion on the venter. This may even be a benefit, as the cuticular presence of the secretion may prolong the repellent effect on nearby predators (Eisner, 1970). Presence of secretion on the cuticle also makes it tempting to hypothesize that *E. floridana* uses the secretion's volatile phase as part of an aposematic suite that further reinforces associative learning in vertebrate predators as Eisner and Grant (1981) found for other arthropods.

The secretion appears to be involved primarily in deterring potential predators based on our data, though it is known to play roles in conspecific interactions. Farine *et al.* (1997) noted that both juvenile and adult *E. floridana* are sensitive to the presence of the secretion and attributed their fleeing from the odor as a response to an alarm pheromone. Alternatively, the secretion may act as a general irritant of arthropods and therefore the attempt to flee is from an adverse stimulus rather than a response to an altruistic alarm pheromone. This would be more consistent with observations of male territoriality (Bell *et al.*, 1979) and use of the secretion in aggressive interactions with conspecifics (David-Henriet *et al.*, 1995).

The ventral abdominal secretion of *E. floridana* is multifunctional, providing communication in conspecific interactions as well as a primary role in predator deterrence. Presumably these effects are mediated by broad-range noxious chemicals that act on common insect and vertebrate sensory receptors. The deterrent aspect of the secretion may act through short-term toxic effects in both invertebrates and vertebrate predators and possibly through longer-term associative learning in vertebrates. The secretion therefore is an effective deterrent to potential predators and can act as an olfactory as well as a contact repellent.

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