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BEHAVIOURAL RESPONSE OF *SOLENOPSIS GEMINATA* (F.) WORKERS (HYMENOPTERA: FORMICIDAE) TO VENOM GLAND EXTRACTS AND LIVE QUEENS

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ABSTRACT. The behavioural response of *Solenopsis geminata* (F) workers to venom gland extracts of queens and other castes, and live queens was studied under laboratory conditions. Of all extracts evaluated, only venom gland extracts of queens, queens collected in nuptial flight and mechanically dealate queens were different with respect to the control. There was no significant difference in the response of minor, media and major workers to the queen venom gland extracts. Extracts induced some response at a concentration of 0.1 to 2 gland equivalents (GE), with a maximum response for 0.5 and 0.8 GE. The response of the workers to the extracts decreased significantly over time. Workers responded better to queens of their own colony than to foreign queens of similar weight. However, when the queens were of different weights, the workers preferred the heavier queen, even if this queen was not their own queen.
KEY WORDS: *Solenopsis geminata*, Formicidae, venom gland, queen pheromone, attraction, aggregation.

RESUMEN. La respuesta conductual de las obreras de *Solenopsis geminata* (F.) a extractos de la glándula de veneno de la reina y de otras castas, y a reinas vivas fue estudiada en condiciones de laboratorio. De todos los extractos evaluados, solamente los extractos de las reinas, reinas virgenes desaladas artificialmente, y reinas colectadas durante el vuelo nupcial fueron atractivos a las obreras. No hubo diferencia estadísticamente significativa en la respuesta de las obreras de diferente tamaño al extracto de la glándula de veneno de las reinas. Se encontró que los extractos de la reina atraen a las obreras en un rango que va desde 0.1 hasta 2 glándulas equivalente (GE). Sin embargo, la mejor respuesta se encontró a dosis de 0.5 y 0.8 GE. La respuesta de las obreras a los extractos decrecio significativamente sobre el tiempo. Los resultados muestran que las obreras responden mejor a sus propias reinas que a reinas extrañas cuando estas tienen un mismo peso corporal. Sin embargo, cuando el peso de las reinas es diferente, las obreras prefieren a la reina de mayor peso, aun cuando no sea la reina de su colonia.
PALABRAS CLAVE: *Solenopsis geminata*, Formicidae, glándula de veneno, feromona de la reina, atracción, agregación.

Ants of the genus *Solenopsis* are characterized by being very aggressive stingers. They have a high reproductive rate, a high population density, an efficient dispersial behaviour, and wide geographical distribution. These ants inhabit disturbed environments, often in association with humans, and are frequently found living in cultivated fields (Trager, 1991; MacKay *et al.*, 1990).

Solenopsis geminata (F.) is a species that was originally distributed from the southern United States to northern South America, but due to commerce, this species has been introduced into both tropical Asia and Africa (Trager, 1991). *S. geminata* is now an extremely abundant predator of arthropods in many disturbed ecosystems in most tropical lowlands (Rish & Carrol, 1982; Perfecto, 1991; Way *et al.*, 1998). For example, it decreased numbers of damaging *Sitophilus* spp (Coleoptera: Curculionidae) on maize by 98% in Mexico (Rish & Carrol, 1982). However, other authors consider that this species can be a pest feeding on seeds, tunnelling through roots, and girdling some plants in crops such as maize and bean (Bhatkar, 1983; del Rio & Casares, 1990).

Many aspects of the biology and ecology of *S. geminata* remain unknown or they have not been studied in detail. One aspect little studied concerns the chemical communication between the queen and her workers, which is fundamental to the organisation of the colonies. The queen is attractive to workers, leading them in many cases to form a retinue and move with her when she moves (Glancey *et al.*, 1983; Glancey, 1986). This phenomenon of aggregation is based on the emission of pheromones by the queen. The only study with *S. geminata* was carried out by Jouvenaz *et al.* (1974), who demonstrated that workers of this species aggregated onto filter paper where their queens had been previously confined. In *Solenopsis invicta* Buren, it was demonstrated that the venom gland is the reservoir of the queen pheromone (Vander Meer *et al.*, 1980). Later, Rocca *et al.* (1983a,b), chemically identified the compounds responsible for activity in *S. invicta* as (*E*)-6-(1-pentenyl)-2H-pyran-2-one and tetrahydro-3,5-dimethyl-6-(1-methyl)-2H-pyran-2-one. A third component, dihydroactinidiolide, was also identified, but it was inactive.

Most of the information on the chemical ecology of *Solenopsis* ants relates to *S. invicta* (Vander Meer, 1983). To determine the generality of the previous findings on *S. invicta* and to understand the chemical communication between the queen and her workers, comparable studies of other species of the genus are needed. In this investigation we take a first step in this direction by extending the study of the queen pheromone of fire ants to *S. geminata*. This work was carried out to investigate the behavioural response of *S. geminata* workers to venom gland extracts and to live queens under laboratory conditions.

MATERIALS AND METHODS

Biological material. Colonies of *S. geminata* were collected from Tapachula (14° 54´ N, 92° 16´ W), Cacahoatan (14° 59´ N, 92° 10´ W), Tuxtla Chico (14° 56´ N, 92°

10´ W) and Mazatan (14° 52´ N, 92° 27´ W) municipalities in the State of Chiapas, Mexico. Nests were excavated with a shovel. The biological material used in the experiments consisted of minor (head width: 0.45-0.80 mm), media (0.85-1.10 mm) and major (1.15-1.50 mm) workers (Tschinkel, 1988), queens, alate virgin queens, mechanically dealate virgin queens and alate queens captured in nuptial flight during the nights of June (95% of these queens were mated).

The queens and alate virgin queens were separated from the workers using two metal wire sieves (mesh size from 4 x 4 mm and 2 x 2 mm, respectively) each of 1 m^2 area. More than one dealate queen was collected in a nest (polygyne colonies). The queens and alate virgin queens were transported to the laboratory in small plastic container (10 cm height x 6 diameter cm) inside an insulated box to avoid death due to the high temperature of the region (35 °C all year round). The workers were transported in plastic containers (50 cm height x 35 cm diameter) and maintained in the laboratory in artificial nests under variable illumination (8-10 h of light), and controlled conditions of temperature (25 °C $\pm$ 3 °C) and relative humidity (70 $\pm$ 5%). Ants were fed *ad libitum* with a diet composed of agar (5 g), water (500 ml), 1 whole hen's egg, honey bee (62 ml), and 1 vitamin-mineral capsule (McKesson Bexel) (Singh, 1977).

The queens, alate virgin queens, mechanically dealate virgin queens, and queen captured in nuptial flight were maintained individually in plastic containers (9 cm height x 5 cm diameter). Soil of the same colony representing 30% of the volume of the container was placed in each plastic container; these insects were maintained under the conditions described above. The queens captured in nuptial flight were dissected immediately after losing their wings (24-36 h after collected).

Preparation of the extracts. Extracts were made from workers, virgin alate queen, mechanically dealate virgin queens (15 days after removing their wings), alate queen captured in nuptial flight, and queens. The venom gland extracts were prepared by dissecting the insects under a binocular microscope, and anaesthetising them lightly with chloroform to avoid release of the gland content. Once the gland was located, it was taken out together with the sting. The sting together with the Dufour´s gland was then removed and the venom gland was placed in a glass vial (3 ml). The gland was macerated in hexane with a small pointed spatula. In each vial, 10 glands of the same treatment were dissolved in one ml of hexane, such that 0.1 ml of the extract corresponded to one gland equivalent (1 GE).

Olfactometer. The olfactometer consisted of a circular plastic container (19 cm diameter x 5 cm height) (Lofgren *et al.*, 1983) without a lid, in which worker ants responded to the extracts as they were introduced in air diffused through a cotton

swab. Two openings at 180^0 from each other were made at the base of container, where the cotton swabs were inserted. One-half of the cotton swab was placed over the narrow end of a Pasteur pipette and the swab was inserted into one of the ports in the container. A similar device was inserted in the other port of the container. Extracts to be evaluated were pipetted onto small strips of filter paper (0.3 cm x 3 cm). After evaporation of the hexane (1 min), the paper was placed inside the Pasteur pipette and then inserted to the cotton swab. In another Pasteur pipette a similar strip of filter paper impregnated with hexane was introduced as a control. To avoid a positional bias, the extract and control were rotated after each replicate. After each bioassay, the ants, cotton swabs, and pipettes were discarded, and the plastic container was cleaned with hot soapy water and rinsed with acetone. When live queens were evaluated, two small cylindrical cages made of copper mesh (mesh size 2.5 mm), instead of the cotton swabs were used. The odour from the extracts or queens was transported into the olfactometer by passing compressed air (0.5 l/ min) through plastic tubing into the pipettes.

Bioassay. The workers used to evaluate the response to the extracts were acclimatised to the olfactometer room conditions for at least 48 h before carrying out the bioassays. All the extracts were evaluated to a concentration of one gland equivalent (1 GE), except for the experiment of dosage-response, in two-choice tests. Twenty ants of similar size were placed in plastic containers (3 cm x 5 cm), after a 5 min period, they were released into the centre of the olfactometer. The number of insects staying in a 2 cm^2 area around the cotton swabs was recorded at intervals of 3, 6, 9, 12 15 minutes. The sum of the 5 counts constituted one replicate. This counting procedure was used because of the typical behaviour response of worker ants to their queens. Generally, workers lick, groom, and feed the queen and collect the eggs she lays; consequently, there is a permanent flow of workers to and from the queen (Lofgren *et al.*, 1983; Rojas unpublished observations). During the bioassays, workers responded to the extracts and occasionally aggregated around the cotton swab, but not receiving other queen-related stimuli they frequently left the count area and then returned. Because of this constant movement in and out of the count area a series of counts gave the most correct score of the worker's responses. The walls of the olfactometer were impregnated with talc to avoid escape of the ants. Each experiment was replicated six times.

The response of the workers was calculated by using the following index: RI = (Npe-Npc)/ (Nt-Npc), where: RI = response index; Npe = number of workers that responded to the extract; Npc = number of insects that responded to the control; Nt = total number of workers released in each bioassay, because the sum of the five counts constituted a replicate, the total of workers observed in each bioassay was 100.

The index value ranged from +1 to -1, positive values indicate attraction, negative values repulsion (Rojas & Cruz-López, 1994).

Response of workers to venom gland extracts from different sources. In this test the response of media sized workers to venom gland extracts of queens, virgin alate queens, mechanically dealate virgin queens, alate queen captured in nuptial flight, and minor, media and major workers was evaluated by using an extract at 1 GE concentration. All bioassays were conducted in two-choice tests, using hexane as a control. Six replicates were carried out for each extract evaluated.

Response of workers of different sizes to the queen venom gland extracts. This experiment was designed to evaluate whether the size of the workers influences the response to the venom gland extracts. Workers were assigned to one of three size categories based on head width (HW): minor workers, HW 0.45-0.80 mm; media workers, HW 0.85-1.10 mm; major workers, HW 1.15-1.50 mm (Tschinkel, 1988). Six replicates for each size were conducted.

Response to different concentration of the queen venom gland extracts. In this experiment the response of media workers to the queen venom gland extracts at different concentrations was evaluated. The concentrations of the extracts were 0.1, 0.5, 0.8, 1.0, 1.5, 2.0, and 3.0 GE. Six replicates for each concentration were made.

Effect of time on activity of venom gland extracts. The objective of this experiment was to evaluate the effect of time on the activity of the venom gland extracts. Filter paper strips (3 x 3 mm) were dipped in either the gland extract at a concentration of 1 GE or in hexane as a control. Once impregnated, they were left at room temperature (26 °C) for 10, 60, or 120 minutes before being placed in the olfactometer for evaluation. Six replicates were made of each treatment.

Response to live queens. This test was designed to evaluate the preference of the workers to queens of their own colonies over queens of foreign colonies. In the first experiment the response of workers to their queens with a similar weight (20 mg vs 19 mg, comparison A x B), or a different weight (21 mg vs 13 mg, comparison C x D) was evaluated. In the second experiment, the response of workers of four different colonies (E-H) to two foreign queens (from colonies C and D) of different weight was recorded. All observations were carried out in two-choice tests.

Statistical analysis. All data were tested previously for homogeneity of variances (Bartlett´s test) and normality (Anderson-Darling test). In the first experiment

(Response of workers to venom gland extracts from a different source), the worker response to the extract and control was compared using a *t* test. Subsequently, only the extracts where there was a significant difference with respect to the control were analysed by using one-way analysis of variance (ANOVA). Data from other experiments were analysed by using *t* test or one-way ANOVA. When ANOVA showed significant treatment effects, a Tukey test was used for separating means. For all analyses, a critical α value of 0.05 was employed.

Table 1

Response (X±SE) of media workers of S. geminata to the venom gland extracts from different sources.

Extract source:	Mean (±SE) number of workers in count area: Extract	Control
Minor workers	20.0±5.1	17.3±3.6 ns
Media workers	19.2±5.3	15.3±5.9 ns
Major workers	14.8±3.3	7.7±1.4 ns
Alate virgin queens	20.2±3.8	12.8±0.8 ns
Alate queens captured in nuptial flight	35.2±3.7	10.3±2.8 ***
Mechanically dealate virgin queens	55.0±3.9	7.0±1.7 ***
Queens	65.8±7.5	4.3±2.2 ***

ns = no significant difference; *** $P < 0.001$, (*t*-test assuming equal variances).

RESULTS

Response of workers to venom gland extracts from different sources. Only venom gland extracts of queens, alate queens collected in nuptial flight and mechanically dealate virgin queens elicited different response to that of the control (Table 1). Comparisons between the response of worker ants to these three active extracts show that they responded better to the queen extract, followed by the mechanically dealate queens. The workers responded significantly less to the extract of the queens collected during nuptial flight ($F= 8.01$; $df = 2, 15$; $P= 0.004$).

Response of workers of different size to the queen venom gland extracts. There was no significant difference in the response of minor, media and major workers to the queen venom gland extracts ($F= 2.29$; $df = 2, 15$; $P= 0.135$) (Fig. 1).

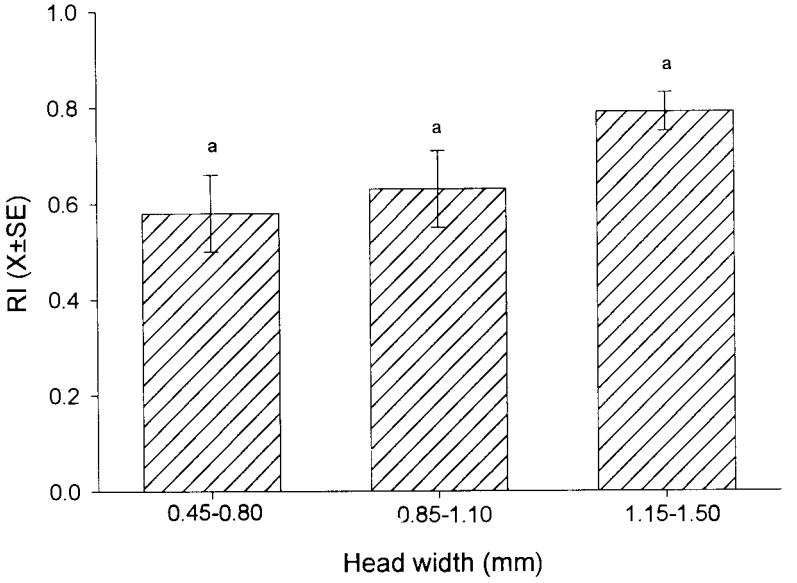

Fig. 1. Response of workers of three different sizes to the queen venom gland extracts. Bars marked by the same letter are not significantly different ($P < 0.05$; Tukey tests).

Response to different concentration of the queen venom gland extracts. The response of the workers to the queen venom gland extract was significantly different depending on concentration ($F = 12.10$; $df = 6, 35$; $P < 0.001$). Some activity was noted at 0.01 GE, but maximum response occurred at 0.5 and 0.8. At 3 GE, the workers were repelled from the queen venom gland extracts (Fig. 2).

Effect of time on efficiency of venom gland extracts. It was found that the extracts remained active for at least 120 min, though, the response of the workers to the extracts decreased significantly over time ($F = 3.937$; $df = 3, 20$; $P = 0.023$) (Fig. 3).

Response to live queens. Workers responded better to queens of their own colony than to foreign queens of similar weight (Table 2, colonies A and B). However, when the queens were of different weights, the workers preferred the heavier queen, even if this queen was not of their own colony (Table 2, colonies C and D). Additional tests with workers of other colonies showed that the weight of the queens was decisive in their attraction to the workers (Table 2, colonies E-H).

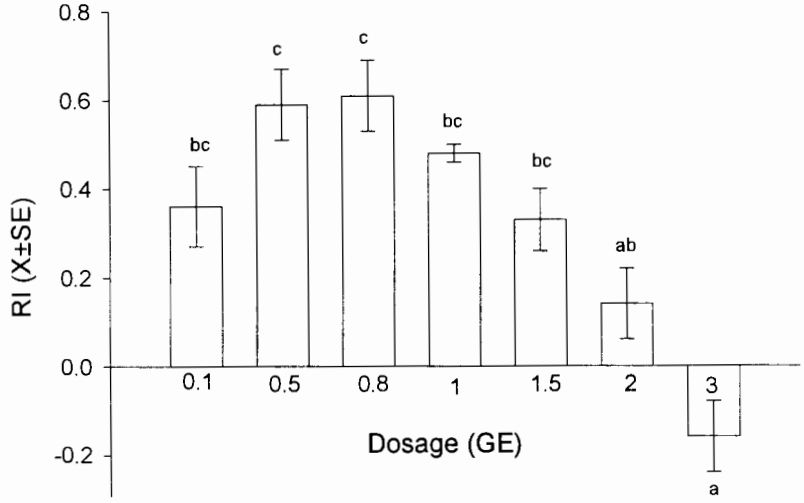

Fig. 2. Response of media workers to different concentration of the queen venom gland extracts. Bars marked by the same letter are not significantly different ($P < 0.05$; Tukey tests).

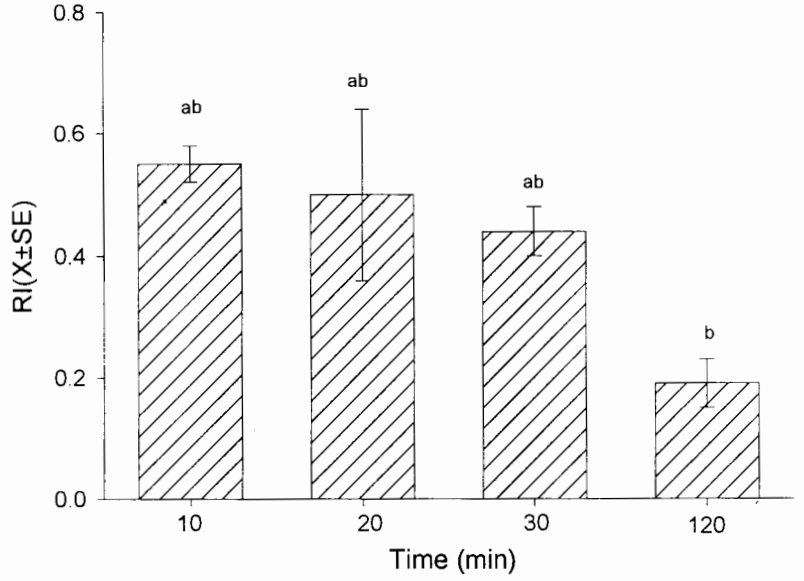

Fig. 3. Effect of time on activity of venom gland extracts. Bars marked by the same letter are not significantly different ($P < 0.05$; Tukey tests)

Table 2

Response (X±SE) of media workers of *S. geminata* from different colonies to their own queens or foreing queens.

Workers from colony:	Mean (±SE) number of workers on queens from colony:			
	A (20 mg)	B (19 mg)	C (21 mg)	D (13 mg)
A	64.2±4.9[a]	4.8±1.1[b]		
B	8.5±1.4[a]	62.5±3.5[b]		
C			75.3±4.1[a]	12.2±3.2[b]
D			58.6±6.1[a]	20.8±5.2[b]
E			62.5±3.5[a]	8.5±1.4[b]
F			64.8±4.7[a]	6.5±0.8[b]
G			56.5±6.1[a]	10±2.9[b]
H			39.7±3.9[a]	6.2±1.5[b]

Data are average of six replications. Means in a row followed by the same letter are not significantly different ($P < 0.05$; t-test assuming equal variances).

DISCUSSION

The results of the present study demonstrated that a pheromone is stored in the venom gland of the *S. geminata* queens that attracts and aggregates workers around them. A similar phenomenon was reported in *S. invicta* (Vander Meer *et al.*, 1980). Although this work only evaluated the attraction (indirectly) and, more properly the aggregation of the workers in the extracts of the queens, the pheromone may affect other worker activities, as was demonstrated in *S. invicta* (Glancey *et al.*, 1983). In the last species, the queen recognition pheromone, as it was called to differentiate it to other queen pheromones (e.g. inhibitory pheromone) mediates transport of brood to the queen, depositing of brood near the queen, formation of the trail to the nest, and guidance of the queen along one of the trails into the nest (Glancey *et al.*, 1983; Vander Meer, 1983). Continuous release of the pheromone by *S. invicta* seems to be dependent upon direct contact between the queens and their workers as evidenced by the fact that queens lose their attraction when isolated from the colony for 30 min and quickly regain it when returned to their colony (Lofgren *et al.*, 1983).

We found that virgin queens of *S. geminata* produce the pheromone 15 days after removal of their wings. A similar phenomenon had been reported in *S. invicta* (Glancey *et al.*, 1981). These authors found that alate queens of *S. invicta* begin to produce pheromone between 6 and 9 days after removal of the wings, reaching their maximum activity 12 days later. A correlation between attractiveness and histolysis of wing muscles, and the presence of large number of eggs was found in this species (Glancey *et al.*, 1981). The production of pheromone may therefore be linked to the biochemical, physiological, or hormonal changes associated with histolysis of wing muscles and production of eggs (Glancey *et al.* 1981). In other ant species it has been shown that virgin queens are not attractive to the workers independent of the presence or absence of wings. For example, Carr (1962) found that virgin queens of the genus *Myrmica* were unattractive to workers whether they were alates or dealates.

The present study found that workers responded to extracts of queens collected during the nuptial flight and evaluated 24-36 h later. Ninety five percent of these females were inseminated since they were observed to contain sperm, and the alary muscles were in the process of histolysis. This seems to indicate that sperm could accelerate the production of pheromone, because in the virgin queens and mechanically dealate virgin queens the pheromone begins to be produced 8 and 15 days after losing the wings, respectively (Fierro Santos, unpublished data). However, many other factors may be involved, for example, the degree of maturity of queens before leaving the nests may vary during the year and so may the onset of pheromone production. In *S. invicta* it has been found that if queens are reared in the spring or summer, there seems to be a high probability that they will leave the nest for a mating flight before fully mature oocytes are present in their ovarioles, but if they overwinter in the parental nest, their ovaries continue to develop very slowly and they begin to oviposit before they leave in early spring (Fletcher & Blum, 1983). The fundamental processes of dealation and oogenesis are usually prevented from occurring while virgin queens are still in the parental nest by the presence of one or more primer pheromones secreted by the mother queen (Willer & Fletcher, 1986). In *S. invicta* it has been shown that queens immediately after the nuptial flight were very weakly attractive (Glancey *et al.*, 1981). The difference between both species may be due to the fact that the process of production of the pheromone is faster in *S. geminata* queens than in S. *invicta* queens.

Our results on the influence of time on extract activity are different to those reported in *S. invicta* by Jouvenaz *et al.* (1974). They found that areas occupied by *S. invicta* queens for an hour attracted workers for more than 24 after removing to the queen. In addition, they demonstrated that when the area treated with hexanic queen extracts, this area remained attractive to the workers for up to 72 h. The difference between both studies may be due to the different method of preparation of the extracts and of

bioassay technique. In the present study extracts were only made from venom glands, while Jouvenaz *et al.* (1974) made their extracts washing the queens with hexane. Using the last method, the extracts could have non-volatile compounds such as cuticular or postpharyngeal gland hydrocarbons (Thompson *et al.*, 1980), which can last longer in the ambient and may affect the behaviour of the workers. In contrast, our bioassay only evaluated the worker response to the volatile compounds of the extract, while that of Jouvenaz *et al.* (1974) can be used to evaluate the worker response to volatile and non-volatile compounds. Another possible explanation of the difference between these studies is that the pheromonal compounds of *S. geminata* may be more volatile than those of *S. invicta*.

The response of workers to different concentrations of the extracts suggests that there is an optimal concentration for attraction and aggregation; the best response occurred at 0.5 and 0.8 GE, whereas at 3 GE a repellent effect of the extracts was found. In *S. invicta*, no negative effect of the extracts was observed, even at doses higher than those evaluated here (Lofgren *et al.*, 1983). The African ant *Myrmicaria eumenoides* provides another example in which behavioural thresholds are related to the quantity of pheromone released (Longhust, 1977). When disturbed this species, produces a droplet at the tip of its sting, which alerts nest mates and attracts them towards the source. However, under high provocation, it sprays the gland contents (the equivalent of about 5 droplets), such a quantity repels sister workers.

The workers of *S. geminata* respond to the pheromone of the queen independently of their size. It would be expected that the minor workers respond better to the pheromone because they play a greater role in queen and brood care, and other activities inside the nests, while the medium and major workers tend toward foraging and retrieving preys (Mirenda & Vinson, 1981). However, in *S. geminata* age has been reported to be an important factor affecting the division of labour among workers; younger ants tend toward brood care while older ants tend toward foraging (Mirenda & Vinson, 1981). In this study, we did not evaluate the influence of this factor on the worker's response to the pheromone, and it would be interesting to carry out such as evaluation in the future. Lofgren *et al.* (1983) reported that the youngest workers of *S. invicta* responded better to the pheromone than older workers.

The observation that workers preferred alien queens over familiar queens under some circumstances was an unexpected result, and seems to run counter to kin recognition theory. These results could be explained in part by the fact that workers from polygyne colonies were used in this study. The occurrence of cohabiting queens tends to dilute genetic relatedness among colony members (Vargo, 1993). Glancey & Lofgren (1988) reported that a method by which polygynous colonies of *S. invicta* perpetuate themselves is via the adoption of newly-mated queens following their mating flight. This indicates that workers from polygynous colonies may accept alien

queens, so explaining the results of the present study.

The weight of the queen appears to be an important factor in queen attractiveness. However, we do not know if this attraction is only mediated by the pheromone stored in the venom gland or if the heavier queens produce more pheromone than lighter queens. Willer & Fletcher (1986) found that heavier queens of *S. invicta* of monogynous and polygynous colonies have a significantly greater inhibitory capability that queens of lesser weight.

In conclusion, this study extends our understanding of the chemical communication between workers and their queens in fire ants of the genus *Solenopsis*, which previously was largely restricted to *S. invicta*. *S. geminata* shares many similarities with *S. invicta*; queens of both species produce a pheromone, which attracts and aggregates workers around them and the source of this pheromone is the venom gland. The chemical identity of the pheromone is known in *S. invicta* (Rocca *et al.*, 1983a,b) and identification of the pheromone in *S. geminata* would help us to understand some of the differences found between these species (e.g. persistence of pheromone). Such information would also be useful in determining whether or not the difference in queen attractiveness to workers is the result of a quantitative variation of queen pheromone. Finally, it would be interesting to compare the worker's response from monogyne colonies to their queens with those reported in the present study.

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