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Foraging in *Blattella germanica* (L.) and aggregation pheromone

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ABSTRACT. *Foraging in* Blattella germanica *(L.) and aggregation pheromone.*– The aim of this paper was to investigate whether conspecifics of the German cockroach (*Blattella germanica* (L.) Blattellidae) act as attractants reinforcing the effect of food stimuli. Attractiveness of four kinds of stimuli combining food and conspecific odours were tested. Dishes containing food were by far the more attractive, even though conditioned filter paper attracted more animals than empty dishes did. The presence of conditioned paper also retained cockroaches in the vicinity of food. Dishes with filter paper attracted more small larvae than medium sized and large ones. However, conspecific odour did not appear to facilitate attraction to food. In addition, food exploitation did not seem to depend on social facilitation.

KEY WORDS . Cockroach, *Blattella germanica,* Aggregation pheromone, Attraction, Feeding.

Introduction

The importance of chemical signals in the life of many insects is well known. Many of the cues that guide insects to food resources, suitable reproductive sites or shelters are chemical (see Matthews & Matthews, 1978, for details). There are many different sorts of attractive chemical stimuli, including pheromones. In particular, aggregation pheromones have been shown to play an important part in the regulation of natural populations, especially in social and in subsocial insects (Masson & Brossut, 1981). There is evidence that larval cockroaches of many species respond to aggregation pheromones (Bell et al., 1972; Brossut, 1970; Brossut, et al., 1974). Ishii & Kuwahara (1967) were the first to report that filter paper which had been conditioned by being placed in a culture of German cockroaches *Blattella germanica,* attracted larvae of the same species. Fatty acids present in the faeces are presumed to be the active factor. Ritter & Persoons (1975) reported that the aggregation pheromone of *B. germanica* appeared to be a complex mixture in which certain free acids play an important role, but they gave no details. Fatty acids act as attractants, but these attractants differ from pheromones in so much that they are not specific (Brossut, 1979). The role of these attractants is to induce "an insect to perform directive locomotory responses toward a source of stimulation" (Dethier, 1956). McFarlane (1984) showed that small (2 to 12 day old) *B. germanica* larvae were in fact repelled by certain volatile fatty acids present in the frass. He concluded that volatile fatty acids do not play a role in aggregation in this species. Indeed, McFarlane (1984) and McFarlane & Alli (1986) pointed out that most of these acids were repellent and that their repellency had to be overcome or masked by other compounds such as lactic acid when German cockroaches were attracted to "conditioned" paper.

Recently, Sakuma & Fukami (1990) found that the attractant components of the aggregation

pheromone of *B. germanica,* isolated from frass contaminated filter paper, were alkylamines. This contrasts with the general view that these aggregation pheromones included fatty acids (Ritter & Persoons, 1975; Brossut, 1975; McFarlane, 1984). Sakuma & Fukami (1991) also reported the presence of arrestant components besides the attractants.

Chemical cues also help German cockroaches *(B. germanica),* detect food, at least in part. It has been known for some time that starved cockroaches are attracted to many kinds of fat soluble substances (Tsuji, 1965, 1966) as well as to fermentation products. Previous observations described how the number of animals in a food patch increased gradually and peaked just before the patch was completely depleted (Rivault & Cloarec, 1991). A relatively important number of animals was attracted simultaneously to a given food source, even when it was nearly exhausted and there were other food sources nearby.

The aim of this paper was to investigate whether conspecific aggregation pheromone can act as an attractant reinforcing the effect of food stimuli. Under natural conditions, small larvae arrive at food sources after larger larvae or adults, but also leave later (Cloarec & Rivault, 1991). As aggregation pheromone has more effect on them, could the fact that they remain longer in the vicinity of an empty food source be related to the deposition of pheromone by animals that had visited the food source earlier ?

Material and Methods

Experimental Area and Set Up

The observations were carried out in a public swimming-baths building. Hygrometry, temperature and photoperiod remained approximately constant. The whole building was lit artificially from 06.00 h until 22.00 h.

The experimental dishes were small (3 cm in diameter) transparent plastic round dishes. The experimental dishes were placed in a line on the 4 m wide tiled pool-side which stretched between a tiled bench placed all along a wall and the edge of the pool. The dishes were placed 0.75 m from the bench and 0.75 m from one another. In this part of the building cockroaches sheltered behind the central heating grids opening under the bench (fig. 1).

Four different categories of stimuli were presented in the dishes:

(B). 0.05 g pieces of dry bread wetted with three drops of beer just before an observation.

(F). Pieces of conditioned filter paper. Strips of filter paper approximately 30 cm long and 3 cm wide were placed in a cage (80 x 28 x 100 cm) containing several thousand individuals of a laboratory reared population of *Blattella germanica* for at least 48 hours prior to an observation. Previous observations had shown that filter paper left in a breeding cage for 24 to 48 h attracted and retained cockroach larvae in empty observation cages (Dabounieau, 1987). A strip of conditioned paper was taken out of a cage just before the start of an experiment and four 3 cm diameter test pieces were cut out to fit two series of dishes (conditioned paper in F and in BF dishes in each series).

(BF). Pieces of paper having been treated like those in (F) were placed together with pieces of bread like those in (B).

(C). A series of empty dishes served as controls (C.

Ten replicates of each type of dishes were tested. The order of the four types of dishes, each containing one of the stimuli, was random within a row. Practically, two sets of dishes were presented at a time (fig. 1), and this set-up was replicated five times.

A 4.5 volt battery light was fixed approximately 0.80 cm above each experimental dish to facilitate observations. This experimental disposition was set up before an observation, before the lights were switched off.

Observations started at 22.00 h as soon as the main lights had been switched off and continued until all the bread in the dishes had been consumed. Counts were made directly by sight. The experimental set-up gave enough light for the observer to distinguish the cockroaches, but did not disturb the animals. Scan records were taken at 2 min intervals. Each record included the number of animals in the

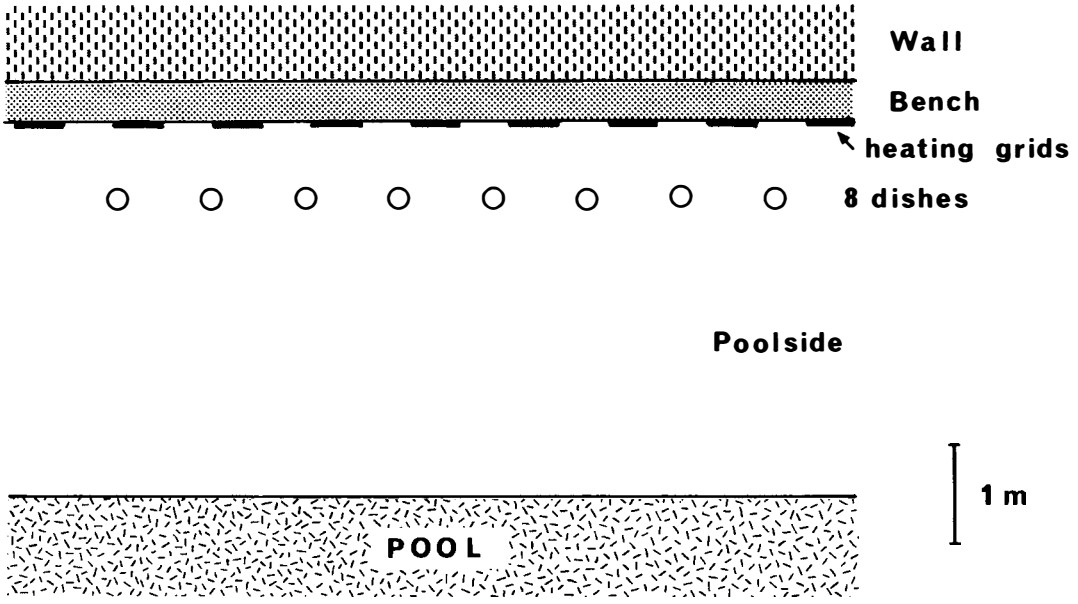

FIGURE 1. Experimental set-up, on poolside, to scale.
[Sistema experimental a escala.]

experimental dishes and within a 20 cm diameter circle around the dishes. When these observations were made the proportion of adults in the general population was exceptionally low. Therefore, because of this deficit in data concerning adults, only larvae were recorded and the larval population was divided into three developmental stages: small: 1st and 2nd instar larvae (Y); medium sized: 3rd and 4th instar larvae (M); and large: 5th and 6th instar larvae (O).

Results

Levels of attractiveness were evaluated directly by the number of animals in, or close to, the experimental dishes, in relation to the numbers of animals in, or close to, control dishes or dishes of the other experimental categories. Comparisons between levels of attractiveness of the different experimental categories were made first for pooled data (i.e. all the animals observed in or around the dishes of each category, without taking developmental stage into account), and then, in more detail, for data concerning each developmental stage. For both pooled data and for detailed analyses, the variations of the numbers of animals in the dishes and close to the dishes were analysed separately.

Pooled Data

First, records of the number of animals observed in the dishes were pooled by experimental category. Then, records for animals observed in the surrounding circles were also pooled by stimulus category.

Experimental category influenced significantly the numbers of animals recorded in the dishes, χ^2=1454, df=3, p<0.001) (fig. 2). B and BF dishes attracted significantly more animals than the two other types of dishes (F, C); but there was no significant difference between the numbers of animals in B and BF dishes, χ^2= 0.88, df=1, p>0.05). F dishes attracted significantly more animals than C dishes did, χ^2=22.7, df=1, p<0.001.

The numbers of animals present in the surrounding circles also differed significantly between categories, (χ^2=219, df=3 p<0.001) (fig. 2). B and BF stimuli attracted significantly more animals than F and C stimuli did, and in addition there were significantly more animals around BF dishes than around B dishes, χ^2=24.03, df=1, p<0.001).

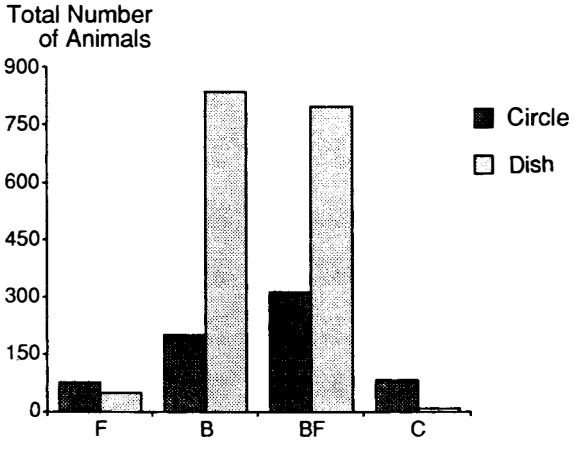

FIGURE 2. Total number of animals recorded during the observations in relation to stimulus category, in the different experimental dishes and in the circles around the dishes. B) dry bread wetted with beer ; BF) dry bread wetted with beer plus a piece of conditioned filter paper; C) empty control dishes; F) conditioned filter paper only.

[Número total de individuos atraidos a los distintos estímulos, en los platos experimentales y en los círculos alrededor de ellos. B) pan seco humedecido con cerveza; BF) pan seco humedecido con cerveza más un trozo de papel de filtro acondicionado; C) platos vacíos como control; F) papel de filtro acondicionado.]

Developmental Stage

For all experimental categories, there were relatively more small larvae than medium stage larvae, which were also more numerous than large larvae in the dishes and around the dishes. In addition, the number of animals of different developmental stages attracted to the experimental dishes differed significantly in relation to the stimulus offered (fig. 3). The type of stimulus had a significant effect on the distribution of cockroaches of all developmental stages observed in the different types of dishes (Kruskal-Wallis: small larvae p=0.013, medium sized larvae p=0.003, large larvae p=0.001). The proportion of large larvae was higher in B and BF dishes. Although on the whole F type dishes attracted only a few animals, these dishes attracted proportionally more small larvae and less medium sized larvae than dishes of the other types. In addition, F type dishes attracted hardly any large larvae. This must be compared to the fact that large larvae were completely absent in C dishes (fig. 3).

Although the number of animals in the different dishes measured directly attractiveness of sources, variations of the numbers of animals in the circles around the dishes were also recorded to test relative attractiveness (fig. 4). No significant differences in distribution were found between categories for circle data (Kruskal-Wallis, p<0.05 for large, medium and small larvae). The proportions of small larvae around all types of experimental dishes were higher than those of medium sized larvae, which in turn were higher than the proportions of large larvae (fig. 4).

Differences in the distribution of animals in relation to developmental stage were observed only at the dish level and not in the surrounding areas.

Discussion

These results show that under these experimental conditions, conditioned filter paper could attract and retain cockroaches, especially small larvae. Even though the total number of insects attracted in

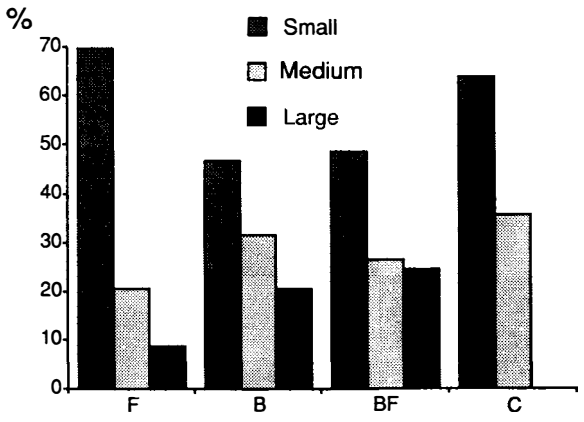

FIGURE 3. Distribution of animals observed in the experimental dishes in relation to their developmental stage (small, medium sized, and large larvae) and in relation to stimulus category. Other details, see fig. 2.

[Distribución de los individuos observados en los platos experimentales en relación a su estado de desarrollo (larvas pequeñas, medianas y grandes) y en relación a los distintos estímulos.]

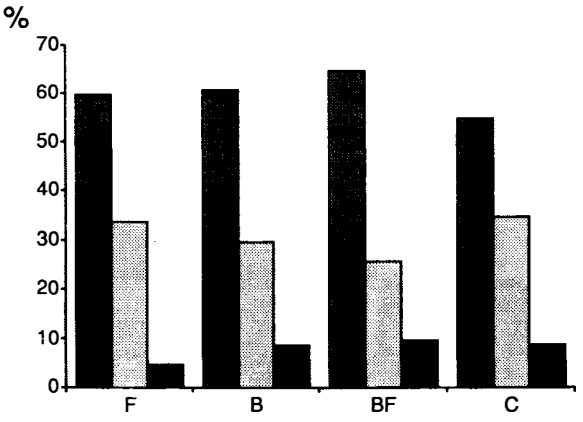

FIGURE 4. Distribution of animals observed in the circles surrounding the different types of experimental dishes in relation to their developmental stage. Other details, see figs. 2 and 3.

[Distribución de individuos observados en los círculos que rodean los platos experimentales en relación a su estado de desarrollo.]

F dishes was low, the proportions of small larvae staying in these dishes were relatively higher than those of animals of other developmental stages in F dishes and of small larvae in dishes of other experimental categories. In agreement with Metzger & Trier's (1975) results, our data suggest that responsiveness to aggregation pheromones decreased with increasing age, although all stages secrete aggregation pheromone in *B. germanica*. Small (first and second instar) larvae remained longer than animals of other developemental stages in and around F type dishes.

In addition, more insects were observed around BF dishes than around B dishes. This seemed to indicate that the presence of conditioned filter paper increased the number of insects attracted to the food sources, but that the presence of conditioned filter paper had no effect on the number of insects feeding. The food proposed in this experiment, bread wetted with beer, appeared to be a very powerful attractant, particularly for medium and large larvae, whether in B or in BF dishes, and more powerful than conditioned filter paper. The question of whether stronger, or longer conditioning of the filter paper could overcome the food attraction in this case remains open. These papers were conditioned sufficiently for social attraction to occur in the absence of choice. Whether pheromones can facilitate location of food sources requires further investigations under more controlled conditions. However, as these observations were made on a natural population, the hunger level of the animals observed could not be evaluated. Wileyto & Boush (1983) compared the attraction of *B. germanica* to various food items and concluded that, under laboratory conditions, the dregs in a beer bottle were the most powerful attractant they had tested. Concentrations of lactic acid in beer, the main attractant

element, range from 65 to 450 mg/liter (Charalambous, 1981), this is very similar to the concentrations that McFarlane & Alli (1986) found aggregated German cockroaches.

Under our experimental conditions the detection and the attraction of food items did not appear to depend on any sort of social facilitation or recruitment as described in ants (Wilson, 1971). However, during trapping experiments we have often found several cockroaches in one trap baited with bread wetted with beer while the nearby traps, which could even be touching each other, remained empty. The presence of conditioned paper increased the attractive effect of the stimulus, but did not increase the number of insects actually feeding in the dishes. The food source alone appeared to attract all the hungry cockroaches and the presence of supernumerary cockroaches when conditioned filter paper was present (BF circle) could not be related to social recruitment around a temporary food source, but rather to an increased attractiveness due to the presence of an extra source of aggregative pheromone.

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Resumen

Alimentación en Blattella germanica *(L.) y feromonas de agregación.*

Se ha analizado la influencia que ejerce el olor a coespecíficos en la comida sobre las larvas de *Blattella germanica* (L.) (Dictyoptera: Blattellidae). Se utilizaron cuatro estímulos distintos que combinaban presencia y ausencia de comida y de olor a coespecíficos: B) pan solo; F) un pedazo de papel de filtro acondicionado (impregnado, en una caja de cría de *B. germanica,* de feromonas de agregación); BF) pan junto con un pedazo de papel de filtro acondicionado; C) un plato vacío. Los resultados ponen de manifiesto que los platos con comida atraen a un número mayor de individuos que los otros. Acuden más individuos al plato con papel acondicionado que al plato vacío, y en este caso más larvas pequeñas que medianas o grandes. Las cucarachas permanecían más tiempo alrededor de las cajas que habían contenido comida cuando había, además, papel impregnado con feromonas. En estas condiciones experimentales el olor a coespecíficos no parece reforzar la atracción que ejerce la comida ni la explotación de una fuente de comida, parece vinculada a facilitación social alguna.

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