IMPORTANCE of SPATIAL and OLFACTORY LEARNING on BAIT CONSUMPTION in the GERMAN COCKROACH

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Abstract The objective of the research presented here was to evaluate the impact of the introduction of a toxic food bait on foraging choice by the German cockroach, *Blattella germanica* (L.). This was done by analysing the importance of learning visual cues associated with feeding sites and the importance of feeding experience. Cockroaches were able to associate visual cues with food and to use these learned cues to forage. A new food type placed in a new site attracted more cockroaches than the known food type in the known site. When the known food type was in a new site and the new food type in the known feeding site, most of the cockroaches oriented towards the known food type and neglected the new one. These results revealed that many factors influence the discovery and ingestion of a food source and that cockroaches take different foraging decisions in relation to the current environmental situation. They are able to distinguish a novel food placed in a novel site from a novel food placed in a site previously occupied by another food type. This also means that cockroaches learn the location of specific food resources and associate particular locations with particular resources. The results show the role of environmental parameters of feeding decisions in cockroaches. This complexity must be taken into account to optimize insecticide treatments with food baits.

Key Words learning, foraging, novelty, bait efficiency

INTRODUCTION

Exploitation of food resources is a fundamental condition for survival for all insects. Before an insect decides to ingest any food, it must make several decisions, such as when to forage (when food is available and risks are low), where to forage, and what type of food to ingest (Begon et al., 1986). Foraging strategies allow animals to deal with all kinds of environmental pressures like unforeseen variations in resource quality, quantity, availability, and distribution. The distribution and accessibility of a food resource influence search, whereas the quality of the resource influences ingestion. Resource distribution is influenced by the position and the number of food patches in the foraging area and their stability. Furthermore, the distribution of food patches in relation to potential shelters and in relation to physical barriers or limits are important environmental traits to be taken into account.

In their natural habitat, cockroaches make decisions because some food sources are spatially stable. These include household equipment, such as refrigerator, cooker, rubbish bin, and bread bin. Other food sources are not stable, such as crumbs, and fallen food scraps; and some of these food sources are large, others not. Cockroaches encounter different types of environment in relation to the stability and dispersion of resources (Rust et al., 1995). They are able to learn the position of their shelter, of a hidden target or of stable food sources in relation to visual landmarks (Rivault and Dabouineau, 1996; Durier and Rivault, 2000a) and they are able to return to food sources.

Household cockroach species are omnivorous and, although they have developed a tendency to exploit food items nearest their shelter first (Rivault and Cloarec, 1991), they can also exploit large areas in their natural habitat where food sources vary in abundance and spatial

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stability. Therefore, learning the spatial representation of food distribution and feeding experience with one type of food may influence how each individual cockroach chooses between the available food sources (Bernays, 1995).

The objective of the research presented here was to study the type of foraging strategies adopted by cockroaches under different environmental conditions, in particular after the introduction of a toxic food bait. To evaluate the influence of a bait on cockroach populations, it is important to understand how these insects exploit their home range and how, when foraging, individuals make decisions in relation to environmental conditions and in relation to previously acquired knowledge of their home range. Therefore, we investigated the capacities of the German cockroach, *B. germanica* (L.) to adjust choice among food sources in relation to feeding experience and to learned spatial representation of food sources.

MATERIALS and METHODS

Insects

Each experiment was conducted with 60 sixth instar nymphs of *B. germanica.* All cockroaches came from a local strain collected in Rennes (France) and were reared in the laboratory at 25°C with a L:D 12:12 h photoperiod. During breeding cockroaches received the same type of food: bread, which was considered to be the Known (experienced) Food Type.

Test Arena

Tests were made in large (1m²) glass arenas equipped with an electric barrier to prevent cockroaches from escaping. The floor of the arena was covered with clean white paper, which was changed before each experiment. During the scotophase, a uniform dim light (3.8W/m²) was present in the room to allow the animals to perceive their environment. A black cardboard shelter (6 x 2 x 2 cm) was placed 45 cm from one corner on the diagonal and two drinking troughs were placed symmetrically each side of the shelter (Figure 1). Each arena included two sets of visual landmarks, S1 and S2, that were used by cockroaches to locate food. S1 was placed near the

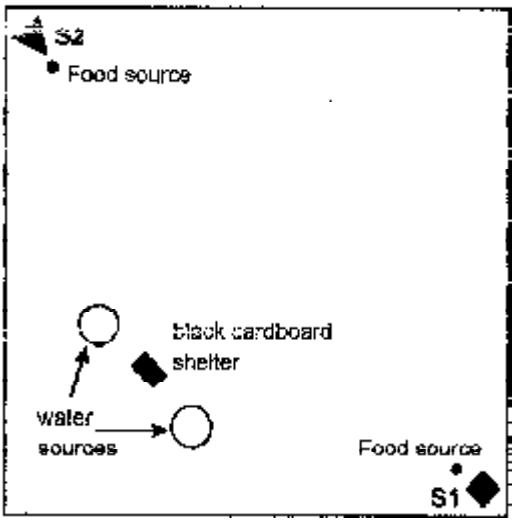

Figure 1. Diagram of the experimental set-up. A 1m² arena equipped with two water sources, one shelter, and two landmarks: S1 and S2.

corner at left-hand and S2 was placed at right-hand from the shelter. Tested food was placed in small dishes (1 cm in diameter) in front of visual landmarks. Two food types were used: bread and a gel bait without its active ingredient (Goliath food base without fipronil, Rhône-Poulenc Agro, Triangle Park, North Carolina).

Testing Protocol

Each experiment was divided into two periods: a training period, which lasted 3 days after introduction, and a test period on the fourth day. During the whole training period, one small dish (1 cm in diameter) containing bread was always placed in front of S2 for 4 hours each day, at the beginning of the scotophase. Thus, the area near the S2 was the Known (experienced) Feeding Area. During the test period, foraging activity was analysed in relation with change of environmental conditions.

Foraging paths were video-recorded with a high-sensitivity video-camera (CCD Ikegami, 0.01 lux) equipped with an infra-red projector. The lens of the camera allowed recording of the foraging paths over the whole surface of the arena. Paths were plotted using an image-processing and trajectometry software which computes several path parameters (Durier and Rivault, 2001). Paths were recorded when cockrocahes left the shelter and reached a feeding area within 5 min. The number of paths obtained per arena depended on the number of nymphs involved in foraging activities and experiments were replicated until sixty to eighty paths were obtained. In each experiment, numbers of cockroaches reaching landmrks S2 and S1 were compared to determine choice of foraging area.

Spatial Learning Experiment

This experiment was designed to determine whether cockroaches were able to learn where to find food in their home range. During the training period, a small dish filled with bread was placed near S2. During tests, there was no food in the arena. The hypothesis was that cockroaches would associate S2 with a the presence of food and use the information they learned during the training period to find it.

Odour Learning Experiment

This experiment was designed to determine how cockroaches orient to their food choice when a food bait is introduced into their familiar home range. In this case the food bait is a new type of food placed in a new area (not previously rewarding). Two hypotheses were considered for this experiment: 1) that cockroaches would orient preferentially towards the known food type (bread) in the known feeding area if they relied on what they learned during the training period; 2) that cockroaches would orient preferentially towards the new food type (Goliath) in the new feeding area if the attractiveness of the known food type had decreased in relation to the attractiveness of the novel food type.

During the training period, the small dish filled with bread was placed near landmark S2. During the test, a small dish with bread was placed near S2 and a small dish with a drop of Goliath gel was placed near landmark S1. Cockroaches could orient either towards the known food type associated with learned visual cues, which was S2, or towards the new food type from a new area, which was S1.

Spatial / Olfactory Learning

This experiment was designed to verify if cockroaches always choose the new food type (or the food bait) wherever it is located in their home range. The hypothesis is that cockroaches will not choose the bait if it was not placed in a new area. In this experiment, cockroaches had the choice between a new food type in the known feeding area and the known food type in a new

area. During the training period, bread was placed near S2. During the test, bread was placed near S1 and a drop of Goliath gel was placed near S2. Cockroaches could orient either towards the new food type associated with learned visual cues or towards the known food type in a new area but no longer associated with the learned visual cues.

RESULTS and DISCUSSION

Spatial Learning Experiment

When no olfactory stimuli were provided, significantly more cockroaches oriented towards S2 than towards S1 ($\chi^2_1 = 13.349$, $p = 0.0003$) (Figure 2). Cockroaches oriented towards the area where food was present during training. During training, they associated S2 with a feeding area and then used the learned information to find this area. Paths were short, not very sinuous with very few arrests and were travelled at slow speed (Durier and Rivault, 2001).

Odour Learning Experiment

In this experiment cockroaches oriented preferentially ($\chi^2_1 = 8.666$, $p = 0.0032$) towards landmark S1 (Figure 2). Cockroaches chose the new food type more often than the known one. Previous experiments demonstrated that bread and Goliath gel are equally attractive feeding stimulants (Durier and Rivault, 2000b). Then, the choice between these 2 food types is not induced by feeding preferences. Therefore, cockroaches were not attracted by the olfactory stimulus of the food type itself but by its novelty in their familiar environment. The perception of a new food type in a new area modified cockroach foraging decision. Cockroaches did not use what they learned during the training period and were attracted by the new olfactory stimulus that they perceived in a new area.

Spatial / Olfactory Learning Experiment

Cockroaches oriented preferentially towards S1 ($\chi^2_1 = 12.553$, $p = 0.0004$), that is towards the known food type in a new feeding area (Figure 2). They did not make the same choice as in the previous experiment. The fact that the odor of the new food type was in the known feeding area induced the cockroaches to reorientate their choice. Paths were more sinuous, longer, included many arrests and were travelled at slower speed than in the previous experiments. Some paths were oriented successively towards both feeding areas. Cockroaches oriented first towards

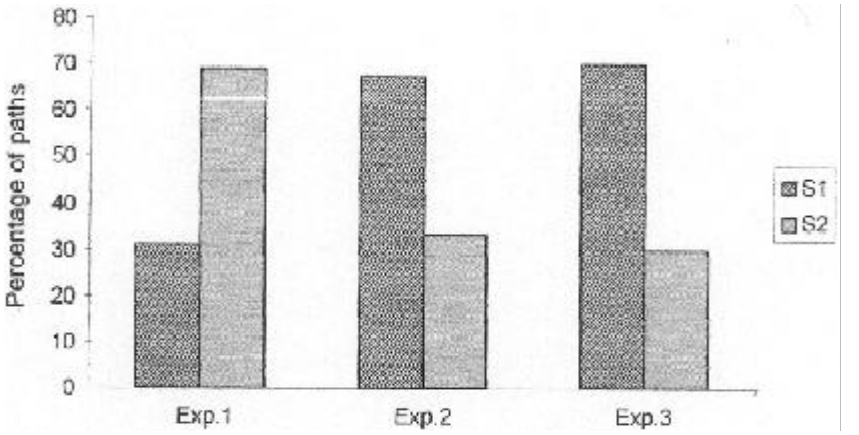

Figure 2. Choice of feeding area. Histograms indicate proportions (in %) of cockroaches orienting towards either food site: S1 or S2.

the new food type. As they neared the new food type, the situation did not fit the training situation. Consequently, they changed their choice and reoriented towards the known food type in the new area. Therefore, the perception of a new food type in an area previously associated with another type of food disturbed their foraging strategies. This result demonstrates that cockroaches know what type of food was to be found in a known area. They learned two types of information during the training period: to locate a previously rewarding area and what type of food was in that area.

In this experiment when the bait was placed in the bread area, they perceived a difference between the ongoing situation and the learned one. The discrepencies induced them to modify their initial choice and to refer to the known food type as a safer choice.

CONCLUSIONS

Our results highlight the part played by many environmental parameters (spatial distribution of food sources) and by learning capacities in food intake decisions in German cockroaches. We demonstrated that cockroaches are able to associate visual cues with food and to use these learned cues to forage (Spatial Learning Experiment). A new food type placed in a new site attracted more cockroaches than the known food type in the known site (Odour Experiment). When the known food type was in a new site and the new food type in the known feeding site, most of the cockroaches oriented towards the known food type and neglected the new one (Spatial Olfactory Experiment). This means that cockroaches learn the location of specific food resources and associate particular locations with particular resources (Durier and Rivault, 2001).

This complexity must be taken into account to optimize insecticide treatments with food baits. Our results help us to understand how cockroaches cope with the introduction of a bait (gel bait or bait station) into their familiar home range. In their home range, baits are perceived as a novelty and their probability of being consumed is related to their placement.

Cockroaches apparently learn two parameters: the position of a food-rewarding area within the home range and its quality. In addition to bait-particular characteristics in terms of attractiveness and feeding stimulation (Durier and Rivault, 2000b), novelty plays also a part in bait efficiency. Nevertheless, novelty has varying efficiency in relation to its position within the home range.

Detailed analysis of cockroach foraging behavior stressed the importance of knowledge in pest biology to improve their control in urban environment. During an insecticide treatment with food baits, we recommend applying food baits nearer the shelters than to any other available food and in places not previously used as foraging sites. This should increase the number of attracted cockroaches and consequently the bait efficiency. Then, detection and estimation of the population living area before the application of bait might be an improvement of this control method.

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