Exploitation of Home Range and Spatial Distribution of Resources in German Cockroaches (Dictyoptera: Blattellidae)

V. DURIER AND C. RIVAULT

Unité Mixte de Recherche 6552, Centre National de la Recherche Scientifique-Université de Rennes 1,
Campus de Beaulieu, 35042 Rennes Cedex, France

ABSTRACT   We analyzed the expression of edge following behavior in German cockroaches, *Blattella germanica* (L.). Structure of the environment and spatial distribution of resources modified both expression of locomotory behavior of cockroaches and its distribution between the edge and the central area of an experimental arena. When they are in a familiar environment, German cockroaches are definitely not edge followers and they exploit similarly the different parts of the accessible surface of their home range. Cockroaches placed in a new environment tended to follow edges more than undisturbed insects. This modification could be assimilated to a response to stressful conditions.

KEY WORDS   *Blattella germanica*, edge effect, exploratory behavior

EXPLORATORY BEHAVIOR ORIENTED by environmental stimuli increases the ability of insects to locate and to exploit resources in their home range. Expression of exploratory behavior varies with the animal's previous experience and appears to be a function of the discrepancy between the perceived ongoing situation and the familiar world (Hinde 1970). A small change in the environment elicits an increase in exploratory behavior, and a major change can induce stress or fear. Fright, in many species, is expressed either by modifications of locomotory activity or by freezing (Hinde 1970). Thus, expression of exploratory behavior and fear can overlap. Motivation and physiological state of the animal interfere with external stimuli to orientate movements. Causes of movements of animals in their home range are multichannelled and depend on a variable and complex ratio between various orienting stimuli (Campan 1997).

Cockroach exploratory behavior facilitates recognition of specific topographic information, which provides an advantage for foraging or retreating to shelter. Cockroaches are able to associate the position of their shelter or of a spatially stable food source with visual landmarks (Dabouineau and Rivault 1995, Rivault and Dabouineau 1996, Durier and Rivault 2000). As it is generally believed that foraging cockroaches travel mainly along edges, it is recommended to place baits and traps at floor-wall junctions, in corners, and next to cracks or crevices to control or monitor the size of the populations in urban areas (Ebeling and Reierson 1974, Reierson 1995). Previous observations of foraging behavior on baited traps placed on the wide, tiled surface around a swimming pool indicate that cockroaches explore areas wider than those defined by simple edges (Rivault 1989, 1990, Rivault and Cloarec 1991, Dabouineau 1992).

The discrepancies between our observations of exploratory movements of cockroaches within their home range and the literature led us to investigate the expression of edge following behavior in cockroaches, and to try to understand the mechanisms of this behavior. The aim of these experiments was to determine whether modifications of cockroach exploratory behavior could be related to the structure of their habitat. We hypothesized, contrary to what is usually claimed, that the presence of edges would not induce an edge following behavior characterized by a high proportion of activity near edges, and that, in the absence of other stimuli, the whole surface of the arena would be explored randomly. Modifications of walking behavior were estimated by the spatial distribution of locomotory activities in the edge area compared with the central area of an experimental arena. To understand these modifications, we analyzed the paths of cockroaches leaving their shelter to forage at the beginning of their active phase and compared them with simulated random paths. Actual paths were characterized in terms of their length, duration, speed, sinuosity, and number of arrests.

Methods

Insects

All German cockroaches, *Blattella germanica* (L.), tested came from a local strain collected in Rennes, France. During breeding, they were provided with an unlimited supply of food (bread) and water and kept at 25°C and 12-h photoperiod.
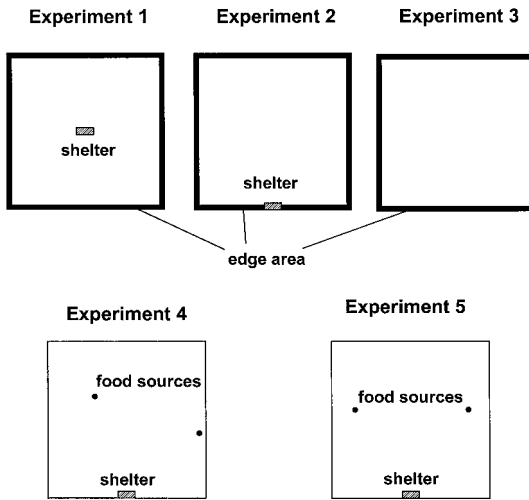
Fig. 1. Experimental setup. Surface of edge areas (experiments 1–3) is indicated in black.

Video Equipment

The paths of cockroaches were recorded by a high sensitivity video camera (CCD Ikegami, 0.01 lux), which recorded the whole surface of the arena. Paths were plotted using an image-processing and trajectometry software (J.-P. Richard, Centre National de la Recherche Scientifique [CNRS], Unité Mixte de Recherche [UMR] 6552). This software computes path characteristics: duration, length, speed, number and duration of arrests, and sinuosity calculated according to Bovet and Benhamou's (1988) formula. Sixth instar nymphs were chosen because of their large size that could be detected by the camera and because they have a great tendency to explore their home range (Rivault 1991).

Experimental Procedures

CO_2-anesthesized cockroaches were introduced into a large glass arena (1 m^2) equipped with an electric barrier to prevent escape. The floor of the arena was covered with clean white paper that was changed between recordings. During the scotophase, a uniform dim white light (3.8 W/m^2) was present in the room to allow the insects to perceive their environment.

Five experiments tested exploration and exploitation of home range (Fig. 1). Experiments 1 and 2 tested the effect of shelter position on edge following. Sixty sixth instar nymphs were introduced into the arena. Cockroaches were placed in the arena at least 30 h before recording their spontaneous locomotory behavior so that they could acclimate to their new environment during a complete light-dark cycle. Under these experimental conditions, only few individuals were active at a time. We did not use isolated animals because their activity level is quite low and they can stay motionless for hours. Aggregation phe-

nomena only occur during the resting phase and not during their active exploratory phase (DeMark and Bennett 1994, Rivault 1989). If overcrowding occurred in the arena, it would be impossible to analyze individual trajectories with the image analyzer and to draw individual paths. Each recording gave us up to eight paths. If these paths were superimposed, it would be impossible to separate and analyze them individually. Cockroach groups were renewed each time so that each path was independent. In relation to their circadian locomotory activity rhythms, experiments were conducted during the scotophase, which is their normal activity phase, to avoid any disturbance. The longer the insects stay in the arena, the better they acclimate. In experiment 1, a black cardboard shelter ($6 \times 2 \times 2$ cm) was placed in the center of the arena. In experiment 2, a black cardboard shelter was placed near an edge. Spontaneous activity of cockroaches was sampled for 2 min at the beginning of the night and their paths were plotted.

Experiment 3 tested the effect of introduction into a novel environment on spontaneous locomotory activity. This condition simulated a stressful situation. At the beginning of the night, eight sixth instar nymphs were placed in the middle of the empty arena, and their activity was recorded immediately. Only eight cockroaches were introduced at the same time into the arena because it was difficult to follow more than eight individual paths simultaneously. The activity of all eight cockroaches was recorded for 2 min and paths were plotted.

Experiment 4 tested the probability of exploitation of a food source in relation to its proximity to an edge. Sixty sixth instar nymphs were introduced into the arena with a black cardboard shelter placed near an edge. Cockroaches were placed in the arena at least 30 h before their locomotory activity was recorded so that they could acclimate to their new environment during a complete light-dark cycle. Before recording, two small dishes (ø = 1 cm), each containing the same amount of bread, were placed in the arena, 60 cm from the shelter. One dish was placed near an edge (2 cm from the edge), and the other one was placed in the middle of the arena (30 cm from the opposite edge). Foraging paths were plotted. Number of recorded paths per arena depended on the number of nymphs involved in spontaneous foraging activities and was always less than eight simultaneously. Cockroaches were considered to forage actively when they left the shelter and reached a food source within 5 min. The other paths were discarded. Paths were plotted, from the time cockroaches left their shelter until they reached one of the feeding areas and started feeding.

Experiment 5 tested the probability of exploitation of a food source in relation to previous rewarding experience at that position. Sixty sixth instar nymphs were introduced in the arena with a black cardboard shelter placed near an edge. Cockroaches were placed in the arena 3 d before recording their activity. During these 3 d, cockroaches were trained to find food in a given position. At the beginning of each night, one small dish (ø = 1 cm) containing bread was placed 5

Table 1. Observed values of parameters used to plot simulated random paths: speed is incremented with 1 cm/s and turn angle with 5°

Exp.	N	Speed (cm/s)		Turn Angle (°)		Sinuosity	
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
1	1,053	3.8	7.8	54	74	0.201	0.529
2	1,601	4.7	9.7	74	99	0.206	0.669
3	1,772	7.7	14.7	24	84	0.138	0.542

N is the number of simulated paths selected in our sample, whose mean sinuosity was between minimum and maximum observed value.

cm in front of a given landmark. The dish was 60 cm from the shelter and 15 cm from an edge. This landmark was a set of two batteries (4.5 V), each equipped with a low intensity light-emitting diode (LED). A second landmark (one battery + one LED), placed 15 cm from the opposite edge, was never reinforced with food. On the fourth day, two small dishes, each containing the same amount of bread, were placed in the arena, in front of each landmark. Foraging paths were plotted as in experiment 4.

Path Analyses

In experiments 1, 2, 4, and 5, the number of recorded paths per arena depended on the number of nymphs involved in spontaneous exploratory activities and was always less than eight simultaneously. Consequently, each individual was able to explore the arena without any interference with others. Within each replicate, obtained paths were independent because: 1) each individual was used only once, and 2) cockroaches explored individually their home range and did not follow each other (Durier and Rivault 2001). All experiments were replicated until at least 50 paths had been recorded. Path characteristics can be measured for defined areas in the arena. We then defined an edge area, 3 cm wide all around the arena and a central area covering the remaining surface (Fig. 1). For experiment 1, 2, and 3 data, ratios were calculated for length of path and number of arrests by dividing their value for the edge area by their value for the total surface of the arena. This ratio was called observed edge ratio.

Simulated Paths

To evaluate the impact of edges on exploratory behavior, we computed simulated paths to understand better the effects of edge constraints. This program was designed for insects that explored individually and randomly a 1-m² arena without spatial specialization. When the simulated insect hits an edge, no parameter induced it to follow the edge.

The simulation plotted random paths using two parameters: 1) speed and 2) turn angle. The range of values used for speed varied between the minimum and maximum values observed in each experimental situation, with 1-cm/s increments. The range of values used for turn angle varied between the minimum and maximum values observed in each experimental situation, with 5° increments (Table 1). Values of these two parameters were combined following a latin

square design. Each simulation, including 50 paths, used one combination of these two parameters. Each simulated path included 1,000 positions. For example, one combination of these two parameters, 54° as angular value and 3.8 cm/s as speed, defines, for each position, the limits of a surface, using a range of 0° ± 54° for turn angle and a range of 3.8 ± 1 cm/s for speed (Fig. 2). The following position was taken randomly within that surface, and so on for the 1,000 positions along a path. Only simulated paths with a mean sinuosity between the minimum and maximum observed sinuosity in each experiment were selected (Table 1). The selected paths were used to calculate a simulated edge ratio using the same protocol as for the observed edge ratio for observed paths. Edge effect was compared between experimental and simulated paths.

Results

Modifications of cockroach exploratory behavior were estimated by the spatial distribution of locomo-
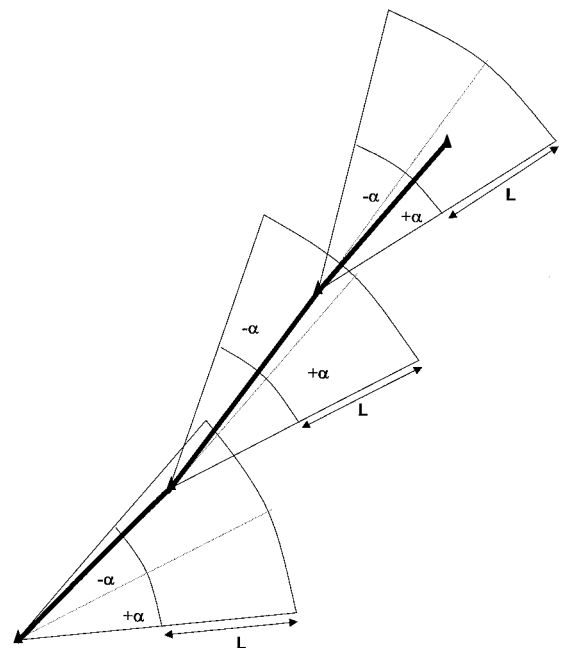
Fig. 2. Simulation of a few random positions within a path, using a combination of turn angle and speed taken from the range of observed values for these parameters. α, maximum turn angle between two positions; L, range of length traveled between two positions for a given speed.

tory activities between the edge area and the central area. The edges of the arena limit their home range and are comparable to floor-wall junctions present in their natural environment. Locomotory behavior was analyzed in relation to: 1) departure position (from the shelter in which cockroaches were resting) and 2) "goal" position (food source for which they are looking).

We compared observed paths in different experimental situations with simulated random paths using parameter ranges (turn angle and speed) observed during these experiments.

Locomotory Behavior in Relation to Departure Position

In experiment 1, we assumed that the presence of edges in the home range confined cockroaches in the edge area. The null hypothesis was that observed and simulated edge ratios had the same distribution. The alternative hypothesis was that the observed edge ratio was different from the simulated edge ratio for which no particular edge following parameter was included. The observed edge ratio for path length was 29.8%, and the simulated edge ratio was 27.8%. These ratios did not differ significantly ($N_{exp.1} = 54$, $N_{simul1} = 1053$, $t = 1.465$, $P = 0.14$). The decision to accept the null hypothesis led us to take a risk of type II error of accepting a false null hypothesis (Sokal and Rohlf 1969). The type II error, β is $9.07 \times 10^{0.09}$ with $\alpha = 0.05$. Therefore, we can conclude that cockroaches did not walk near edges more than indicated by simulated random paths. Nevertheless, cockroaches tended to make more arrests in the edge area than expected from path length in that area. The observed edge ratio for number of arrests, 39.4%, was significantly greater than the observed edge ratio for path length of 29.8% ($t = 5.345$, $P < 0.05$). Speed of paths near edges was significantly lower than in the central area ($t = 4.091$, df = 48, $P < 0.05$). The presence of the edge of the arena induced slight modifications of exploratory behavior. Cockroaches made relatively more arrests and moved more slowly near edges than in the central area, although they did not walk significantly more along edges. When their shelter was placed in the central area, they explored the whole area and did not tend to be confined to the edge area.

In experiment 2, we hypothesized that the position of the shelter near an edge of the arena should increase the presence of cockroaches in the edge area. The observed edge ratio for path length was 22.6%, and the simulated edge ratio was 22.5%. These ratios did not differ significantly ($N_{exp.2} = 65$, $N_{simul2} = 1601$, $t = 0.023$, $P = 0.98$). The decision to accept the null hypothesis was taken with a small risk of type II error ($\beta = 9.19 \times 10^{0.05}$ with $\alpha = 0.05$). Compared with simulated random paths, cockroaches did not walk near edges relatively more than in the central area (Fig. 3a). Again, cockroaches tended to make more arrests in the edge area than expected from path length in that area. The observed edge ratio for number of arrests, 36%, was significantly greater than the

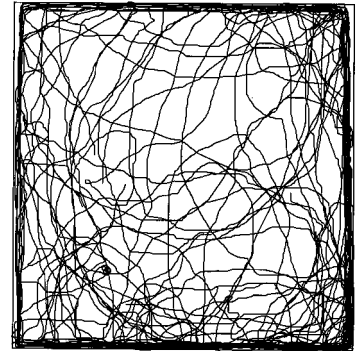**Experiment 2**

shelter
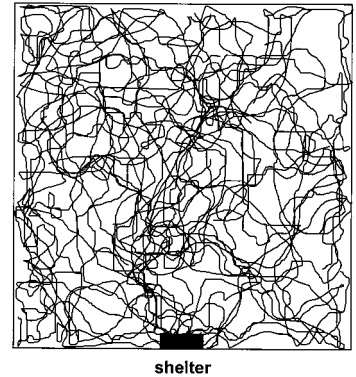
Experiment 3

Fig. 3. Twenty video-filmed path trajectories were superimposed for experiments 2 (top) and 3 (bottom). These superimposed path trajectories revealed the importance of the edge following in experiment 3.

observed edge ratio for path length (22.6%) ($t = 4.728$, $P < 0.05$). Speed of paths near edges was significantly less than in the central area ($t = 2.405$, df = 59, $P < 0.05$). As in experiment 1, cockroaches made relatively more arrests and moved more slowly near edges than in the central area. Even though their shelter was near an edge, they did not confine their locomotory activity to the edge area. The position of the shelter in the arena, and consequently the departure of the path, did not modify the spatial distribution of exploratory behavior in their familiar environment.

In experiment 3, we hypothesized that the exploratory behavior of cockroaches placed in a new environment should differ from that observed in a familiar environment. The observed edge ratio for path length was 55.4%, and the simulated edge ratio was 49.1%. These ratios differed significantly ($N_{exp.3} = 76$, $N_{simul3} = 4772$, $t = 2.748$, $P < 0.05$). Cockroach locomotory activity was significantly greater in the edge area than expected from simulated paths. Cockroaches made more arrests in the edge area than expected from path length in that area. The observed edge ratio for number of arrests (86.1%) was significantly greater than the observed edge ratio for path length (55.4%) ($t = 14.167$, $P < 0.05$). Speed of paths near edges was significantly less than in the central area ($t = 8.985$, df = 75, $P < 0.05$). Cockroaches made relatively more

arrests and moved more slowly near edges. Compared with simulated random paths, nymphs walked relatively more near edges than in the central area (Fig. 3b). They were confined more to the edge area, and their tendency to follow the edges in an unknown arena was greater than was expected with random simulations.

Comparisons between experiments 1, 2, and 3 indicated that the observed edge ratios for path length and for number of arrests were greater in experiment 3 than in experiments 1 and 2 (analysis of variance (ANOVA), path length, $F = 47.562$, df = 2,192, $P < 0.05$; number of arrests, $F = 102.114$, df = 2,192, $P < 0.05$). Paths in the edge area or in the central area were traveled more rapidly in experiment 3 than in experiments 1 and 2 (ANOVA, edge area, $F = 49.52$, df = 2,183, $P < 0.05$; central area, $F = 58.443$, df = 2,191, $P < 0.05$). Durations of arrests in the central area or in the edge area were longer in experiment 3 than in experiments 1 and 2 (ANOVA, central area, $F = 51.21$, df = 2, 1753, $P < 0.05$; edge area, $F = 5.77$, df = 2, 2417, $P < 0.05$). Paths in the central area or in the edge area were less sinuous in experiment 3 than in experiments 1 and 2 (ANOVA, central area, $F = 60.93$, df = 2,191, $P < 0.05$; edge area, $F = 17.22$, df = 2,168, $P < 0.05$). Differences in observed path characteristics indicated that cockroaches did not explore an unknown environment (experiment 3) in the same way as they did a familiar environment (experiments 1 and 2). The observed differences in the values of path characteristics were considered to indicate stress.

The presence of an edge induced modifications of cockroach exploratory behavior. Reduced speed and increased number of arrests were observed under all experimental conditions in the edge area. The greater tendency to follow edges, observed in experiment 3, was induced by novelty of experimental conditions, which could be related to stressful conditions.

Locomotory Behavior in Relation to Goal Position

In experiments 4 and 5, when cockroaches were given a choice between two similar food sources, we hypothesized that the position of food sources in the home range would modify choice and exploratory behavior in relation to the proximity of food to an edge and to previous experience.

In experiment 4, cockroaches consumed the source placed near the edge as often as the source placed in the central area ($N_{near} = 37$, $N_{far} = 31$, $\chi^2 = 0.53$, $P = 0.47$). Proximity of a food source to an edge did not facilitate its discovery. In experiment 5, cockroaches consumed the food placed in the training area as often as the food placed in a new area ($N_1 = 35$, $N_2 = 41$, $\chi^2 = 0.325$, $P = 0.57$). Experienced rewarding position of a food source did not influence cockroach choice. Under these experimental conditions, choice between two identical food sources was influenced neither by the position of food sources in relation to their distance from an edge, nor by previous experience of the location of a food source.

However, length and duration of the paths as well as the number of arrests were significantly greater in experiment 4 than in experiment 5 (length, $t = 3.612$, $P < 0.05$; duration, $t = 4.993$, $P < 0.05$; number of arrests, $t = 5.172$, $P < 0.05$). Duration of arrests and sinuosity of paths did not differ significantly between experiments 4 and 5 (duration, $t = 1.33$, $P = 0.18$; sinuosity, $t = 1.76$, $P = 0.08$). Paths were traveled at a slower speed in experiment 4 than in experiment 5 ($t = 3.68$, $P < 0.05$). Comparison of path characteristics indicated that paths in experiment 5 were more direct than that in experiment 4. Although the olfactory stimulus from both sources was identical in both experiments, path characteristics differed. Thus, previous experience of a food source in experiment 5 improved foraging efficiency.

Discussion

Our results show that the structure of the environment and the spatial distribution of resources can modify both the expression of locomotory behavior of cockroaches and its distribution in the environment. Our experimental results (experiments 1 and 2) reveal two main points. First, the expression of exploratory behavior was modified by the presence of an edge that induced a decline in walking speed and an increase in the number of arrests. Second, exploratory behavior in a familiar environment was not confined to the edge area and covered the whole surface of the arena (Fig. 3a). Comparisons between simulated random paths and experimental cockroach paths showed that when cockroaches were in a familiar environment, they did not tend to follow edges. Furthermore, the starting point of an exploratory path, either near an edge or in the central area, did not induce an edge following tendency. Similarly, in a richer environment, the goal position, materialized by a food source, was not found more easily when it was placed near an edge or in the central area (experiment 4). Under these experimental conditions, previous experience with a rewarding food source did not influence the choice of a food source, but it increased foraging efficiency by shortening paths (experiment 5). Important edge following was observed only in cockroaches placed in a new environment (experiment 3) (Fig. 3b). Path characteristics were highly modified when cockroaches were introduced into a novel environment. In this case, cockroaches moved at very high speed, made long arrests near edges, and spent longer following edges.

In a familiar environment, cockroaches had the opportunity to form relationships between landmarks and presence of different resources (DeMark et al. 1993, Durier and Rivault 2001), and they did this in experiments 1 and 2, in which all environmental factors were maintained unchanged. In a field situation, cockroaches are established in a familiar environment, which they explore regularly and where they spend most of their life (Rivault 1990). In this familiar environment, a few components might change between two exploratory phases so they have to update continuously their knowledge of their home range by

exploring novelties and by learning new spatial associations (Durier and Rivault 2002). When many environmental components change, cockroaches find themselves in situations more or less similar to those in experiment 3, in which they could use no known navigation cues and had to refer to direct stimuli such as thigmotaxis.

Our results contradict the general belief that cockroaches travel along edges (Ebeling and Reierson 1974, Reierson 1995). This is true only when cockroaches are in an unfamiliar environment, a fact that could be assimilated to a stressful situation. When they are in their familiar environment, they are definitely not edge followers. Cockroaches exploit similarly the different parts of the accessible surface of their home range (Silverman and Bieman 1996). When cockroaches are stressed, they head toward a refuge in which thigmotactic contacts can be positively reinforced (Darchen 1954). As proximity to an edge satisfies their thigmotactism, it induces edge following only under stressful conditions. As edge following is not expressed frequently in a familiar environment, recommendations to place insecticidal baits along walls to control cockroach populations do not take into account all their natural behavioral features and may not be the more efficient tactic. Other methods of cockroach control, as sticky traps or jars, rely on their tendency to explore novelties and to enter into dark refuges, as demonstrated by Appel (1998).

Acknowledgments

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