A model of animal movements in a bounded space

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Abstract

Most studies describing animal movements have been developed in the framework of population dispersion or population dynamics, and have mainly focused on movements in open spaces. During their trips, however, animals are likely to encounter physical heterogeneities that guide their movements and, as a result, influence their spatial distribution. In this paper, we develop a statistical model of individual movement in a bounded space. We introduced cockroaches in a circular arena and quantified accurately the behaviors underlying their movement in a finite space. Close to the edges, we considered that the animals exhibit a linear movement mode with a constant probability per unit time to leave the edge and enter the central zone of the arena. Far from the walls cockroaches were assumed to move according to a diffusive random walk which enabled us to overcome the inherent problem of the quantification of the turning angle distribution. A numerical model implementing the behavioral rules derived from our experiments, confirms that the pattern of the spatial distribution of animals observed can be reliably accounted for by wall-following behaviors combined with a diffusive random walk. The approach developed in this study can be applied to model the movements of animals in various environment under consideration of spatial structure.
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1. Introduction

Random walk and diffusion models are commonly used to describe animal movements in their environment, analyse their dispersion and predict their spatial distribution (Okubo, 1980; Kareiva and Shigesada, 1983; McCulloch and Cain, 1989; Berg, 1993; Turchin, 1998; Byers, 2001). These models have been used for instance to describe the foraging patterns of ants (Crist and McMahon, 1991), the search for resources in butterflies (Root and Kareiva, 1984) or the migration patterns of vertebrates (Bergman et al., 2000).

Land cover types and landscape spatial heterogeneities (e.g. patch boundaries or habitat edges) can affect the spatial distribution of organisms through their influence on their movement patterns (Crist et al., 1992; Johnson et al., 1992; Wiens et al., 1993; Morales and Ellner, 2002). In particular, the influence of small-scale physical heterogeneities of the environment will be important for small size walking or crawling species. For instance, it is known that ants and termites orient their movements along the structural guidelines created by rocks, crest lines or grooves (Jander and Daumer, 1974; Klotz and Reid, 1992, 1993; Klotz et al., 2000). The tendency for an organism to orient itself in space by mechanical contacts has been termed thigmotaxis (Fraenkel and Gunn, 1961), and the trend to move along edges has been defined as wall-following behavior (Creed and Miller, 1990). In these cases, animals are not attracted towards physical heterogeneities by long-range stimulations (as it is the case in phototaxis or chemotaxis) but rather, they move randomly in the environment until establishing a physical contact with an obstacle that will guide their motion.

In this paper we investigate how the motion patterns of organisms are affected by the presence of physical edges in a simple situation in which the tracking and

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quantification of animals' movements can be easily conducted. We study the movements of the German cockroach *Blattella germanica* (L.) when introduced in a circular arena. In this situation cockroaches display both exploratory and wall-following behaviors (Darchen, 1957). First, we identify and quantify the behavioral rules that were assumed to contribute to the spatial distribution of the cockroaches. We then built a statistical model of individual motion to verify that these behavioral rules can explain the spatial distribution of cockroaches in an enclosed area, qualitatively as well as quantitatively.

2. Methods and results

2.1. Experimental set-up, data collection and definition of individual behaviors

2.1.1. Experimental animals

Experiments were performed with first instar larvae (24-h old) of *B. germanica* (L.) (Dictyoptera: Blattellidae). At this stage of development the body length is about 3 mm (excluding the antennae), the body width 2 mm and the antennae length 3 mm. The experimental arena was 11 cm in diameter and 0.3 cm in height. It was covered with a glass plate to avoid air currents and to prevent larvae from escaping. The arena was cleaned before each experiment with hot soapy water and alcohol to remove any residual chemical cues. The set-up was placed on a table surrounded with white curtains to homogenize the light and to mask visual landmarks. At the beginning of an experiment an individual was introduced under CO_2 narcosis at the center of the arena. Each experiment was set to 60 min and the larvae were used only once. A total of 19 replications were performed.

2.1.2. Path analysis

The behavior of the cockroaches was recorded continuously with a high definition camera (Sony CDR-VX 2000 E) placed above the arena. The paths were then digitized at a sample rate of one point every 0.68 s with an automatic video-tracking software (Ethovision®, version 1.90, Noldus Information Technology). Calibration factors were 0.06 cm pixel^{-1} on the Y-axis and 0.05 cm pixel^{-1} on the X-axis. The sampling rate was chosen so as to avoid both undersampling (which induces a loss of information due to low temporal resolution) and oversampling (which introduces some noise due to the wobbling movement of the larva). The paths were converted as a series of Cartesian coordinates and were characterized by several parameters (that will be detailed in the result section).

2.1.3. Criteria for wall-following behavior

When introduced in the arena, the cockroaches spent most of their time (about 50%, see below) walking close to the edge of the arena, with their ipsilateral antenna dragging along the wall. When a cockroach moves along the edge, it holds its antennae forward in a slightly lateral position and maintains its relative position to the wall with the mechanoreceptors associated to the antennae (Camhi and Johnson, 1999; Okada and Toh, 2000). In our experiments, we distinguished two kinds of movements depending on the distance between the larva and the edge of the arena. We considered that a cockroach displayed wall-following behavior when it was less than 0.5 cm from the wall. This corresponds to the minimal distance required for a larva to establish an antennal contact with the wall. Hereafter, we will call this zone the peripheral zone (of the arena) (Fig. 1). The rest of the arena will be defined as the central zone.

2.1.4. Definition of a path

We assumed that a cockroach remained motionless when the two following conditions were fulfilled: (1) its displacement between two successive steps was less than 0.1 mm and (2) the stop duration was at least 1.36 s (corresponding to two successive observations). In the peripheral zone, the beginning of a path was determined by the occurrence of one of the two following events: (1) a motionless cockroach in the peripheral zone started a new displacement or (2) a moving larva reached the peripheral zone from the central zone. A path ended
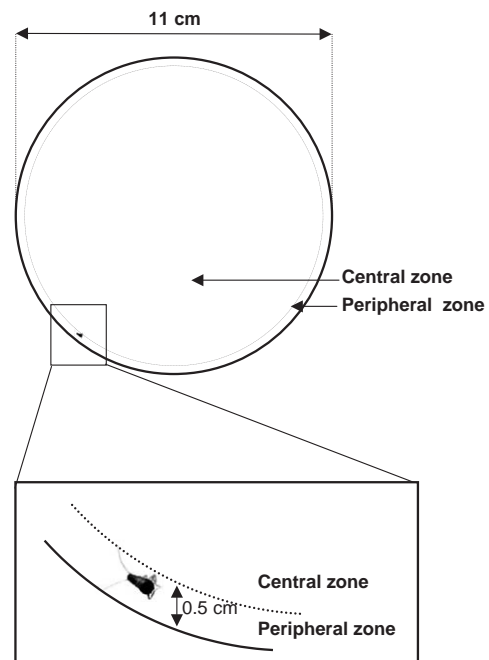

Fig. 1. Experimental arena (cockroach and arena are represented at approximately the same scale). A cockroach was considered to walk in the peripheral zone when it could establish an antennal contact with the wall (see enlargement).
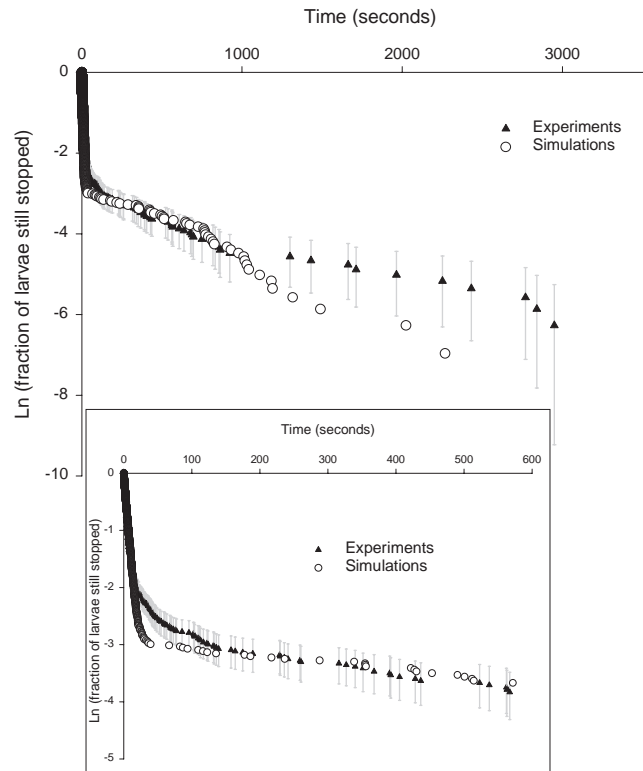
Fig. 2. Natural logarithm of the fraction of cockroaches that are still stopped as a function of time for experimental data ($\pm 95\%$ confidence interval) and from simulations (that assume a double exponential distribution of stop durations). Note that each plot corresponds to the survival curve of 1060 stopping durations. The insert shows both curves for stopping durations less than 600 s.

each time a larva stopped its movement or when it left the peripheral zone. In the central zone, we considered that a path began when either (1) a larva had just left the peripheral zone and entered the central zone or (2) a motionless cockroach in the central zone started to move. A path ended each time a larva entered the peripheral zone or stopped its displacement in the central zone.

2.2. Statistical modeling of individual behaviors

This section is devoted to the statistical quantification of individual behaviors based on the observed movements. The data collected for the 19 cockroaches were pooled.

2.2.1. Duration of stops in the peripheral and central zones of the arena

There was no significant difference between the duration of the motionless state in the peripheral ($n = 634$) and the central zone of the arena ($n = 426$) (Mann–Whitney test, $Z = -1.37$, $P > 0.05$). If the probability for a larva to initiate a new displacement was constant over time then the log-survival curve of the number of cockroaches still motionless either in the central or the peripheral zone of the arena should fit a straight line (Haccou and Meelis, 1992). However, as shown in Fig. 2,

the curve suggests that the duration of the stops was either short or long. We thus assumed that each cockroach can be in two states that control the duration of the stops. This hypothesis is supported by behavioral observations. Indeed, when a cockroach stops it may remain either active and display antennal movements ("awake" state) or inactive without performing any antennal movement ("resting" state). The "awake" state is characterized by short stops and the "resting" state by long stops. We hypothesized that each kind of stops follows an exponential law. We then estimated the probability p_{Short} for a cockroach to be in the "awake" state and the mean duration of short and long stops (respectively τ_{Short} and τ_{Long}) by fitting the fraction of cockroaches $F(t)$ still motionless at time t with the following equation (using the least squares method):

$$F = p_{Short}e^{-t/\tau_{Short}} + (1 - p_{Short})e^{-t/\tau_{Long}}.$$

The best fit was obtained with $p_{Short} = 0.93$, $\tau_{Short} = 5.87$ s and $\tau_{Long} = 700$ s. Using these parameter values, we computed a theoretical distribution of stop durations ($n = 1060$) with Monte Carlo simulations. There were no significant differences between the theoretical and experimental distributions (Mann–Whitney test, $Z = -0.6$, $p > 0.05$). The good agreement suggests that stopping times can be satisfactorily explained by the two internal states we hypothesized.

2.2.2. Wall-following movement

Paths characteristics in the peripheral zone: The cockroaches were assumed to exhibit a linear motion mode, i.e. the larvae were considered to move tangentially along the arena wall at a distance of 0.5 cm.

Mean velocity in the peripheral zone: We measured the angular difference θ_i of the position of the cockroach at the beginning and the end of each path (as defined above) with respect to the center of the arena (arena radius: r) and its relative duration t_i. Taking into account all the paths collected for all larvae, the average velocity $\langle v_p \rangle$, was then computed as follows:

$$\langle v_p \rangle = \frac{\sum_{i=1}^{i=n}(r\theta_i)}{\sum_{i=1}^{i=n} t_i}.$$

Using this formula we found that the average velocity at the peripheral zone was $1.06 \, \text{cm s}^{-1}$ ($n = 1418$).

Probabilities to stop and to exit the peripheral zone: We computed the duration of each path of the cockroaches in the peripheral zone and then calculated the fraction $F(t)$ of cockroaches that did not stop or leave the periphery as a function of time t, i.e. $F(t)$ is the fraction of individuals still moving at time t. Fig. 3 shows the resulting extinction curve on a semi-logarithmic scale. This curve can be fitted by a linear function

$$\ln(F(t)) = -\frac{t}{\tau}.$$

The extinction curve of the two behaviors is thus characterized by an exponential decay and the probability per unit time to perform one of the two behaviors is independent of the duration of the path previously covered by the cockroach (Haccou and Meelis, 1992). This corresponds to a memory-less process, τ gives the characteristic time before a cockroach leaves the periphery or stops and dt/τ gives the probability that one of these events occurs during the time interval dt. Leaving the periphery and making a stop are two exclusive events which means that during a time interval dt, only either of these events might occur; therefore the probability that a cockroach performs one of these behaviors during dt is given by

$$\frac{dt}{\tau} = \frac{dt}{\tau_{Exit}} + \frac{dt}{\tau_{Stop,p}},$$

where $\tau_{Stop,p}$ and τ_{Exit} are the characteristic times, respectively, before a stop in the peripheral zone or an exit. It can easily be shown that

$$\frac{1}{\tau_{Stop,p}} = \frac{1}{\tau}\left(\frac{N_{Stop,p}}{N}\right),$$

where $N_{Stop,p}$ is the number of paths that ended with a stop and N is the total number of paths that ended either with a stop or an exit from the peripheral zone.
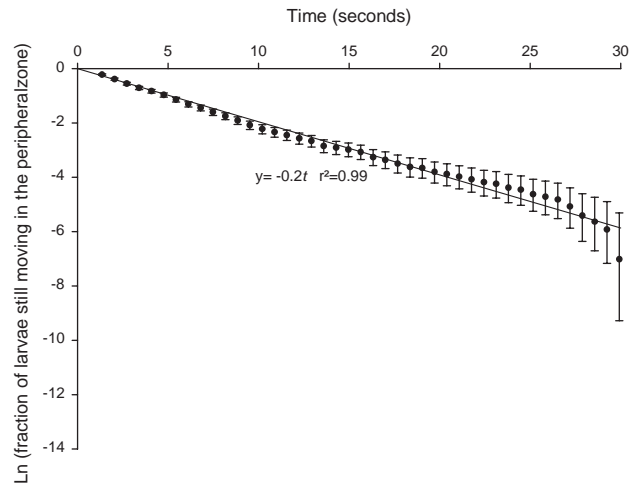

Fig. 3. Natural logarithm of the fraction of cockroaches that did not stop or exit the peripheral zone as a function of time ($n = 1418$). Error bars are 95% confidence intervals.

In the experiments we found $N_{Stop,p} = 567$, $N = 1418$ and $1/\tau = 0.20 \, \text{s}^{-1}$ (Fig. 3). It follows that

$$\frac{1}{\tau_{Stop,p}} = 0.08 \, \text{s}^{-1},$$

$$\frac{1}{\tau_{Exit}} = 0.12 \, \text{s}^{-1}.$$

2.2.3. Movement in the central zone

Mean velocity in the central zone: We considered each path i recorded in the central zone of the arena (as defined above) and measured its length l_i and its relative duration t_i. Considering all the paths collected for all larvae, the average velocity, $\langle v_c \rangle$ was computed as follows:

$$\langle v_c \rangle = \frac{\sum_{i=1}^{i=n}(l_i)}{\sum_{i=1}^{i=n}(t_i)}.$$

Using this formula we found that the mean velocity of a moving cockroach in the central zone of the arena was $1.1 \, \text{cm s}^{-1}$ ($n = 1332$).

Path characteristics in the central zone of the arena: The continuous movements of the cockroaches can be approximated by a series of straight line interrupted by angular reorientations (Turchin et al., 1991). Their trajectories can thus be characterized by a mean free path (l) which corresponds to the average length covered by a cockroach between two successive changes of direction and a phase function $p(\theta'/\theta)$, which represents the probability distribution for a cockroach with an initial direction θ to continue in a direction θ' (Bovet and Benhamou, 1988). The degree of anisotropy of the phase function (g) gives a measure of the tendency to move in the same direction; this parameter is defined by the

formula

$$g = \langle \cos(\theta) \rangle = \int_{2\pi} p(\theta' \mid \theta) \cos(\theta') \, d\theta', \quad g \in [-1; 1].$$

A value of g close to 1 indicates a high degree of directional persistence, whereas a value close to -1 indicates frequent reversal of direction. When the frequency distribution of changes of direction is uniform $g = 0$ and the diffusion is isotropic.

The calculation of the distribution of turning angles requires an unbiased criterion to establish accurately at which moment a cockroach significantly changed the direction of its path (Tourtellot et al., 1991; Turchin, 1998). However, finding such a criterion without making arbitrary assumption is a difficult task. An alternative method is to compute the transport mean free path, l^*. The value l^* represents the distance for which the random walk become uncorrelated. Diffusion theory states that, for an isotropic phase function and after a few diffusive events, the spatial distribution of organisms can be reliably reproduced with an isotropic phase function and the transport mean free path (Case and Zweifel, 1967). The calculation of l^* does not require the characterization of the phase function:

$$l^* = \frac{l}{1 - g} \quad l^* \in \left[\frac{l}{2}; +\infty \right[.$$

The net squared displacement of a moving individual is given by (Kareiva and Shigesada, 1983)

$$\langle R_n^2 \rangle \approx n \int_0^{+\infty} l^2 p(l) \, dl,$$

where $p(l) \, dl$ is the probability that the length of each path has a value between l and $l + dl$. $\langle R_n^2 \rangle$ corresponds to the straight line distance between the beginning of a path and the position of the individual after n consecutive steps. In the case of a diffusive random walk, assuming an exponential distribution of the path lengths with a characteristic length l^*:

$$p(l) = \frac{1}{l^*} \, (e^{-l/l^*}).$$

Then,

$$\langle R_n^2 \rangle \approx n \int_0^{+\infty} l^2 \frac{1}{l^*} (e^{-l/l^*}) \, dl \approx 2n(l^*)^2. \tag{1}$$

Assuming that the velocity v is constant:

$$n = \frac{tv}{l^*} \tag{2}$$

and substituting Eq. (2) in Eq. (1) we finally get

$$\langle R_n^2 \rangle \approx 2v(l^*)t \quad \text{and} \quad l^* = \frac{\langle R_n^2 \rangle}{2vt}. \tag{3}$$

For each path and each time step, we calculated the square of the distance, R_n, between the beginning of the path (x_0, y_0) and the position (x, y) of the cockroach
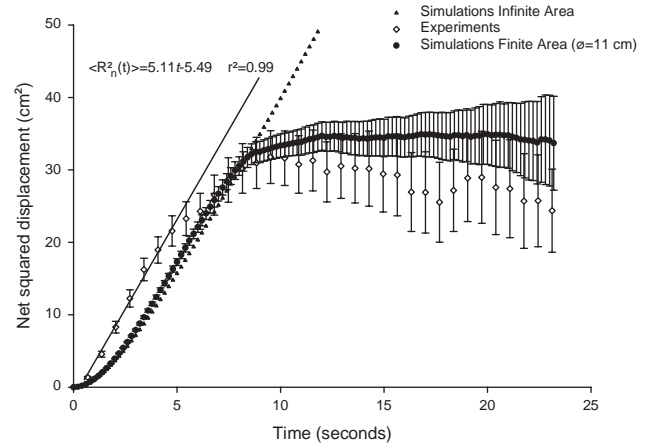

Fig. 4. Mean net squared displacement as a function of time. The solid line represents the linear regression of the initial part of the experimental curve. Simulations were performed either in an infinite (filled triangles) or in a finite (Ø = 5.5 cm) arena size (filled circles). Error bars are 95% confidence intervals.

after n steps:

$$R_n^2 = (x_n - x_0)^2 + (y_n - y_0)^2.$$

Fig. 4 shows the average squared distances $\langle R_n^2 \rangle$ as a function of time obtained for all paths recorded in the central zone of the arena. During the diffusive regime, the mean squared net displacement increases linearly with time, it then reaches a plateau as a consequence of finite space provided by the arena that prevents cockroaches to diffuse further away.

Fitting the initial linear part of the curve to get the slope, we obtained (Fig. 4)

$$\langle R_n^2(t) \rangle = 5.11t - 5.49, \quad r^2 = 0.99. \tag{4}$$

With $v = 1.1 \, \text{cm s}^{-1}$, and using Eqs. (3) and (4), we get the value of the transport mean free path $l^* = 2.32 \, \text{cm}$.

The experimental values of $\langle v_c \rangle$ and l^* were then used in Monte Carlo simulations of a diffusive random walk model (simulation details will be described below) with an arena size similar to the one used in our experiments. The mean squared displacement was computed with the same procedure as that described for the experimental paths (Fig. 4). The qualitative agreement between the results of the experiments and the simulations suggests that the movement of the cockroaches in the central zone of the arena can be confidently modeled by a diffusive random walk model with the experimentally assessed parameters. The simulations done with an arena of infinite size confirm that the plateau reached in the second part of the curve is due to the confinement in a finite space. It also confirms that the confinement effect is not prejudicial for the application of the random walk model. Note that the minor disagreement between experiments and simulations concerning the transition between the ballistic (initial part of the curve) and the diffusive

regime does not bias the assessment of the transport mean free path. This deviation results from the variation in the velocity of the cockroaches during the experiments while the velocity is assumed to remain constant in the model.

Probability to stop in the central zone: To assess the probability for a larva to stop in the central zone we used only the paths of the cockroaches that started in the peripheral zone of the arena and that either stopped in the central zone or returned to the periphery. Assuming a constant velocity v_c, the fraction $F_{Stop,c}$ of cockroaches that stopped from the entry point in the central zone of the arena can be expressed by the formula

$$F_{Stop,c} = 1 - \int_0^{+\infty} p(L)e^{-L/v_c\tau_{Stop,c}}\, dL$$
$$= 1 - \left\langle e^{(-L/v_c\tau_{Stop,c})} \right\rangle, \qquad (5)$$

where $1/\tau_{Stop,c}$ is the probability to stop per unit time. The second term in Eq. (5) represents the mean exponential attenuation over all possible paths of length L defined on $[0; +\infty[$. To compute $1/\tau_{Stop,c}$, we need to characterize the distribution $p(L)$ of the lengths of the diffusive paths (which began and ended at the periphery). Under the assumption that $\tau_{Stop,c}$ is larger than the characteristic time required to cross the whole area, one can use the approximation

$$\left\langle e^{-L/(v_c\tau_{Stop,c})} \right\rangle \approx \left\langle 1 - \left(\frac{L}{v_c\tau_{Stop,c}}\right) \right\rangle$$

and Eq. (5) simplifies to

$$F_{Stop,c} \approx \left(\frac{\langle L \rangle}{v_c\tau_{Stop,c}}\right).$$

Then,
$$\frac{1}{\tau_{Stop,c}} = \frac{v_c(F_{Stop,c})}{\langle L \rangle}. \qquad (6)$$

Blanco and Fournier (2003) have shown that in the case of a pure diffusive process with an isotropic incidence, the average trajectory length $\langle L \rangle$, defined as the mean length of the random walk trajectories from the entry point to the first exit out of the diffusive area, is independent of the diffusion path features and depends only on the geometry of the system. For our circular arena we get

$$\langle L \rangle = \frac{d\pi}{4}, \qquad (7)$$

where d is the diameter of the arena (10 cm for the central zone) over which the diffusive process occurs. This yields a value of $\langle L \rangle = 7.85$ cm. In the present case, however, the incidence is not strictly isotropic. Computing $\langle L \rangle$ from experiments and from Monte Carlo simulations based on the behavioral rules derived from the experiments (see below), we obtained a value of 7.54 ± 0.37 cm (mean $\pm$ SE, $n = 949$) and 7.43 ± 0.069 cm

(mean $\pm$ SE, $n = 10,000$), respectively. Both values are close to the theoretical one. This indicates that the theoretical value computed from Eq. (7) can be used confidently (even for a non strictly isotropic incidence). It also confirms that the use of a random walk model in the central zone of the arena was justified.

Therefore, from Eqs. (6) and (7) we get

$$\frac{1}{\tau_{Stop,c}} = \frac{4v_c(F_{Stop,c})}{\pi d}.$$

In the central zone of the arena, the fraction $F_{Stop,c}$ was 21% ($n = 1207$). Thus, the probability per unit time to stop in the central zone of the arena is

$$\frac{1}{\tau_{Stop,c}} = 0.03 \text{ s}^{-1}.$$

2.2.4. Coupling cockroaches movement in the peripheral and central zones

In the preceding sections we characterized cockroach movements either in the central or in the peripheral zone of the arena. To explain the observed spatial distribution of cockroaches in the arena, the next step is to link both categories of movements. To do this, we need to characterize the distribution of changes of direction when a cockroach enter the central zone from the peripheral zone, and conversely the peripheral zone from the central zone. We first considered the case of a cockroach that goes from the peripheral to the central zone of the arena. We computed the angle between the direction of the cockroach at the periphery, assuming it walked tangentially to the wall, and the direction of its trajectory after it has just entered the central zone. The cockroaches can only depart from the peripheral zone with angles ranging from 0° to 180°; the latter case corresponds to a U-turn (Fig. 5). The distribution of directional changes shown in Fig. 5 is skewed to the left, which indicates that most directional changes are
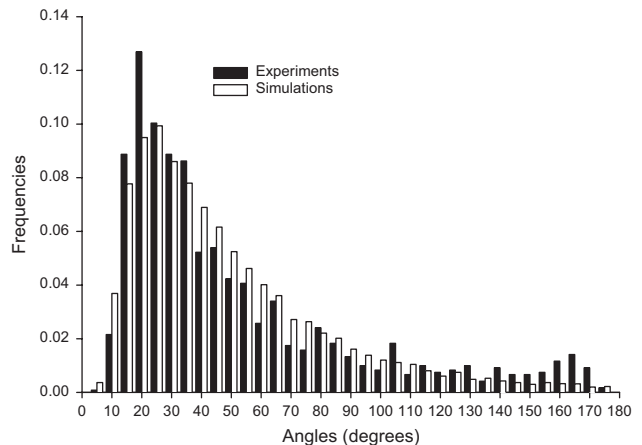
Fig. 5. Frequency distribution of turning angles for cockroaches leaving the peripheral zone to enter the central zone for experiments ($n = 1207$) and simulations ($n = 10000$).

close to the forward direction. The experimental distribution was fitted with a log-normal distribution (widespread in biological systems: Limpert et al., 2001), specified by two parameters that can easily be incorporated into a simulation model (geometric mean $\times$ / SD $= 36.6 \times /2.14$ degrees, $n = 1207$).

When a cockroach moved from the central zone and entered the peripheral zone, the problem was to determine in which direction it turned once it was in the peripheral zone. Behavioral observations indicated that a cockroach, reaching the periphery, pursued its walk forwardly, i.e. the larva minimized its angular deviation in relation to the previous direction of its path in the central zone.

2.3. Model description and comparison of the model's predictions with experimental results

At this stage, all behavioral rules we identified were translated into a statistical model of individual motion behavior in a bounded area. In this section, we describe the numerical implementation of the model and compare the average spatial distribution of larvae and the fraction of time a larva spent either moving or motionless with the values obtained in the experiments.

2.3.1. Numerical model description

We developed a spatially explicit numerical model based entirely on the individual behaviors measured in the experiments. All the parameters estimated are summarized in Table 1. In the model, the cockroaches move in 2 dimensions preserving the time and the spatial scales of experiments with a time step $\delta t = 0.2\,\text{s cycle}^{-1}$. At the beginning of a simulation, the cockroaches are placed at the center of the arena and are in a moving state. In the subsequent cycles, each individual can be in one of two possible states: either it is moving or it is stopped. Each larva adjusts its behavior according to its current position (center or periphery) and to the rules determined in the experiments. A larva in the peripheral zone can move, stop or enter the central zone. The angle with which a cockroach leaves the peripheral zone is
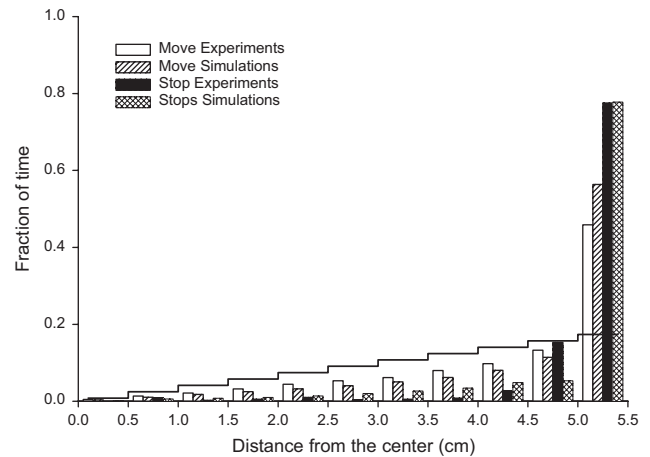

Fig. 6. Fraction of time spent by a cockroach in the arena as a function of its distance from the center and its motion state, for experiments ($n = 19$) and simulations ($n = 1000$). The solid line represents the relative surface of each ring.

determined by generating random deviates according to a log-normal distribution (see Fig. 5). A cockroach in the central zone can either stop or walk randomly until it reaches the peripheral zone. When a cockroach stops, it first decides whether it is in the "awake" or "resting" state and then determines the duration during which it will remain in that state. A total of 1000 simulation runs have been performed.

2.3.2. Comparison of the model's predictions with experimental results

The radial distribution of larvae, in experiments and simulations, was determined from the Cartesian coordinates recorded over an interval of 60 min. For convenience, the arena was divided in 11 rings of 0.5 cm width. To compare the output of the simulations with the experimental results, we computed in both cases the fraction of time a cockroach spent in the different rings. Fig. 6 shows the fraction of time a larva spent either moving or stopped as a function of its radial position. There were no significant differences between experiments and simulations in the fraction of time spent moving (Kolmogorov–Smirnov two sample test, $N_1 = N_2 = 11$; $Z = 0.43$; $P > 0.05$) or stopped (Kolmogorov–Smirnov two sample test, $N_1 = N_2 = 11$; $Z = 1.28$; $P > 0.05$). In both cases, the cockroaches spent about 80% of their stopping time and about 50% of their moving time in the peripheral zone. In the central zone, the moving times in each ring are approximately proportional to the surface.

3. Discussion

This study confirms that the spatial distribution of cockroaches is affected by the presence of edges through

Table 1

	Central zone	Peripheral zone	
Mean speed	$1.1\,\text{cm s}^{-1}$ ($n = 1332$)	$1.06\,\text{cm s}^{-1}$ ($n = 1418$)	
Probability to stop	$0.03\,\text{s}^{-1}$	$0.08\,\text{s}^{-1}$	
Probability to exit		$0.12\,\text{s}^{-1}$	
Transport mean free path	2.32 cm		
Geometric mean for angle departure	Isotropic phase function	$36.6 \times /2.14^{\circ(1)}$ ($n = 1207$)	
Mean Stop duration	P_{Short} 0.93	τ_{Short} 5.87 s	τ_{Long} 700 s

(1) The symbol $\times$ / is taken from Limpert et al. (2001).

thigmotaxis. In order to characterize animal movements in a bounded space, we proposed a method of statistical modeling of individual motion. Compared to the standard procedures used to model animal movements, two points are worth noting in the method we used:

(1) Close to the edge, we assumed a linear displacement mode with a constant probability to leave the peripheral zone per unit time. When they reached the periphery of the arena, cockroaches were 'trapped' and followed the walls. Similar results have been reported in *Paramecium bursaria* or *Dysdercus cingulatus* (Fabr.) (Farine and Lobreau, 1984; Kitamura 1986; Sikora et al., 1992). In our experiments, the time spent in the peripheral zone was greater than that expected when calculated from the relative surface of the external ring. This result suggests that cockroaches exhibit an active tendency to walk along the walls of the arena. It is worth noting that an individual might exhibit an 'active' tendency to perform a behavior (such as thigmotaxis), while the termination of this behavior obeys a memory less process (exit from the periphery). In foraging ants, for example, workers can be actively engaged in trail-following, but nonetheless they exhibit a constant probability per unit of distance to leave the trail (Calenbuhr and Deneubourg, 1992).

(2) The use of a random walk to model the movement in the central zone of the arena enabled us to overcome the problem of the quantification of the turning rate (due to the artifacts inherent to path discretization when using a time basis to digitize trajectories and to the wobbling associated to the animal micromovements). The transport mean free path computed, associated with an isotropic phase function, reproduces correctly the observed patterns of diffusion of the cockroaches in the central zone. It might be argued that path modeling is not reducible to a purely random walk but requires knowledge of the changes of direction of the animals (Bovet and Benhamou, 1988). We argue however that our approach is more parsimonious and precise as long as one wants only to explain and reproduce the global pattern of animal movement. Furthermore, our method allows us to apply an invariant diffusive property of random walks (the average length of trajectories only depends on the system geometry), to easily compute the probability to stop in the central zone of the arena.

Wall-following behavior in cockroaches is primarily a response to tactile stimuli and is not affected by vision (Creed and Miller, 1990). In natural conditions, cockroaches are mainly active during the night (Rivault, 1974) and, although cockroaches possess other navigational capabilities (Durier and Rivault, 1999), their thigmotactic behavior could help them to reach a shelter which are often located within cracks and crevices in walls. In addition, because physical heterogeneities affect the spatial distribution of organisms, wall-following behavior might increase the probability to encounter conspecifics close to the edges. As a consequence, thigmotactic behavior can influence the collective behavior exhibited by a group of animals. For example, the initiation of aggregation is favored close to the edges of an arena in the heteroptera *Dysdercus cingulatus* (Fabr.) (Farine and Lobreau, 1984). The same is true for the schooling behavior when fish are introduced in a water tank (Suzuki et al., 2003).

Further work should investigate how the radius of curvature of the arena or, conversely, the presence of convex walls influence departures from the periphery, and how the presence of physical heterogeneities (i.e. obstacles) in the central or peripheral zone influence the spatial distribution of individuals. The approach developed here might be extended to other experimental contexts such as the analysis of the collective motion of animals confined in a finite space or ecological contexts such as the modeling of the foraging patterns of species that combine orientation along structural guidelines and random walk in open space.

At a larger scale, the characterization of animal movements at habitat edges in spatially complex landscapes could be combined with the modeling approaches already developed in landscape ecology (e.g. Johnson et al., 1992) to predict the distribution and dynamics of populations. For instance, an approach taking into account the behavioral changes occurring close to edges could be useful to describe the patterns of animal movement through line corridors with sharp boundaries, such as hedgerows or fencerows (Tischendorf and Wissel, 1997) or to understand the spatial distribution of species in patchy landscapes, such as birds whose spatial distribution is affected by forest boundaries that act as movement conduits (Desrochers and Fortin, 2000).

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