



## Self-organized aggregation in cockroaches

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Aggregation is widespread in invertebrate societies and can appear in response to environmental heterogeneities or by attraction between individuals. We performed experiments with cockroach, *Blattella germanica*, larvae in a homogeneous environment to investigate the influence of interactions between individuals on aggregations. Different densities were tested. A first phase led to radial dispersion of larvae in relation to wall-following behaviours; the consequence of this process was a homogeneous distribution of larvae around the periphery of the arena. A second phase corresponded to angular reorganization of larvae leading to the formation of aggregates. The phenomenon was analysed both at the individual and collective levels. Individual cockroaches modulated their behaviour depending on the presence of other larvae in their vicinity: probabilities of stopping and resting times were both higher when the numbers of larvae were greater. We then developed an agent-based model implementing individual behavioural rules, all derived from experiments, to explain the aggregation dynamics at the collective level. This study supports evidence that aggregation relies on mechanisms of amplification, supported by interactions between individuals that follow simple rules based on local information and without knowledge of the global structure.

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The most common collective behaviour among living organisms is probably grouping, which occurs in a wide range of taxa, including bacteria, arthropods, fish, birds and mammals (Parrish & Hamner 1997; Parrish & Edelstein-Keshet 1999; Parrish et al. 2002). Depending on the species, these assemblages may be labelled as herds, shoals, flocks, schools or swarms and are more broadly denoted as aggregations (Allee 1931). In reference to the spatial distribution of organisms, an aggregation could be

defined as any assemblage of individuals that results in a higher density of individuals than in the surrounding area (Camazine et al. 2001).

Studies on aggregation have investigated mainly the benefits from association with conspecifics or differences in fitness related to the spatial position of individuals in groups (Hamilton 1971; Parrish 1989; Krebs & Davis 1993; Krause 1994; Romey 1995; Watt & Chapman 1998; Krause & Ruxton 2002). Much less attention has been paid to proximal causes, addressing the question of the underlying mechanisms, with the exception of studies on fish (Krause & Tegeder 1994; Parrish & Hamner 1997; Croft et al. 2003) and social amoebae (Raper 1984). Attempts have been made to classify aggregations according to the cues leading to these assemblages and the relations between their components (Allee 1931 and references therein; Parrish & Hamner 1997). Aggregates could be formed incidentally by passive collection of organisms resulting from abiotic factors. For example, zooplankton could aggregate in response to physical constraints such as marine currents (Hamner & Schneider 1986). Aggregation

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could also result from active movements of individuals (Parrish & Hamner 1997).

Two types of active aggregation can be distinguished. In one case, aggregation results from common individual taxis responses to environmental heterogeneities on clumped resources. External cues, which are generally fixed features of the environment, act as templates specifying the final aggregation patterns, which are therefore independent of the initial conditions and of density, with the exception of overcrowding (Camazine et al. 2001). Once the environmental heterogeneities are removed or the food patches are exhausted, individuals might disperse. For example, aggregations of the fly *Stomoxys calcitrans* result from the movements of individuals towards a common zone of preferred temperature (Fraenkel & Gunn 1961). In the second case, aggregation results from social interactions involving attraction between the members of the group. The term congregation was coined to describe groups formed and maintained by mutual attraction (Parrish & Hamner 1997; Turchin 1998). Congregations range from basic aggregates, such as mosquito swarms, fish schools or bird flocks, to more complex and integrated groups, such as those found in eusocial insects or primates (Romey 1997). The presence of environmental heterogeneities (e.g. light or temperature gradients) can also affect individual behaviour such as resting time or path features; a template combined with social interactions could favour the initiation of clustering in a particular site or reinforce the intensity of aggregation.

One approach to understanding how group patterns arise is to investigate the action of individuals in relation to their local environment, without reference to the global structure (Gueron et al. 1996). Based on the interactions between members of the group, self-organized systems are able to produce clusters starting from a homogeneous distribution of animals in a uniform environment (Camazine et al. 2001; Theraulaz et al. 2002; Depickère et al. 2004). The aggregation patterns result from interactions between individuals that follow simple rules based on local information, without reference to the global pattern (Deneubourg et al. 2002). One key mechanism of self-organization in social systems is the existence of positive feedbacks (Bonabeau et al. 1997). Aggregation of individuals relies on the amplification of a dynamic signal provided by other individuals; more aggregated individuals provide a stronger impetus for aggregation. For example, in the bark beetle, *Dendroctonus micans* (Deneubourg et al. 1990), or in the social amoebae *Dictyostelium discoideum* (Marée & Hogeweg 2001), aggregates emerge from interattraction and amplification processes mediated by the production and diffusion of chemicals (aggregation pheromone and cAMP, respectively).

In this study, we focused on aggregations of larvae of the German cockroach, *Blattella germanica* (L.), in a uniform environment, to highlight the expression of the social component of aggregation. In the wild, the German cockroach forms mixed clusters of males and females, with generation overlap (Rivault 1989, 1990). In cockroaches, aggregation might underlie different benefits such as reduction of physical stresses (Dambach &

Goehlen 1999), facilitation of coprophagy (Kopanic et al. 2001), increase in the efficiency of alarm responses and antipredator behaviour, faster development and more efficient reproduction (Schal et al. 1997). Although aggregation patterns are observable at the macroscopic level, our modelling effort aimed to understand their emergence from the microscopic level of interacting individuals (Ebeling & Schweitzer 2001). We used an individual-based approach to understand the link between these two levels of analysis: the individual level, i.e. the behaviour of a single larva, and the collective level, characterized by the aggregation dynamics and the spatial distribution of individuals. We assumed that cockroaches have access only to local cues, without long-range information on the global structure. Based on experimentally derived individual behavioural rules, we built an individual-based numerical model to assess the influence of individual rules on the production of spatiotemporal aggregation patterns.

## METHODS

### Study Species and Experimental Set-up

Cockroaches came from a strain reared since 1987 in a laboratory in Rennes, France. Mature ootheca were taken from gravid females and placed in individual dark boxes with a moist sponge to maintain humidity. Temperature was kept at 25°C, and dog pellets and water were provided ad libitum. Experiments were performed with first-instar larvae (24 h old). Bodies of first-instar larvae are approximately 3 mm long (excluding the antennae) and 2 mm wide, and antennae are 3 mm long. For all experiments, larvae were introduced under CO<sub>2</sub> narcosis in the centre of a circular arena. The experimental arena was 11 cm in diameter and 0.3 cm high, covered with a glass plate to prevent air currents and larvae from escaping. Before each experiment, the arena was cleaned with hot soapy water and alcohol to remove chemical cues. We ensured that the surroundings of the set-up were homogenous to avoid spatial heterogeneities that might bias cockroach behaviour. Each experiment lasted 60 min and was carried out at 25°C and 35% RH. For experiments involving several individuals, each group was composed of cockroaches hatched from the same ootheca, and all larvae were used only once.

### Individual Behaviour

Each individual can be in two states, moving or stopped. A stopped cockroach (alone or in an aggregate) could start moving either spontaneously or after collision with a moving larva. While moving, a cockroach could encounter other stopped or moving larvae. Our aim was to quantify the path features of a cockroach and the transition probabilities from one behaviour to another as a function of a cockroach's immediate neighbourhood. Individual behaviour was recorded continuously with a high-definition camera (Sony CDR-VX 2000 E) placed

above the arena coupled with a videotape recorder (Panasonic AG 5700).

### Paths analysis for individual larva

When introduced into the arena, cockroaches spent most of their time walking close to the edge of the arena, with their ipsilateral antenna dragging along the wall. We considered that a cockroach displayed this wall-following behaviour when it was less than 0.5 cm from the wall (0.5 cm is the minimal distance required for a larva to establish antennal contact with the wall). We designated this zone the peripheral zone (of the arena) and the rest of the arena as the central zone. To model the path of a single cockroach in the circular arena, we assumed that the motion patterns result from the combination of wall-following behaviour and a diffusive random walk in the central zone (see also Jeanson et al. 2003).

Single larvae were introduced into the experimental arena and their paths were digitized with videotracking software (Ethovision version 1.90, Noldus Information Technology, Wageningen, The Netherlands) at a sample rate of one frame every 0.68 s. We analysed 19 individual paths.

**Peripheral zone.** We assumed that cockroaches move linearly in the peripheral zone (i.e. the sinuosity of the path was neglected in this zone of 0.5 cm width). The average speed at the periphery ( $v_p$ ) was computed from the experiments as the total length of all paths divided by the total moving time. From the duration of the paths in the peripheral zone and knowing the fraction of paths that ended either by a stop or by the departure from the external ring to enter the central zone, we computed the probabilities per unit of time of stopping in the peripheral zone and of leaving the peripheral zone (respectively,  $1/\tau_{\text{Stop,p}}$  and  $1/\tau_{\text{Exit}}$ , where  $\tau_{\text{Stop,p}}$  and  $\tau_{\text{Exit}}$  are the characteristic times before a stop in the peripheral zone or an exit; Appendix, equations A2, A3).

For cockroaches that left the peripheral zone, we computed the angle between the direction of the cockroach at the periphery (assuming that it walked tangentially to the wall) and the direction of its trajectory after it had just entered the central zone. Cockroaches departed from the peripheral zone at angles of 0–180°; 180° corresponds to a U turn.

**Central zone.** The average velocity in the central zone ( $v_c$ ) was computed as the total length of all paths (collected for all larvae) divided by the total moving time. The individual paths can be characterized by the average length between two direction changes (mean free path) and the frequency distribution of the scattering angles for each direction change (phase function) (Turchin et al. 1991; Berg 1993; Turchin 1998). The characterization of this phase function requires an objective criterion when a cockroach significantly changes its direction (Tourtellot et al. 1991). Practically, this is difficult and characterized by large uncertainty. As an alternative, we modelled the spatial distribution of larvae using the transport mean free path  $l^*$  ( $l^*$  represents the distance for which incidental

direction and direction of diffusion are no longer correlated; Case & Zweifel 1967) associated with an isotropic phase function (Jeanson et al. 2003).

Knowing the velocity of individuals and the proportion of paths in the central zone that ended with a stop, we computed the probability per unit time of stopping spontaneously in the centre of the arena ( $1/\tau_{\text{Stop,c}}$ ; Appendix, equation A6).

### Interactions between larvae

One crucial point was to determine at what distance an individual detects another larva. We assumed that the perception between larvae required at least antennal contact. The antennae are 3 mm long (the same length as the body), so we assumed that two cockroaches could perceive each other if their head-to-head interindividual distance was equal to or less than 6 mm (Fig. 1a). For convenience, we defined a detection area (within which a cockroach could perceive conspecifics) as circle with a 3-mm radius with the animal's head as the centre. Thus, a moving cockroach could perceive a stopped larva across a maximal distance of 12 mm (Fig. 1b). Within its perception radius, we assumed that a moving or a stopped cockroach can detect up to three larvae.

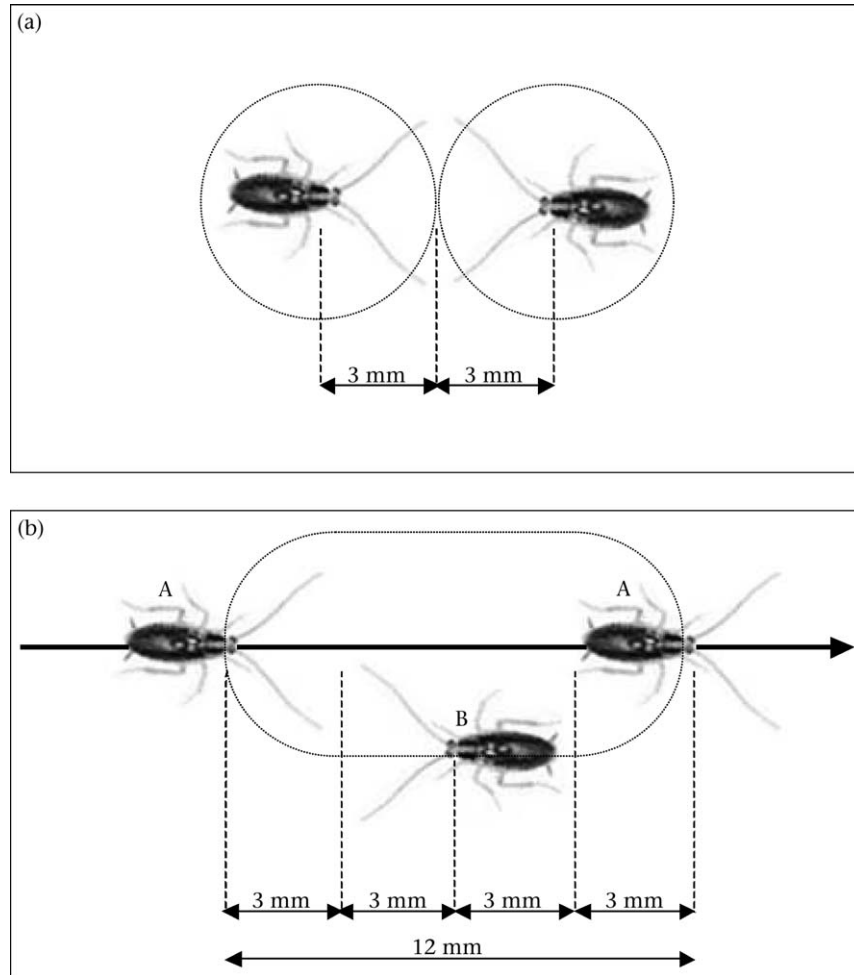
To analyse interactions between individuals, i.e. to determine the behavioural rules based on local information, we introduced groups of two, three and four larvae into the experimental arena.

### Probability of stopping in an aggregate

Our numerical individual-based model required the estimation of rates (i.e. time- or distance-dependent probabilities). From our experiments, we were able to compute only the fraction  $F_{\text{Stop},N}$  of moving cockroaches that stopped when encountering  $N$  stopped larvae within their detection radius ( $1 \leq N \leq 3$ ). Assuming that the probability of stopping when perceiving  $N$  stopped larvae was constant per unit time (i.e. a Markovian process), we computed the rate at which a larva would stop ( $1/\tau_{\text{Stop},N}$ ) when it perceived  $N$  cockroaches within its perception radius ( $\tau_{\text{Stop},N}$  is the characteristic time between detection of an aggregate by a moving larva and its stop; Appendix, equations A7, A8).

### Collisions

A stopped larva, either aggregated or isolated, could start moving after a collision. We assumed that each stopped larva in an aggregate of  $N$  individuals ( $2 \leq N \leq 3$ ) could detect moving larvae within their detection radius and had the same probability of being collided with. From experiments, we computed the fraction  $F_{\text{Collision},N}$  of encounters between a moving larva and an isolated larva or an aggregate that ended with the departure of a cockroach (in almost all cases, when a collision occurred, only one larva left the aggregate). This fraction divided by the size of the aggregate gave the individual probability of starting to move. Assuming that the probability of moving was constant per unit time when a moving cockroach detected a stopped one, we computed the probability  $1/\tau_{\text{Collision},N}$  per unit time of moving during a collision,



**Figure 1.** (a) Circles represent the detection radius for each cockroach. Two cockroaches detect each other when their interindividual distance (with reference to the head) is equal to or less than 6 mm. (b) A moving cockroach A encounters a stopped cockroach B. Based on the assumption of the detection radius, A perceives B (and reciprocally) at a maximum of 12 mm. The whole area of mutual perception is represented by the ellipse.

with  $\tau_{\text{collision},N}$  the characteristic time between the detection of the moving larva and the departure of the stopped cockroach (Appendix, equations A9, A10).

#### Spontaneous probability of starting to move

Experiments were designed to assess the probabilities that a stopped individual (alone or in an aggregate) would start moving. We introduced into the arena a number of larvae equal to the number in the aggregate for which we wanted to characterize the lifetime. The lifetime of an aggregate of a given size was assessed as the time between a moving individual in the cluster stopping and the spontaneous departure of one of the aggregated cockroaches. Log-linear plots of the survival curve of lifetimes of isolated larvae or aggregates of different sizes ( $2 \leq N \leq 4$ ) all showed a bilinear pattern (double exponential on normal scale), which could be explained by dividing the distribution of stopping times into two classes with different mean times. This hypothesis of two stopping states seemed supported by behavioural observations: a cockroach that stops moving may remain either active and display antennal movements ('awake'

state) or display no antennal movements ('resting' state). We fitted these survival curves to a double exponential function. Thus, for isolated larvae and for each aggregate size  $N$  ( $2 \leq N \leq 4$ ), the probability  $p_{\text{Short}}$  of a larva belonging to the category of short-stop duration, and the mean durations for short and long stops (respectively,  $\tau_{\text{Short}}$  and  $\tau_{\text{Long}}$ ) are estimated by fitting the equation

$$F(t) = \sum_{I=0}^{I=N} \frac{N!}{I!(N-I)!} p_{\text{Short}}^I (1 - p_{\text{Short}})^{N-I} e^{-\left(\frac{It}{\tau_{\text{Short},N}} + \frac{(N-I)t}{\tau_{\text{Long},N}}\right)} \quad (1)$$

to the experimental fraction of aggregates  $F(t)$  of size  $N$  not dissolved at time  $t$  ( $I$  is the number of cockroaches in the category of short-stop duration).

#### Validation of local cues assumption

To validate our assumption about the use of local cues, we checked whether the quantified individual behavioural



rules (collisions, transition to a motionless state and stop durations) correctly predicted experimental probabilities measured for isolated larvae, aggregates of two and three larvae and for aggregates greater than the number of larvae that a cockroach could detect within its perception radius. From simulation runs (see below for a description of the numerical model), we computed the fraction of moving cockroaches that stopped when encountering isolated larvae or aggregates of 2, 3, 7, 10 and 15 cockroaches and the proportion of encounters that ended with the departure of a stopped cockroach after a collision. Lifetime distributions for aggregates of 2, 3, 7, 10 and 15 cockroaches were predicted with similar Monte Carlo simulations. All these predictions were compared to experimental data.

## Collective Behaviours

Groups of 10 larvae ( $N = 20$  replications) or 20 larvae ( $N = 22$  replications) were deposited at the centre of the experimental arena under  $\text{CO}_2$  narcosis. A camera (Philips-LDH 0371/00) placed above the arena was coupled with a computer (Amiga 1200/68060). An image-processing software (J. P. Richard, unpublished software) computed the position of each individual every 10 s for 60 min. To avoid misinterpretations from sampling noise related to the automatic detection of cockroaches in experiments, we assumed that two cockroaches belonged to the same aggregate if their interindividual distance was less than or equal to 1 cm.

After recovery from  $\text{CO}_2$  narcosis, cockroaches ran about in an excited way. Furthermore, not all the larvae in a group introduced into the arena awoke simultaneously. Therefore, to estimate individual behavioural rules in relation to social interactions and to characterize the dynamics of aggregation, we discarded the first 5 min of the experiments. For each experimental replication and simulation run, we computed the size of the largest aggregate every 10 s.

## RESULTS

### Individual Behaviour

#### Paths analysis

Table 1 gives the experimental results on path characterization. The probability  $1/\tau$  per unit time of performing either a stop or an exit from the periphery of the arena was given by the slope of the straight line fitting the

log-survival curve of the fraction of cockroaches that did not stop or exit the periphery as a function of time ( $1/\tau = 0.21/\text{s}$ ). Forty per cent ( $N = 1418$ ) of the paths ended with a stop. Therefore, the probability per unit time to stop on the periphery (Appendix, equations A2, A3) was:

$$\frac{1}{\tau_{\text{Stop,p}}} = 0.08/\text{s} \quad \text{and} \quad \frac{1}{\tau_{\text{Exit}}} = 0.13/\text{s}$$

The distribution of angles for individuals that left the peripheral zone for the centre of the arena was fitted by a log-normal distribution (Limpert et al. 2001), specified by two parameters that could easily be incorporated into a numerical model (geometric mean  $^{\times}/\text{SD} = 36.6^{\times}/2.14$  degrees,  $N = 1207$ ). The usual symbol  $\pm$  used for normal distributions is replaced by the symbol  $^{\times}/$ , because of the multiplicative properties of the log-normal distribution; for further details see Limpert et al., 2001.

The fraction  $F_{\text{Stop,c}}$  of paths in the centre of the arena that ended with cockroaches stopping before reaching the periphery was 21% ( $N = 1207$ ). From, equation A6 (Appendix), we obtained

$$\frac{1}{\tau_{\text{Stop,c}}} = 0.03/\text{s}$$

The transport mean free path  $l^*$  (computed from the coordinates of larvae in the centre of the arena) was 2.32 cm. Jeanson et al. (2003) showed that these parameters describe individual path features correctly and reproduce the spatial distribution of a cockroach in the arena.

#### Homogeneity of the experimental set-up

To determine whether the final distribution of individuals was influenced by spatial heterogeneity, phototaxis or residual chemical cues, we pooled the coordinates of all individuals for experiments with 10 larvae ( $N = 20$  replications) and with 20 larvae ( $N = 22$  replications) at 60 min. In both cases, the spatial distribution of individuals was uniform (random: Rao spacing test: 10 larvae,  $U = 137.61$ , NS; 20 larvae,  $U = 140.66$ , NS; Batschelet 1981).

#### Probability of stopping in an aggregate

We counted in the experiments the proportion of encounters with a stopped larva or with an aggregate of  $N$  individuals that ended with a moving larva stopping. Using equation A8 (Appendix), we computed the time-dependent probabilities for a moving cockroach to stop

**Table 1.** Path characteristics of single cockroaches as a function of their spatial position in the arena

	Centre	Periphery
Mean speed	$v_c = 11.0$ mm/s ( $N=1332$ )	$v_p = 10.6$ mm/s ( $N=1418$ )
Probability of stopping	$1/\tau_{\text{Stop,c}} = 0.03/\text{s}$	$1/\tau_{\text{Stop,p}} = 0.08/\text{s}$
Probability of exiting		$1/\tau_{\text{Exit}} = 0.13/\text{s}$
Mean free path	23.2 mm	
Geometric mean $^{\times}/\text{SD}$ for angle departure	Isotropic phase function	$36.6^{\times}/2.14$ degrees ( $N=1207$ )

Sample sizes are given in parentheses.

**Table 2.** Fraction of moving cockroaches that stopped when encountering  $N$  larvae within their perception radius ( $F_{\text{Stop},N}$ ) and relative individual probabilities of stopping ( $1/\tau_{\text{Stop},N}$  from equation A8), fraction of stopped cockroaches that left the motionless state after collision with a moving larva ( $F_{\text{Collision},N}$ ) and relative individual probabilities of starting to move after a collision ( $1/\tau_{\text{Collision},N}$  from equation A10)

Size of aggregate	Stops		Collisions	
	$F_{\text{Stop},N}$	$1/\tau_{\text{Stop},N}$	$F_{\text{Collision},N}$	$1/\tau_{\text{Collision},N}$
$N=1$ ( $n=280$ )	0.42	0.49/s	0.26	0.27/s
$N=2$ ( $n=260$ )	0.50	0.63/s	0.11	0.052/s
$N=3$ ( $n=109$ )	0.51	0.65/s	0.07	0.021/s

Sample sizes are given in parentheses.

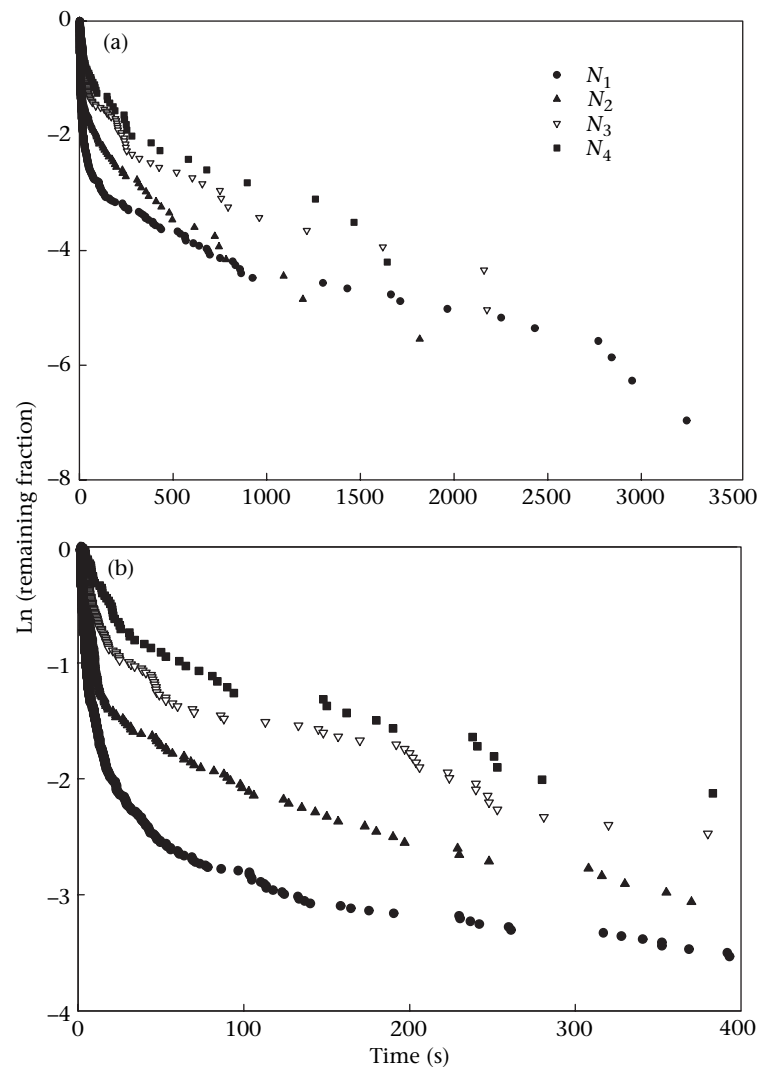
when encountering a stopped larva (or an aggregate). The probability for a cockroach to stop increased as the number of larvae in its neighbourhood increased (Table 2).

### Collisions

We determined the proportion of individuals that started moving after a moving larva had collided with them. Equation A10 (Appendix) gives the individual probability ( $1/\tau_{\text{Collision},N}$ ) per unit time of starting to move after a collision. As the number of larvae in the vicinity increases; individual probabilities to leave the stopping state after a collision decrease (Table 2).

### Spontaneous probability of starting to move

For isolated larvae and for each aggregate size, the survival curve plotted on a log-normal scale showed a bilinear pattern. This suggested that stop durations belonged to two subpopulations (Fig. 2). For each aggregate size, the experimental survival curves were fitted with equation (1) by minimizing the residual sum of squares to estimate  $P_{\text{Short}}$ ,  $\tau_{\text{Short}}$ ,  $\tau_{\text{Long}}$  (Table 3). For each type of stop duration (short or long), the inverse of the mean lifetime ( $\tau_{\text{Short}}$  and  $\tau_{\text{Long}}$ ) gave the individual probability per unit time to end spontaneously the motionless state. As the



**Figure 2.** (a) Natural logarithm of the fraction of isolated larvae ( $N_1$ ) that are still stopped, and of aggregates ( $N_2$ ,  $N_3$ ,  $N_4$ ; respectively, aggregates of 2, 3 and 4 larvae) not dissolved, as a function of time. (b) Curves for times below 400 s.

**Table 3.** Individual probabilities for stopped cockroaches to display short stops and mean lifetime of stop durations as a function of the number of neighbours ( $N = 1$ : isolated larva;  $N = 2$ : aggregate of two cockroaches, etc.)

Size of aggregate	$P_{\text{Short}}$	$\tau_{\text{Short}}$ (s)	$\tau_{\text{Long}}$ (s)
$N=1$ ( $n=1059$ )	0.93	5.87	700
$N=2$ ( $n=256$ )	0.66	16	1248
$N=3$ ( $n=154$ )	0.34	18.5	1062
$N=4$ ( $n=67$ )	0.24	34.1	1719

Sample sizes are given in parentheses.

numbers of conspecifics increased, stopping duration as well as the probability of belonging to long-stop durations increased. In other words, as the number of neighbours increased, the probability of a cockroach leaving an aggregate decreased.

## Collective Results

### Description of numerical individual-based model

The spatially explicit numerical model was written in Java and was based entirely on the experimental measures of individual behaviour. We used it to explore model predictions by Monte Carlo simulations. In this model, cockroaches moved in two dimensions preserving time and spatial scales of experiments with time steps of 0.2 s/cycle. The basic units in the model were individual cockroaches that were characterized by their spatial location, orientation and motion state (moving or stopped). At the beginning of a simulation run, cockroaches were initialized in a moving state in the central zone of the arena. Each larva then adjusted its behaviour depending on its spatial location (i.e. centre or periphery of the arena) and on its neighbourhood (number of cockroaches within its detection radius) according to the behavioural rules derived from experiments (Tables 1, 2, 3). We assumed that the presence of conspecifics did not influence individual path features (no coordinated collective movement).

At each time step, a moving cockroach determines whether it stops depending on the number of larvae in its neighbourhood and according to experimental

probabilities (Table 2). The same probabilities ( $1/\tau_{\text{Stop},N}$ ) were used in the periphery and the centre areas. When a cockroach stops (spontaneously or when encountering an aggregate), it determines whether it belongs to the category of short- or long-stop duration ( $P_{\text{Short}}$ ). However, the parameters  $P_{\text{Short}}$ ,  $1/\tau_{\text{Short}}$  and  $1/\tau_{\text{Long}}$  were assessed for each aggregate size, so each time that a stopped larva detects changes in the number of stopped larvae within its perception radius, it determines, according to its updated environment, whether it belongs to the short- or long-stop durations (Table 3). It starts moving spontaneously with probabilities  $1/\tau_{\text{Short}}$  and  $1/\tau_{\text{Long}}$ , or with probability  $1/\tau_{\text{Collision}}$  when it perceives a moving cockroach (collision). We also performed simulations with cockroaches that behaved as isolated individuals without any interactions. We designated simulations performed with social interactions as ‘social simulations’ and simulations performed without social interactions as ‘nonsocial simulations’. We performed 200 simulation runs for each condition ( $N = 10$  social and nonsocial larvae, 20 social and nonsocial larvae).

### Validation of the ‘local cues’ assumption

Simulations were performed to ensure that our assumption on the use of local cues (i.e. information available only within the perception radius) was sufficient to reproduce the experimental proportions of individuals that stopped and induced collisions when encountering isolated larvae or aggregates of 2, 3, 7, 10 and 15 larvae (Table 4). In all cases, no differences were found between experiments and social simulations. There were no differences in lifetimes between experiments and social simulations for the aggregates of two larvae (Mann–Whitney  $U$  test:  $Z = -1.62$ ,  $N_{\text{exp}} = 256$ ,  $N_{\text{sim}} = 250$ , NS), three larvae ( $Z = -1.04$ ,  $N_{\text{exp}} = 154$ ,  $N_{\text{sim}} = 250$ , NS), four larvae ( $Z = -0.05$ ,  $N_{\text{exp}} = 67$ ,  $N_{\text{sim}} = 250$ , NS), seven larvae ( $Z = -1.40$ ,  $N_{\text{exp}} = 59$ ,  $N_{\text{sim}} = 250$ , NS), 10 larvae ( $Z = -1.62$ ,  $N_{\text{exp}} = 35$ ,  $N_{\text{sim}} = 250$ , NS) and 15 larvae ( $Z = -1.14$ ,  $N_{\text{exp}} = 49$ ,  $N_{\text{sim}} = 250$ , NS). The agreement between the experimental results and the social simulation outputs suggested that our assumption on the use of local cues was sufficient to explain the behaviour of a moving larva facing a large aggregate.

**Table 4.** Proportions of larvae that stopped and induced collisions (departure of a stopped larva) when encountering isolated cockroaches or aggregates in experiments and social simulations

$N$ larvae	Proportion of stops			Proportion of collisions		
	Experiments	Simulations	$P^*$	Experiments	Simulations	$P^*$
1	0.42 [0.36–0.47] ( $n=280$ )	0.39 ( $n=1000$ )	0.29	0.26 [0.22–0.32] ( $n=280$ )	0.23 ( $n=1000$ )	0.28
2	0.50 [0.43–0.55] ( $n=260$ )	0.45 ( $n=1000$ )	0.06	0.11 [0.07–0.15] ( $n=260$ )	0.09 ( $n=1000$ )	0.18
3	0.51 [0.42–0.61] ( $n=109$ )	0.45 ( $n=1000$ )	0.20	0.07 [0.03–0.14] ( $n=109$ )	0.07 ( $n=1000$ )	0.73
7	0.60 [0.50–0.70] ( $n=98$ )	0.53 ( $n=1000$ )	0.17	0.12 [0.06–0.21] ( $n=98$ )	0.09 ( $n=1000$ )	0.29
10	0.75 [0.62–0.85] ( $n=63$ )	0.63 ( $n=1000$ )	0.06	0.10 [0.04–0.20] ( $n=63$ )	0.09 ( $n=1000$ )	0.84
15	0.71 [0.54–0.85] ( $n=35$ )	0.70 ( $n=1000$ )	0.85	0.09 [0.02–0.23] ( $n=35$ )	0.09 ( $n=1000$ )	0.99

Experimental proportions are given with lower and upper 95% confidence limits in brackets; sample sizes are in parentheses.

\*Chi-square test.

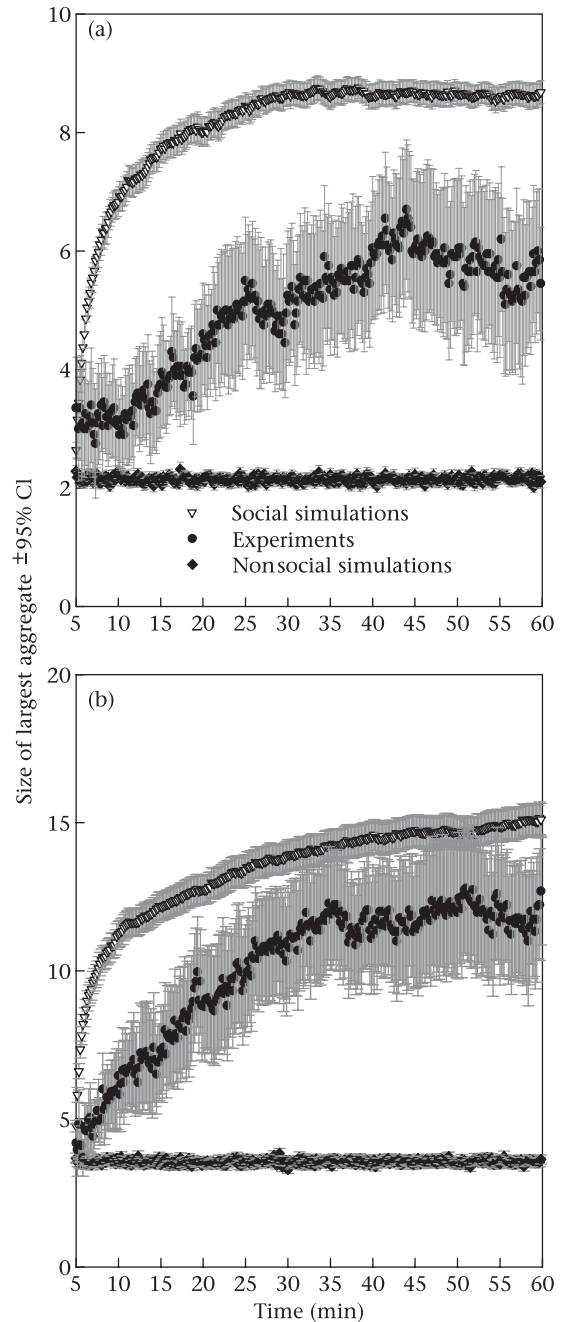
### Simulation results and comparison with experiments

At 60 min, we computed the average distance from the centre of the arena for all larvae in the experiments and in the simulations. Cockroaches were distributed mainly at the periphery of the arena both in experiments ( $\bar{X} \pm \text{SD}$ : 10 larvae:  $49.32 \pm 2.60$  mm,  $N = 20$ ; 20 larvae:  $48.60 \pm 0.71$  mm,  $N = 22$ ) and in social simulations (10 larvae:  $48.91 \pm 3.68$  mm,  $N = 200$ ; 20 larvae:  $49.65 \pm 0.66$  mm,  $N = 200$ ). We determined the temporal evolution of the mean size of the largest aggregate every 10 s for 55 min for 10 and 20 cockroaches (Fig. 3). The main discrepancy between experiments and social simulations was caused by the intensity of aggregation, which was about 30% greater in social simulations. Figure 4 shows the spatio-temporal aggregation patterns for independent experiments, social simulations and nonsocial simulations with 10 and 20 cockroaches. Experiments and simulations showed qualitatively the same dynamics: a small cluster was formed from an initial uniform individual distribution, which was then amplified and stabilized over time to lead finally to an aggregate gathering almost all cockroaches. No such aggregation occurred in the nonsocial simulations where larvae remained uniformly distributed throughout the arena.

## DISCUSSION

Cockroach larvae in an experimental arena first distributed themselves homogeneously at the periphery of the arena. The wall-following behaviour caused the presence of cockroaches to be higher close to the edges. This increased the probability that conspecifics met near the wall and thus the probability of initiating a cluster at the periphery. The emergence of an aggregate relies on a positive feedback; the greater a cluster, the more cockroaches tended to rest in its vicinity. We showed that individuals modulate their behaviour depending on the presence of conspecifics in their vicinity; the probability of stopping and resting times were more important when the number of larvae was larger. We built an individual agent-based numerical model implementing behavioural rules derived from experiments to test the hypothesis that aggregation relies on the use of local cues. In the literature there are many theoretical models dealing with similar aggregation processes, but few of these models have received experimental validation of the suggested underlying mechanisms. Although our numerical model reveals a quantitative disagreement with experiments, it nevertheless offers strong evidence that aggregation can be explained in terms of interactions between individuals that follow simple rules based on local information without knowledge of the global structure.

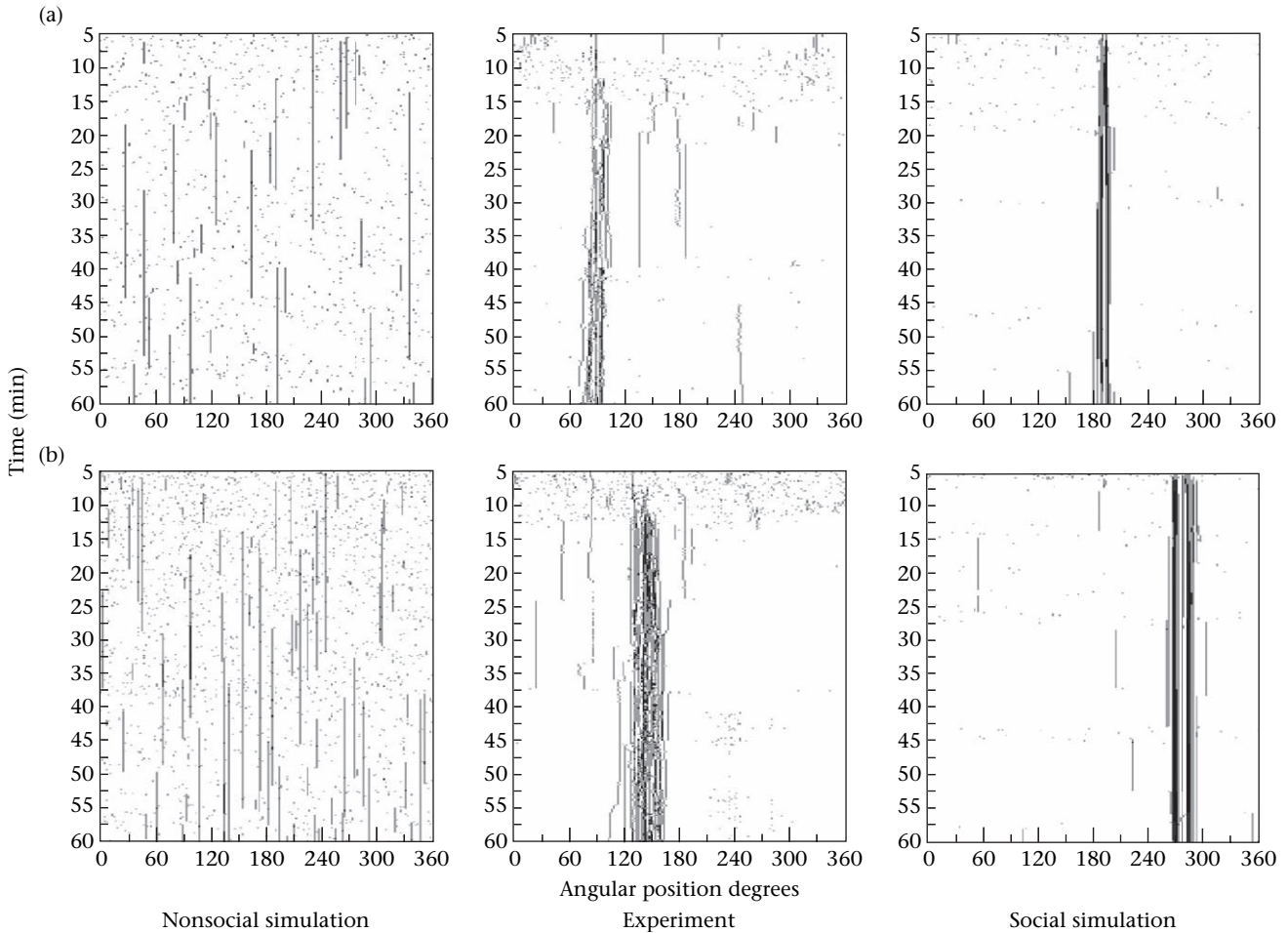
We showed that the behaviour of a larva (i.e. probability of stopping and resting time) is affected by the presence of conspecifics in its immediate vicinity. However, we did not explore how larvae assess this local density. Several mechanisms are possible. Aggregation intensity increases when humidity decreases (Ledoux 1945), suggesting that grouping might induce a reduction of net water loss per individual by the formation of a local microclimate



**Figure 3.** Temporal evolution of the mean size of the largest aggregate for (a) 10 larvae and (b) 20 larvae for experiments (10 cockroaches:  $N = 20$ ; 20 cockroaches:  $N = 22$ ), social simulations (10 cockroaches:  $N = 200$ ; 20 cockroaches:  $N = 200$ ) and nonsocial simulations (10 cockroaches:  $N = 200$ ; 20 cockroaches:  $N = 200$ ). Error bars show 95% confidence intervals.

around the larvae (Dambach & Goehlen 1999). Dambach & Goehlen (1999) suggested that a moving cockroach could use the water diffusion field of a neighbour as a cue to stop. This water field might also affect stop duration of cockroaches, depending on their neighbourhood, and contribute to the stabilization of the aggregate. Previous studies on cockroach aggregations dealt mainly with the characterization of chemical compounds involved in





**Figure 4.** Spatiotemporal aggregation dynamics for experiments, social simulations and nonsocial simulations with (a) 10 and (b) 20 larvae. Black dots: positions of cockroaches as a function of time and angular position.

grouping. Although many investigations have attempted to identify the aggregation pheromones in *B. germanica*, these studies yielded ambiguous results. Substances produced by the rectal pad cells and adsorbed on the cuticle (Ishii & Kuwahara 1967, 1968) or cuticular hydrocarbons (Rivault et al. 1998) appear to be involved in aggregation. Some of these compounds exhibit an arresting action (Scherkenbeck et al. 1999) that might affect the probability of stopping when encountering conspecifics or influence stop durations. Although some volatile compounds have been identified, it seems that the aggregation pheromones exert an action through direct contact or at least attract only at short distances (Rivault et al. 1998). In the beetle *D. micans* (Deneubourg et al. 1990) and the amoebae *D. discoideum* (Raper 1984), aggregation relies on chemoattraction based on the production and diffusion of chemical signals (aggregation pheromone or cAMP, respectively), but aggregation in cockroaches appears to require close contact between individuals. Thus, during their random walk in the arena, it seems unlikely that moving cockroach larvae are attracted towards conspecifics by long-range stimulation, but rather stop after encountering conspecifics at close

contact. However, we cannot rule out the influence of an aggregation pheromone on the stabilization of the aggregate. In the long term, after the eventual dispersion of individuals, chemical marking of the substrate favoured and enhanced reaggregation at the previous clustering site (unpublished observations). After their individual foraging trip under natural conditions, cockroaches might benefit from the passive marking of a common resting site to gain a common shelter and thus to maintain the cohesion of the group.

Aggregation requires modulation of individual behaviour in relation to social or environmental changes perceived in the immediate vicinity. For instance, cockroaches increased their resting time inside a group as its size increased, leading to an amplification process and to the formation of a main aggregate. In other contexts, this modulation of individual behaviour might lead to the collective selection of a common aggregation site (Deneubourg et al. 2002; Jeanson et al. 2004a). In cockroaches, the aggregation behaviour described in this study might lead to the selection of a common shelter without invoking other activities, except the modulation of individual resting time depending on the intrinsic characteristics

of the shelter. In both cases, the probability of a cockroach leaving a resting site decreased as a function of the number of conspecifics in the site (Rivault & Cloarec 1998; Amé et al. 2004). Workers of the ant *Oecophylla longinoda* hang on to one another to form chains to bridge empty spaces between leaves or branches (Hölldobler & Wilson 1990). The formation of a unique and efficient chain results from a positive feedback based on the modulation of individual probabilities of entering and leaving the chain, probabilities that depend strongly on the number of ants already present in the chain (Lioni et al. 2001).

Even though implementation of the individual behavioural rules differs according to species, the underlying mechanisms of aggregation rely mainly on the amplification of a social signal that can cover a wide range of modes, such as silk in spiders (Saffre et al. 1999; Jeanson et al. 2004b) or caterpillars (Fitzgerald 1995), trail pheromones in ants (Hölldobler & Wilson 1990). Hence, the identification of the behavioural rules governing the interactions and communication between individuals is a promising approach to understanding the emergence of spatiotemporal patterns in animal groups.

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## Appendix

### Probability of stopping in peripheral zone

Plotting the survival curve (the fraction  $F(t)$  of larvae that did not stop or exit as a function of the moving time) of the durations of the paths in the peripheral zone on a semi-logarithmic scale, we obtained a straight line that can be fitted by

$$\ln(F(t)) = -\frac{1}{\tau}t \quad (\text{A1})$$

This indicates that the survival curve of both behaviours corresponded to an exponential decay (Haccou & Meelis 1992). The parameter  $\tau$  gives the characteristic time before an exit or a stop and  $dt/\tau$  gives the probability of performing either a stop or an exit during the interval  $dt$ . Thus, the probability  $1/\tau_{\text{Stop,p}}$  of stopping per unit time at the periphery is given by

$$\frac{1}{\tau_{\text{Stop,p}}} = \frac{1}{\tau} \left( \frac{N_{\text{Stop,p}}}{N} \right) \quad (\text{A2})$$

where  $N_{\text{Stop,p}}$  is the number of paths at the periphery that ended with a stop.

The probability of exiting per unit time is

$$\frac{1}{\tau_{\text{Exit}}} = \frac{1}{\tau} - \frac{1}{\tau_{\text{Stop,p}}} \quad (\text{A3})$$

### Probability of stopping in centre of arena

Assuming a constant speed  $v_c$ , the fraction  $F_{\text{Stop,c}}$  of cockroaches that stopped at a distance  $L$  from the entry point in the centre of the arena is given by

$$\begin{aligned} F_{\text{Stop,c}} &= 1 - \int_0^{+\infty} p(L) e^{-\frac{L}{v_c \tau_{\text{Stop,c}}}} dL \\ &= 1 - \langle e^{-\left(\frac{L}{v_c \tau_{\text{Stop,c}}}\right)} \rangle \approx \left( \frac{\langle L \rangle}{v_c \tau_{\text{Stop,c}}} \right) \end{aligned} \quad (\text{A4})$$

where  $1/\tau_{\text{Stop,c}}$  is the probability per unit time of stopping in the central zone and  $p(L)$  the distribution of the lengths of the diffusive paths (which began and ended at the periphery). Blanco & Fournier (2003) showed that, in the case of a diffusive process, the average trajectory length  $\langle L \rangle$ , defined as the mean distance between the first

entry and first exit point from the centre, depends only on the geometry of the system

$$\langle L \rangle = \frac{\pi \delta}{4} \quad (\text{A5})$$

where  $\delta$  is the diameter of the arena (10 cm for the centre) over which the diffusive process occurs. Therefore, the probability per unit time of stopping in the centre of the arena is

$$\frac{1}{\tau_{\text{Stop},c}} = \frac{4v_c(F_{\text{Stop},c})}{\pi \delta} \quad (\text{A6})$$

#### *Rate of stopping when encountering stopped larvae*

The fraction of cockroaches that stopped when encountering  $N$  stopped larvae is given by

$$F_{\text{Stop},N} = 1 - e^{-\frac{d}{v(\tau_{\text{Stop},N})}} \quad (\text{A7})$$

where  $d$  is the distance when a moving cockroach could perceive a stopped larva, and  $v$  is the velocity of a cockroach. Based on its detection radius, a moving larva could perceive a stopped cockroach or an aggregate for

$d = 12$  mm at maximum (Fig. 1). The rate  $1/\tau_{\text{Stop},N}$  is thus estimated by

$$\frac{1}{\tau_{\text{Stop},N}} = -\frac{v(\ln(1 - F_{\text{Stop},N}))}{12} \quad (\text{A8})$$

#### *Probability of moving during a collision*

The fraction  $F_{\text{Collision},N}$  of larvae that left their stopping state because of a collision is given by

$$F_{\text{Collision},N} = N \left( 1 - e^{-\frac{d}{v(\tau_{\text{Collision},N})}} \right) \quad (\text{A9})$$

where  $N$  is the number of stopped larvae that detect the moving cockroach and  $v$  the mean speed of a larva. Based on its detection radius, a stopped larva could perceive a moving cockroach for  $d = 12$  mm at maximum (Fig. 1). Therefore, the probability  $1/\tau_{\text{Collision},N}$  is given by

$$\frac{1}{\tau_{\text{Collision},N}} = -\frac{v(\ln(1 - \frac{F_{\text{Collision},N}}{N}))}{12} \quad (\text{A10})$$