



Cockroach aggregation based on strain odour recognition

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Blattella germanica (L.) cockroaches are gregarious during their resting period. Binary choice tests with groups of larvae indicated a strong tendency to aggregate on a single resting site. This was observed even when all sites were identical or when larvae came from either one or two strains. Previous results showed that gregarious behaviour is mainly based on recognition of cuticular hydrocarbons characterizing strain odour and that larvae prefer their own strain odour to that of another strain. Nevertheless, when groups in tests came from two different strains and had the choice between their two strain odours, they aggregated on only one of the sites. A mathematical model relying on a minimum number of functioning rules was devised to reproduce these experimental collective responses. The model is based on a fundamental parameter representing individual variation in the resting period on a given site in relation to the number of individuals on that site. Taking only this parameter into account, the model predicted that different strains are able to aggregate on the same site despite a weak interstrain interattraction parameter. *Blattella germanica* is thus an interesting biological model to investigate different aspects of aggregation and interindividual recognition.

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Spatial distribution of individuals is an important subject in many fields because it determines the level of interactions between individuals, and more generally the structuring as well as the organization of populations (Okubo 1980). In many species, individuals form groups and local population density is higher in some areas in relation to surroundings (Southwood 1966). The spatial and temporal cohesion of such groups of individuals, as well as their complexity and diversity of the clustering phenomenon, has been explained in various ways. Ecologists stress the importance of environmental stimuli (Southwood 1966), whereas ethologists stress existing relationships between group members (Ledoux 1945; Grassé 1952). An aggregation may form by the attraction of individuals to the same environmental stimulus (Hamner & Schneider 1986; Stocker 1999), or by mutual attraction between group members (Allee 1931; Okubo 1980; Parrish & Edelstein-Keshet 1999). Social aggregations that involve interindividual attraction necessitate

information transfer. Rules governing individual movements within an aggregation and the emergent properties or 'group behaviour' are not easily understood (Parrish & Hamner 1997).

The study of proximal causes, that is, the mechanisms involved in group formation, can benefit from concepts of self-organization (Deneubourg & Goss 1989; Bonabeau et al. 1997; Camazine et al. 2001). Detailed information on how aggregations form would lead to a better understanding of why they form and how selection acts on mechanisms that increase individual fitness and thereby the inclusive fitness of the group (Pulliam & Caraco 1984). These groups find their origin and their cohesion in the attraction between individuals: group members are then the source of attraction (Camazine et al. 2001). In most situations, the behaviour of the group as such is considered as an emergent process that arises from attractions between the individuals of a group and between the individuals and their immediate environment (Camazine et al. 2001). Modelling allows the testing of some rules of association based on minimal hypotheses and so helps to verify whether results of computer-generated simulations answer the same rules of association as the observed animal aggregations (Camazine et al. 2001).

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Studies on cockroaches, particularly on *Blattella germanica* (L.), have described their aggregative distribution in a natural environment where different age classes share the resources that are present in their home ranges. Cockroaches tend to gather in safe shelters during their resting period (Rivault 1989; Rivault & Cloarec 1991; Rust et al. 1995) and select shelters on physical characteristics (Reiersen 1995; Appel & Smith 1996). Therefore, shelters are important environmental resources for these insects. The formation of aggregations depends on both environmental factors and mutual attraction. Experiments have shown that cockroaches are able to use environmental cues such as learned spatial information to return to their shelters (Rivault & Dabouineau 1996; Durier & Rivault 1999) as well as the odour produced by each group member to reinforce the cohesion of aggregations observed during resting periods (Rivault & Cloarec 1998; Rivault et al. 1998). In eusocial insects (Vandermeer et al. 1998; Lenoir et al. 1999) and in gregarious cockroaches (Rivault et al. 1998), cuticular hydrocarbons act as a recognition signal inducing attraction between individuals.

Therefore, cockroaches provide us with an interesting model to investigate the link between interindividual recognition abilities and the organization of populations in aggregations and to discuss its evolutionary consequences. Our aim in this study was to investigate how groups are formed. We used experimental results and a theoretical model with few functioning rules to investigate the emergence of aggregations.

METHODS

Experimental Data

Aggregation in choice tests

Binary choice tests were done with groups of 20 first-instar cockroach larvae, *B. germanica*, following the same experimental procedure as described in Rivault & Cloarec (1998). Tests were done in petri dishes with filter papers acting as attractive resting sites that were large enough to house the entire group, without any overcrowding. Tested groups of cockroaches came from either a single strain or two different strains. A strain descends from cockroaches collected from a given urban location and bred in isolated cages in the laboratory after capture. All strains are kept under strictly identical rearing conditions (climatized room, type of cage, diet and rearing densities) to minimize environmental effects (for details see Rivault et al. 2002).

We used data from Rivault & Cloarec (1998) and additional experimental data. In the 1998 paper, tests with two control papers showed that groups of cockroaches from a single strain formed a single aggregation on one of the papers. Furthermore, cockroaches preferred a strain odour-conditioned paper to a control paper, and they chose the paper conditioned with their own odour in preference to a paper conditioned with a different strain odour.

Because cockroaches are able to discriminate and select their own strain odour, we conducted additional experiments done under the same conditions as those used in

1998. We tested groups of cockroaches from two strains to verify their ability to segregate. The proportions of each strain in the groups were either equal or different: 0.95, 0.90, 0.85, 0.75, 0.65, 0.60, 0.55 and 0.5. Cockroaches received two control papers and we counted the individuals on each paper at the end of the tests. Only tests when at least 80% of larvae were resting on papers were taken into account.

Influence of conspecifics on individual resting time

To study individual behaviour and the influence of conspecifics on resting time, we did a series of experiments with eight larvae observed for 20 min under the same experimental conditions as described above. We used 57 resting durations to calculate the relation between resting time and the number of conspecifics on the site. The mean resting time was measured when larvae were either alone or with one or two conspecifics. We have sufficient experimental data only for situations with one, two and three larvae in the set-up. The distribution of resting times in all situations is an exponential equation (e^{-Qx}). Q is the probability of leaving the site and in this case the mean resting time is the inverse of probability Q (Table 1).

By analogy with other experimental results (e.g. Therulaz et al. 2002; Depickère et al. 2004), we tested the empirical function:

$$Q = \frac{\theta}{k + X^n} \quad (1)$$

This function Q means that the probability of leaving decreases with the number of conspecifics (X) on the site. Values of θ and k were estimated by fitting equation (1) and experimental data. $\theta/(k+1)$ is the highest probability of leaving a site (i.e. when one individual is alone on the site). k and n are parameters that modulate the influence of the other individuals. k corresponds to a threshold in relation to the number of individuals (X) and n is the sensitivity to this number. The characteristics of the site influence θ , k and consequently the resting durations of individuals. The fitting implies $\theta = 0.06$, $k = 6$ and $n = 2$ ($r = 0.96$, $P = 0.001$).

Model

The hypotheses on which our model is based require a minimum number of behavioural rules. Taking these

Table 1. Probability of leaving the site (Q) in relation to the number of individuals (X) on the site calculated from experimental data

X	Q (s)	df	r	P
1	0.0086	18	0.96	0.001
2	0.006	26	0.94	0.001
3	0.004	13	0.96	0.001

For each number of individuals (X), the value of Q is given by a linear regression.

behavioural rules into account, the model aims to predict the results of our experiments on the collective dynamics of cockroach aggregation.

Mean field formulation

The model describes the dynamics of the groups on each of the two resting sites and consequently the traffic of individuals between the two sites. The differential equations describe the variations in the mean numbers of individuals on each site in relation to time. These equations have two terms: (1) a positive part reflects the arrivals of individuals on the site and (2) a negative part describes their departures.

One strain. All the individuals belonged to the same strain and were considered to be identical. Each individual explored the petri dish randomly and had the same probability at each time step of encountering one of the two sites. The equation evaluates the number of individuals on each site (X_1 = number of individuals on site 1, X_2 = number of individuals on site 2). This hypothesis was based on observations that, under these conditions, there is no trail (Durier & Rivault 2001), no long-range interactions between the insects (e.g. between the aggregated larvae on the resting site and the larvae exploring the petri dish) and no memory effect (or that they were insignificant). We assumed that exploration durations were short and exchanges between sites were direct. In this model individuals travelled immediately from one site to the other, and the durations of the exploratory phase were omitted. The model can be generalized for several sites, but we limited our study to two sites.

The probability of moving from i to j depends on the probability of leaving site i (Q_i). At each time step, each individual on site i has a probability of leaving site i depending on the number of individuals (X_i) on site i : the greater X_i is, the lower the probability of leaving the site i (Q_i). Q_i is defined by equation (1).

$$Q_i = \frac{\theta}{k + X_i^2} \quad \text{with } \theta = 0.06 \text{ and } k = 6 \quad (2)$$

The flux of individuals between the two sites can be explained as follows:

$$\phi_{ij} = X_i Q_i = \frac{\theta X_i}{k + X_i^2} \quad i = 1, j = 2 \quad i = 2, j = 1 \quad (3)$$

Because sites are identical, all the parameters that characterize both sites are equal. The equations of the mean field model can be written as:

$$\frac{dX_i}{dt} = -\frac{\theta X_i}{k + X_i^2} + \frac{\theta X_j}{k + X_j^2} \quad i = 1, j = 2 \quad i = 2, j = 1 \quad (4)$$

Two strains. The model can be generalized for groups of individuals from different strains. Here, we considered only groups formed by two strains. We used X for strain 1 and Y for strain 2. In mixed groups, the probability of one individual belonging to either strain leaving is always a function of the number of individuals present on the

site. Because larvae prefer their own strain odour to that of other strains (Rivault et al. 1998), the influence of individuals belonging to the same strain can be more important than that of individuals belonging to the other strain. In this case, the basic model must be completed with parameters of attraction between strains i and j : β_{ij} .

X_i and Y_i are, respectively, the numbers of individuals of strains 1 and 2 on site i . We supposed that the interaction of strain 1 on strain 2 is the same as that of strain 2 on strain 1 and therefore $\beta_{12} = \beta_{21} = \beta$. The parameters of attraction between strain members, already present in the single strain model, are always considered equal to 1 ($\beta_{11} = \beta_{22} = 1$). $\beta < 1$ expresses the fact that an individual of one strain tends to stay more with an individual of the same strain than with an individual of another strain. When $\beta = 0$, the two strains behave independently. It is difficult to estimate β experimentally and currently we have no experimental value for this parameter. The probabilities of leaving site i for an individual depend on X_i ($Q_{x,i}$) or Y_i ($Q_{y,i}$):

$$Q_{x,i} = \frac{\theta}{k + (X_i + \beta Y_i)^2} \quad Q_{y,i} = \frac{\theta}{k + (Y_i + \beta X_i)^2} \quad (5)$$

When there are two strains X and Y , the model equations can be written as:

$$\begin{aligned} \frac{dX_i}{dt} &= -Q_{x,i}X_i + Q_{x,j}X_j & i = 1, j = 2 \quad i = 2, j = 1 \\ \frac{dY_i}{dt} &= -Q_{y,i}Y_i + Q_{y,j}Y_j \end{aligned} \quad (6)$$

with $X_1 + X_2 = N_x$, $Y_1 + Y_2 = N_y$, where N_x , N_y are the numbers of individuals of each strain and $N = N_x + N_y$ is the total number of individuals.

Monte Carlo simulations

To understand the main effects arising from the fluctuations of the dynamics, we used Monte Carlo simulations where the random aspect of the process is automatically incorporated. The simulations were based on the same mechanisms defined in the differential system of equations (4) or (6). The different steps can be summarized as follows: (1) initial conditions: the number of individuals on each site was fixed at $N/2$; (2) decision process: two states are possible for each individual if we consider that exchanges with the outside environment can be neglected: on site i or on site j . At each time step (t), the position of each individual was checked. Then its probability of moving from i to j is given by Q_j (equation 2) for one strain or $Q_{x,i}$ and $Q_{y,i}$ (equation 5) for two strains. Its position at $t+1$ depends on the comparison between the calculated value Q_j and a random number sampled from a uniform distribution between 0 and 1. If its value is less than or equal to Q_j , the individual leaves site i and goes to site j . If not, it stays on site i .

The probability Q_i of moving from i to j is updated at each simulation step in relation to the number of individuals already present on site i . The process was

repeated for a sufficient number of steps to reach the stationary state. Monte Carlo simulations were run 1000 times. Simulation results allowed us to follow progress towards the stationary state on sites i and j in relation to time. The distributions of the numbers of individuals present on sites i and j in relation to time and at stationary state were calculated.

RESULTS

One Strain

Experimental results

The observed distribution of experiments in relation to the different proportions of larvae on one site (Fig. 1) was bimodal and differed from a binomial distribution. This means that the majority of larvae aggregated on one of the sites. In 75% of the experiments, 80% of the larvae were on the same site.

Mean field model

With one strain and two identical sites, the model has three stationary solutions. The first solution is symmetrical (dispersal) with equal numbers of individuals on both sites:

$$X_{1,2} = 0.5N \quad (7a)$$

The other two solutions are asymmetrical (heterogeneous), with unequal numbers of individuals on each site. This means that one of the sites was selected:

$$X_{1,2} = 0.5 \left(N \pm (N^2 - 4k)^{0.5} \right) \quad (7b)$$

The three solutions are represented by a typical pitchfork bifurcation diagram (Fig. 2a) of X/N as a function of N . This diagram has a dispersal state (equal use of the two sites) that becomes unstable from $N = 2k^{0.5}$. If $N < 2k^{0.5}$, the dispersal state is stable and the other two solutions do not exist. If $N \geq 2k^{0.5}$, the dispersal state is unstable and one of the two asymmetrical solutions is selected. If $k = 6$, when the total number of individuals is greater than five, the formation of a group on one of the sites induced the selection of one site to the detriment of the other. This

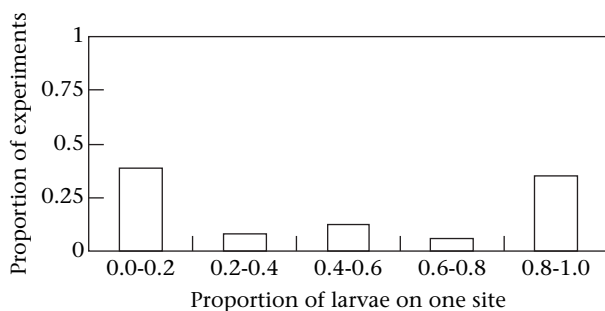


Figure 1. Proportion of experiments in relation to the proportion of larvae on one of the two sites for a group of 20 larvae from the same strain in the presence of two control papers (49 experiments).

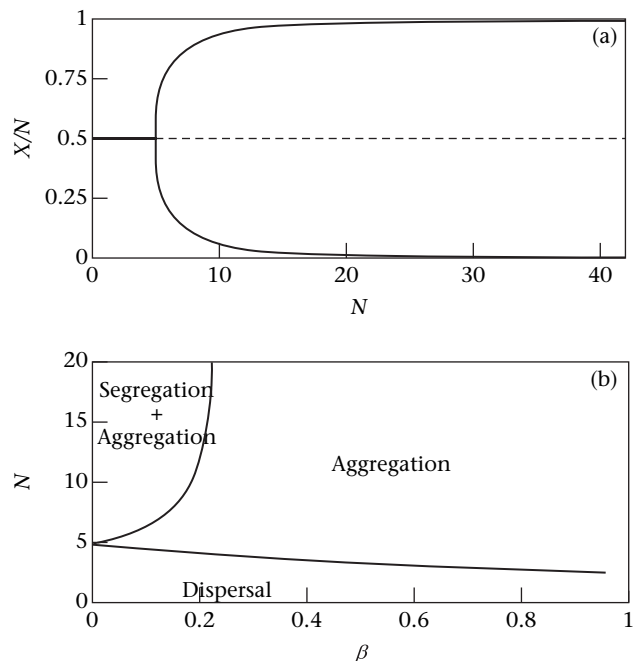


Figure 2. Diagrams of solutions for the one-strain and two-strains mean field model: (a) model of the fraction of the total number of individuals on one site (X/N) in relation to the total number of individuals on both sites (N) (bifurcation diagram).—: Stable solutions; - - -: unstable solutions. (b) Diagram of the mean field model solutions as a function of the attraction parameter β and N for the same proportion of individuals from each strain.

selection occurs through amplification. The greater N is, the greater the clustering asymmetry.

Monte Carlo simulations

Monte Carlo simulations confirm the analytical results, and provide supplementary information. At the end of the simulation process (12 h, corresponding to the duration of the resting period), for small sample sizes $N < 5$ (e.g. $N = 4$, Fig. 3a), frequencies of computer simulations of the different proportions of individuals on one site were uniformly distributed. As the dynamics were defined with interaction between individuals, the resulting distribution did not fit a binomial. However, the small number of individuals is not enough to induce the selection of one site. For a larger N , we observed a U-shaped distribution of the simulations as a function of the fraction of the total population on each site. This showed that the majority of individuals aggregate on the same site and the greater N is, the stronger the aggregation level (Fig. 3b, c, d). With sample sizes $5 \leq N < 16$, the numbers of individuals on one site were never large enough to reach a stable state: each site was selected alternately (Fig. 4a). With sample sizes $N \geq 16$, individuals selected one of the sites and choice reversals were no longer observed (Fig. 4b). We can assume that when N increases, there are fewer reversals (Fig. 4c), higher clustering tendency and higher clustering stability on one site. However, we stress that it took time to reach a high level of aggregation and the stationary state. For $N = 20$, the stable state for one site to be selected

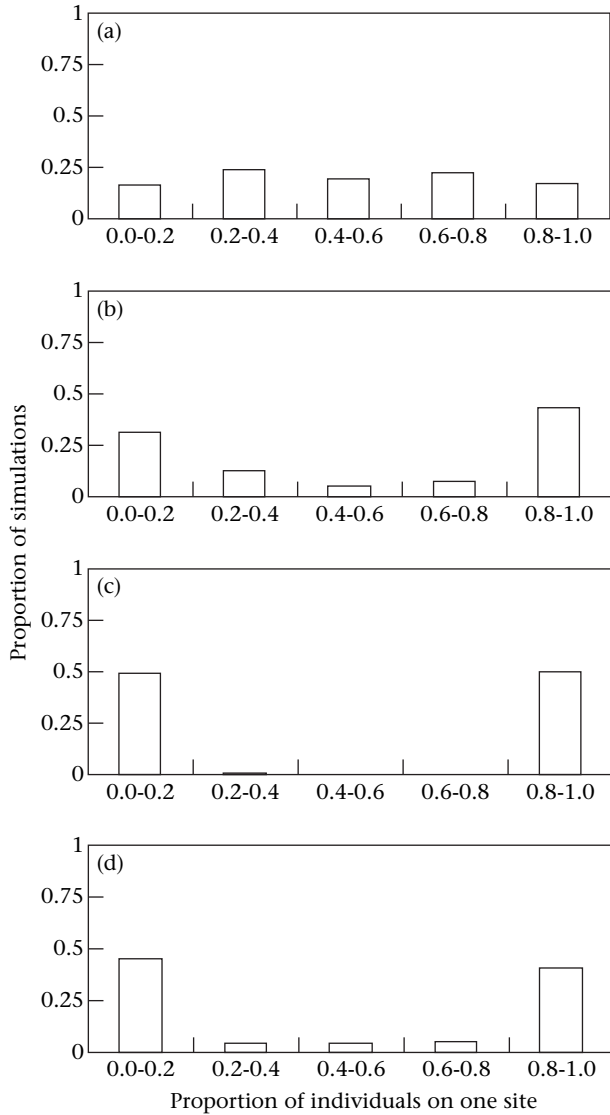


Figure 3. Proportions of simulations in relation to the proportions of individuals on one of the two sites for different groups of N individuals (simulation duration: 12 h). (a) $N = 4$, (b) $N = 10$, (c) $N = 20$ and (d) $N = 80$.

was reached after a short delay of 26 min. For $N = 80$, the same state was reached after 7 h (Fig. 4d), and for $N = 100$ after 21 h.

With one strain, the predictions of the simulations and the experimental results agreed. Indeed, for $N = 20$, the theoretical (Fig. 3c) and experimental distributions (Fig. 1) do not differ. In 75% of the experiments and in 80% of the simulations, at least 80% of individuals selected one site.

Two Strains

Experimental results

The observed distribution of experiments in relation to the different proportions of the total numbers of individuals (two strains cumulated) was bimodal and differed from a binomial distribution (Fig. 5a–c). This means that

the majority of individuals from the two strains aggregated on one of the sites. This was observed for all tested proportions of strains and no differences were observed for the different proportions. More than 80% of larvae were observed on the same site, in more than 75% of the experiments (Fig. 5c). Furthermore, no differences were observed between the experiments with one strain and experiments with different proportions of two strains.

Mean field model

The model has nine stationary solutions. We discuss only the simplest case from a mathematical point of view: equal numbers ($N_x = N_y = N$) of individuals from the two strains. The first solution, stable for N around 5, corresponds to a dispersal of individuals of both strains on both sites:

$$X_i = Y_i = 0.5N, \quad i = 1, 2 \quad (8a)$$

A group of two conjugate solutions corresponds to a heterogeneous distribution of individuals. Most individuals of both strains select the same site:

$$X_i = Y_i = X_{\pm} \quad i = 1, 2$$

$$X_{\pm} = 0.5N \pm 0.5 \sqrt{N^2 - \frac{4k}{(1+\beta)^2}} \quad (8b)$$

These solutions correspond to the aggregation of the individuals of both strains on the same site. They exist and are stable if:

$$N > \frac{2k^{0.5}}{1+\beta}$$

A second group of two conjugate solutions corresponds to segregation between the two strains, the majority of one strain is on one site, and the majority of the second strain is on the second site:

$$X_i = Y_j \quad i = 1, j = 2 \text{ and } i = 2, j = 1$$

$$X = 0.5N \pm \sqrt{N^2 - \frac{4(k+N^2\beta^2)}{(1-\beta)^2}} \quad (8c)$$

These solutions do not exist if (1) $\beta > 0.333$ and (2) if $\beta \leq 0.333$ and $N^2 > 4k/(1-2\beta-3\beta^2)$. However, these solutions are stable for: $\beta < \beta_{\text{asymp}} - 2k^{0.5}N^{-2}$ with $\beta_{\text{asymp}} \approx 0.236$. A last group of four conjugate solutions corresponds to a mixture of individuals of both strains on both sites. The solutions are always unstable (never observed).

Figure 2b summarizes these results. Three sectors can be defined when N varies as a function of β : dispersal, aggregation plus segregation and aggregation alone. To summarize, the model shows that only for small values of β (< 0.25) and $N > 5$ may the population adopt two different patterns: both strains are aggregated on the same

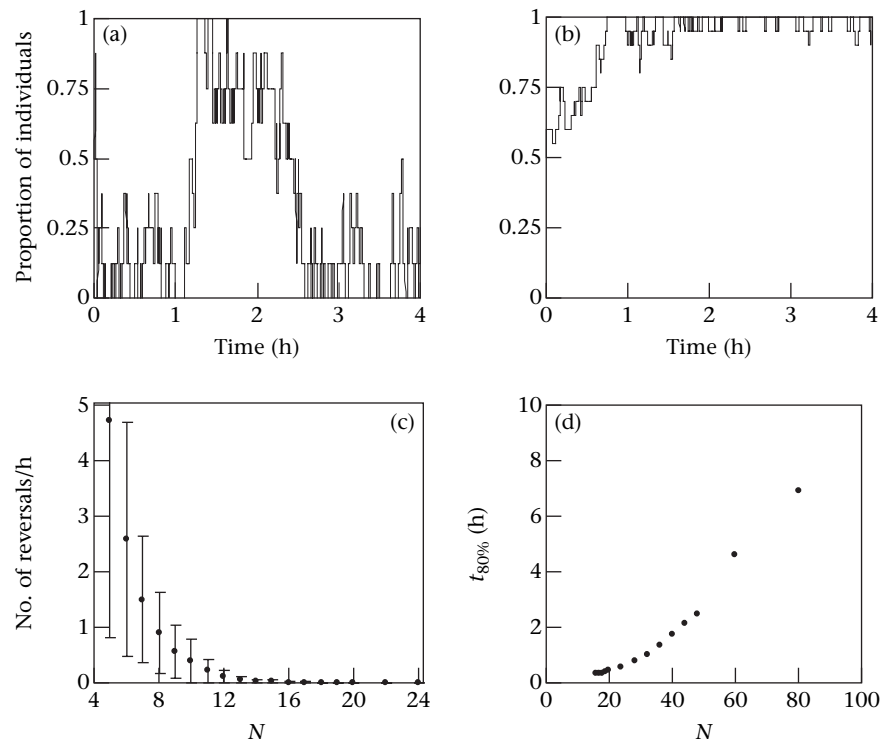


Figure 4. Time effect in the simulations on the aggregation dynamics of the model (a, b). Development of the proportion of individuals on one of the two sites during the first 4 h. (a) $N = 8$, (b) $N = 20$. (c) Number of reversals as a function of N . (d) Time needed to aggregate 80% of the population on one site as a function of N .

site or both strains are segregated. Monte Carlo simulations show the selection frequencies for the different patterns. For a small N , both strains are distributed on both sites and are mixed. For larger N and β , the individuals of both strains aggregate on the same site.

Monte Carlo simulations

First, we analysed the influence of the attraction between the strains (β) and the influence of the proportion of one strain in relation to the other strain for a total number of individuals: $N = 20$ (as in the experiments). At the level of pooled individuals of both strains, for very low values of β and a proportion of each strain of about 0.5, we observe, a trimodal distribution of the simulations in relation to the proportion of the total number of individuals on each site. At the level of each strain, we observe a U-shaped distribution (Fig. 6a). This shows that each strain often 'selects a site' independently of the other and interacts weakly with the other strain. However, when the proportion of one strain in relation to the other differs from 0.5, the trimodal distribution tends to be U-shaped. Thus segregation is observed less frequently when the proportion of one strain increases in relation to the other. When β increases, the trimodal distribution of pooled strains rapidly tends to a well-marked U-shaped distribution for all tested strain proportions (e.g. $\beta = 0.2$, equal proportion of both strains, Fig. 6b). When $\beta \geq 0.2$, in more than 75% of the simulations, mixed groups are aggregated on one site

(Fig. 6c). The proportion of individuals from each strain weakly influences the mixed aggregation of both strains.

These theoretical results show that small values of β are sufficient to aggregate both strains on the same site as shown by the experiments. Furthermore, the final aggregation does not differ between the two-strains and the one-strain situations. The total size of the population influences the aggregation. For a fixed value of β , the higher N is, the higher the proportion of simulations where both strains are aggregated on the same site (Fig. 6d).

Comparisons between computer simulations and experimental results showed that, for a value of attraction between strains of $\beta = 0.2$, all results were statistically similar (Figs 5c and 6c, for a proportion of experiments $> 80\%$, chi-square test: $\chi^2_8 = 2.75$, $P = 0.01$).

DISCUSSION

In our experiments, groups of cockroaches were presented with a choice between two resting sites that were more than large enough to house the entire group. The fact that the group tested included individuals from either one or two strains did not influence the aggregation pattern, although these cockroaches had the capacity to discriminate between strain odours and to choose resting sites impregnated with their own strain odour in preference to resting sites impregnated with odours of other strains (Rivault & Cloarec 1998).

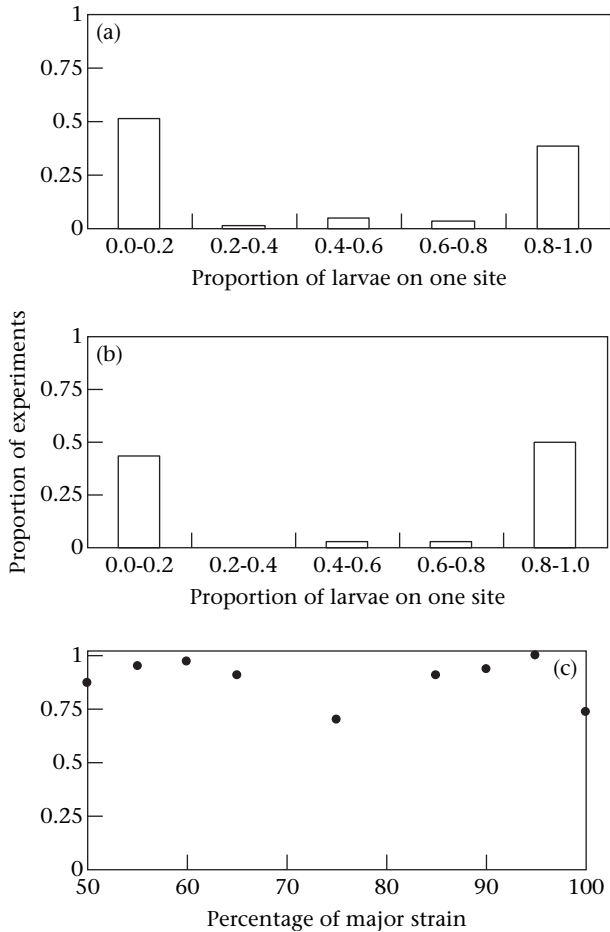


Figure 5. Proportions of experiments in relation to the proportions of larvae on one of the two sites: (a) for all experiments whatever the proportion of individuals from the two strains (229 experiments) and (b) for 90% of individuals from one strain (32 experiments). (c) Proportions of experiments characterized by more than 80% of larvae on the same site in relation to the percentage of the major strain. Numbers of experiments used for each percentage of the major strain: (100%, 49 experiments), (95%, 24), (90%, 32), (85%, 21), (75%, 30), (65%, 22), (60%, 33), (55%, 20), (50%, 47).

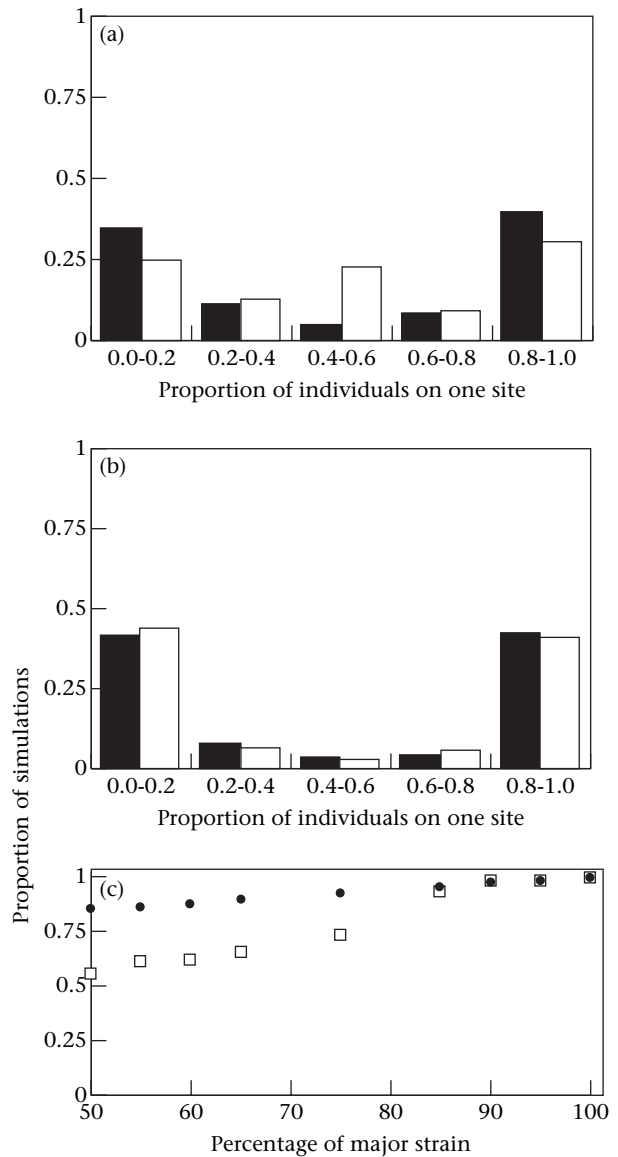


Figure 6. Proportions of simulations in relation to the proportions of individuals on one of the two sites for different proportions of individuals from two strains, for a total of 20 individuals and two values of the attraction parameter β : 0.05 and 0.2. We ran simulations for 12 h. ■: Individuals from the major strain on the site (when the mixed group included the same number of individuals, 50%, from each strain); □: cumulated data for individuals from the two strains. (a) $\beta = 0.05$, 50%. (b) $\beta = 0.2$, 50%. (c) Proportions of experiments characterized by more than 80% of larvae on the same site in relation to the percentage of the major strain for $\beta = 0.05$ (□) and $\beta = 0.2$ (●). (d) Proportions of experiments characterized by more than 80% of larvae on the same site in relation to the total population for $\beta = 0.2$ (when the mixed group included the same number of individuals, 50%, from each strain; simulation duration: 12 h).

The hypotheses underlying our model rely on a minimum number of functioning rules that lead to amplification. Amplification is modulated by the time spent on a site (resting time), which is sufficient to produce the pattern independently of any signalling. The presence of already resting conspecifics on a site, which acts as a signal, induces newcomers to increase their resting time on that

site. Agreement between our model and experimental results enabled us to conclude that behavioural traits regulate the formation of aggregations in *B. germanica*. Consequently, the formation of aggregations does not require any active signalling.

Our model predicts that this behavioural trait enables aggregations to form only when the number of individuals already present on the site is large enough. When the number of individuals is small, the aggregation level is weak and the model suggests that, automatically, different strategies operate in relation to the total number of individuals. Nevertheless, under natural conditions, other sets of behavioural traits involved in navigation, reproduction and population dispersion could act to maintain locally high population densities (Rivault 1989; Reiersen 1995; Durier & Rivault 2001). For example, the model does not take into account ground marking of resting areas with cuticular hydrocarbons that could reinforce the aggregation, although tests with conditioned papers showed that insects stayed longer on a well-marked site and thus aggregated there faster (Rivault et al. 1998). This external memory effect is ineffective in the short term (a few hours) but stabilizes the aggregations in the longer term (Depickère et al. 2004).

The model predicts that when individuals came from two strains, an interstrain attraction parameter (β), much weaker than the intrastrain attraction parameter, leads to the formation of a single mixed aggregation, similar to the one-strain aggregation. Despite many difficulties, these results suggest further experiments are needed to investigate the influence of conspecifics from different strains on resting times and to quantify the value of β .

The model showed that it is not necessary to add complementary rules to obtain this result. So by using this model there is no need to consider chemical signatures as a behavioural modification to interpret the emergence of segregation or aggregation. We verified the characteristics of this model by varying the values of the different attraction parameters. Nevertheless, we do not exclude the possibility that mixed aggregations would increase chemical exchanges between individuals and would accelerate the appearance of a new chemical signature, common to all individuals and reinforcing the mixing of the strains, as observed in ant colonies (Dahbi et al. 1997; Dahbi & Lenoir 1998).

The value of the interstrain attraction parameter (β) can be compared to the genetic proximity between strains: β increases when the relationship between strains becomes closer. This parameter can be influenced by other factors such as similar diets or use of environmental materials (Lenoir et al. 2001). As stated above, small values of β are sufficient to induce the emergence of a mixed aggregation. Strains may be separated randomly only when the values of β are very small. Consequently, segregation has a higher probability of emerging when levels of relatedness between strains are low.

We have discussed our results only for situations with two shelters and two strains. However, analysis of the theoretical model for more than two sites and for more than two strains (not summarized in this paper) predicts a similar collective response and mainly the systematic

aggregation of all strains together despite a weak attraction between the strains.

Our study reveals powerful mechanisms in presocial insects and suggests that these 'self-organized scripts' (Camazine et al. 2001) could be numerous, even though, in terms of individual or group benefits, the situations could differ. Indeed, the mechanisms involved in the aggregation of cockroaches have their equivalent in many gregarious arthropods and social insects (Eickwort 1981; Camazine 1991; Deneubourg et al. 1991; Franks & Sendova-Franks 1992; Lioni et al. 2001; Depickère et al. 2004). Thus, we can state, by taking specific traits into account, that our model and rule of thumb can be applied to a number of gregarious species as well as to a set of situations where social activities are based on an aggregation phenomenon such as building behaviour (Franks & Deneubourg 1997; Rasse & Deneubourg 2001) or defence (Millor et al. 1999). The selection of the collective solution results from amplification mechanisms and competition between different amplifications. In these situations, resting times increase with the numbers of conspecifics. Our model and experimental results help, on the one hand, to explain a wide range of responses that appear to be adaptive and, on the other hand, to establish a link between cognitive processes (Sherman et al. 1997; Rivault et al. 1999) and collective responses where weak interstrain attraction is sufficient to induce emergence of mixed aggregations. This property characterizes all systems where clustering is a by-product of the competition between different amplification mechanisms (Saffre et al. 1999).

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