

Collective Decision-Making Based on Individual Discrimination Capability in Pre-social Insects

Jean-Marc Amé, Jesus Millor, José Halloy,
Grégory Sempo, and Jean-Louis Deneubourg

Service d'Ecologie sociale, CP 231, Université Libre de Bruxelles,
Bd Fr. Roosevelt, B-1050 Bruxelles, Belgium
jldeneub@ulb.ac.be

Abstract. Gregarious insects, like cockroaches, aggregate in shelters during their resting period. How do individuals reach a collegial decision? What is the relation between the distributions of the individuals and the parameter values characterizing the population and the environment? With a model based on experimental data, we demonstrated that the collegial decision is based on the relation between the individual resting time in a shelter and the population in this shelter. We extended this model to the case where different sub-groups may interact and where the crowding effect under the shelters influences the aggregation. This second model shows that depending on the interaction between the sub-groups and the crowding effect, different patterns are observed such as segregation of the different sub-group or the aggregation of the whole population.

1 Introduction

Grouping is the most common collective behaviour among living organisms. This phenomenon extends over the entire diversity of taxon and spans many biological characteristics like life-history strategy, degree of mobility... [1][2]. Many species from bacteria to higher vertebrates form groups more or less stable in time and space in response to environmental heterogeneities and environmental constraints or to attraction between individuals [3]. The level of interactions among individuals in a population relies on the spatial distribution of individuals that influences the structure and the organization of populations [4]. Aggregation can be defined as a higher temporal and spatial density of individuals than in the surrounding area [5][2]. The origin and the stability of social aggregates result from mutual inter-individual interactions which are mediated by information transfer between individuals. This can induce emergent group behaviours, patterns or functions that are not merely the sum of the individual behaviours [6]. Self-organized systems allow understanding how non-linear interactions can lead to complex and non-intuitive behaviours even with basic rules or information transfer at the individual level [2].

In cockroach species, during the diurnal phases of their rhythm of activity the most widespread collective behaviour is gregariousness [7-9]. Studies on cockroaches and

especially on *Blattella germanica* have shown that clustering results from inter-attraction between individuals in response to a signal mediated by chemical cues [10][11] and that this aggregation can be considered as a social phenomenon [12]. Different benefits result from aggregation such as reduction of stresses, increase in efficiency of alarm responses and antipredator behaviour, faster development and more efficient reproduction. Cockroaches tend to gather in shelters during their resting period. In *Eublabeus distanti* individuals are able to discriminate individuals belonging from the same strain or from another strain [13]. Ishii & Kuwahara [14] have shown that groups of cockroach larvae were able to select an aggregation shelter according to its odour conditioning in binary choices tests. Different strains of cockroaches imply different individual chemical signals per strains. Recent studies based on recognition of cuticular hydrocarbons profiles in *Blattella germanica* show that strains discriminate the signals and this leads to resting shelter selection. In a recent experimental binary choices study based on odour discrimination between species or strains of cockroaches, Leoncini and Rivault [15] have shown that segregation can occur when the carrying capacity of shelters is a limiting factor. In relation to the crowding effect sub-groups aggregate under the same shelter or segregate between the two shelters.

The bases to model this kind of collective phenomena have been introduced in previous studies [16-18]. We present here collective decision making linked to aggregation problems between different sub-groups of individuals by taking into account the crowding effect. Our aim is to show that inter-attraction can lead, in relation to the limited carrying capacity of shelters, to different patterns of aggregation from a homogeneous distribution of individuals to segregation between sub-groups. Modulating the level of inter-attraction between strains and the crowding effect, we show in this study that either segregation or aggregation can be emergent patterns due to local interaction between individuals without global knowledge of the system.

We describe the differential equations model that derives from the previous ones [16-18] and the stochastic description of the model by using master equations to take into account the fluctuations characterizing such systems and determine the probability distribution of individuals from each sub-group under shelters.

This model study will be useful to determine how the properties observed at the individual-level can explain the patterns that emerge at the collective-level without an active signal.

2 Formalizing the Model

2.1 Meanfield Formulation of the Model

Previous experiments provided data to build a dynamical model of aggregation based on the individual behaviour [18][19]. In previous studies on mechanisms that induce collective choices in binary choice tests, we have analyzed on one hand similar models based on strain recognition without a crowding effect [16][17]. On the other hand, we have analyzed the effect of crowding on one strain on binary choices and multiple choices tests and describe the patterns that appear [18]. The present model

mixes these studies and takes into account the crowding effect of shelters in binary choices tests for two strains and thus the effect of limited space due to the carrying capacity of shelter on strain repartition.

We present first the general model for p strains ($i=1\dots p$) and two shelters ($j=1,2$) with a limited carrying capacity (S_j). We assume that the number of individuals from each strain is equal to N and that the maximum number of individuals that each shelter can harbor is equal ($S_j=S$). $X_{i,j}$ is the number of individuals of the strain i under the shelter j .

$$\sum_{j=1}^2 X_{i,j} = N \quad \forall i = 1\dots p \tag{1}$$

At each time step, each individual in the shelter j has a probability $Q_{i,j}$ to leave this shelter and to explore the arena. It has the same probability at each time step to encounter and to join the shelter h (R_h).

Neglecting the time outside shelters, we can write the evolution of the number of individuals of strain i under shelter j as follow:

$$\frac{dX_{i,j}}{dt} = -R_h Q_{i,j} X_{i,j} + R_j Q_{i,h} X_{i,h} \quad j = 1,2 \quad h = 1,2 \quad h \neq j \quad \forall i = 1\dots p \tag{2}$$

The probability to join the shelter j is given by:

$$R_j = \mu \left(1 - \sum_{i=1}^p \frac{X_{i,j}}{S} \right) \quad j = 1,2 \quad \forall i = 1\dots p \tag{3}$$

Where μ is the maximal kinetic constant for entering in shelter j . R_j is equal to 1 as we have neglected the time outside the shelter thus individuals dynamic only depend to the probability to leave a shelter to reach directly another one.

The probability $Q_{i,j}$ for one individual belonging to one strain to leave a shelter is in relation to the number of individuals present under this shelter. Experimental tests showed that larvae prefer their own strain odour to that of other strains [19]. In this case, the influence of individuals belonging to the same strain can be more important than that of individuals belonging to other strains. Thus the basic model must be completed with parameters of inter-attraction between strains i and l : β_{il} .

We suppose that the interaction of strain i on strain l is the same that l on i and that each strain has the same interaction with others, therefore $\beta_{il} = \beta_{li} = \beta$.

The parameters of inter-attraction inside a strain already present in the single strain model are always considered equals to 1 ($\beta_{ii} = 1$). To express that an individual of one strain tends to stay more with an individual of the same strain than with individual of another strain, $0 \leq \beta \leq 1$. If $\beta = 0$, we have p independent strains with no inter-attraction between them. If $\beta = 1$, we have p strains that interact in the same way with others.

The experimental results show that the probability $Q_{i,j}$ of leaving shelter j decreases with the density of individuals $\frac{X_{i,j}}{S}$ under this shelter [16]:

$$Q_{i,j} = \frac{\theta}{1 + \rho \left(\frac{X_{i,j}}{S} + \sum_{\substack{l=1 \\ l \neq i}}^p \frac{\beta X_{l,j}}{S} \right)^n} \quad j = 1,2 \quad \forall i = 1 \dots p \tag{4}$$

where θ is the maximal probability of leaving the shelter j per unit of time, and ρ is a reference surface ratio for estimating the carrying capacities. From personal measures, we assume that $n \approx 2$ [16].

We can resume the evolution of the number of individuals of each strain under the two shelters after normalization ($x_i = X_i/N$) as follow:

$$\sum_{j=1}^2 x_{i,j} = 1 \quad \forall i = 1 \dots p$$

$$\frac{dx_{i,j}}{dt} = - \frac{\theta x_{i,j}}{1 + \rho \left(\frac{x_{i,j}}{\sigma} + \beta \sum_{\substack{l=1 \\ l \neq i}}^p \frac{x_{l,j}}{\sigma} \right)^2} \left(1 - \frac{\sum_{l=1}^p x_{l,h}}{\sigma} \right) + \frac{\theta x_{i,h}}{1 + \rho \left(\frac{x_{i,h}}{\sigma} + \beta \sum_{\substack{l=1 \\ l \neq i}}^p \frac{x_{l,h}}{\sigma} \right)^2} \left(1 - \frac{\sum_{l=1}^p x_{l,j}}{\sigma} \right) \tag{5}$$

where $\begin{cases} j = 1 & h = 2 \\ j = 2 & h = 1 \end{cases}$ with $\sigma = \frac{S}{N}$

Shelters can't hold more than the total number of individuals per strains (N). These conditions imply for p strains that $2S \geq pN$ or $\sigma \geq \frac{p}{2}$ (e.g. $p=1 \Rightarrow \sigma \geq 0.5$; $p=2 \Rightarrow \sigma \geq 1$).

2.2 Stochastic Formulation of the Model

A stochastic description of the model can be done by using master equations to take into account the fluctuations characterizing such systems and determine the probability distribution of individuals from each strain under shelters.

$X_{i,j}$ is the number of individuals of strain i under shelter j . The systems is characterized by $(N + 1)^p$ states Ω per strain $i (1 \dots p)$ and per shelter j :

$$\Omega(X_{i,j}) = X_{1,j}, \dots, X_{i,j}, \dots, X_{p,j}$$

Thus, we associate to each state $\Omega(n)$ a probability (P) to be in this state at time t : $P(\Omega(n), t) \quad \forall i = 1 \dots p$

We can define the transition probability between states W : $W(\Omega(n)|\Omega(n'))$.

The following dynamical equation counts the processes leading to the state $\Omega(n)$ and the processes removing it from this state:

$$\frac{dP(\Omega(n),t)}{dt} = \text{contribution of transition } \Omega(n') \rightarrow \Omega(n) \quad n \neq n' \\ - \text{contribution of transition } \Omega(n) \rightarrow \Omega(n') \quad (6)$$

$$\frac{dP(\Omega(n),t)}{dt} = \sum_{\substack{n' \\ n' \neq n}} (P(\Omega(n'),t)W(\Omega(n')|\Omega(n))) - \sum_{\substack{n' \\ n' \neq n}} (P(\Omega(n),t)W(\Omega(n)|\Omega(n'))) \quad (7)$$

$$\text{with } P(\Omega(n),t=0) = P_0(\Omega(n))$$

In term of probability, the incoming individuals on site j per unit of time of state $\Omega(n)$ come from transitions of all states $\Omega(n')$ where the probability of occupation at time t is $P(\Omega(n'),t)$ to state $\Omega(n)$ with a transition probability $W(\Omega(n')|\Omega(n))$. Else the outgoing of individuals from site j per unit of time of state $\Omega(n)$ is proportional to its probability of occupation at time t $P(\Omega(n),t)$ with a transition probability $W(\Omega(n)|\Omega(n'))$.

At each time step, $X_{i,j}$ can either unchanged or vary by only 1 or -1 , corresponding to the individual movements between the shelters:

$$\Omega(X_{i,j} - 1) = X_{1,j}, \dots, X_{i,j} - 1, \dots, X_{p,j}$$

$$\Omega(X_{i,j} + 1) = X_{1,j}, \dots, X_{i,j} + 1, \dots, X_{p,j}$$

For two sites, assuming $X_{i,2} = N - X_{i,1}$ we can define the contributions of transition for state $\Omega(X_{i,1})$ per unit time under shelter 1. For example $W_i(\Omega(X_{i,1} - 1)|\Omega(X_{i,1}))$ is the transition probability per unit time of going from state $\Omega(X_{i,1} - 1)$ to state $\Omega(X_{i,1})$. It corresponds to the movement of an individual of strain i between the shelter 2 and the shelter 1. $P(\Omega(X_{i,1} - 1), t)$ is the probability of being at state $\Omega(X_{i,1} - 1)$ at time t .

$$W_i(\Omega(X_{i,1} - 1)|\Omega(X_{i,1})) = \frac{\theta(X_{i,2} + 1)}{1 + \rho \left(\frac{(X_{i,2} + 1)}{S} + \beta \sum_{\substack{l=1 \\ l \neq i}}^p \frac{X_{i,2}}{S} \right)^2} \left(1 - \frac{\left(\sum_{i=1}^p X_{i,1} \right) - 1}{S} \right) \quad (8)$$

To obtain the contribution of transition to the state $\Omega(X_{i,1})$, we sum over all states that can lead to this state in a single step, corresponding to the movement of individuals of the p strains. Similarly the contribution from the state $\Omega(X_{i,1})$ per unit time is the product of the probability of being in state $\Omega(X_{i,1})$ at time t , times the sum of the transition probabilities per unit time from $\Omega(X_{i,1})$ to all other states accessible from $\Omega(X_{i,1})$.

Thus the stochastic evolution per unit of time of the number of individuals of strain i under the shelter 1 is given by the equation (9):

$$\frac{dP(\Omega(X_{i,1}),t)}{dt} = \sum_{i=1}^p (W_i(\Omega(X_{i,1}-1)|\Omega(X_{i,2}))P(\Omega(X_{i,1}-1),t) + W_i(\Omega(X_{i,1}+1)|\Omega(X_{i,1}))P(\Omega(X_{i,1}+1),t)) - \sum_{i=1}^p (W_i(\Omega(X_{i,1})|\Omega(X_{i,2}-1))P(\Omega(X_{i,1}),t) + W_i(\Omega(X_{i,1})|\Omega(X_{i,1}+1))P(\Omega(X_{i,1}),t)) \tag{9}$$

3 Results

3.1 Meanfield Model

From the general model (Eq. 5), for two strains ($i=2$) we can resume the evolution of the number of individuals of these strains under the two shelters as follow:

$$\frac{dx_{i,j}}{dt} = - \frac{\theta x_{i,j}}{1 + \rho(\frac{x_{i,j}}{\sigma} + \beta \frac{x_{l,j}}{\sigma})^2} (1 - \frac{x_{i,h} + x_{l,h}}{\sigma}) + \frac{\theta x_{i,h}}{1 + \rho(\frac{x_{i,h}}{\sigma} + \beta \frac{x_{l,h}}{\sigma})^2} (1 - \frac{x_{i,j} + x_{l,j}}{\sigma}) \tag{10}$$

where $\begin{cases} i = 1 & l = 2 \\ i = 2 & l = 1 \end{cases}$ et $\begin{cases} j = 1 & h = 2 \\ j = 2 & h = 1 \end{cases}$

With two strains and two identical shelters, the model has nine stationary solutions that correspond to different distributions of individuals under shelters. We resume below these analytical solutions and their analytical stability.

(a) The symmetrical state

These first solutions correspond to the dispersal of individuals between shelters (dispersal) with an equal number of individuals on each strain on both shelters:

$$x_{1,1}=x_{1,2}=x_{2,1}=x_{2,2}=0.5.$$

The symmetrical state exists for all values of σ and β and whatever the value of the parameter ρ . This state is stable when no other states exist (Fig. 1a & 2); see below for the conditions of existence of the aggregative and the segregative states.

Thus for small values of σ ($S \approx N$) and $\beta > 0.3$, and for huge values of σ , the shelters collect half the number of individuals of each strain (equipartition).

(b) The two aggregative states

Another group of two solutions is asymmetrical (heterogeneous), with an unequal number of individuals whatever the strain under each shelter: one shelter is selected, the two strains aggregate under the same shelter:

$$x_{1,1}=x_{2,1}; x_{1,2}=x_{2,2}.$$

These two aggregative states are always stable when they exist (Fig. 1a & 2).

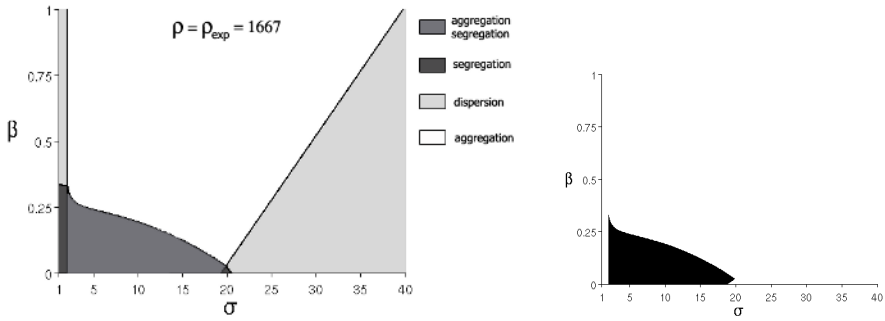


Fig. 1. Existence and stability of the different states for two strains and two shelters in relation to (σ, β) . Assuming equation (5), $\sigma \geq 1$ and $\rho = \rho_{exp} = 1667$. a- the homogeneous state, the aggregative and segregative states. b- the four mixed states (always unstable).

(c) The two segregative states

One group of solutions, are symmetrical (but heterogeneous), with an equal number of individuals whatever the strain under each shelter. This means that one shelter was selected by one strain, the other shelter by the other strain. The two strains segregate:

$$x_{1,1} = x_{2,2}; x_{1,2} = x_{2,1}.$$

The existence of the two segregative states depends on the level of interaction between strains and on the carrying capacity of shelters (Fig. 1a & 2). The following inequality gives the domain of existence of those states:

For low values of σ and β , these states are stable but when β increases and when these states exist, they become unstable.

(d) The four mixed states

This group of 4 solutions correspond to an unequal number of individuals of each strain under each shelters: $x_{1,1} \neq x_{2,2} \neq x_{1,2} \neq x_{2,1}$.

The four mixed states exist if the aggregative and the segregative states exist in the same time and are always unstable (Fig. 1b).

The segregative solutions are always stable when they exist in the same range of values that the symmetrical state only i.e. for small values of σ ($\sigma < 2$, Fig. 1), and in a range of huge value of σ ($\sigma \approx 20$ for $\rho = 1667$) and small values of β (Fig. 1a & 2). Despite the aggregative states, even if σ is small, the segregative states exist while the coefficient of inter-attraction between strains is small ($\beta < 0.3$) but their stability is limited with the existence of the four mixed states that is always unstable (Fig. 1b & 2, $\sigma = 5$). The segregative states disappear when $\sigma > 21$ for $\rho = 1667$. The aggregative states exist from $\sigma = 2$ but disappear in relation to the inter-attraction and the carrying capacity of shelters due to the non limited space of shelters (Fig. 1a). For $S \gg N$, the symmetrical state become the stable state.

3.2 Stochastic Study

The numerical resolution of master equations aims to follow the time evolution of the distribution of individuals under shelters and gives the probability of each states

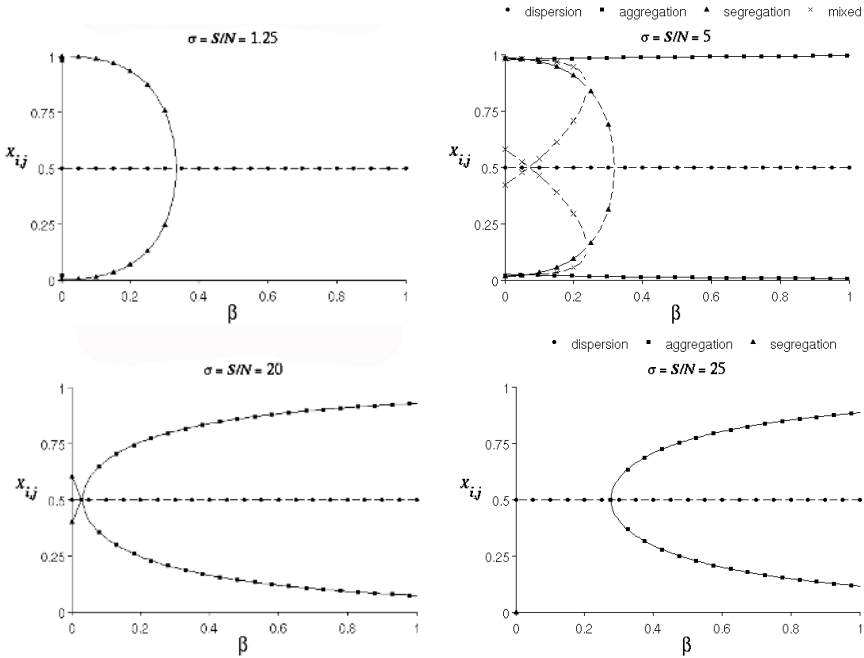


Fig. 2. Bifurcation diagrams as a function of β for four values of σ and $\rho = 1667$. Dashed lines represent unstable branches and solid lines, stable branches. (●) represent the symmetrical state (dispersion), (▲), the segregative states, (■), the aggregative ones and (×), the four mixed states.

$\Omega(X_{i,j})$ at the stationary regime. The time to reach the stationary regime increases in relation to N .

For small values of σ ($\sigma < 2$) and β lower than 0.3 (Fig. 3a & 3b), the segregative states are selected; for β greater than 0.3, only the symmetrical state exist and is selected (Fig. 3c). So for a fixed carrying capacity, the greater is N , the more the segregation is selected if the strains few interact.

For medium values of σ and small values of β we have coexistence of the aggregative states and the segregative ones (Fig. 3a & 3b) but for very small values of β the segregative states is more often selected and for upper values of β the aggregative states is more selected than the other ones (Fig. 3 & Fig. 4).

In a range of values of σ between 2 and 19, the aggregative states and/or the symmetrical state are selected in relation to β (Fig. 3). The greater is σ in this range and/or β the smaller is the probability to select the segregative states instead of the aggregative ones (Fig. 3).

However for huge values of σ ($\sigma > 20$), in a first hand the segregative states disappear and in a second hand the aggregative ones in relation to β . For $\sigma \geq 40$, the symmetrical state is the only existing state as predicted in the meanfield model (Fig. 3 and see Fig. 1a).

This stochastic model shows similar results with experiments [15]. In those experiments, we can assume that $S=25$ and by approximation with the results of the model that $\beta \approx 0.15$. For two strains, with populations of 5 ($\sigma=5$) and 10 ($\sigma=2.5$) individuals and for this small value of β , the segregation decreases face to the aggregation in relation to the increase of σ (Fig. 3b).

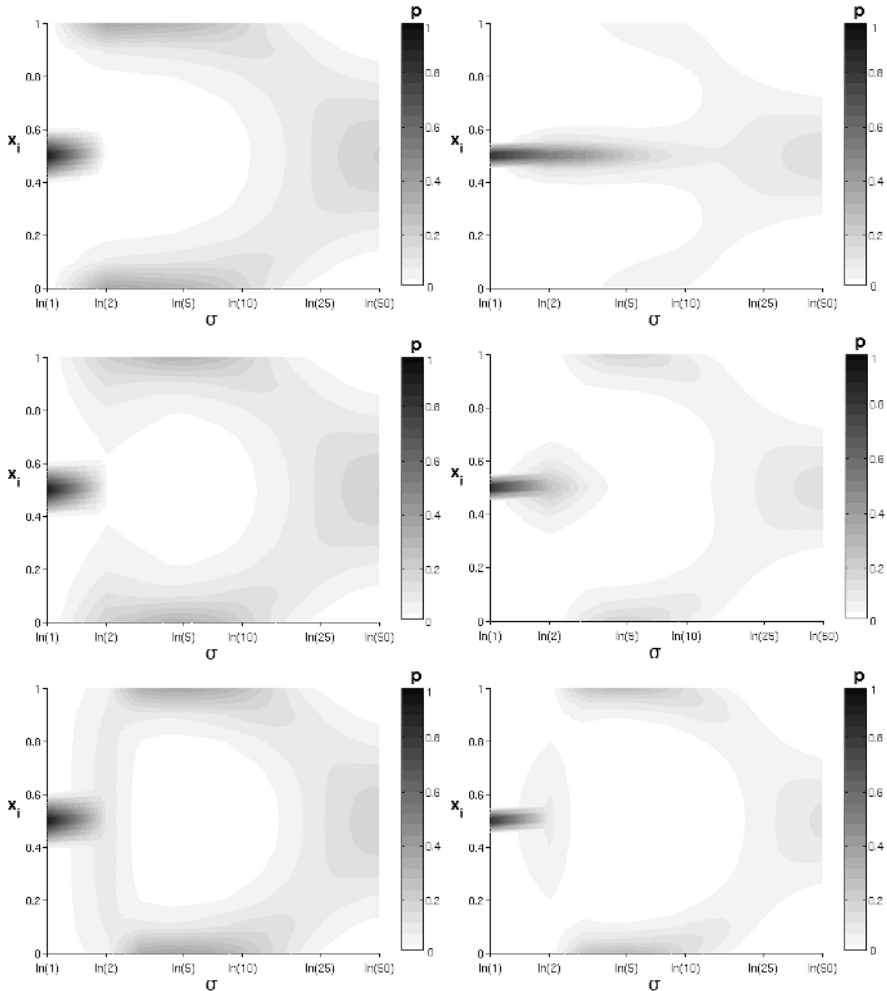


Fig. 3. Stochastic resolution of the two-strain model for $\rho = 1667$. The figures give the probabilities to be in state $\Omega(X_i)$ associated to the proportions of individual in relation to σ (logarithmic scale on this figure). In the left column, x_i is the proportion of individuals under one shelter for one of the two strain; in the right column, x_i is the proportion of individuals under one shelter for both strains. a- probabilities for $\beta=0.05$; b- probabilities for $\beta=0.15$; c- probabilities for $\beta=0.35$.

4 Discussion

Results show that solutions are not qualitatively different from the model without crowding effect [16][17]: collective patterns that emerge at the collective level without and with the crowding effect are identical. Whereas the crowding effect which is represented by the carrying capacity of shelters (S) limits the range of existence and of stability of the aggregative and segregative states for huge values of S . At the stationary regime, only 3 parameters characterize the model: $\sigma (S/N)$, β (inter-attraction parameter) and ρ (reference surface ratio) that are linked to group properties but not to the individual behaviour. β is the parameter of interaction between strains (or between species of cockroaches). When $\beta > 0.3$, there is no difference between a two-strains group or a one-strain group. For $\beta < 0.3$ and small value of σ , the segregative states are stable. For larger values of σ , both aggregative and segregative states are stable, but the greater is the values of σ , the lower is the probability of observing the segregative states.

Modulating the inter-attraction β , the total number of individuals (N) and the carrying capacity of the shelter (S), a diversity of solutions is generated (emergence of segregation, co-existence of segregation and aggregation, ...) without any modulation of the individual behaviour and individual knowledge of the global system: the greater the number of individuals under a shelter is, the lower the probability of leaving this shelter. However, the crowding effect (environmental constraint) plays a role on the probability of joining a shelter by limiting to a critical value the number of individuals accepted under a shelter.

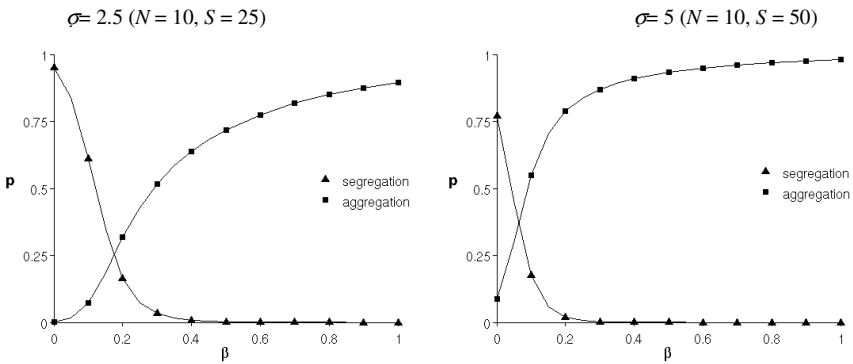


Fig. 4. Probability to reach the aggregative states or the segregative states at the stationary regime with 80% of individuals of each strains under shelters for $N = 10$ and $S = 25$ ($\sigma = 2.5$) and 50 ($\sigma = 5$). (\blacktriangle) represents the segregative states and (\blacksquare), the aggregative ones.

This study shows that this kind model based on minimal rules of inter-attraction between individuals can explain the distribution of groups in a population (clustering and gregariousness between animal species or strains). By taking account positive feedbacks due to individual behaviours and negative feedbacks due to environmental constraints, collective choices can lead to the segregation or the aggregation of groups of animals [2][17][18]. This should describe a relevant and generic process for

understanding the dynamics of aggregation and segregation between sub-groups or species without the need of sophisticated behaviours modulated by the density [15][17]. Self-organised mechanisms govern many cases of aggregation and collective choice. Behavioural positive feedbacks, based on different type of signals (pheromone, silk, mechanical...), are the keystones of the dynamics of aggregation [20-24]. Our hypothesis is that for all these cases, the coupling between crowding and these positive feedbacks leads to a diversity of patterns similar to those of the cockroaches.

References

1. Parrish, J.K. & Edelstein-Keshet, L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284**, 99-101.
2. Camazine, S., Deneubourg, J.L., Franks, N., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2001. *Self-Organization in Biological Systems*. Princeton Univ. Press, Princeton.
3. Parrish, J.K., Viscido, S.V. & Grünbaum, D. 2002. Self-organized fish schools: An examination of emergent properties. *Biol. Bull.* **202**, 296-305.
4. Okubo, A. 1980. *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, Berlin.
5. Southwood, T.R.E. 1966. *Ecological Methods*. London, Methuen.
6. Parrish, J.K., Hamner, W.M. & Prewitt, C.T. 1997. Introduction - from individuals to aggregations: unifying properties, global framework, and the holy grails of congregation. *In: Animal Groups in three Dimensions* (Parrish, J. K. & Hamner, W. M., eds). Cambridge Univ. Press, Cambridge, pp. 1-14.
7. Bell, W.J., Parsons, C. & Martinko, E.A. 1972. Cockroach aggregation pheromones: analysis of aggregation tendency and species specificity (Orthoptera: Blattidae). *J. Kans. Entomol. Soc.* **45**, 414-421.
8. Rivault, C. 1990. Distribution dynamics of *Blattella germanica* in a closed urban environment. *Entomol. Exp. Appl.* **57**, 85-91.
9. Appel, A.G. 1995. *Blattella* and related species. *In: Understanding and Controlling the German Cockroach* (Rust, M.K., Owens, J.M. & Reiersen, D.A., eds). Oxford Univ. Press, Oxford, pp. 1-20.
10. Ishii, S. & Kuwahara, Y. 1968. Aggregation of German cockroach *Blattella germanica* nymphs. *Experientia* **24**, 88-89.
11. MacFarlane, J.E. & Alli, I. 1987. The effect of lactic acid and volatile fatty acids of the aggregation behaviour of *Periplaneta americana*. *Comp. Biochem. Physiol.* **86**, 45-47.
12. Ledoux, A. 1945. Etude expérimentale du grégarisme et de l'inter-attraction sociale chez les Blattidés. *Annales des Sciences Naturelles Zoologie et Biologie Animale* **7**, 76-103.
13. Brossut, R. 1979. Gregarism in cockroaches and in *Eublaberus* in particular. *In: Chemical Ecology: Odour Communication in Animals* (Ritter, F.J., ed.). Elsevier, Amsterdam, pp. 237-246.
14. Ishii, S. & Kuwahara, Y. 1967. An aggregation pheromone of the German cockroach *Blattella germanica* (Orthoptera: Blattellidae). 1. Site of the pheromone production. *Appl. Entomol. Zool.* **2**, 203-217.
15. Leoncini, I. & Rivault, C. 2005. Could species segregation be a consequence of aggregation processes? Example of *Periplaneta americana* (L.) and *P. fuliginosa* (Serville). *Ethology* **11**(5), 527.

16. Amé, J.M., Rivault, C. & Deneubourg, J.L. 2004. Cockroach aggregation based on strain odour recognition. *Anim. Behav.* **68**, 793-801.
17. Millor, J., Amé, J.M., Halloy, J. & Deneubourg, J.L. 2006. Individual discrimination capability and collective decision-making. *J. Theor. Biol.* **239**, 313-323.
18. Amé, J.M., Halloy, J., Rivault, C., Detrain, C., Deneubourg, J.L. Collegial decision making based on social amplification leads to optimal group formation. *PNAS* **103** (15), 5835-5840.
19. Rivault, C. & Cloarec, A. 1998. Cockroach aggregation: discrimination between strain odours in *Blattella germanica*. *Anim. Behav.* **55**, 177-184.
20. Saffre, S., Furey, R., Krafft, B. & Deneubourg, J.L. 1999. Collective decision-making in social spiders: dragline-mediated amplification process acts as a recruitment mechanism. *J. Theor. Biol.* **198**, 507-517.
21. Detrain, C. & Deneubourg, J.L. 2002. Complexity of environment and parsimony of decision rules in insect societies. *Biol. Bull.* **202**, 268-274.
22. Depickère, S., Fresneau, D. & Deneubourg, J.L. 2004. A Basis for Spatial and Social Patterns in Ant Species: Dynamics and Mechanisms of Aggregation. *J. Insect Behav.* **17**, 81-97.
23. Jeanson, R., Deneubourg, J.L. & Theraulaz, G. 2004. Discrete dragline attachment induces aggregation in spiderlings of a solitary species. *Anim. Behav.* **67**, 531-537.
24. Sumpter, D.J.T. & Pratt, S.C. 2003. A modelling framework for understanding social insect foraging. *Behav. Ecol. Sociobiol.* **30**, 109-123.