

Individual discrimination capability and collective decision-making

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Abstract

Amplification is the main component of many collective phenomena in social and gregarious insects. In a society, individuals face a mixed palette of odours coming from different groups (lines, strains) and individuals present discrimination capabilities. However, often at the collective level, different groups may cooperate and act together. To understand this apparent contradiction, we use a model of food recruitment where each group of foragers have its own blend of pheromone trail that is partly recognized by the others groups. The model shows that a low level of recognition between signals is sufficient to produce a collaborative pattern between groups and that beyond a critical value of recognition, only the aggregation of all the groups around the same food source is observed. The comparison between this model and one describing the site selection by gregarious insects (e.g. cockroach) suggests that such collective response is a generic property of social phenomena governed by amplification processes.

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1. Introduction

It is well established that many social insects are able to discriminate between nestmates and non-nestmates (Vander Meer and Morel, 1998; Lenoir et al., 1999; Zanetti et al., 2001; Breed et al., 2004), but kin discrimination inside a colony is largely controversial. In honeybees the queen can mate with up to 20 drones that give rise to a colony with 20 patriline or sub-families (Estoup et al., 1994). Each sub-family has a hydrocarbon profile used by workers as sub-family discrimination (Page et al., 1991; Arnold et al., 1996). In laboratory conditions workers can discriminate between supersisters (same patriline) and half-sisters (other patriline) (Getz and Page, 1991; Moritz and Heisler, 1992). Despite individual discrimination capabilities, when the collective behaviour takes place, it seems that individuals behave independently of their sub-family

origin. In swarming honeybees, Kryger and Moritz (1997) did not find differences between the sub-families composition of the primary and the after-swarm. Kirchner and Arnold (2001) did not find evidences for sub-family discrimination between bee dancers and followers in a colony of two sub-families neither in a colony of 17 sub-families. In *Leptothorax* ants, workers prefer to follow their own trail but collective trails still emerge (Aron et al., 1988). The gregarious behaviour of the cockroaches (e.g. *Blattella germanica* L.) is mainly based on the cuticular hydrocarbons recognition characterizing the strain odour. The individuals prefer their own strain odour from those of another strain (Rivault et al., 1998). However, groups of two different strains of *Blattella germanica* L. (with different odours) settle together in the same shelter (Amé et al., 2004).

All these examples involve amplification mechanisms that are widespread in social insects and gregarious arthropods. Amplification governs behaviours like: aggregation-sorting (Deneubourg et al., 1990; Deneubourg et al., 1991; Couzin and Franks, 2003; Depickère

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et al., 2004; Leoncini and Rivault, 2005), defence (Millor et al., 1999), exploration (Detrain et al., 1991; Fourcassié and Deneubourg, 1994), food recruitment (Pasteels et al., 1987; Seeley et al., 1991; Detrain et al., 1999) or nest moving (Vissher and Camazine, 1999).

Our hypothesis is that amplification processes, despite a low level of recognition between groups can lead to aggregation. To test this hypothesis we will use a model of food recruitment as a case study. Recruitment is often seen as the “archetype” of amplification mechanism leading to collective decision. In our model, each group have its own blend of pheromone and the probability for an individual to choose a trail laid down by members of its group is greater than the probability to choose the trail of another group. The comparison between this model and one describing the site selection by a multi-strains population of gregarious individuals (Amé et al., 2004) will show that such collective response is a generic property of social phenomena governed by amplification processes.

2. Model of recruitment by chemical trail

The model, based upon empirical findings about the behaviour of the individual ants, describes the evolution of the concentration of trail pheromone and, as a consequence, the traffic of ants over each trail. It is an extension of a model that has already been applied to different types of choice experiments (Deneubourg and Goss, 1989; Beckers et al., 1992, 1993; Nicolis and Deneubourg, 1999; for a review see e.g. Detrain et al., 1999; Sumpter and Beekman, 2003; Sumpter and Pratt, 2003). In a mass recruitment, when the ant finds a food source it lays a trail pheromone that leads the other ants to this food source. When ants are faced with a multiple choice (in the laboratory, represented by a bridge with s

branches, Fig. 1) they are faced with two decisions: the decision to leave the nest and those to choose one of the trails leading to one of the identical food sources equidistant from the nest (s food sources). The probability to choose one of the branches depends on the pheromone concentration on this branch.

The ant departure from the nest to the food source is based on the probability ϕ (s^{-1}) to leave the nest per time unit (the flow of departure). In this model, we neglect the time variation of ϕ . This approximation does not affect the dynamics of the collective choice (Camazine et al., 2001). An ant leaves the nest, chooses a path, reaches a food source, ingests food and promptly returns to the nest laying a trail pheromone. We can quantify the ant decision at a choice point by equation (1) that depends on the values of the pheromone concentration c_i on each trail i (Deneubourg and Goss, 1989):

$$P_i = \frac{(k + c_i)^n}{\sum_{l=1}^s (k + c_l)^n}, \quad i = 1, \dots, s, \quad (1)$$

- n determines the level of nonlinearity in the response. A high value of n means that if one branch has only a very slightly higher amount of pheromone than the others, the next ant that arrives at the branch fork will have a very high probability of choosing it.
- k corresponds to the intrinsic degree of attraction of an unmarked branch. The greater the k , the greater the marking necessary for the choice to become significantly non-random.

On its return journey from a food source, each ant lays a quantity of pheromone q . Since in this case the time needed to visit the food sources and return is equal for both sources, we neglect the time delay between the choice and the ant's return. The evaporation rate of the

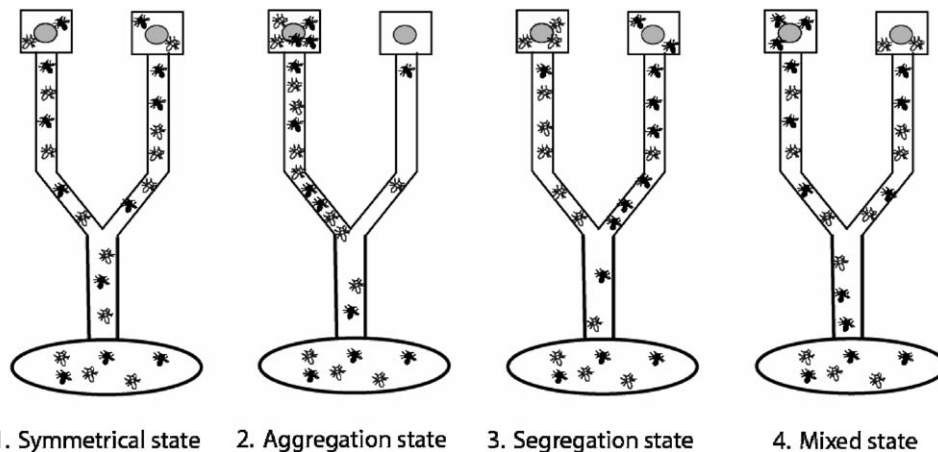


Fig. 1. Schema representing the different stationary states of the model. Individuals from the two strains can choose between the two branches of the bridge leading to two identical food sources equidistant from the nests (see text).

trail pheromone will be proportional to the pheromone concentration and to a constant v . This constant is the inverse of the mean lifetime of the trail pheromone. Thus, pheromone concentration is directly proportional to the flux of individuals (ϕ) in the system. At each unit of time a quantity $q\phi P_i$ of pheromone is added to the trail i and vc_i is the rate of evaporation of this trail pheromone. Here we give a dimensionless form of the equation in relation to v and k by replacing c_i and ϕ , respectively, by $C_i = c_i/k$, $\Phi = q\phi/(kv)$ and $\tau = vt$. These relationships can be expressed in the following system of s differential equations which describe the rate of change in concentration of pheromone on trails 1 to s .

$$\frac{dC_i}{d\tau} = \Phi P_i - C_i, \quad i = 1, \dots, s. \tag{2}$$

Here we consider g groups of foragers. Each group has its own blend of pheromone (e.g. a mix of trail pheromone and footprint hydrocarbons) that may influence the decision of the individuals of the other groups. Ants choose a trail in relation to the relative concentration on all trails. The probability to choose a trail increases with the concentration of the pheromone on this branch deposited by the individuals of the different groups. The trail pheromone of one group can be partially recognized by the other groups. The influence between individuals belonging to the same group is more important than that between individuals from different groups. To take this into account, we will include to Eq. (1) a parameter β_{jl} of inter-attraction between groups l and j .

$$P_{il} = \frac{(1 + \sum_{j=1}^g \beta_{jl} c_{ij})^n}{\sum_{k=1}^s (1 + \sum_{j=1}^g \beta_{jl} c_{kj})^n}, \quad l = 1, \dots, g \text{ and } i = 1, \dots, s, \tag{3}$$

where P_{il} is the probability for an individual of the group l to choose the trail i .

These probabilities increase with the concentration of the pheromone on each branch deposited by the individuals of the different groups adjusted by the parameter $0 \leq \beta_{jl} \leq 1$ that measures the level of recognition between both strains odour (j and l). $\beta_{il} = 0$ corresponds to two independent groups and $\beta_{jl} = 1$ to an identical signal for the group j and l ($\beta_{jl} = 1$). We will suppose that the inter-attraction of group j on group l is the same that l on j and from then $\beta_{jl} = \beta_{lj}$ and all the parameters q , n , and v are identical for the different groups-pheromones.

Eq. (4) describes the rate of change in concentration of pheromone on trail i for the group l

$$\frac{dC_{il}}{d\tau} = \Phi P_{il} - C_{il}. \tag{4}$$

The flow of ants for the group l choosing the trail i is ΦP_{il}

For two groups and two food sources, the rates of change in concentration of pheromone are given by the following expressions:

$$\begin{aligned} \frac{dC_{11}}{d\tau} &= \Phi \frac{(1 + C_{11} + \beta C_{12})^2}{(1 + C_{11} + \beta C_{12})^2 + (1 + C_{21} + \beta C_{22})^2} - C_{11}, \\ \frac{dC_{21}}{d\tau} &= \Phi \frac{(1 + C_{21} + \beta C_{22})^2}{(1 + C_{21} + \beta C_{22})^2 + (1 + C_{11} + \beta C_{12})^2} - C_{21}, \\ \frac{dC_{12}}{d\tau} &= \Phi \frac{(1 + C_{12} + \beta C_{11})^2}{(1 + C_{12} + \beta C_{11})^2 + (1 + C_{22} + \beta C_{21})^2} - C_{12}, \\ \frac{dC_{22}}{d\tau} &= \Phi \frac{(1 + C_{22} + \beta C_{21})^2}{(1 + C_{22} + \beta C_{21})^2 + (1 + C_{12} + \beta C_{11})^2} - C_{22}, \end{aligned} \tag{5}$$

where C_{11} and C_{21} are the pheromone concentrations on the branch 1 and 2 for the group 1, and C_{12} and C_{22} the pheromone concentrations on the branch 1 and 2 for the group 2.

3. Results

At the stationary states, the flow of individuals of group l choosing the path i , is proportional to C_{il} . System (5) has four types of stationary states corresponding to different distributions of the individuals around the food sources (summarized in Figs. 1 and 2). The details of the algebra are given in Appendix A.

(1) *The symmetrical state*: The pheromone concentrations are equal on both paths and for both groups: $C_{il} = \Phi/2$ and the flows of both groups are equal on each trail. This symmetrical states exist for all the values of Φ and β . The stability analyse shows that this solution is only stable for low flux values:

$$\Phi < \frac{2}{(1 + \beta)} \tag{6}$$

As $0 \leq \beta \leq 1$, this implies that for $\Phi > 2$, $C_{il} = \Phi/2$ is always unstable.

(2) *The two aggregative states*: The activity of the two groups is focused on the same food source meaning both groups have selected the same branch. The pheromone concentrations are equal for both groups on both branches. However, the selected branch presents a higher concentration than the non-selected one. In this case, the flows of both groups along one trail are equal. The selected branch is chosen randomly (i.e. with a probability of 0.5). This is summarized by the formula $C_{11} = C_{12} < C_{21} = C_{22}$ or $C_{11} = C_{12} > C_{21} = C_{22}$. These solutions are:

$$\begin{aligned} C_{11} = C_{12} &= \frac{\Phi}{2} \pm \frac{\sqrt{\Phi^2 - (4/(\beta + 1))^2}}{2}, \\ C_{21} = C_{22} &= \Phi - C_{11}. \end{aligned} \tag{7}$$

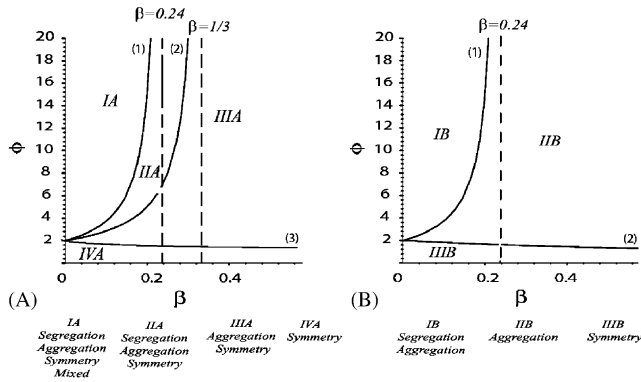


Fig. 2. The stationary states in relation to the level of trail recognition between groups (β) and the flux of individuals (Φ). Areas of the condition of existence (A) and the condition of stability (B) of the stationary states. The first curve (1) in (A), corresponds to the condition of existence of the mixed states: $\Phi > 2(1 + \beta)/(1 - \beta^2 - 4\beta)$ (asymptote value $\beta = 0.24$, dashed line), the second curve (2) to the condition of existence of the segregative states: $\Phi > 2/(1 - 3\beta)$ (asymptote value $\beta = 1/3$, dashed line) and the third one (3) to the condition of existence of the aggregative states $\Phi < 2/(1 + \beta)$. In (B), the first curve (1) represents the condition of stability of the segregative states: $\Phi > 2(1 + \beta)/(1 - \beta^2 - 4\beta)$ (asymptote value $\beta = 0.24$, dashed line) and the second curve (2) the condition of stability of the symmetrical states (identical to the condition of existence): $\Phi < 2/(1 + \beta)$ (see text). Dashed lines represent the asymptotes of the conditions of solutions existence and stability.

These stationary states exist if $\Phi > 2/(\beta + 1)$ and under this condition are always stable for any value of Φ and β .

(3) *The two segregative states:* The majority of the individuals of one strain focus their activity on one branch and the individuals of the second strain on the other one. In this case, the segregative steady states are $C_{11} = C_{22} \neq C_{21} = C_{12}$ and the pheromone concentrations are giving by

$$C_{11} = C_{22} = \frac{\Phi}{2} \pm \frac{\sqrt{\Phi^2 - 4(\Phi\beta + 1)^2/(\beta - 1)^2}}{2},$$

$$C_{21} = C_{12} = \Phi - C_{11}. \tag{8}$$

The segregative states exist if $\Phi > 2/(1 - 3\beta)$ and never appear for $\beta > 1/3$. They are stable under the condition (see Appendix A):

$$\Phi > \frac{2(1 + \beta)}{(1 - \beta^2 - 4\beta)} \tag{9}$$

Inequality (9) shows that the stability of the segregative states depends on the level of recognition between the trails of the groups (β) but also on the flux of individuals (see Fig. 2B). The lower the flux, the lower must be β to observe a stable “split” or segregation between both groups. Moreover, for $\beta > \sqrt{5} - 2 \approx 0.236$, the segregative states are always unstable.

(4) *The four mixed states:* In this case $C_{11} \neq C_{22} \neq C_{21} \neq C_{12}$: the pheromone concentrations and the traffic are different on both trails and for both

groups. The four combinations of solutions are (see Appendix A):

$$C_{11} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2}, \tag{10a}$$

$$C_{11} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2}, \tag{10b}$$

$$C_{11} = \frac{\Phi}{2} + \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{-M^{0.5} - (M - 4\Omega)^{0.5}}{2}, \tag{10c}$$

$$C_{11} = \frac{\Phi}{2} + \frac{-M^{0.2} - (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{-M^{0.2} + (M - 4\Omega)^{0.5}}{2}, \tag{10d}$$

with

$$M = \frac{(\beta - 1)^2 \Phi \beta (1 + (\Phi/2) + (\beta\Phi/2))}{(\beta^2 - 1)} - \left(1 + \frac{\Phi}{2} + \frac{\Phi\beta}{2}\right) \left(1 - \frac{\Phi}{2} + \frac{3\Phi\beta}{2}\right),$$

$$\Omega = 1 + \frac{\Phi}{2} + \frac{\beta\Phi}{2}.$$

$$\Phi > \frac{2(1 + \beta)}{(1 - \beta^2 - 4\beta)}$$

and

$$\beta < \sqrt{5} - 2. \tag{11}$$

Eq. (11) is the same as Eq. (9). Indeed when the mixed states disappear, the segregative states become unstable (see Appendix A and Fig. 3).

The bifurcation diagrams show the value of the stationary states (the trail concentration for one group on one of the two branches) and their stability in relation to the individual flux Φ for a recognition parameter of $\beta = 0.22$ (Fig. 3A) and in relation to the recognition parameter β for a flux of $\Phi = 10$ (Fig. 3B). For $\Phi > 2$ the solution $C_{11} = C_{12} \geq C_{21} = C_{22}$ (aggregative states) exists and is always stable (Fig. 3A). The segregative states ($C_{11} = C_{22} \neq C_{21} = C_{12}$) become stable only for large value of $\Phi (> 34)$ when $\beta = 0.22$. For $\Phi = 10$ (Fig. 3B) the aggregative states are always stable and the segregative states are stable for small value of $\beta (\beta < 0.185)$. When $\beta > 0.185$, the mixed states disappear.

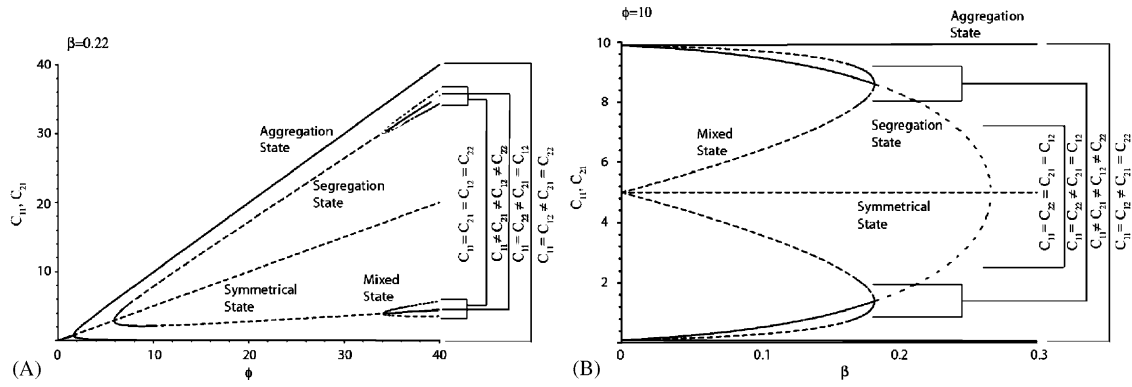


Fig. 3. Concentrations values of the trail odour for strain 1 on branches 1 and 2 in relation to Φ for $\beta = 0.22$ (A) and in relation to β for $\Phi = 10$ (B). ----- unstable states; — stable states.

The phase space diagram illustrates the dynamics of the system. Fig. 4 represents this phase space diagrams putting the values of the trail odour concentration on one branch for one group (C_{11}) as a function of the trail odour concentration on the same branch for the other group (C_{12}).

For low flux values of $\Phi = 1$ and low recognition $\beta = 0.1$ (Fig. 4A) only the symmetrical state exists. When Φ is large and β small ($\beta = 0.1$) all the states appear (Fig. 4B). The unstable mixed states surround the segregative one. The system will tend, depending of the initial conditions, to the aggregative or the segregative states that are stable for these parameters values. Fig 4B shows that the basin of attraction of the segregative states is small compared to those of the aggregative states. So despite the fact that both solutions are stable, the system is characterized by a higher probability to adopt one of the aggregative states. For $\Phi = 10$ and $\beta = 0.25$ (Fig. 4C) the mixed states disappear and the system tends to the stable aggregative states. For $\beta > 0.33$ (Fig. 4D) just the symmetrical and aggregative states remain and the individuals from the two groups “aggregate” using the same path and visiting the same food source.

4. Discussion

With one unique strain, a pitchfork bifurcation appears in the exploitation pattern of the food sources leading to the collective selection of only one path (Deneubourg and Goss, 1989). This selection is based on the reinforcement of the trail: the highest the concentration of the trail i in front of the concentration of the other trail, the highest the ants probability to choose this trail (P_i) and to reinforce it. In the present model the choice function P_{ij} (3) assumes that the chemical signal of one group increases the probability of the other group to choose the same path. On one hand, the pattern obtained by the recruitment amplification mechanism depends on the size of the groups (ϕ) and on the other

hand, on the level of discrimination between strain odours. For small population size, the individuals distribute themselves in a symmetrical way on the two food sources, i.e. both branches are concomitantly exploited by both groups. As soon as the flow exceeds a threshold, the pattern switches to the aggregative or segregative states depending on the β value that measures the level of strain odours recognition. For low values of β (< 0.24), groups can segregate on the food sources because the odour signal from the other strain plays only a little role on the amplification process in comparison with its own trail odour. For these small values of β , aggregative states are also stable. The initial conditions will determine whether the system chooses between segregative or aggregative solutions. However, the analysis of the model shows that the selection of the aggregative states is dominant due to the relative size of their attraction basins. As soon as β reached a critical value ($\beta > 0.24$), the two groups focus their activity on the same food source. To summarize, our results show that a high discrimination between groups (corresponding to a weak inter-attraction between them) permits to keep segregation states between the groups when the individuals rely solely on the amplification mechanisms presented here. Moreover, the model shows that different collective responses occur without the need of changing the individual behaviour or the communication system.

The analysis for more than two groups and/or more than two sources (not summarised in this paper) predicts similar collective response and mainly the systematic aggregation between groups with a weak inter-attraction between them.

Another example is given by the aggregative behaviour on cockroaches. Gregarious behaviour in the German cockroaches (*Blattella germanica*) is mediated by the recognition of cuticular hydrocarbons. The larvae prefer their own odour to that of other strains (Rivault et al., 1998). However, Amé et al. (2004) have shown that different strains are able to aggregate on the same site and segregation is infrequently observed. The

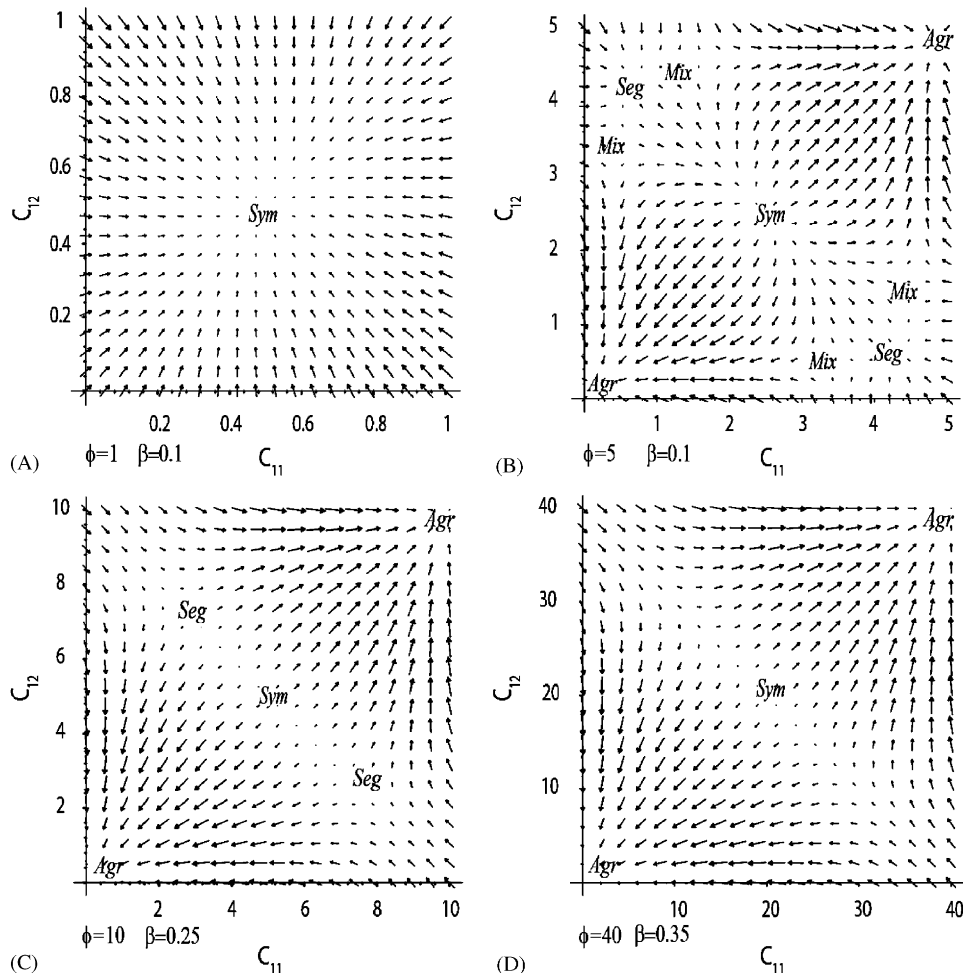


Fig. 4. Phase space representing the values of the trail odour concentration on one branch for one group (C_{11}) in relation to the trail odour concentration on the same branch for the other group (C_{12}) for different values of Φ and β . Agr: aggregative states; seg: segregative states, sym: symmetrical states, mix: mixed states.

amplification mechanisms regulating site selection are based on the modulation of the individual resting time on the site. The probability for one individual belonging to one strain (e.g. strain x) to leave (Q_x) is a decreasing function of the number of individuals present on the site (X_i): $Q_x \approx X_i^{-n}$. The influence of individuals belonging to the same strain is more important than that of individuals belonging to the other strain. In this case, the probability is completed with parameters of inter-attraction between strains x and y : $\beta(Q_i \approx (X_i + \beta Y_j)^{-n})$, being the number of individuals of strain y on the site i . 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, β is lower than 1. A good agreement between the experimental results and the stochastic version of the model (Monte-Carlo simulation) was obtained. The preliminary study of the differential equations version (Amé et al., 2004) confirmed by the detailed analysis of this model (see Appendix B) shows that both models have the same behaviour. This strongly suggests that any phenomenon

based on similar modulation of the amplification between groups or strains, shows the same collective behaviours described in this paper.

This could be the case for many gregarious arthropods species that form aggregates which persist due to attraction modulated by chemical and thigmotactic signals (Eickwort, 1981) or for insect societies that organize items or workers spatially (Camazine et al., 2001; Deneubourg et al., 1991; Franks and Sendova-Franks, 1992). Many other collective behaviours in social insects, like swarming, food recruitment or defence are processes where amplification mechanisms are involved (Visscher and Camazine, 1999; Seeley and Visscher, 2004; Camazine and Sneyd, 1991; Millor et al., 1999). Our results allow to understand why during these collective behaviours there is no evidence of kin-discrimination even if an individual is able to perform such discrimination (Heinze et al., 1997; Kryger and Moritz, 1997; Kirchner and Arnold, 2001).

The value of the recognition parameter β expresses the capability to respond to a signal of another

individual belonging to a different group. If $\beta = 0$, the individual is blind to this signal. We may formulate different hypothesis on the origin of this recognition factor. For social insects and many other arthropods, the communications are largely based on pheromones such as trail pheromones, cuticular hydrocarbons, ... Values of β may correspond to a certain overlapping between the chemical signatures of two groups. This chemical profile is under genetic control but is also determined by the environment and food consumption (Page and Robinson, 1991; O'Donnell, 1998; Arnold et al., 2000; Julian and Fewell, 2004; Wyatt, 2003). So, genetic proximity or sharing common resource may increase the similitude between two signals and contribute to large value of β . In recruitment, the amplification can be mediated by generic signals common to all individuals (e.g. the trail pheromone) and by specific signals such as the cuticular hydrocarbons (*Lasius* sp., Yamaoka and Akino, 1994). In these situations, the value of parameter β is mediated by the relative contribution of the generic and specific signals.

In this model we considered that β was a constant. However, the interactions between individuals may lead to a mixing of different chemical signatures and to the apparition of a blended signature that may favour the aggregation of different groups (ants: Lenoir et al., 2001; between bumblebees species: Dronnet et al., 2005; between cockroaches species: Everaerts et al., 1997). This corresponds, in the model, to the increase of β as a function of the interactions between the individuals. We hypothesize that coupling the dynamics of our model with the increase of β could systematically lead to the aggregation of the different groups, even if the system starts with small β .

One of the main hypotheses of the model is that the resources are abundant and no crowding reaches significant level (i.e. large shelters compared to the size of the population, no traffic congestion, Dussutour et al., 2004). We have shown that in such conditions, where competition is weak between individuals, the system adopts aggregative states. Preliminary analysis of a modified version of the model that includes crowding effects or limitation of the resource shows that the segregative states are favoured, but the aggregative states are still possible for a vast region in parameter space. A second important hypothesis of the model is that there is no agonistic behaviour between the individuals of the different groups. However, if such antagonistic behaviours are not too strong, preliminary results of the model show that similar results are still found. The main consequence is the increase of the β value for which segregative states disappear. Others behaviours, that may affect such collective dynamics, are not included in the model. Among them, there is a lack of modulation of the emission of the signals as a

function of the social or chemical environment (Devigne et al., 2004) or the odour familiarization of individuals reared in multiple groups (Errard and Hefetz, 1997; Lenoir et al., 2001).

To summarize, this model shows that collective choice can be shared by different groups without the need of specific signals or sophisticated behaviours. We focused the discussion on the chemical communications of insects. However, the basic elements of the model are not specific to these types of communications or species (e.g. vertebrates: Couzin and Krause, 2003; Hemelrijk, 2002; Parrish and Edelstein-Keshet, 1999). Similar models could be developed for different structures based on visual or sound communications and could explain some aspects of the formation of inter-specific groups of fishes, birds and mammals (Overholtzer and Motta, 2000; Stensland et al., 2003).

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Appendix A. Solutions and stability of the system

At the steady states, the concentrations C_{ii} remain constant and their rate is equal to zero. The algebraic equations (A.1) (for two groups and two food sources) correspond to the steady states of Eq. (5):

$$C_{11} = \Phi \frac{(1 + C_{11} + \beta C_{12})^2}{(1 + C_{11} + \beta C_{12})^2 + (1 + C_{21} + \beta C_{22})^2}, \quad (\text{A.1a})$$

$$C_{21} = \Phi \frac{(1 + C_{21} + \beta C_{22})^2}{(1 + C_{21} + \beta C_{22})^2 + (1 + C_{11} + \beta C_{12})^2}, \quad (\text{A.1b})$$

$$C_{12} = \Phi \frac{(1 + C_{12} + \beta C_{11})^2}{(1 + C_{12} + \beta C_{11})^2 + (1 + C_{22} + \beta C_{21})^2}, \quad (\text{A.1c})$$

$$C_{22} = \Phi \frac{(1 + C_{22} + \beta C_{21})^2}{(1 + C_{22} + \beta C_{21})^2 + (1 + C_{12} + \beta C_{11})^2}. \quad (\text{A.1d})$$

The ratio between C_{11} and C_{21} and C_{12} and C_{22} gives:

$$\frac{C_{11}}{C_{21}} = \frac{(1 + C_{11} + \beta C_{12})^2}{(1 + C_{21} + \beta C_{22})^2}, \quad (\text{A.2a})$$

$$\frac{C_{12}}{C_{22}} = \frac{(1 + C_{12} + \beta C_{11})^2}{(1 + C_{22} + \beta C_{21})^2}. \quad (\text{A.2b})$$

The sum of the pheromone concentration of each strain on the two branches is equal to the dimensionless flux Φ and we can write:

$$C_{21} = \Phi - C_{11} \quad \text{and} \quad C_{22} = \Phi - C_{12}. \quad (\text{A.3})$$

The substitution of Eq. (A.3) in Eq. (A.2) gives:

$$\frac{C_{11}}{(\Phi - C_{11})} = \frac{(1 + C_{11} + \beta C_{12})^2}{(1 + \Phi - C_{11} + \beta(\Phi - C_{12}))^2}, \quad (\text{A.4a})$$

$$\frac{C_{12}}{(\Phi - C_{12})} = \frac{(1 + C_{12} + \beta C_{11})^2}{(1 + (\Phi - C_{12}) + \beta(\Phi - C_{11}))^2}, \quad (\text{A.4b})$$

or

$$C_{11}(1 + \Phi - C_{11} + \beta(\Phi - C_{12}))^2 = (\Phi - C_{11})(1 + C_{11} + \beta C_{12})^2, \quad (\text{A.5a})$$

$$C_{12}(1 + (\Phi - C_{12}) + \beta(\Phi - C_{11}))^2 = (\Phi - C_{12})(1 + C_{12} + \beta C_{11})^2. \quad (\text{A.5b})$$

If we define the variables Z , W and Θ :

$$Z = C_{11} - \frac{\Phi}{2}, \quad (\text{A.6a})$$

$$W = C_{12} - \frac{\Phi}{2}, \quad (\text{A.6b})$$

$$\Theta = 1 + \frac{\Phi}{2} + \frac{\beta\Phi}{2}, \quad (\text{A.6c})$$

we can rewrite Eq. (A.5):

$$Z\Theta^2 + Z(Z + \beta W)^2 - \Phi\Theta(Z + \beta W) = 0, \quad (\text{A.7a})$$

$$W\Theta^2 + W(W + \beta Z)^2 - \Phi\Theta(W + \beta Z) = 0. \quad (\text{A.7b})$$

Eqs. (A.7a)+(A.7b) and Eqs. (A.7a)–(A.7b) gives:

$$(Z - W)((Z + W)^2 - ZW(\beta - 1)^2 + \Theta^2 - \Phi\Theta(1 - \beta)) = 0, \quad (\text{A.8a})$$

$$W\Theta^2 + W(W + \beta Z)^2 - \Phi\Theta(W + \beta Z) = 0. \quad (\text{A.8b})$$

Eqs. (A.8) have four groups of solutions:

$$Z = W = 0, \quad (\text{A.9a})$$

$$Z = W \neq 0, \quad (\text{A.9b})$$

$$Z = -W \neq 0, \quad (\text{A.9c})$$

$$Z = \frac{\Omega}{W}, \quad (\text{A.9d})$$

with

$$\Omega = \frac{\Phi\Theta\beta}{\beta^2 - 1} = \frac{\Phi(1 + (\Phi/2) + (\beta\Phi/2))\beta}{\beta^2 - 1}.$$

Eq. (A.9a–d) corresponds respectively to the symmetrical states ($C_{il} = \Phi/2$), the two aggregation states (Eq. (7)), the two segregation states (Eq. (8)) and the four mixed states (Eq. (10)).

For the mixed states, coupling Eq. (A.9d) with (A.8a,b) we obtain:

$$(Z + W)^2 = M = \frac{(\beta - 1)^2\Phi\beta(1 + (\Phi/2) + (\beta\Phi/2))}{(\beta^2 - 1)} - \left(1 + \frac{\Phi}{2} + \frac{\Phi\beta}{2}\right)\left(1 - \frac{\Phi}{2} + \frac{3\Phi\beta}{2}\right), \quad (\text{A.10a})$$

$$Z + W = \pm M^{0.5}, \quad (\text{A.10b})$$

$$Z^2 \mp M^{0.5}Z + \Omega = 0. \quad (\text{A.10c})$$

Eq. (A.10c) gives four stationary states:

$$Z^{++} = \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$W^{+-} = \frac{M^{0.5} - (M - 4\Omega)^{0.5}}{2},$$

$$Z^{+-} = \frac{M^{0.5} - (M - 4\Omega)^{0.5}}{2},$$

$$W^{+-} = \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$Z^{-+} = \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$W^{-+} = \frac{-M^{0.5} - (M - 4\Omega)^{0.5}}{2},$$

$$Z^{--} = \frac{-M^{0.5} - (M - 4\Omega)^{0.5}}{2},$$

$$W^{-+} = \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2}.$$

Or for C_{11} and C_{12} :

$$C_{11} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{M^{0.5} - (M - 4\Omega)^{0.5}}{2}, \quad (\text{A.11a})$$

$$C_{11} = \frac{\Phi}{2} + \frac{M^{0.5} - (M - 4\Omega)^{0.5}}{2},$$

$$C_{12} = \frac{\Phi}{2} + \frac{M^{0.5} + (M - 4\Omega)^{0.5}}{2}, \quad (\text{A.11b})$$

$$\begin{aligned} C_{11} &= \frac{\Phi}{2} + \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2}, \\ C_{12} &= \frac{\Phi}{2} + \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2}, \end{aligned} \tag{A.11c}$$

$$\begin{aligned} C_{11} &= \frac{\Phi}{2} + \frac{-M^{0.5} - (M - 4\Omega)^{0.5}}{2}, \\ C_{12} &= \frac{\Phi}{2} + \frac{-M^{0.5} + (M - 4\Omega)^{0.5}}{2}. \end{aligned} \tag{A.11d}$$

For C_{21} and C_{22} we have:

$$C_{21} = \Phi - C_{11} \quad \text{and} \quad C_{22} = \Phi - C_{12}$$

The solutions are real and positive if $M > 0$. This condition implies that:

$$\Phi > \frac{2(1 + \beta)}{1 - \beta^2 - 4\beta} \quad \text{and} \quad \beta < \sqrt{5} - 2 \tag{A.12}$$

The other condition is $M - 4\Omega > 0$ that gives:

$$\Phi > \frac{2(1 - \beta)}{1 + 2\beta + \beta^2} \tag{A.13}$$

However if Eq. (A.12) is verified, Eq. (A.13) is also verified. Indeed:

$$\frac{2(1 + \beta)}{1 - \beta^2 - 4\beta} > \frac{2(1 - \beta)}{1 + 2\beta + \beta^2}. \tag{A.14}$$

A.1. Stability of stationary states

For the analysis of stability for the symmetrical states, the Jacobian matrix gives four eigenvalues:

$$\frac{\Phi + \beta\Phi - 2}{2 + \Phi + \beta\Phi}; \quad -\frac{3\beta\Phi + 2 - \Phi}{2 + \Phi + \beta\Omega}; \quad -1; \quad -1 \tag{A.15}$$

The solutions are stable if the eigen values are negative. The denominators are always positive. Then the conditions of stability are:

$$\Phi + \beta\Phi - 2 < 0 \Rightarrow \Phi < \frac{2}{(\beta + 1)}, \tag{A.16a}$$

$$3\beta\Phi - \Phi + 2 > 0 \Rightarrow \Phi < \frac{2}{(1 - 3\beta)}. \tag{A.16b}$$

For $\beta > 0$, $(\beta + 1)$ is always greater than $(1 - 3\beta)$ and thus the first condition prevails.

For the stability of the stationary states for the aggregation states, the Jacobian matrix gives four eigen values:

$$-\frac{\Phi + \beta\Phi - 2}{\Phi(\beta + 1)}; \quad -\frac{\Phi(\beta + 1)^2 + 2\beta - 2}{\Phi(\beta + 1)^2}; \quad -1; \quad -1 \tag{A.17}$$

As $\Phi > 2/(\beta + 1)$ the numerators of the two first values are always positive (denominators are always positive).

This implies that these two values are always negative and the stationary states are always stable.

For the segregation states, the Jacobian matrix gives the following eigenvalues:

$$\frac{2 - \Phi + 3\beta\Phi}{\Phi(1 - \beta)}; \quad \frac{\Phi\beta^2 + 4\beta\Phi - \Phi + 2\beta + 2}{\Phi(\beta^2 - 2\beta + 1)}; \quad -1; \quad -1. \tag{A.18}$$

For $0 < \beta < 1$ the denominators are always positive. Then the conditions of stability are:

$$2 - \Phi + 3\beta\Phi < 0 \Rightarrow \Phi > \frac{2}{(1 - 3\beta)}, \tag{A.19a}$$

$$\Phi\beta^2 + 4\beta\Phi - \Omega + 2\beta + 2 < 0 \Rightarrow \Phi > \frac{2(\beta + 1)}{(1 - \beta^2 - 4\beta)} \tag{A.19b}$$

The first condition is the same than the condition of existence. For the second one when $\beta > \sqrt{5} - 2$ (A.19b) becomes positive and the segregation state is unstable.

Thus $\beta < \sqrt{5} - 2 \approx 0.236$ represents a necessary condition of stability for the segregation states.

For the mixed states, numerical resolutions show that the solutions, that exist for $\beta > \sqrt{5} - 2$, are always unstable.

Appendix B. The cockroach aggregation model

The model describes the variations of the mean number of individuals on each of the resting sites and consequently the traffic of individuals between the sites. We have limited the study to two identical sites and two strains having the same number of individuals (N). X_i and Y_i are, respectively, the number of individuals of strain X and Y in this site i . These equations have two terms: first, a positive part reflects the arrivals of the insects on the site and second, a negative part describes their departure:

$$\frac{dX_1}{dt} = -Q_{x,1}X_1 + Q_{x,2}X_2 \tag{B.1a}$$

$$\begin{aligned} \frac{dY_1}{dt} &= -Q_{y,1}Y_1 + Q_{y,2}Y_2, \\ X_2 &= N - X_1, \\ Y_2 &= N - Y_1, \end{aligned} \tag{B.1b}$$

Q_{xi} and Q_{yi} are, respectively, the probabilities for an individual X or Y to leave at each time step the site i for the site j :

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

The greater X_i , Y_i , the lower the individual probability to leave the site i . The influence of individuals belonging to the same strain can be more important than that of individuals belonging to the other strain. One individual tends to stay more with individuals of the same strain than with individuals of another strain. β ($0 \leq \beta \leq 1$) is similar to the β used in the model of trail recruitment.

If we define $Z = X_1 - 0.5N$ and $W = Y_1 - 0.5N$ and we follow the same procedure as in Appendix A, we show that the stationary solutions of this model are similar to those of the model of recruitment (see text and Appendix A).

The symmetrical state

$$X_1 = Y_1 = \frac{N}{2}. \quad (\text{B.3a})$$

The two aggregative states

$$\begin{aligned} X_1 = Y_1 &= 0.5N + \left(0.25N^2 - \frac{k}{(1+\beta)^2}\right)^{0.5}, \\ X_1 = Y_1 &= 0.5N - \left(0.25N^2 - \frac{k}{(1+\beta)^2}\right)^{0.5}. \end{aligned} \quad (\text{B.3b})$$

These states are real and positive if $N > 2k^{0.5}/(1+\beta)$.

The two segregative states

$$\begin{aligned} X_1 &= 0.5N + \left(0.25N^2 - \frac{k + \beta^2 N^2}{(1-\beta)^2}\right)^{0.5}, \\ Y_1 &= 0.5N - \left(0.25N^2 - \frac{k + \beta^2 N^2}{(1-\beta)^2}\right)^{0.5} \\ \text{and} \\ X_1 &= 0.5N - \left(0.25N^2 - \frac{k + \beta^2 N^2}{(1-\beta)^2}\right)^{0.5}, \\ Y_1 &= 0.5N + \left(0.25N^2 - \frac{k + \beta^2 N^2}{(1-\beta)^2}\right)^{0.5}. \end{aligned} \quad (\text{B.3c})$$

These states are real and positive if $\beta < 1/3$ and $N > 2k^{0.5}/(1-2\beta-3\beta^2)^{0.5}$.

The four mixed states

$$\begin{aligned} X_1^{++} &= 0.5N + \left(\frac{-(A+2\Theta) + \sqrt{(A+2\Theta)^2 - 4\Theta^2}}{2}\right)^{0.5}, \\ Y_1^{++} &= \frac{\Theta}{X_1^{++} - 0.5N} + 0.5N, \\ X_1^{-+} &= 0.5N - \left(\frac{-(A+2\Theta) + \sqrt{(A+2\Theta)^2 - 4\Theta^2}}{2}\right)^{0.5}, \\ Y_1^{-+} &= \frac{\Theta}{X_1^{-+} - 0.5N} + 0.5N, \end{aligned}$$

$$\begin{aligned} X_1^{+-} &= 0.5N + \left(\frac{-(A+2\Theta) - \sqrt{(A+2\Theta)^2 - 4\Theta^2}}{2}\right)^{0.5}, \\ Y_1^{+-} &= \frac{\Theta}{X_1^{+-} - 0.5N} + 0.5N, \\ X_1^{--} &= 0.5N - \left(\frac{-(A+2\Theta) - \sqrt{(A+2\Theta)^2 - 4\Theta^2}}{2}\right)^{0.5}, \\ Y_1^{--} &= \frac{\Theta}{X_1^{--} - 0.5N} + 0.5N, \\ \Theta &= \frac{0.5\beta N^2}{\beta - 1}, \quad A = k - 0.25N^2 + \beta N^2 + 0.25\beta^2 N^2. \end{aligned} \quad (\text{B.3d})$$

The mixed states are real and positive if $A < 0$. If $\beta > \sqrt{5} - 2$, A is always > 0 .

The stability properties of these different states are the same as the corresponding states of the trail model.

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