



The effect of aggregates on interaction rate in ant colonies

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Direct contact between individuals is important for the organization of social insects. The question has been raised whether in ant colonies contact may also provide a mechanism to allow ants to estimate the density of the population in a nest and regulate their behaviour accordingly, as reflected by a subquadratic dependence of the number of interactions as a function of the density. We developed a kinetic model of encounters between individuals, and conducted an experiment with different densities of the species *Lasius niger*. These suggested that the subquadratic law is not due to active regulation by ants but arises, rather, as a consequence of the kinetics of the encounter process and the presence of small, temporary clusters of individuals.

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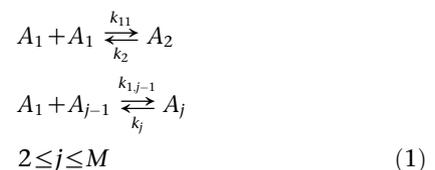
It is well established that direct contact between individuals is important for social organization in connection with, for instance, information exchange, exchange of nutrient material (trophallaxis), mutual helping (allogrooming), vector transmission, agonistic and gregarious behaviour (Davison 1973; Krasnov & Khokhlova 2001). Social insects constitute a striking, and important, example where the effects arising from direct contact can be observed and analysed in a detailed manner. Hölldobler & Lumdsen (1980) have proposed that defence recruitment behaviour in ant society depends on the number of encounters of an individual with others from a different colony. Furthermore, encounters constitute an essential step in the process of aggregation. In addition, direct contact may provide a mechanism allowing individuals in a colony to estimate the density of the population in a nest and regulate their behaviour accordingly. In particular, Gordon et al. (1993) studied the number of encounters between individuals per unit time as a function of the overall density and found that it follows a power law with an exponent less than the expected value of 2. They interpreted this difference as evidence that the physical characteristics of the individuals' trajectories (velocity, mean free path) were modified as a result of the encoun-

ters. Stated differently, the individual behaviour is altered as individuals begin to regulate their encounter rate according to the density they perceive, thereby preventing, for instance, unnecessarily high numbers of individuals from being involved in a given task.

In the present paper, we propose an alternative explanation of the subquadratic law followed by the encounter rate. We developed a kinetic model of encounters between individuals accounting for such a dependence and conducted an experiment to test it.

THE MODEL

Consider N ants on a surface S . In the absence of any specific stimuli, individuals will spend most of their time in free motion or as parts of aggregates A_j involving at least two ants ($j \geq 2$). Let A_1 denote the free individual. Experiments show that the aggregates A_j ($j \geq 2$) remain immobile and only the isolated individuals are in motion (Nicolis 2003). It therefore seems reasonable to assume that a j -aggregate is formed predominantly by adding A_1 to a $(j - 1)$ aggregate and, conversely, that when such an aggregate decays it will predominantly free one individual at a time. This leads us to stipulate the following kinetic scheme



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Here M is the largest aggregate observed, $k_{1,j-1}$ the rate of aggregation towards the j th aggregate and k_j the rate of decay of this aggregate.

The development of the population of different A_j 's in time will be determined by the probability of the (A_1, A_{j-1}) encounters and by the lifetime of this aggregate. Let σ_{j-1} be the characteristic linear dimension of A_{j-1} . In the absence of geometric effects, free ants A_1 that meet this aggregate within a time interval Δt are necessarily within a distance $(\sigma_1 + \sigma_{j-1})/2$ from the symmetry axis of the aggregate and within a distance $\bar{v}\Delta t$ from a cross-section of it transversal to the axis, as illustrated in Fig 1 (Frost & Pearson 1965). In reality, ants are asymmetric objects and, furthermore, one expects an encounter to be effective only when the sensory organs are, at the appropriate time, at a distance less than or equal to 0.5 cm (Depickere et al. 2004). We account for these restrictions by introducing an 'efficiency factor' q , counting the percentage of encounters that will actually result in aggregate formation. In our analysis of the model equations we take the value of this factor to be 1/2.

The number of $A_1 - A_{j-1}$ encounters, $I^{(1,j-1)}$ in a surface ΔS will then be given by

$$I^{(1,j-1)} = N^{(j-1)} \left[\frac{\sigma_1 + \sigma_{j-1}}{2} \right] \frac{\bar{v}\Delta t}{\Delta S} N^{(1)} \quad j \geq 2$$

$$I^{(1,1)} = \frac{1}{2} (N^{(1)})^2 \frac{\sqrt{2}\bar{v}\Delta t}{\Delta S} \quad (2)$$

where $N^{(1)}$ is the number of free ants in ΔS , $N^{(j-1)}$ the number of A_{j-1} in ΔS . The factor 1/2 in the second equation is introduced to avoid counting twice a given pair of free individuals (assumed to be identical). $\sqrt{2}\bar{v}$ is the mean relative velocity of two free individuals, where the factor $\sqrt{2}$ arises from the averaging over all possible approach angles using a uniform distribution. In the following we are interested in the development over time, and steady-state behaviour, of the mean densities, n_j , of A_1, \dots, A_j, \dots

$$n_j = \frac{N^{(j)}}{\Delta S}$$

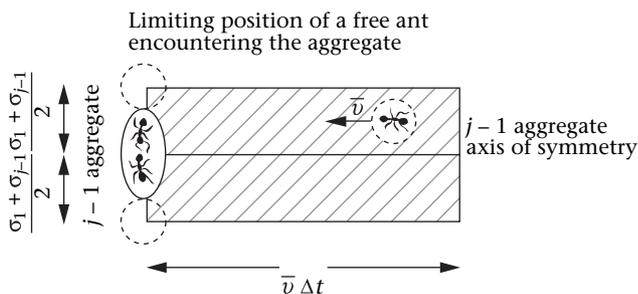


Figure 1. Effective interaction surface in an encounter between a free ant and an aggregate involving $j - 1$ ants to form a j -aggregate. \bar{v} is the mean velocity of free ants, σ_1 its characteristic linear size, σ_{j-1} is the characteristic linear size of the aggregate, and t is time.

The rate of change of n_j associated with an aggregation process will then be given by

$$\left(\frac{dn_j}{dt} \right)_{\text{agg}} = \frac{I^{(1,j-1)}}{\Delta t \Delta S}$$

or using equation (2)

$$\left(\frac{dn_j}{dt} \right)_{\text{agg}} = k_{1,j-1} n_1 n_j \quad (3)$$

where the effective rate constant $k_{1,j-1}$ is given by

$$k_{1,j-1} = \left[\frac{\sigma_1 + \sigma_{j-1}}{2} \right] \bar{v}$$

$$k_{11} = \sqrt{2} \frac{\sigma_1 \bar{v}}{2} \quad (4)$$

Combining all these processes and assuming that the motion of free ants is sufficiently random to maintain spatial homogeneity, one may write the following equations resulting from scheme (1)

$$\frac{dn_1}{dt} = - \underbrace{2k_{11}n_1^2}_I + \underbrace{2k_2n_2}_II - n_1 \underbrace{\sum_{j=2}^{M-1} k_{1,j}n_j}_{III} + \underbrace{\sum_{j=3}^M k_jn_j}_{IV}$$

$$\frac{dn_j}{dt} = k_{1,j-1}n_1n_{j-1} + k_{j+1}n_{j+1} - k_jn_j - k_{1,j}n_1n_j \quad (5)$$

$$\frac{dn_M}{dt} = k_{1,M-1}n_1n_{M-1} - k_Mn_M$$

$$2 \leq j \leq M - 1$$

In the first equation, I represents the aggregation rate of two isolated ants, II , the disintegration of an aggregate of two, hereafter referred to as a dimer by analogy with chemistry, III , the absorption of an isolated ant joining an aggregate, and IV , the emission of an individual from an aggregate of three, hereafter referred to as a trimer again by analogy with chemistry, or from larger aggregates. These equations all satisfy the conservation condition

$$\sum_{i=1}^M in_i = n = \frac{N}{S} \quad (6)$$

where i is an integer number accounting for the number of individuals in aggregates of increasing order and N is the total number of ants. On the other hand, at the steady state ($dn_j/dt = 0$) all forward processes in equation (1) are cancelled by the backward ones and one obtains

$$n_j = \frac{k_{1,j-1}}{k_j} n_{j-1} n_1 \quad (7)$$

Substitution into equation (6) leads to the following closed equation for n_1 ,

$$n_1 + 2 \frac{k_{11}}{k_2} n_1^2 + \dots + M \frac{k_{11} \dots k_{1,M-1}}{k_2 \dots k_M} n_1^M = n \quad (8)$$

Since we assume that aggregates form when lone individuals join other individuals or existing aggregates,

the total number of interactions per unit time in the population, I_{tot} , can be evaluated as

$$I_{\text{tot}} = n_1 (k_{11}n_1 + k_{12}n_2 + \dots + k_{1,M-1}n_{M-1})$$

$$= n_1 \left(k_{11}n_1 + \frac{k_{11}k_{12}}{k_2}n_1^2 + \dots + \frac{k_{11}\dots k_{1,M-1}}{k_2\dots k_{M-1}}n_1^{M-1} \right) \quad (9)$$

where, in going from the first to the second line, we used equation (7). We solve equation (9) later on, evaluate it for some representative cases and compare the results with the experimental observations.

Note that the encounter rates in the model equation (5) are quadratic with respect to the densities n_i of the species involved. This is analogous to the law of mass action familiar from chemical kinetics (Frost & Pearson 1965). We emphasize that this is not tantamount to a quadratic dependence of I_{tot} with respect to the average density n since I_{tot} is a collective variable, depending in a complex way on the individual n_i 's.

EXPERIMENTAL VALIDATION

Methods

In this section we report experimental work providing justification of the assumptions underlying the proposed model, along with quantitative information on the parameter values. The experimental set-up consisted of a circular arena of diameter 30 cm. The temperature was maintained at 25°C and a light source of 40 W was used. The ants, *Lasius niger*, collected from earth banks of the faculty campus (Campus de la Plaine, ULB, Brussels) with the permission of the Dean of the Faculty, were deprived of food for 4 days and were brought from the nest directly to the arena. Measurements were started 2 h later, when a (statistically) quasi steady-state regime was likely to have been reached (Depickere et al. 2004). In each measurement, the individuals were followed by a camera for 45 min. The number of isolated individuals and of the aggregates, defined as clusters of individuals (at rest) within relative distances of less than 5 mm, were identified during four intervals of 2 min. These intervals were chosen at minutes 0, 13, 28 and 43 in the 45-min period. We counted the ants on four circular areas 9 cm in diameter whose centres were 5 cm from the boundaries. We tested three densities: 0.03, 0.07 and 0.22 per cm².

Results and Discussion

Figure 2 depicts the distribution of survival times of dimers and trimers. We observed a law close to the exponential. This is compatible with one of the main assumptions underlying the model, namely, that the decay of an aggregate is a random process. Indeed, a basic result from the theory of such processes (Feller 1968) is that the probability that a state (here the maintenance of a stable aggregate) lasts until an event leading to its decomposition occurs at time t follows a negative exponential law. The reciprocal of the factor multiplying the

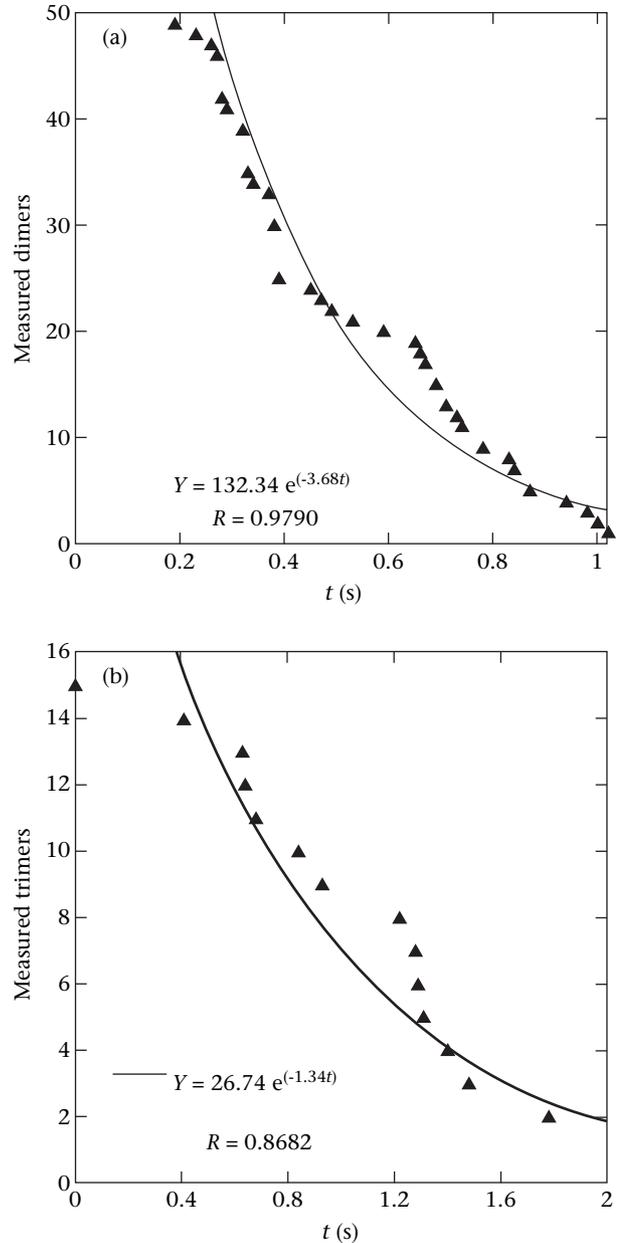


Figure 2. Lifetime distribution of (a) aggregates of two and (b) aggregates of three, referred in the text as dimers and trimers, respectively, by analogy to chemistry, for the density $N = 0.07$ per cm². t is time. An exponential curve fit (plain line) is superimposed on the experimental data.

time variable in the exponent provides the mean lifetime of the aggregate. The factor itself (i.e. the reciprocal of the mean lifetime) determines the rate at which the aggregate decays, and is to be identified with the factor k_i in equation (1). To reach a stable result one needs to take averages over the lifetimes of large numbers of individual dimers and trimers. One arrives in this way at trimer lifetimes that are two or three times greater than those of dimers (respectively, 0.272 s and 0.745 s). This is in agreement with recent results (Depickere et al. 2004) showing that aggregate stability increases with size. Practically no tetramers or higher order aggregates were

detected during the measurement. The specific distributions in Fig. 2 were obtained for a density of 0.07 per cm². The analysis was repeated for the other two densities tested. The results on the mean lifetimes and the quality of the exponential fit were statistically indistinguishable from those of Fig. 2.

Finally, we inferred the ants' speed from the mean distance covered by 20 individuals over 1 min. This mean speed includes an individual's pauses and its observed value is 2.56 cm/s. The linear size of an individual is 0.3 cm.

FREE ANTS AND THEIR ENCOUNTER DYNAMICS

The Monomer–Dimer Case

The simplest instance where encounters between individuals lead to a nontrivial pattern corresponds to setting $M = 2$ in equations (1), (5), (8) and (9). A given ant then shares its time between free motion and a state in which it is part of a pair. The steady-state percentages of these two forms can be deduced from equation (8) which becomes in this limit

$$n_1^2 + \frac{k_2}{2k_{11}}n_1 - \frac{k_2}{2k_{11}}n = 0 \tag{10}$$

The only physically acceptable solution of this equation is

$$n_1 = \frac{k_2}{4k_{11}} \left(-1 + \sqrt{1 + 8\frac{k_{11}}{k_2}n} \right) \tag{11}$$

and the corresponding interaction number per unit time is given by (cf. equation 9)

$$I_{\text{tot}} = \frac{k_2^2}{16k_{11}} \left(2 + 8\frac{k_{11}}{k_2}n - 2\sqrt{1 + 8\frac{k_{11}}{k_2}n} \right) \tag{12}$$

Expanding equation (12) in series of n in the weak density limit (i.e. the mean distance between individuals is much larger than their linear dimension) one sees straightforwardly that I_{tot} starts with a quadratic dependence in n . This behaviour changes for densities around the value $k_2/8k_{11}$ and tends asymptotically (for large n) to a linear function of n . There is, therefore, no remnant of quadratic behaviour in the high-density region. Nevertheless, if the parameter k_2 increases, or, equivalently, the number of dimers decreases, the quadratic law will persist for higher densities. Figure 3a depicts the results of the numerical evaluation of equations (11)–(12). The curves in the middle are obtained by using parameter values derived from experimental measurements. The other graphs are obtained for two different hypothetical velocities and rates. We see that linear n dependence is indeed postponed when the lifetime of the dimer is short (k_2 large).

The Monomer–Dimer–Trimer Case

Let us now account for the fact that one individual can, with a non-negligible probability, interact with a dimer

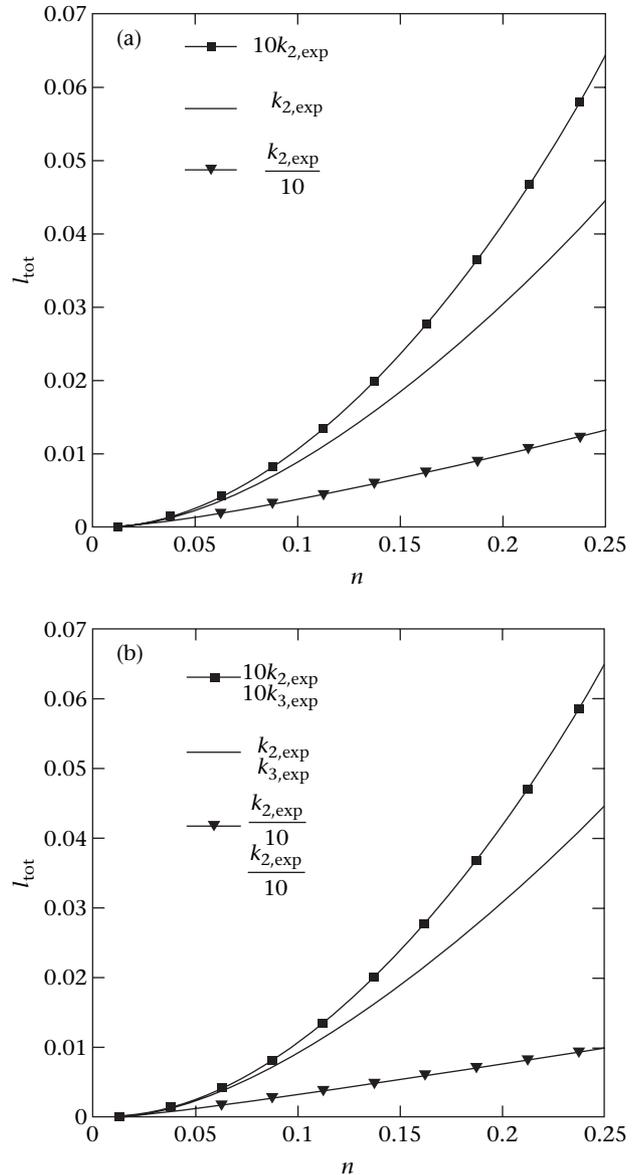


Figure 3. Number of theoretical collisions (I_{tot}) implied in the formation of (a) aggregates of two (dimers) and (b) aggregates of three (trimers) as a function of density (n). Parameter values are: rate of encounter between two free individuals $k_{11} = 1.08 \text{ cm}^2/\text{s}$, rate of encounter between a free individual and a dimer $k_{12} = 0.768 \text{ cm}^2/\text{s}$, as deduced from the experimentally determined values of mean velocity \bar{v} and linear dimension σ_1 and σ_2 , experimental rate of decomposition of a dimer $k_{2,\text{exp}} = 1.881 \text{ per s}$ and of a trimer $k_{3,\text{exp}} = 0.833 \text{ per s}$.

and form, for a certain time, a trimer. This situation corresponds to setting $M = 3$ in equations (1), (5), (8) and (9). Equation (8) becomes

$$n_1^3 + \frac{2k_3}{3k_{12}}n_1^2 + \frac{k_2k_3}{3k_{11}k_{12}}n_1 - \frac{k_2k_3}{3k_{11}k_{12}}n = 0 \tag{13}$$

and the corresponding interaction number per unit time is (cf. equation 9)

$$I_{\text{tot}} = n_1 \left(\frac{k_{11}}{2} n_1 + \frac{k_{11} k_{12}}{k_2} n_1^2 \right) \quad (14)$$

where we replace n_1 by the numerical solution of the cubic equation (equation 13). Figure 3b summarizes the results of the evaluation of I_{tot} . The qualitative behaviour is similar to that in Fig. 3a. A number of quantitative differences are nevertheless worth noting, in particular, that the presence of trimers tends to slow down the growth rate.

DISCUSSION

In this paper, we developed a simple kinetic model of encounters between individuals which could be one of the primary mechanisms of the aggregation phenomenon. This model, in conjunction with experiment conducted with different ant densities, allowed us to calculate the number of interactions between two and three individuals and the durations of these interactions. We found that the law that follows the total number of aggregates as a function of individual density is not universally quadratic. This phenomenon is amplified when the number of individuals involved in the aggregates increases.

Gordon developed experiments to determine the rate of antennal interactions between individuals as a function of their densities (Adler & Gordon 1992; Gordon et al. 1993; Gordon 1995) and observed a nonquadratic law. She concluded that a behavioural modification of the individuals was responsible for altering the trajectories as a function of encounters. Her major (and correct) argument (Gordon 1996) is that if individuals have identical exploratory behaviour (the same random walk which is not modified over time) the number of encounters is bound to be proportional to N^2 . Because she did not observe this law in her experiments, she suggested that the contacts modify the nature of the trajectory of the individuals involved in collisions.

Our model and experimental data suggest that the switching from a quadratic to a linear regime at high density is not due to an active regulation by ants but to the kinetics of the collision process itself and, particularly, to the presence of aggregates: because the encounter process takes a finite time, say τ on average, the maximum number of interactions during an experimental period T is limited to the value T/τ . The contact rate thus cannot increase with the density of ants beyond this limit. We do not rule out that active regulation by ants may well be present in a number of instances in ant biology. The principal message of this paper is that under the conditions of the present work, it simply does not apply, and is superseded by a computationally less expensive mechanism inherent in the kinetics of the collision process.

The model proposed here is in many respects generic, and hence applicable to a variety of situations involving the formation of aggregates, beyond social insect biology, such as aggregation in the absence of direct contact

(Okubo 1980; Gerard et al. 2002), Lanchester battle scenarios in combat evolution (Franks & Partridge 1993; Adams & Mesterterton-Gibbons 2003), or epidemics (Krasnov & Khokhlova 2001). It would undoubtedly be interesting to address such applications. In this context, different ways of quantifying the information flux underlying the processes present should also be explored.

The model does not explicitly take into account the spatial dependence of the different processes at work. It would be interesting to generalize our study to a spatially extended model. One can expect that taking account of spatial effects in this kind of process can lead to a breaking of symmetry. Recent work on ants (Theraulaz et al. 2002) and on cockroaches (Jeanson et al., in press) already shows the essential role of the spatial dimension. Furthermore, it is believed that many factors can affect trajectories (and thus the contact rate) without any regulation by the individuals. For example, it is well known that ants have a strong capacity to follow heterogeneities (thigmotaxis) and that the concentration of pheromone secreted during the process has a significant influence on the trajectories. The role of these additional effects will be the subject of future work.

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