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Collective decision through self-assembling

Received: 18 December 2002 / Accepted: 7 March 2004 / Published online: 8 April 2004
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Abstract The ant genus *Oecophylla* is well known for forming chains that allow a gap to be bridged. Using a set-up where the ants are given the choice of building a chain on two identical sites, we show that they always end up focusing their activity on a single one. A mathematical model suggests that this result depends on probabilities of entering and leaving the chain that depend on its size. The same model allows some predictions to be made on the influence of the nest size. Thus, a critical population size is needed in order to observe the formation of at least one chain. Over this size we observe the transitory coexistence of two chains, for which the duration is positively correlated to the nest size. However, this coexistence always leads to the formation of one chain and to the break-up of the other one. Following on from these results we give similar examples in gregarious arthropods and discuss the possibility of these mechanisms being generic for a wide range of collective activities and decisions.

Introduction

Aggregation is a widespread phenomenon in biological systems (Parrish and Keshet 1999; Ben-Jacob et al. 2000; Krause and Ruxton 2002). In social insects, its expression varies from the gathering of individuals at a single site to their splitting between different ones. It also expresses a wide variety in terms of interactions and structures, from no physical contact between individuals to their self-assemblage (Anderson et al. 2002; Whitesides and Grzybowski 2002). The arboreal ant *Oecophylla* self-assembles to form chains that allow the bridging of an empty space or the building of the nest (Ledoux 1950; Hölldobler and Wilson 1990). In a previous paper we showed

that the formation of a single chain is mainly under the control of individual probabilities to enter and leave it, depending on the number of ants in the chain and modulated by a visual stimulus (Lioni et al. 2001). In this paper, experimental results show that when two identical sites can be used to form chains, the colony ends up focusing its self-assembling activity on one of them. A mathematical model suggests that this collective decision lies in the individual probabilities to enter and to leave a chain depending on the chain size, and does not refer to any cognitive capacity such as a comparison between sites. It also shows how the colony size affects the dynamics of competition between chains in terms of size and time.

Materials and methods

Experiments on *Oecophylla smaragdina* were conducted in May 1997 in semi-laboratory conditions (Station King Leopold III, Laing Island, Papua New Guinea). We used a binary choice set-up composed of a vertical bar leading to two horizontal and identical branches forming a 60° angle where ants can form chains at the end of the horizontal branches (see insert Fig. 1a) and surrounded by a white sheet to isolate the workers from any visual stimulus. Two replicates per day were conducted during daylight and separated by 2 h. Each replicate ($n=15$) lasted for 20 min. For each of them we used new horizontal branches and the vertical bar was cleaned with alcohol. Each nest, collected 12 h before its first use, was replaced every 2 days by a new one picked up from the same colony (same tree holding few tens of nests).

Data were collected with a video recording system that allowed observation of the individuals as well as the formation of chains. The variables measured were the number of ants (1) that come from the nest and pass on to the two horizontal branches per second (ϕ_i); (2) that join the chains per second (ϕ_{ei}); and (3) that leave the chains per second (ϕ_{li}) (see Fig. 1).

These measurements allow the calculation of each chain's population at time t ($X_i(t)$): $X_i(t) = X_i(t-1) + \phi_{ei}(t) - \phi_{li}(t)$. ϕ_{ei} is equal to the individual probability of entering the chain i (P_{ei}) multiplied by the incoming flow of ants from the nest on the corresponding horizontal branch (ϕ_i). ϕ_{li} is equal to the individual probability of leaving the chain i (P_{li}) multiplied by the number of ants in the corresponding chain (X_i).

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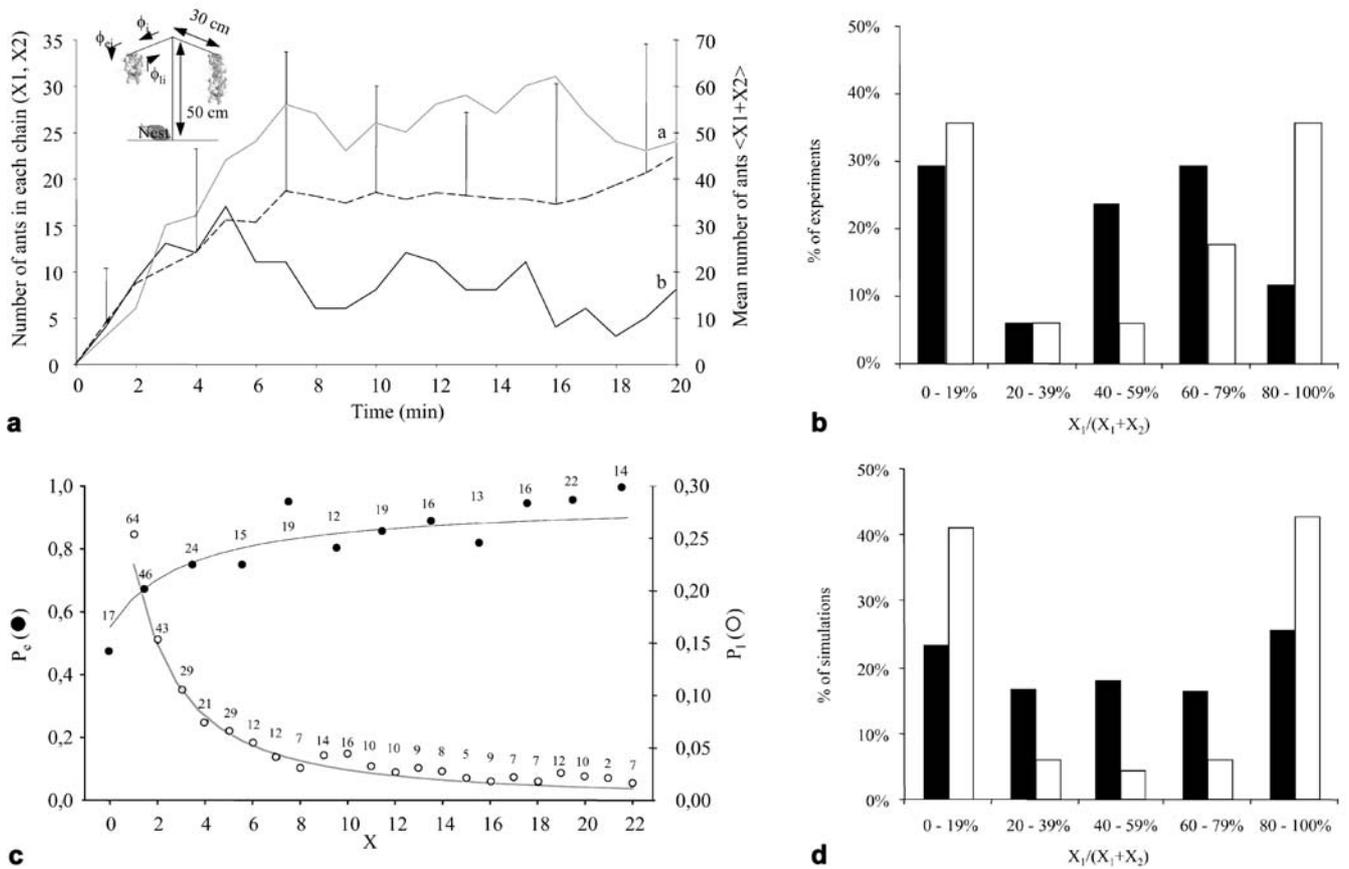


Fig. 1 **a** Example of the evolution of the number of ants constituting a chain on branches *a* and *b* over a period of 20 min and mean experimental evolution (*dashed line*) of the number of ants in both chains (X_1-X_2). The *insert* shows the binary-choice experimental set-up used to study chain competition (for ϕ_i , ϕ_c and ϕ_l , see text). **b** Percentage of experiments ($n=15$) as a function of the percentage of ants in one chain on the total number of ants in each chain ($X_1/(X_1+X_2)$) at times 2 min (*black columns*) and 20 min (*white*

columns). **c** Experimental individual probabilities of entering, P_e (●), and leaving, P_l (○), a chain depending on its size and their respective fitting (*solid lines*). Each *dot* is associated with its sample size used for the calculation of the probabilities. **d** Percentage of simulations ($n=1,000$) as a function of the percentage of ants in one chain on the total number of ants in each chain ($X_1/(X_1+X_2)$) at times 2 min (*black columns*) and 20 min (*white columns*)

Considering a sample of measurements for each chain size (X) we calculate the corresponding P_e and P_l as follows:

$$P_e(X) = \phi_{ei}(t)/\phi_i(t)$$

$$P_l(X) = \phi_{li}(t)/X_i(t-1)$$

To make the link between the individual behaviours and the collective dynamics, a stochastic model is developed using the values of the experimental parameters (Camazine et al. 2001; Lioni et al. 2001).

Experimental results

The ants' behaviour can be described as follows: ants leave the nest and choose one or other of the horizontal branches. When reaching the end of the branch they can either join or start a chain, or turn away and walk back onto the horizontal branch to the nest. At the same time, ants forming the chain can either stay or leave to go back to the nest.

With two symmetrical nearby sites on which to build a chain, there is a dynamic leading to one chain after a few

minutes. Considering an example (Fig. 1a), we observe firstly a similar increase in the number of ants in both chains. After 4 min one chain (*a*) still increases to reach a plateau value of ~ 30 individuals, and the second one (*b*) decreases symmetrically. In the same way, the mean evolution of ants in the chains observed over a period of time also shows a rapid increase followed by a plateau. Figure 1b expresses the percentage of ants in the right-branch chain over the total number of ants in both chains. At time 2 min, both chains on each branch are regularly distributed, i.e. chain growth shows no preference for a specific branch. At time 20 min, more than 80% of the experiments show that the collective activity is focused on a single chain, equally distributed between the right or left branches.

This gradual increase in asymmetry in terms of chain size is not due to a difference in the mean incoming flow (ϕ_i), which remains equal on both branches. A linear correlation between the mean flow over 20 min on the winning branch and the losing one gives a slope equal to one ($r=0.93$, $n=15$, $P<0.001$), which indicates an equal

probability for the ants coming from the nest to choose one or the other branch.

The incoming flow slightly decreases with the increase of the population in the chains (X_1 and X_2), which suggests a linear dependency on the flow with the population remaining in the nest ($Pop - X_1 - X_2$). The link between the incoming flow (ϕ_i) and P_0 , which corresponds to the individual probability to leave the nest, is:

$$\phi_i = 0.5P_0(Pop - X_1 - X_2)$$

with $P_0=0.01 \text{ s}^{-1}$ and $Pop=100$ ($r=0.9$, $n=15$, $P<0.001$).

Using two phenomenological functions similar to those already found for a single-branch situation (Lioni et al. 2001), we identified the relationship between the individual probabilities to enter (P_e) and to leave (P_l) and the number of individuals in the chain (X) (Fig. 1c).

$$P_e = C_{e0} + \frac{C_{e1}X}{C_{e2} + X}$$

The function P_e expresses the idea that the probability of joining the chain grows with X and reaches a plateau value equal to $C_{e0}+C_{e1}$. C_{e0} is the rate of spontaneous hanging when no chain is yet formed ($X=0$). Fitting the experimental data gives: $C_{e0}=0.55$, $C_{e1}=0.4$, $C_{e2}=3.56$, ($r=0.89$, $n=12$, $P<0.001$).

$$P_l = \frac{C_{l1}}{C_{l2} + X^v}$$

The function P_l expresses the decrease in the probability of leaving the chain as X increases and tends to 0. Fitting the experimental data gives: $C_{l1}=0.7$, $C_{l2}=2.1$, $v=1.3$ ($r=0.92$, $n=30$, $P<0.001$).

Theoretical results

Each second, the model describes the evolution of the number of individuals in both chains (X_1 , X_2). At the beginning ($t=0$) the total population (Pop) is in the nest so that $X_1=X_2=0$. The chain dynamics are under the control of three events: (1) the ants leaving the nest with an individual probability P_0 for each of them and an equal probability (0.5) to choose one or the other horizontal branch; (2) the individual probability to join a chain (P_e); (3) and to leave it (P_l). When they do not join the chain or when they leave it, they go back to the nest.

Experimental and theoretical distribution of the proportion of ants in the right branch chain over the total of ants in both chains at times 2 and 20 min, shows a strong similarity (Fig. 1d) [for 2 min : $\chi^2=0.5$, $df=2$, $P>0.05$; for 20 min: $\chi^2=2.32$, $df=2$, $P>0.25$]. The model reproduces both the asymmetry in terms of time and percentages of population in the chains as well as the mean evolution of ants in the chains depending on the time (e.g. at 20 min for $Pop=100$ (Fig. 2a)).

This agreement between experimental and theoretical results validates our model and allows its extension to study the role of the nest population size (Pop). Figure 2a shows the mean number of ants both in the bigger and

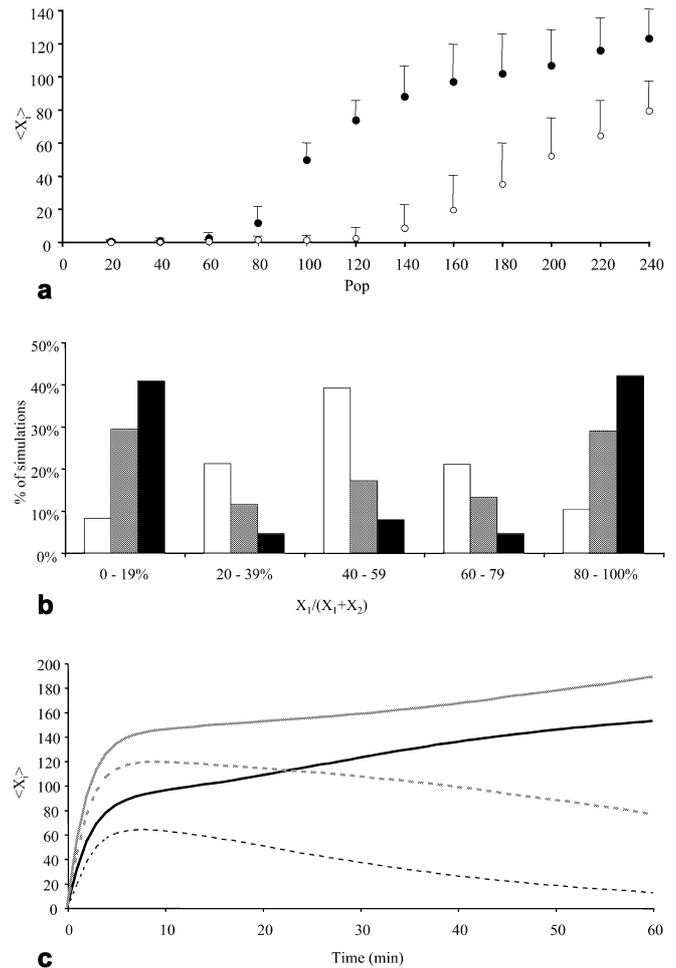


Fig. 2 a Mean theoretical evolution ($n=1,000$) of the bigger (*black circles*) and smaller (*white circles*) chain size depending on the population value (Pop) at time 20 min. **b** Percentage of simulations ($n=1,000$) as a function of the percentage of ants in one chain on the total number of ants in each chain ($X_1/(X_1+X_2)$) at times 20 (*white columns*), 40 (*grey columns*), 60 (*black columns*) minutes and considering an initial population $Pop=200$. **c** Mean theoretical evolution ($n=1,000$) of the bigger (*solid lines*) and smaller (*dashed lines*) chain size over 60 min considering a population size (Pop) of 200 (*black*) and 300 (*grey*)

smaller chains at time 20 min as a function of the nest population. For $Pop \approx 60$ no chain appears. For larger populations, two chains grow symmetrically, always followed by the break-up of the smaller one: the bigger the nest population, the bigger the chains and the longer their coexistence. Considering the case of a population of 200 ants and the distribution of the number of ants in the right-branch chain over the total number of ants in both chains over the time (Fig. 2b) leads to a majority of simulations showing a symmetry (time 20 min), whereas an asymmetry appears and is amplified at times 40 and 60 min. In terms of mean chain size, a nest population of 200 also leads, at time 20 min, to an average population of 100 and 50 ants respectively for the bigger and the smaller chains. In this case, the smaller chain reaches the same size as a situation that involves a population $Pop=100$ ants which

corresponds to our experimental data. As long as the population remaining in the nest ($Pop - X_1 - X_2$) is bigger than (± 50 ants) both chains symmetrically grow and when most of the population is in the chains, the real competition between them occurs through the individual probabilities of entering and leaving, leading to the total break-up of the smaller chain (Fig. 2c). From a theoretical point of view, these solutions correspond to the well-known bifurcation phenomenon: in a symmetrical environment, the system adopts an asymmetrical solution (Camazine et al. 2001).

Discussion

Our results show that the logic used in chain building in *Oecophylla* does not refer to complex cognition such as direct comparison between sites. The spatial focus of the activity depends on the interplay between the colony size and the individual response to the local number of nestmates in the chain: the bigger the chains, the greater the probability to enter (P_e) and the lower the probability to leave (P_l). A small population will never produce a chain, due to an incoming flow unable to compensate for the departure from the chains, characterised by a high leaving probability. Above this nest size, the choice of sites for a chain is preceded by the symmetrical growth of two chains and their transitory coexistence, for a duration that is positively correlated to the size of the nest population.

In a natural situation, the functionality of self-assembling behaviour is to form a bridge, which requires a minimum length. When the population is too small, the interplay between the incoming flow and the probabilities (P_e and P_l) prevents the formation of any chain. Considering a medium nest population size, a colony could end up forming either a single functional chain or two chains, neither of which would be large enough to form a bridge. Our model suggests that the functional solution is reached by constraining the colony to focus its activity on one site. This prevents the colony from committing to a large percentage of the population to an unsuccessful task. On the other hand, the same mechanisms give a degree of flexibility since they also allow the transitory coexistence of at least two chains if the colony is big enough. In short, the colony adopts an efficient response depending on its size.

Furthermore, any activity, such as recruitment, that leads to an increase in the local density could favour chain formation. Chemical trails laid by nestmates constituting a bridge (Hölldobler and Wilson 1978) might amplify and stabilise the collective choice, which is initially under the control of the entering and leaving probabilities. Considering the exploitation of a source of food, it also suggests that the break-up of the selected chain will be strongly correlated with the exhaustion of the resource by decreasing the passing flows of workers.

The striking point of these results is to show, beyond the process of chain formation, how living groups make collective choices. This self-organised system (Camazine

et al. 2001; Hemelrijk 2002) falls within the family of Local Activation–Long-range Inhibition models originally suggested by Gierer and Meinhardt (1972). We basically observe a competition between amplification (within a range of a few centimetres, the local density of nestmates modulates the probability for an individual to be part of the chain) and inhibition mechanisms, which arises automatically as a result of the depletion of the nest. Many collective decisions in animal societies obey similar principles. An example of such processes is the competition between recruitment to multiple food sources in social insects or gregarious arthropods, where the inhibition also arises as the result of the depletion of the number of available individuals (Camazine and Sneyd 1991; Seeley et al. 1991; Fitzgerald 1995; Detrain et al. 1999). Despite the difference in terms of mechanisms, both the dynamics of chain formation and trail recruitment lead to a bifurcation characterised by the emergence of an asymmetry in the number of individuals in the chains or around the food source (Sumpter and Pratt 2003). In the same way, an increase in the total population shows an abrupt change in the chain's population or on the trail (Beekman et al. 2001).

Self-assembling is an extreme case of the widespread phenomenon of aggregation. In different species of ants or cockroaches the dynamics of aggregation between individuals are also governed by an individual probability of joining or leaving an aggregate modulated by its size (Franks and Sendova-Franks 1992; Rivault and Cloarec 1998; Theraulaz et al. 2001; Depickère et al. 2004; Amé et al. 2004). Through the modulation of these individual probabilities, a wide range of spatial organisation can be observed, from a total aggregation to a segregation of individuals or items.

The ability of a colony to gather individuals and items could be one of the selected key mechanisms for the emergence of higher forms of co-operation, working in synergy with other parameters such as genetic and individual variability (Page and Erber 2002) and history (Weidenmüller 2002). We make the assumption that this basic mechanism should be generic and of particular importance in the patterns and dynamics observed in many collective tasks performed by insects and other animals. In this way aggregation, which is often only seen as a gathering of individuals, could be one of the keystones for a multiplicity of collective activities and decisions. It leads to an economy in terms of individuals and time and to the production of a wide variety of spatio-temporal structures (Camazine 1991; Hammerstein and Leimar 2002), well-adapted and fully integrated into some more general activities.

Acknowledgements We thank Prof. J.-M. Pasteels for his interest and his help in making the study possible on Laing Island, Papua New Guinea. This work was supported by the SWARM-BOTS Project, funded by the Future and Emerging Technologies programme (IST-FET) of the European Commission, under grant IST-2000-31010 and by grant numbers 2.4510.01 and 2.9008.90 for Belgian Joint Basic Research.

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