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Chain Formation in *Œcophylla longinoda*

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The aggregation phenomenon is very common in numerous activities of social insects, however, it is often their functional aspects that are studied, leaving their mechanisms not so well understood. With the example of chain formation in Œcophylla longinoda, *we present the mechanisms responsible for these collective structures. Our experimental results show that a change in the probability that a worker will decide to join or leave a chain is (1) strongly dependent on the number of ants present in the chain and (2) slightly dependent on the presence of a visual stimulus. The determining role of these probabilities is validated with the use of a mathematical model that reproduces the formation and breakup of the chain. Moreover, it predicts other properties of aggregation such as the influence of nest population size.*

KEY WORDS: Aggregation; chains; model; ants; *Œcophylla.*

INTRODUCTION

Aggregate formation is one of the most frequently observed phenomena in a wide range of behavior types demonstrated by social insects. A particular type of aggregation can be defined as self-assembling, which occurs when individuals grip on to each other. These structures are involved in bivouac formation in the genus *Eciton* (Rettenmeyer, 1963; Schneirla, 1971; Gotwald, 1995), chain formation in *Linepithema humile* (Bonabeau *et al.*, 1999; Lioni

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et al., in prep), raft formation in *Solenopsis invicta* (Morrill, 1974) and in swarms (Morse, 1963), and festoons of building honeybees (Darchen, 1959).

Ants of the genus *Œcophylla* (Ledoux, 1949; Hölldobler and Wilson, 1978, 1990) are characterized by their capacity to form two types of chains: one which allows the bridging of an empty space, for example, between two branches (Fig. 1), and another allowing the binding of leaves during nest

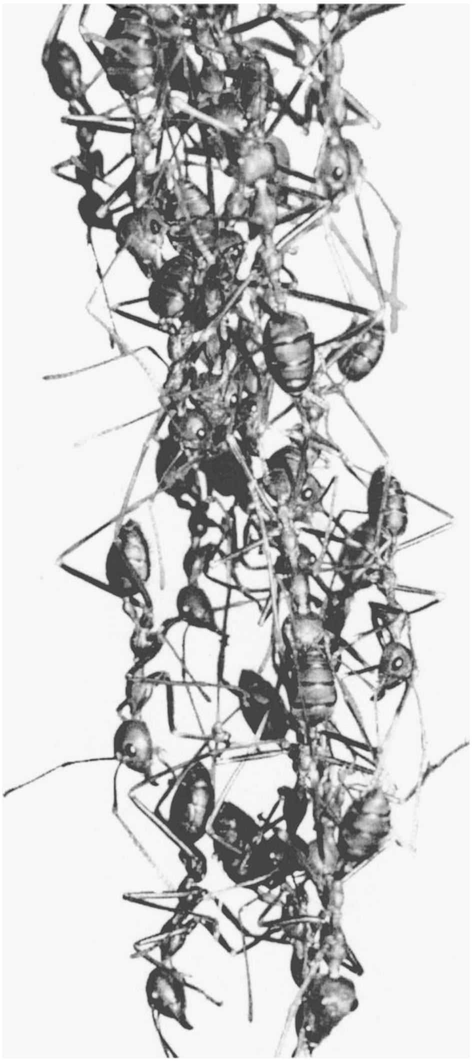

Fig. 1. Chain formation in the experimental setup.

construction (see, e.g., Hölldobler and Wilson, 1990, pp. 618–629). These chains are collective structures due to the capacity of the individuals to hang on to each other. This is due, in part, to their very strong, well-developed, adhesive arolia under the tarsus (Wojtusiak, 1995).

Our objective was to study the behavioral mechanisms implied in chain formation, which allows the bridging of gaps demonstrated by *Œ. longinoda*. These collective structures are formed by the progressive attachment of workers holding on to each other by their legs and remaining motionless. This paper describes results from experiments conducted under laboratory conditions and those from a model that makes the link between individual behaviors and collective dynamics.

METHOD

The ants used came from nests collected in March 1995 in the Cameroon. Their installation in the laboratory was carried out under the same conditions as used by Ledoux (1949). The original nests were placed at the foot of a lemon tree in which the ants spontaneously installed themselves, and in a few days they had built several nests from the leaves. The total population recovered amounted to several thousand workers. The colony was fed every 2 days with honey and dead crickets. The ambient temperature was around 27°C.

The experimental apparatus was built using preliminary observations where we were able to show how workers responded to a visual stimulus (a dark object imitating a thin branch). The workers attached themselves to each other in an attempt to reach the object. As soon as this stimulus was removed this hanging behavior disappeared.

The experimental apparatus (Fig. 2) used to study chain formation consisted of a horizontal metal branch connected to a box into which 150 workers, removed from the nest exterior, were introduced. The experiment began 1 h after the introduction of the workers into the box. A black bar (width, 1 cm; length, 30 cm) was placed 6 cm below the artificial branch and situated 15 cm from the beginning and 3 cm from the end of the horizontal part. The apparatus was enclosed in white card to isolate the workers from environmental visual stimuli. The experimental group was used in two or three experiments, then replaced in the foraging area. Experiments carried out on the same day were separated by a 2-h interval.

This apparatus allowed the ants which were placed in the box to travel around the metal bar and rapidly from a chain just above the zone where the black bar was placed. The chain formed progressively by the successive integration of new ants into the chain (Fig. 1). This apparatus was a good compromise between the possibility of observing the chain formation phenomenon and that of observing its reproduction in a natural situation.

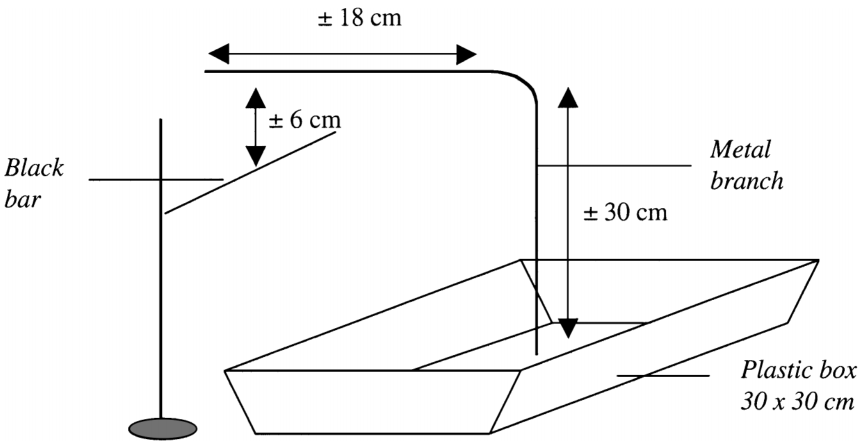

Fig. 2. Experimental setup (see text).

Data collection was done using a video that allowed observation of the individual as well as the global behaviors. In the experimental set conducted ($N = 10$), the attractant was put in place for 20 min, then removed, which allowed the breakup of the chain to be observed. It was noted that no chain was produced without the use of a visual attractant. Recording started as soon as the black bar was put in position and was stopped when the chain had completely broken up.

The measurements considered for chain formation and breakup dynamics were as follows.

(1) The number of workers that pass above the visual stimulus per second (ϕ_p).
(2) The number of workers which join the chain per second (ϕ_e). Observations were limited to the 5-cm zone above the attractant.
(3) The number of workers which leave the chain via the artificial branch per second (ϕ_s). When the attractant is reached workers can leave the chain in two ways: by the artificial branch or by the attractant. Due to the short length of chains observed, very few workers reached the attractant (less than 1% of over 1152 ants leaving the chain left it via the attractant). Thus these data were grouped with the number of workers leaving via the artificial branch.

These two values (ϕ_e, ϕ_s) allowed calculation of the chain size at time t(X: number of workers):

$$X(t) = X(t-1) + \phi_e(t) - \phi_s(t)$$

The probability that an individual will join the chain was defined as the flow of workers joining the chain, divided by the passing flow on the artificial branch:

$$P_e(t) = \phi_e(t)/\phi_p(t)$$

The probability of an individual to leave a chain (P_s) in 1 s was defined as the mean number of workers leaving the chain divided by the chain size at time $t - 1$ s:

$$P_s(t) = \phi_s(t)/X(t-1)$$

Measurements of the hanging time of workers at the end the chain was also considered. In this case, only workers that were motionless and without any other individual hanging onto them were counted.

EXPERIMENTAL RESULTS

Description of Chain Formation

To allow the reader to visualize the phenomenon, a short description is given. Figure 3 illustrates one of the typical evolutions of worker number in a chain with and without an attractant and the cumulative number of workers entering a chain in a time course. These dynamics evolved in four stages (a, b, c, and d in Fig. 3) and were observed in all chains studied.

(a) At the beginning of the experiment a few workers were seen walking on the artificial branch. The flow and the number of hanging workers were generally very low.
(b) The flow increased with time until it reached a high value where it remained constant (mean flow for this example = 0.13 worker/s); meanwhile there was an increase in workers hanging above the attractant and forming a chain.
(c) Then a plateau period was observed, where the number of workers in the chain remained relatively stable: in this example, between 25 and 30 workers, for about 400 s.
(d) Finally, a rapid breakup of the chain occurred when the attractant was removed. This occurred despite a flow of entrants equivalent to that observed in the presence of the attractant. In most of the experiments, when the number of ants in the chain reached a population close to 20–30, we observed that the passing flow slowed down slightly.

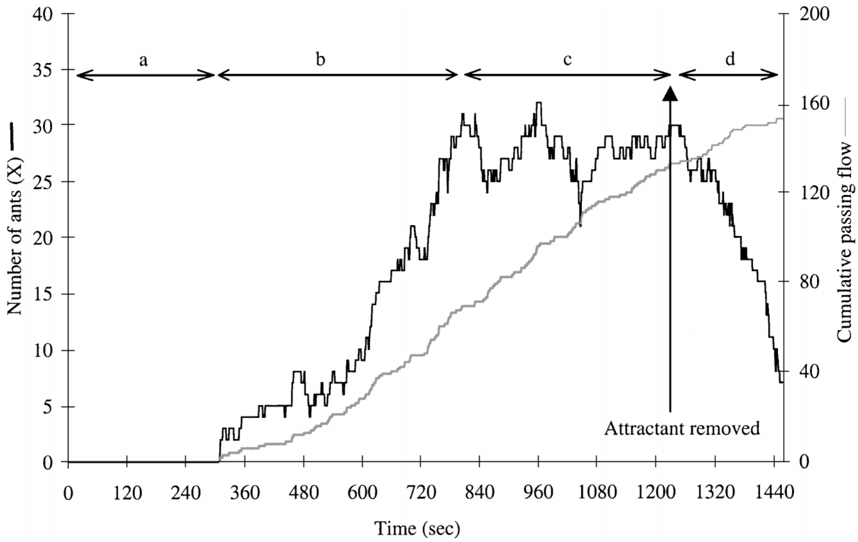

Fig. 3. Typical evolutions of the worker number in a chain (----) with and without attractant and the cumulative passing flow (grey) in a time course. To smooth the fluctuations of the passing flow, the cumulative passing flow is used. This flow at time *t* is the total number of ants that pass between time 0 and time *t*. The four stages of the dynamics are (a) the beginning of the experiment, when a few workers are walking on the metal branch; (b) the increase in workers hanging above the attractant and forming a chain; (c) the plateau period; and (d) the breakup of the chain when the attractant is removed.

These first results demonstrate the importance of a visual attractant in the chain formation behavior of this ant. In our experiments, most of the chains observed were short, not long enough to reach the attractant. An explanation for this situation can be found in the total population number, the passing flow, and the distance of the attractant (see The Model, below). The growth of the chain resulted from the addition of ants coming from the artificial branch, gripping at the beginning of the chain, or traveling along it to remain motionless at its end for a while. After being motionless (if other workers did not block them by gripping,) workers traveled up and left the chain.

Global Dynamics

Figure 4 illustrates the mean evolution of the chains that formed in the zone above the attractant for each experiment. The latency stage was highly variable (mean = 260 s, SD = 130 s), and the flow was close to zero, so we focused on the growth stage. As a consequence, $t = 0$ is not the beginning

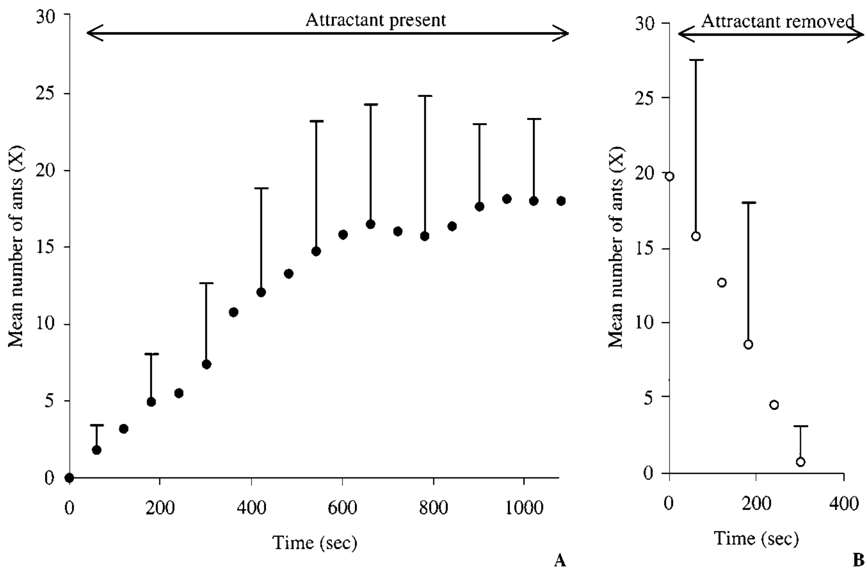

Fig. 4. Mean and standard deviation of the number of ants in the chain and breakup for the 10 experiments. (a) Mean growth with attractant. $t = 0$ is the beginning of the growth. (b) Mean breakup without attractant. Time $t = 0$ corresponds to the removal of the attractant.

of the experiment but the beginning of the growth (stage b in Fig. 3). Due to the fact that the attractant was removed after 1200 s (from the start of the experiment), the mean time of growth was reduced to 1080 s, which was the shortest experimental time observed from $t = 0$ to $t = 1200$ s (Fig. 4a). There was an initial growth in worker number in the chain, followed by the beginning of a stabilization around a mean value of 18 workers, for a mean flow of arrivals of 0.12 worker/s ($\pm$SD = 0.02).

When the attractant was removed, a rapid decline in the number of workers in the chain was observed, despite an entrance flow equal to the situation with attractant [0.12 worker/s with attractant, 0.11 worker/s without ($\pm$SD = 0.02)]. After 5 min, all the chains had disappeared (Fig. 4b).

Individual Probabilities

This second part shows the mechanisms responsible for the chain formation and the chain breakup after the attractant was removed. We are particularly interested in the individual probabilities of entering and leaving the chains to understand their role in the dynamics observed. To do this and to distinguish the role of the attractant from that of the number of ants in the chain, these probabilities were measured as a function of the chain population.

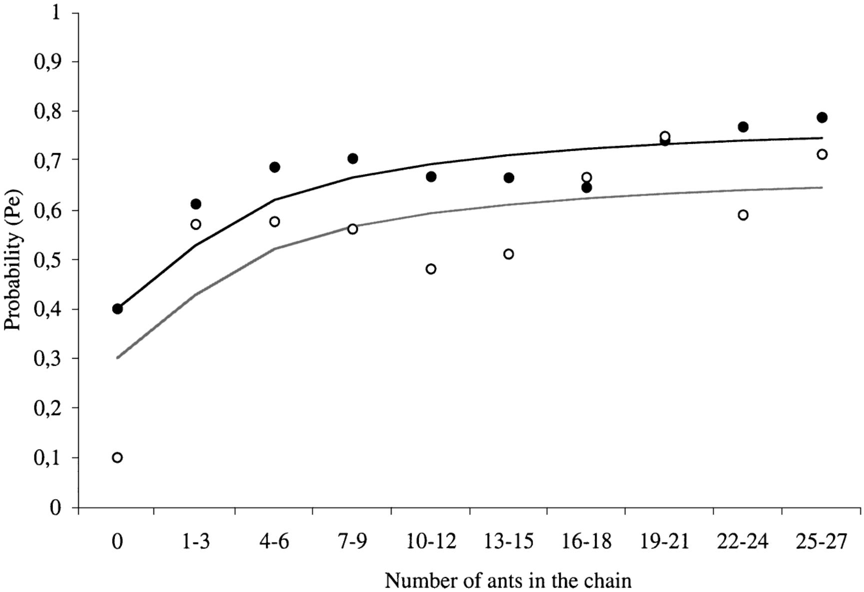

Fig. 5. Individual probabilities of entering a chain depending on the number of ants in the chain. (•) With attractant; (○) without attractant.

The Probability of Entering a Chain (P_e)

Figure 5 shows the individual probabilities of entering a chain in the presence and absence of an attractant. The probability of spontaneous hanging (in the absence of a chain) is 0.4 with an attractant and 0.1 without (numbers of passing ants observed are 198 and 74, respectively). When a chain was present, the data were divided into groups of three due to the low frequency of observations. The probability of entering was quite stable, with a mean value of 0.7 with the attractant and 0.6 without.

The Probability of Leaving a Chain (P_s)

Figure 6 illustrates that the individual probabilities of leaving a chain were dependent on the chain size. The probabilities of leaving a chain were higher in the situation without an attractant than in the one with an attractant. These probabilities are mean values of the different events that occurred in the chain (gripping at the beginning or at the end of the chain, traveling up and down). In both the presence and the absence of an attractant, the probabilities of leaving decreased rapidly, until a plateau value was reached

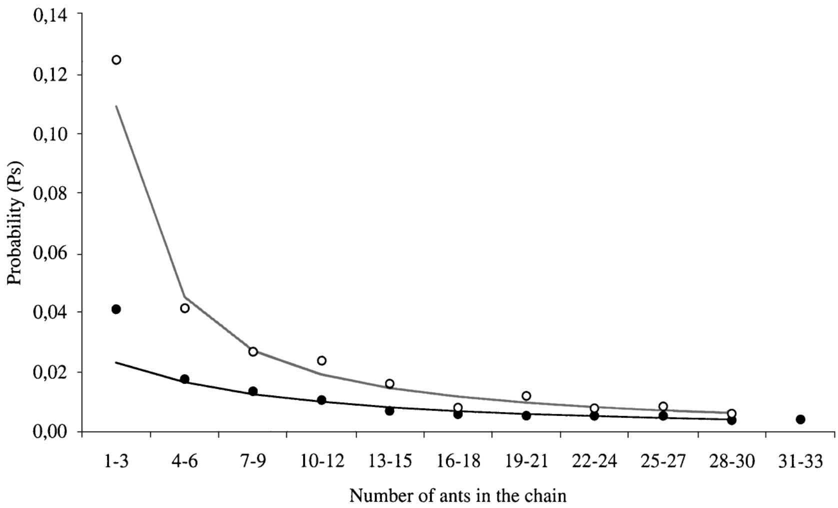

Fig. 6. Individual probabilities of leaving a chain depending on the number of ants in the chain. (•) With attractant; (○) without attractant.

around 0.005. This decrease showed a form of group effect between the workers. The presence or absence of a visual stimulus did not qualitatively affect the relationship between the chain size and the probability of leaving.

The Motionless Time at the End of a Chain

We investigated the behavior of workers situated at the end of a chain by measuring the time they remained motionless. These ants were particularly important to the leaving dynamics. Qualitative observations showed that a large number of ants that left the chain were situated at its extremity. The question was whether this motionless time was ruled by an individual memory effect or by a collective mass effect. These results concerned only workers at the end of a chain, with no other ant hanging onto them. Figure 7 shows the fraction of ants (w) that remained motionless (inverse cumulative distribution in hanging time). For the two experimental situations, an exponential decrease in the fraction of ants (w) as a function of the hanging time at the end of the chain was observed:

$$w = e^{-\frac{t}{T_m}}$$

where T_m represents the mean hanging time at the end of a chain, which was 10.5 s ($r = 0.99$, $P < 0.001$, df $= 28$) with an attractant and 4.6 s ($r = 0.99$, $P < 0.001$, df $= 10$) without an attractant. There is a significant difference between these two times (Student test: $t = 3.89$, $P < 0.001$, df $= 105$).

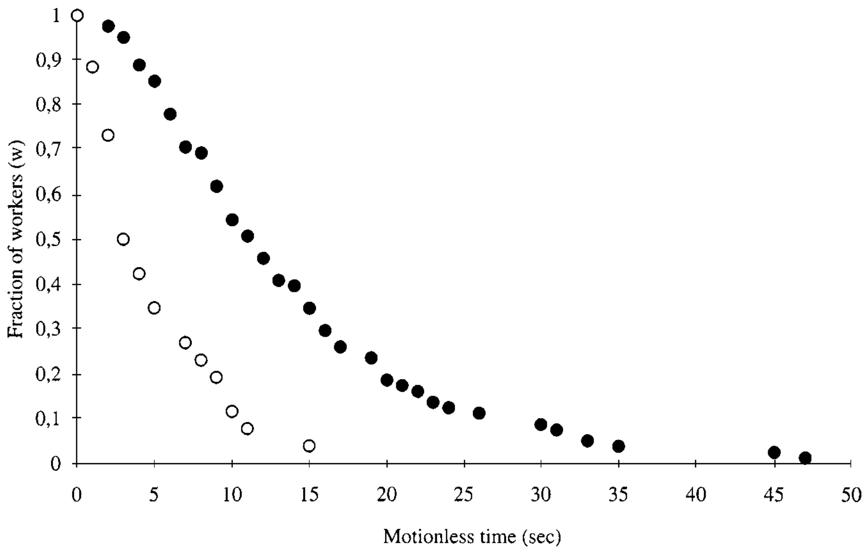

Fig. 7. Fraction of ants (w) still remaining motionless at time t (inverse cumulative distribution in hanging time). (•) With attractant; (○) without attractant.

The probability of leaving the end of a chain was constant and independent of the time spent at this extremity [for a discussion of such exponential laws see, e.g., Pasteels *et al.* (1986)].

THE MODEL

A stochastic model has been developed using the experimental results [Monte Carlo simulation (Sobol, 1994; Gillespie, 1992; Camazine *et al.*, 2001)]. This model describes the evolution of the number of individuals in the chain, corresponding first to the growth phase with an attractant present and then to the breakup phase when the attractant is removed. In the first phase (verification) we determined whether this model correctly reproduced the three stages of the dynamics observed (growth, plateau, and breakup). In the second phase (prediction), using the validated model we tested the influence of a key parameter, the number of ants available, on the dynamics of chain formation.

Description

At each second, the chain contained X individuals. The chain dynamics were under the control of three events: the passing flow and the probabilities of entering and leaving the chain. At the beginning ($t = 0$) the total population (Pop) was in the box and $X = 0$. At each second, each ant in the box had a probability P_0 of leaving it and arriving above the attractant. These ants had a probability (P_e) of entering the chain. At the same time, each ant in the chain had a probability (P_s) of leaving it. This allowed the calculation of the number of ants in the chain (X) each second. These three probabilities were defined as follows.

P_0: The mean passing flow was fairly constant, with a slight decrease when the population in the chain (X) became large. This strongly suggested a linear dependence on the flow with the population remaining in the box (Pop $-$ X). The link between the mean passing flow (ϕ_p) and P_0 was

$$\phi_p = P_0(\text{Pop} - X)$$

To respect the mean experimental passing flow at the beginning of the growing phase, P_0 was equal to 0.0012 s^{-1}.

P_e and P_s: We have shown under Experimental Results that the probabilities of entering (P_e) and of leaving (P_s) depended on the number of individuals making up the chain. We have identified the relationship between these probabilities and the number of individuals (X) to use them in the model:

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

$$P_s = C_{s0} + \frac{C_{s1}}{C_{s2} + X^{\nu}}$$

The function P_e expresses the idea that the probability of joining the chain growth with X and reaching a plateau value is equal to $C_{e0} + C_{e1}$. C_{e0} is the value of spontaneous hanging when $X = 0$. P_s decreases with X and reaches C_{s0} for large X values. The parameter values are listed in Table I.

Results

Verification of Growth and Breakup Dynamics

Figure 8 compares the mean evolution of number of ants in the chain for 2000 simulations with the experimental mean. The model does not include a latency time before the establishment of an arrival flow on the artificial branch, that is, all chains begin at $t = 0$. This also reduced the total duration of the experiments (limited to 1080 s). Looking at the growth dynamics we can see a strong similarity between the two curves. A χ^2 test shows that the two curves are similar ($P = 0.99$, df $= 17$, $\chi^2 = 3.046$). Comparing theory and experiments for the mean chain breakup also gives a close agreement. The two curves show a rapid reduction in the number of ants for comparable

Table I. Parameter Values Used in the Model

	Pop = 150	
	Attractant present	Attractant absent
P_e		
C_{e0}	0.4	0.1
C_{e1}	0.4	0.4
C_{e2}	4	4
ν	1	1
r	0.71	0.25
P_s		
C_{s0}	0	0
C_{s1}	0.26	0.36
C_{s2}	9	1.3
ν	1.2	1.2
r	0.95	0.96

time scales. A χ^2 test shows that the two curves are not statistically different ($P = 0.52$, df $= 5$, $\chi^2 = 4.18$).

Prediction Flow Effect

Our theoretical and experimental results show the dominant role of a visual attractant in chain formation and breakup. The model allowed us to

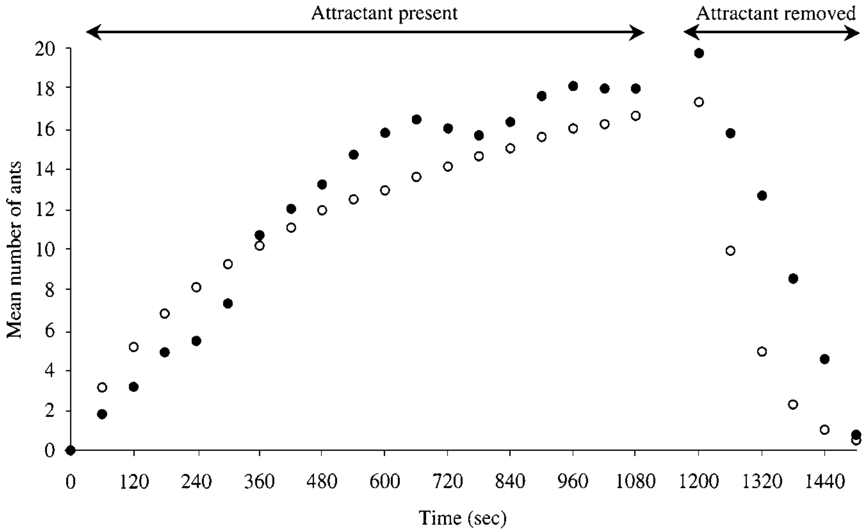

Fig. 8. Mean number of ants in the chain over time. (•) Experimental results; (○) simulation results.

explore the influences of parameters such as the passing flow and the total population available. Remember that the passing flow is dependent on the total population in the box [$\phi_p = P_0(\text{Pop} - X)$]. As the population (Pop) increased the mean passing flow also increased (for example, there were 0.18 and 0.24 ant/s, respectively, for population sizes of 150 and 200 ants at a fixed probability).

Figure 9a shows the mean number of ants in the chain as a function of the population (Pop) for a probability of leaving the box (P_0) fixed at the experimental value of 0.0012. Curves 1 and 2 correspond to the situations with attractant at 20 and 100 min, respectively, which correspond to the stationary value (mean maximum number of ants in the chain). Curves 1 and 2 show that the mean number of ants in the chain is under the control of the total population. Below populations of ≈120–130 ants, chains were small. Above these populations there was a linear increase in the number of ants in chains. It was as if there was a threshold value of the population size above which chains could form. This threshold was not the result of a change in the behavior of individuals relating to the size of the population, but simply resulted in hanging and leaving dynamics.

Figure 9b gives the fraction of ants in a chain depending on the population size for times 20 and 100 min. It is a better illustration of how small variations in the population act on chain growth and, thus, particularly in the stationary state (curve 2). We note that a 70% increase in the population size (from 150 to 250 workers) leads to a fivefold increase in the proportion of individuals involved in the chain. We note that the larger the population, the larger the proportion of individuals in the chain.

We use the simulation to analyze the influence of the total population on the dynamics under the presence of an attractant (for 20 min) and its removal (see experimental). Figure 10 shows the mean evolution (and the standard deviation) of the number of ants in the chain depending on the time, for five population sizes (Pop = 150, 300, 375, 450, and 500). When the attractant was present (Fig. 9b), we saw the influence of the population size on the rate of growth of the chain. When the attractant was removed, two situations were observed: with and without breakup. Above a population size of ≈350, the removal of the attractant did not lead to chain breakup. The population of workers in the chain decreased slightly and stayed more or less stable.

Similar simulations were done without any attractant for 100 min. This means that we started the simulations with the entering and leaving probability values corresponding to the absence of an attractant (see Table I). As shown in the previous situations, the dynamics were strongly linked to the total population. For a population smaller than 350, no chains were observed. For larger populations (Pop $>$ 500), we always observed the formation of a chain (Fig. 11a).

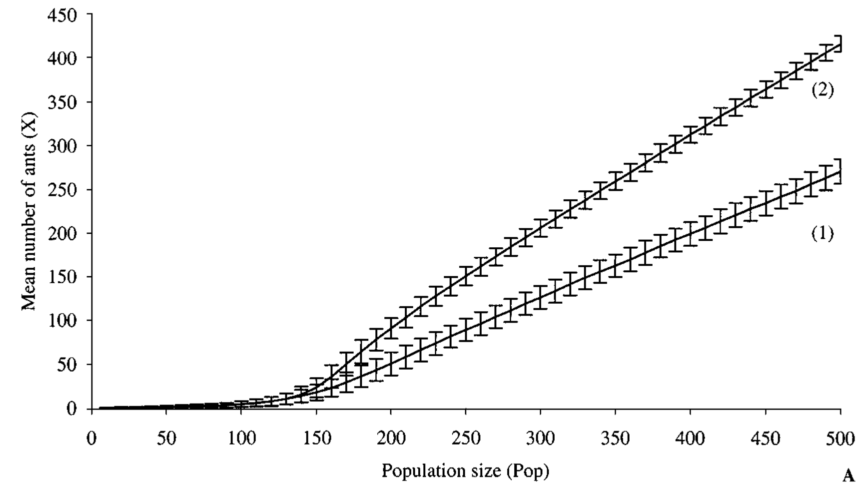

Fig. 9. (a) Mean number of ants in the chain (mean X) with attractant depending on the population size (Pop). (1) After 20 min; (2) after 100 min. The latter value corresponds to the stationary state of the model. (b) Mean fraction of the total population in the chain (mean X/Pop) depending on the population size (Pop). (1) After 20 min; (2) after 100 min.

Between these population values (350 < Pop < 500), we observed both results. Some simulations led to the formation of a chain, and others did not. Figure 11b illustrates the result of two simulations for a population size equal to 375. One leads to no chain (1) and one reaches a population of 100 ants in the chain (2). To summarize, as the population size increased, the

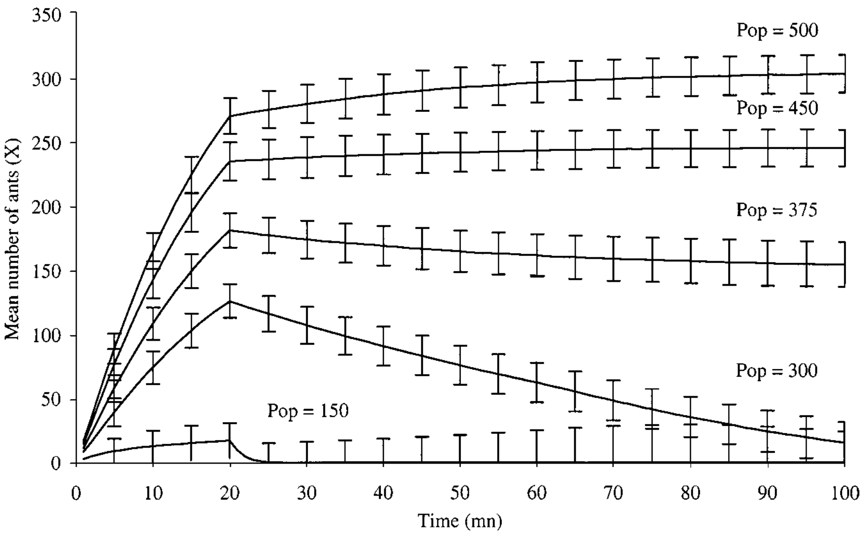

Fig. 10. Mean and standard deviation of the number of ants in the chain over time for five population values: 150, 300, 375, 450, and 500. The attractant is present from $t = 0$ to $t = 20$ and then removed.

fraction of simulations leading to the chain formation increased. For example, for population sizes of 375, 450, and 500, we observed that 3, 60, and 96%, respectively, of the chains had at least 20 individuals.

These results show that the dynamics are not only under the control of the attractant and its influence on the entering and leaving probabilities, but also, surprisingly, under the control of the population size available and the history of the chain.

DISCUSSION

Our experimental results showed that workers were sensitive both to the presence of an attractant and to the number of workers in the chain. The higher the number of workers in a chain, the higher the probability to join the chain and to stay in it. To summarize, we have demonstrated the key role of the number of ants in the chain, which acts as a positive feedback for the entrances and a negative feedback for the leavings. We have no information on the nature of the stimulus responsible for this attractiveness. It could be tactile and/or chemical.

The model showed that, without changing any behavioral rules, chain formation was also very sensitive to the flow of ants passing above the chain, which was under the control of the population size (Pop in the model). It

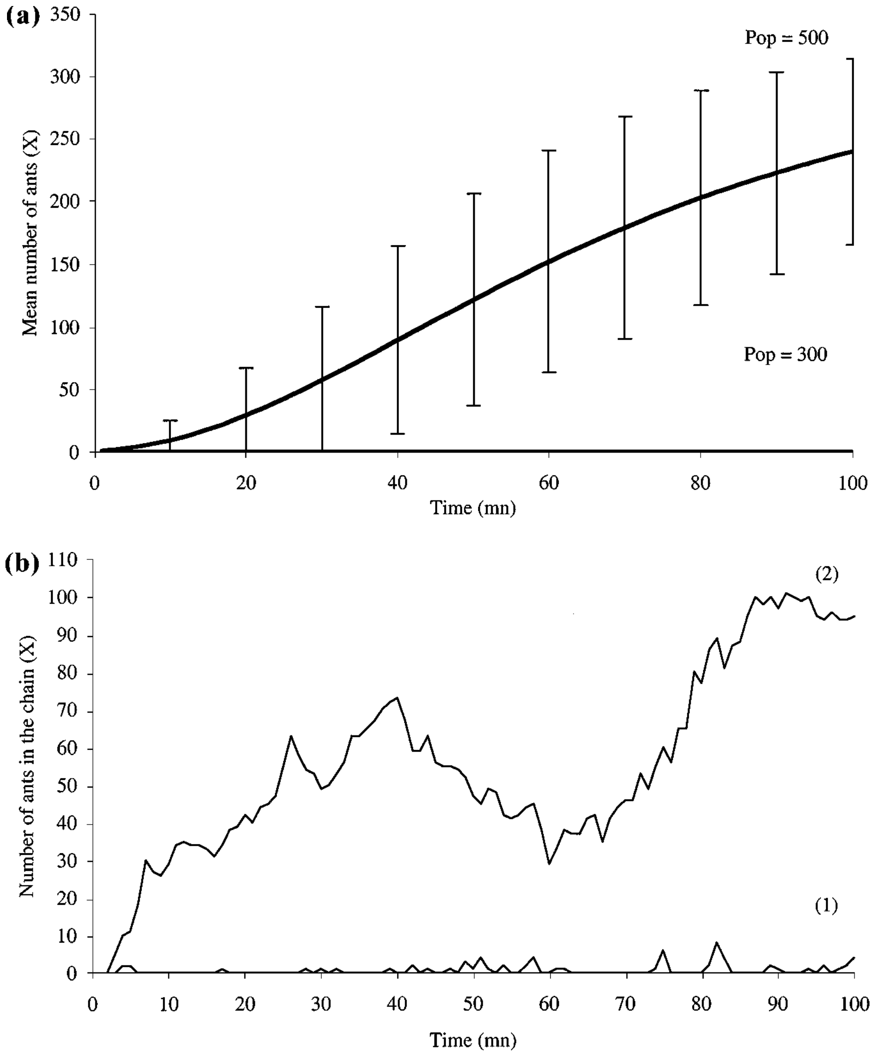

Fig. 11. (a) Mean and standard deviation of the number of ants in the chain over time for two population values (300 and 500) without any attractant. (b) Two examples of changes over time in the number of ants in the chain for a population size = 375. (1) No chain is observed; (2) the number of workers reaches 100.

showed that with an attractant a slight increase in this population produced a rapid growth of the number of ants in the chain (X) as well as an increase in the proportion of individuals involved in the chain (X/Pop). Surprisingly, it also showed that for a population (Pop) larger than 350, the removal of the attractant did not lead to breakup, but to the maintenance of the number of ants in the chain. Moreover, for large populations (Pop > 500), large chains could be formed without any attractant.

We did not present the results concerning the influence of the probability of entering (P_0), which can be related to the motivation of ants to go onto the artificial branch. Some similar conclusions might be obtained when the population size (Pop) is fixed but the probability value of leaving the box (P_0) is increased.

To conclude this discussion, these experimental and theoretical results must be reintroduced to the context of the natural colony activity, in which visual stimuli can vary in size and distance. Therefore the theoretical results suggest that for the same physical or visual environment, a chain may emerge spontaneously if the density of the ants (corresponding to Pop in the model) in the area is sufficient. Any event that leads to an increase in density will favor chain formation or its maintenance, where it is needed. This is particularly the case in events such as food recruitment, nest moving, and defensive activity (Hölldobler and Wilson, 1978, 1991). For example, food recruitment, which favors an increase in the flow of ants, may lead to the formation of a chain, which then becomes integrated into the path. The theoretical results suggest that due to this increase in population, the chain can remain stable and last until food exhaustion (end of the recruitment). In such an activity, the chain becomes a living bridge where recruiting ants also trail on their nestmates (Hölldobler and Wilson, 1978).

Chain formation is one particular example of aggregation in ants and other social arthropods. Moreover, numerous social activities involve aggregation or steps that may be seen as an aggregation. The method used in this study could be extended to these numerous cases (e.g., Rivault *et al.*, 1999). It could test the hypothesis that these dynamics of aggregation are ruled by similar probabilities of joining and of leaving the cluster depending on its size and on the environmental characteristics (Deneubourg *et al.*, 1990: Millor *et al.*, 1999). If this hypothesis were confirmed, it would show the robustness of these simple mechanisms, which implicate an economy based on time, avoiding the coding of specific behavior patterns or activities and how they may lead to a diversity of responses toward changes in physiological, social, and environmental characteristics.

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