

# Phase transition between disordered and ordered foraging in Pharaoh's ants

Madeleine Beekman\*<sup>†</sup>, David J. T. Sumpter<sup>‡</sup>, and Francis L. W. Ratnieks\*

\*Laboratory of Apiculture and Social Insects, Department of Animal and Plant Sciences, Sheffield University, Sheffield S10 2TN, United Kingdom; and  
<sup>‡</sup>Centre for Mathematical Biology, Mathematical Institute, Oxford University, 24-29 St. Giles, Oxford OX1 3LB, United Kingdom

Communicated by I. Prigogine, Free University of Brussels, Brussels, Belgium, June 7, 2001 (received for review August 12, 2000)

The complex collective behavior seen in many insect societies strongly suggests that a minimum number of workers are required for these societies to function effectively. Here we investigated the transition between disordered and ordered foraging in the Pharaoh's ant. We show that small colonies forage in a disorganized manner, with a transition to organized pheromone-based foraging in larger colonies. We also show that when food sources are difficult to locate through independent searching, this transition is first-order and exhibits hysteresis, comparable to a first-order phase transition found in many physical systems. To our knowledge, this is the first experimental evidence of a behavioral phase transition between a maladaptive (disorganized) and an adaptive (organized) state.

Systems consisting of simple interacting units often exhibit phase transitions caused by changes in the interactions among units (1–3). For example, heating a ferromagnet increases the relative strength of the disordering thermal forces relative to the ordering magnetic forces, and at a critical temperature the metal is demagnetized. Similar transitions have been observed in biochemical and biological systems ranging from enzyme kinetics (4), to the growth of bacterial populations (5), and brain activity (6). In insect societies, workers often use multiple interactions and simple rules to produce complex and adaptive behavior at the colony level (7). Examples include foraging (8–14), nest construction (13, 15–18), and nest-site selection (19–21). These examples suggest that phase transitions should occur in insect societies (8, 22). We investigated the transition between disordered and ordered foraging in ants.

In many ants, foragers lay pheromone trails from food sources back to their nest. These trails allow nestmates to locate and exploit the source easily. As more ants collect food they reinforce the trail. Although the pheromone trail is volatile, it can be maintained if sufficient ants use it. The probabilities that an individual ant joins and remains on the trail increase with trail strength (23). In this article, we have modeled how the total increase in the number of ants walking to a single food source depends on colony size. The model makes three important predictions: (i) the increase in the number of ants walking to the food source along the trail is a nonlinear function of colony size; (ii) when independent discoveries of the food source are infrequent, there is a first-order (discontinuous) phase transition from relatively low levels of foraging without a pheromone trail to trail-based foraging as colony size increases; (iii) this discontinuous transition exhibits hysteresis—for intermediate-sized colonies; either no trail or a well used trail occurs depending on initial conditions. In other words, intermediate-sized colonies find it difficult to start a trail but can sustain an existing one. We tested the model by using Pharaoh's ants *Monomorium pharaonis* (L.).

## The Model

We modeled the total increase,  $x$ , in the number of ants walking to a single food source as a function of colony size,  $n$ . The model assumes that the probability that an ant begins foraging at the food source depends on both the probability per min per

individual,  $\alpha$ , that she finds it through independent searching, and the probability per min per individual,  $\beta x$ , that she is led to it by the pheromone trail. The  $x$  ants following the pheromone trail lose it with rate  $sx/(s+x)$ , where  $s$  is a constant determining the maximum rate at which ants can leave the trail. In other words, trail strength increases as more ants use the trail, and ants are less likely to lose a stronger trail.  $\alpha$ ,  $\beta$ , and  $s$  are constants that depend on the topology of the foraging environment and the ability of individual ants to follow pheromone trails. Thus, the rate of change in foragers walking to the food source is given by the following mean-field equation:

$$\begin{aligned} \frac{dx}{dt} &= (\text{ants beginning to forage at feeder}) \\ &\quad - (\text{ants losing pheromone trail}) \\ &= (\alpha + \beta x)(n - x) - \frac{sx}{s + x}. \end{aligned}$$

This equation is solved for  $x$  at  $dx/dt = 0$ , or equivalently,

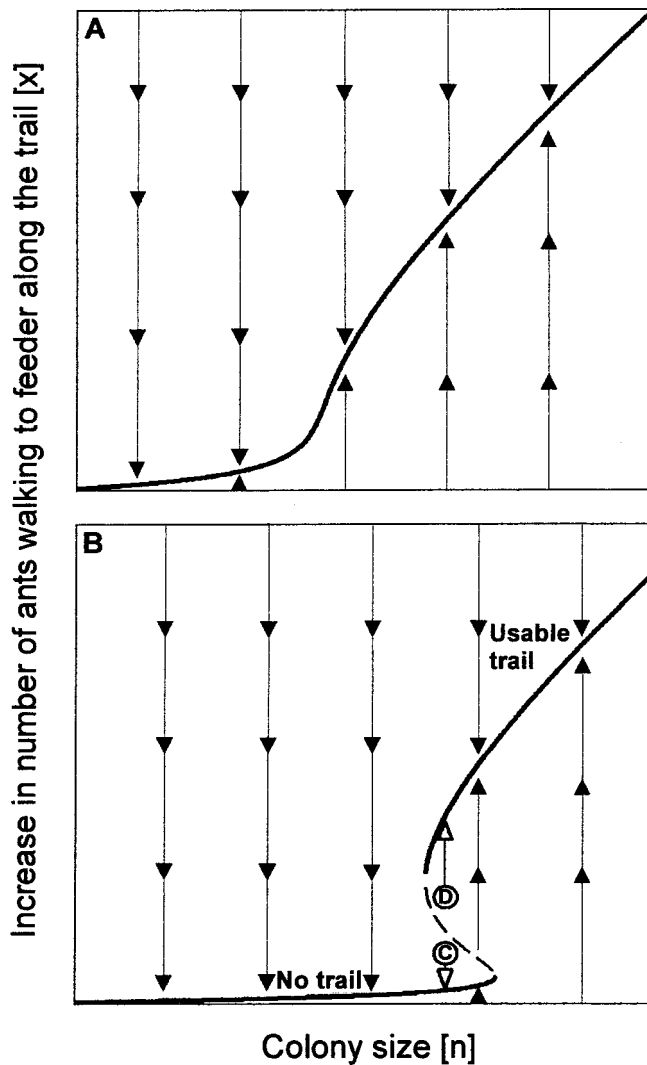
$$\beta x^3 + (\beta s + \alpha - \beta n)x^2 + (s(1 + \alpha - \beta n) - \alpha n)x - \alpha ns = 0, \quad [1]$$

to give equilibrium solutions. This cubic equation gives either one or three solutions depending on parameter values. Fig. 1 shows the predicted equilibrium increase,  $x$ , in the number of ants walking to a single food source as a function of colony size,  $n$ , when the feeder is frequently ( $\alpha = 0.021$  ants per min; Fig. 1A) and infrequently ( $\alpha = 0.0045$  ants per min; Fig. 1B) found by independently searching ants. In Fig. 1,  $\beta = 0.00015$  and  $s = 10$  are fixed. In Fig. 1A and B, there is a nonlinear increase in the number of ants walking to the feeder with colony size.

Where there is only one equilibrium solution, as in Fig. 1A, it is stable, and the total increase in foragers at the feeder is uniquely predicted by that solution. In this case, the increase in foraging with colony size is said to exhibit a continuous (second-order) phase transition. Where there are three equilibria, as in Fig. 1B, two are stable and depending on the initial value of  $x$ , the total increase in foragers may correspond to either solution. In Fig. 1B, the solid lines are the stable equilibria, whereas the dashed line is the unstable equilibrium. The stable equilibria do not meet and Fig. 1B is said to exhibit a discontinuous (first-order) phase transition. The coexistence of two stable equilibria in Fig. 1B for certain values of  $n$  implies that hysteresis occurs, meaning that the equilibrium distribution of ants walking to the feeder critically depends on the initial number at the feeder. In Fig. 1B, if fewer ants than the unstable equilibrium initially discover the source (point C), then the total increase in foragers

<sup>†</sup>To whom reprint requests should be addressed at: Schools of Biological Sciences and Mathematics and Statistics, University of Sydney A12, Sydney NSW 2006, Australia. E-mail: mbeekman@bio.usyd.edu.au.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

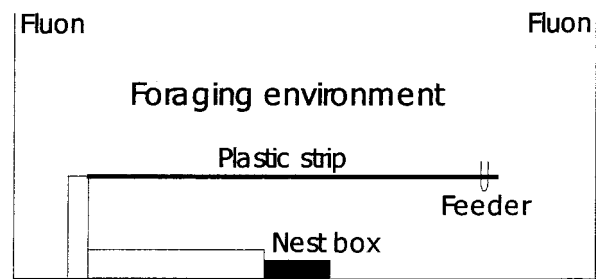


**Fig. 1.** The predicted total increase,  $x$ , in the number of ants walking to a single food source as a function of colony size,  $n$ , when the feeder is found (A) frequently ( $\alpha = 0.021$ ) and (B) infrequently ( $\alpha = 0.0045$ ) by independently searching ants. The other parameters,  $\beta = 0.00015$  and  $s = 10$ , are fixed. A and B correspond to solutions of Eq. 1. A has a unique solution for all  $\alpha$ , whereas B has two stable solutions (solid lines) for a range of  $\alpha$  values. The dashed line is the unstable equilibrium. If fewer ants than the unstable equilibrium initially discover the source (point C), then the total increase in foragers will be determined by the lower stable equilibrium. However, if the initial discovery is by a larger group (point D), then the increase will be to the upper equilibrium. The arrows A and B visualize where a point in phase space will move to from its initial position. For example, in A, a point in the upper left-hand corner will move to the lower left-hand corner. When there is more than one stable equilibrium, as in B, for intermediate-sized colonies, a point in phase space can move to one or the other equilibria depending on its initial condition (points C and D).

will be determined by the lower stable equilibrium. However, if the initial discovery is by a larger group (point D in Fig. 1B), then the increase will be to the upper equilibrium. Hysteresis can occur whenever there are three equilibrium solutions to Eq. 1, but in particular, we predict its occurrence for small  $\alpha$  and intermediate-sized values of  $n$ .

### Materials and Methods

We chose the Pharaoh's ant *Monomorium pharaonis* as a model species because the workers lay pheromone trails and are small, 2-mm long, which facilitates laboratory study. In addition, colony



**Fig. 2.** Diagrammatic representation of the experimental set-up. Brood is located inside the nest box. Ants are prevented from escaping by a layer of Fluon (Sigma) applied to the rim of the container that serves as a foraging environment.

size can easily be manipulated because Pharaoh's ants have multiple queens and lack nestmate recognition, thus colonies can be combined and divided (24, 25). Our basic experimental protocol was to manipulate the number of ants in a colony, and hence indirectly the total number of foragers, and then observe whether a pheromone trail built up to a syrup feeder 50 cm away. Study colonies had several queens, brood (eggs, larvae, and pupae), and  $n$  workers. They were housed in a heated room kept at  $20 \pm 2^\circ\text{C}$  and fed with egg yolk and dead insects. The colony was housed in a wooden nest box ( $11 \times 2 \times 8$  cm) in a plastic box ( $45 \times 30 \times 15$  cm) that acted as a foraging environment (see Fig. 2 for details). A feeder, an Eppendorf vial with three small holes at 1 mm above ground level, filled with a 1 M sucrose solution was placed 50 cm from the nest at the end of a plastic strip (3-cm width). Before the start of each experimental trial, ants were deprived of syrup for 1–3 days.

During each experimental trial, we counted the number of ants crossing a line 5 cm from the feeder per min at intervals of 10 min, starting 5 min after the first ant(s) found the feeder. We made 7 such measurements per trial. To obtain the increase in ants foraging at the feeder for each trial, we took the mean of the 3 consecutive measurements with the largest combined increase and subtracted from that mean the initial number of ants crossing the line before the feeder was set up (1 measure per trial). In this way we were sure of comparing the maximum foraging response in each trial. In particular, this measure eliminates the possibility that different delays in the onset of foraging among trials cause anomalous differences in the results. The initial number of ants crossing the line in absence of the feeder was used as an estimate of the independent discovery rate,  $\alpha$ .

### Results

Fig. 3 shows the increase in the number of ants walking to the feeder along the trail in relation to colony size  $n$ . For colonies of 100–600 ants, the increase in the number of ants is small (pooled mean  $\pm$  variance  $0.6 \pm 1.36$ ) and not significantly different from a normal distribution fitted with the same mean and variance ( $\chi^2 = 8.22$ ;  $P = 0.4$ ). The number increases steeply for colonies exceeding 600 ants and does not fit the same normal distribution (for 700 or more ants  $\chi^2 > 1000$ ;  $P < 0.00001$ ). This significant change in both the mean and the variance clearly demonstrates that a nonlinear process underlies ant foraging.

Our data support the hypothesis that there is a phase transition from disorganized (without using a pheromone trail) to organized (trail-based) foraging as the number of ants increases. In particular, colonies of 600 ants or fewer cannot form a trail toward a feeder, whereas larger colonies can. However, larger colonies do not always form a trail. There are two possible reasons for this occasional failure of trail build-up. The first reason relates to unavoidable variation in the study colonies. We

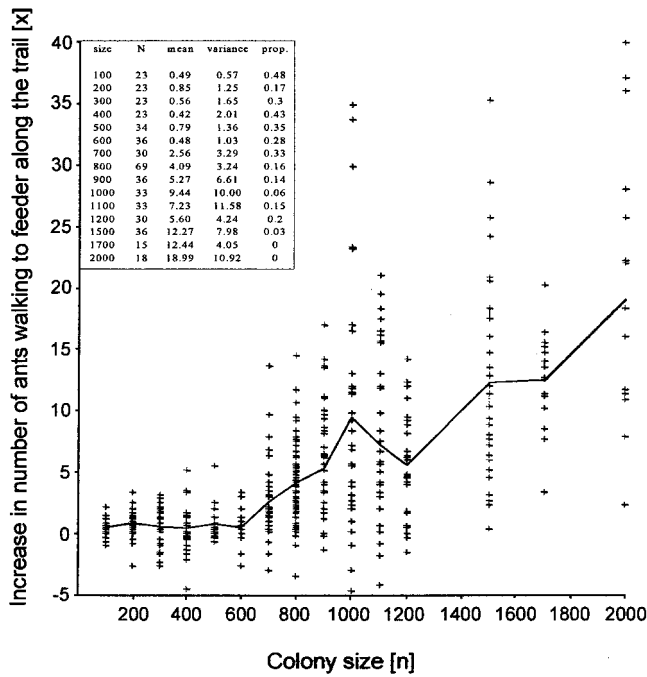


Fig. 3. Colony size ( $n$ ) vs. the increase in the number of ants walking to the feeder along the trail. Note that here  $n$  refers to the total number of ants in the colony, whereas in Fig. 1,  $n$  denotes the number of foragers. The line connects the means of all trials at a given colony size. Crosses represent single trials. Also shown are the numbers of trials per colony size, mean, variance, and the proportion of trials with a mean increase of less than 1 ant per min. Each colony was used on 3 consecutive days, so the total number of different colonies used is  $N/3$ .

precisely manipulated the number of workers in each colony, but there would still be variation among the studied colonies in the actual age structure of the workers or worker-brood ratio, both of which are known to affect the ant's motivation to forage (25). Also, the colonies were deprived of syrup for 1–3 days, which will cause variation in motivation. In addition, we could manipulate only the total number of ants in the colony and not the number of ants engaged in foraging. The second reason relates directly to the second and third model predictions—that a first-order phase transition and hysteresis will occur for intermediate-sized colonies.

In the model, a first-order transition occurs when independent finds of the feeder by workers are infrequent. These infrequent finds are what actually occur. [The independent discovery rate ( $\alpha$ ) was only 0.0052 per ant per min.] In intermediate-sized colonies we expect that, because of short-term fluctuations, the number of foraging ants can be either above or below the unstable equilibrium (dashed line in Fig. 1B), giving rise to a strong chance element in trail formation and a widening of the distribution of trail strengths. However, because the significant increase in variance of number of ants walking to the feeder for colonies of more than 700 ants is also consistent with colony variation caused by unavoidable differences between colonies of the same size, we cannot use this fact alone as proof of a first-order transition.

To test directly for the occurrence of hysteresis we conducted additional trials by using colonies of 300 and 700 ants. This time we caused a short-term increase in the number of foraging ants by initially placing the feeder beside the nest and then moving it to the normal 50-cm location when 20–40 ants were feeding. Despite this help, there was no significant change in the increase of ants walking to the feeder for colonies of 300 (Fig. 4). In contrast, colonies of 700 had a mean increase of 4.7 ( $\pm 3.3$ ) when

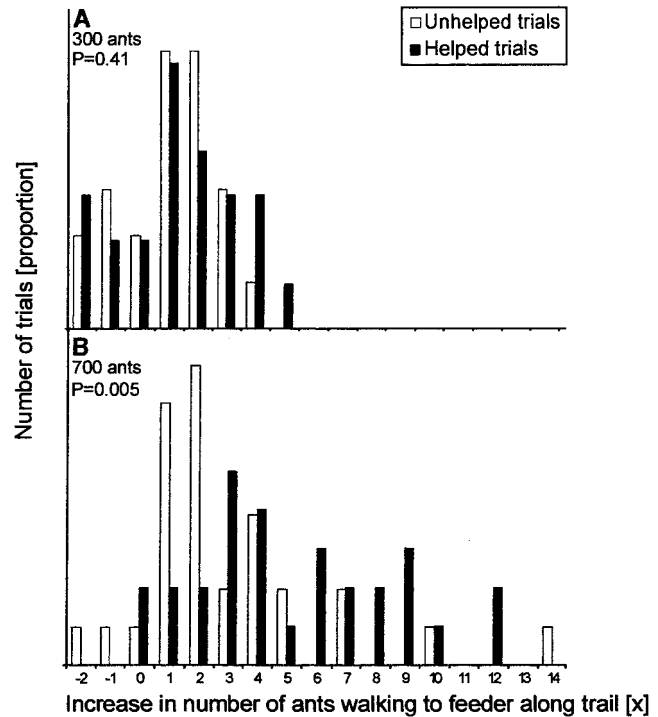


Fig. 4. Frequency distributions of the increase in number of ants walking to the feeder in unhelped and helped colonies of 300 (A) and 700 (B) ants. Maximum value on y axis is 0.5. The data for the helped trials of 300 ants are normally distributed with mean 0.56 and variance 1.65, and are not significantly different for unhelped trials ( $\chi^2 = 7.38$ ;  $P = 0.41$ ,  $N$  unhelped 23,  $N$  helped 24). Because the data do not conform to a standard [normal or logarithm (log)-normal] distribution in the unhelped 700-ant colonies, we quantified the difference between the two distributions by using a G test (32). The distributions found for the unhelped and helped 700-ant experiments are significantly different ( $n_p = 29$ ,  $m = 9$ ,  $G_{adj} = 22.7$ , and  $P = 0.005$ ,  $N$  unhelped 30,  $N$  helped 29). For the colonies with 300 ants, the distributions are not significantly different ( $n_p = 24$ ,  $m = 7$ ,  $G_{adj} = 6.27$ , and  $P = 0.41$ ). For each colony size, we selected the maximum number of frequency bins ( $m$ ) that ensured that no bin was empty and calculated the G test over these

$$G = 2n_p \sum_{\text{all bins, } i} p_i \log \left( \frac{n_p p_i}{n_q q_i} \right),$$

where  $p_i$  (respectively  $q_i$ ) is the proportion of replicates in bin  $i$  and  $n_p$  (respectively  $n_q$ ) is the total number of replicates in the helped (respectively unhelped) experiments. Applying the William's adjustment to  $G$  ensures that it is distributed according to a  $\chi^2$  distribution with  $m-1$  degrees of freedom (32).

helped to start a trail vs. 2.6 ( $\pm 3.3$ ) when not helped. When helped, only 4 of 29 trials showed an increase of less than 1 (i.e., no increase; see Fig. 4). Thus, whereas colonies of 300 ants were incapable of maintaining a trail to the food source, colonies of 700 ants were usually able to maintain a trail when helped to initiate it. The fact that colonies of 700 ants have different foraging patterns when helped or not indicates the existence of more than one stable equilibria, and confirms hysteresis as predicted by the model.

## Discussion

The existence of hysteresis shows directly that foraging organization in Pharaoh's ants is influenced by colony size in a nonlinear and discontinuous way. Our study shows that even quite large colonies of 600 ants are unable to forage in an organized manner to a feeder only 50 cm away. This failure is

presumably because the trail pheromone is highly volatile. Preliminary experiments had earlier shown that a well established trail formed by hundreds of returning foragers decays completely in  $\approx 10$  min under similar conditions (F.L.W.R., unpublished results). To overcome the constraint on colony size set by the volatility of the trail pheromone, ants could presumably evolve less volatile pheromones. Although some ant species do use long-lasting trails (trunk trails) to connect the nest to important foraging locations such as trees for collecting honeydew (26) or leaves (27), this is maladaptive for ants that feed on ephemeral food sources.

Ants have evolved various mechanisms to overcome the constraint set by colony size on pheromone-trail foraging. Pharaoh's ants (28) and other trail-recruiting species (29) deposit an attracting pheromone when exploring new areas, even when no food has been found. This mechanism may serve to increase the local ant density thus increasing the probability of forming a trail when food is found. Other ant species use tandem or group recruitment, whereby a successful forager guides one or more recruits directly to the food source (30). Group recruitment is not subject to a minimum colony size and is typically found in ants with small colonies such as ponerines and *Leptothorax* (25). Some species with larger colonies [e.g., *Tetramorium caespitum* and *Camponotus socius* (8, 11, 30)] use both group recruitment and pheromone trails. Such a dual mechanism will have an effect similar to our hysteresis experiment with an initial period of group recruitment helping to establish the new trail, thus overcoming the constraint set by colony size.

The transition between disordered (no trail) and ordered (trail-based) foraging at a critical colony size is strongly analo-

gous to first-order transitions in physical systems, such as the discontinuous change from water to ice at a critical temperature (31). Furthermore, the observed hysteresis is reminiscent of supercooling, where water cooled rapidly to below the critical temperature will not turn into ice for a long transient period. In contrast to physical systems, in many biological systems natural selection can act against the occurrence of certain states, such as disordered foraging, by fine tuning the rules by which patterns emerge (7). For example, group recruitment exploits the supercooling property of foraging to allow the ants to begin laying useable trails below the critical colony size. In this sense, natural selection is the intersection between alternative stable and adaptive states. We expect most complex biological systems that are shaped by natural selection to be in an adaptive state, but by experimental manipulations, such as those we have made here, rarely encountered maladaptive states can be generated.

We thank Lisbeth Børgesen (Univ. of Copenhagen, Denmark) for providing us with the ants. We also thank Carl Anderson, David Broomhead, Johan Calis, Edmund Crampin, Martin Depken, Nigel Franks, Ana Sendova-Franks, Leah Henderson, Florian Merz, Stephen Pratt, and the anonymous referees for useful discussions and/or comments. M.B. was supported by a postdoctoral fellowship from the research network "Social Evolution" of the Universities of Århus, Firenze, Keele, Sheffield, Uppsala, Würzburg, and the Eidgenössische Technische Hochschule, Zürich, financed by the European Commission via the Training and Mobility of Researchers (TMR) program. D.J.T.S. was supported by the Engineering and Physical Sciences Research Council (EPSRC) and the Association for the Study of Animal Behavior (ASAB).

- Kauffman, S. A. (1993) *The Origins of Order. Self-Organization and Selection in Evolution* (Oxford Univ. Press, Oxford).
- Grimmett, G. (1999) *Percolation* (Springer, Berlin).
- Ball, P. (1999) *The Self-Made Tapestry. Pattern Formation in Nature* (Oxford Univ. Press, Oxford).
- Murray, J. D. (1991) *Mathematical Biology* (Springer, Berlin).
- Nicolis, G. & Prigogine, I. (1977) *Self-Organization in Nonequilibrium Systems. From Dissipative Structures to Order Through Fluctuations* (Wiley, New York).
- Kelso, J. A. S., Bressler, S. L., Buchanan, S., Deguzman, G. C., Ding, M., Fuchs, A. & Holdroyd, T. (1992) *Phys. Lett. A* **169**, 134–144.
- Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., Aron, S. & Camazine, S. (1997) *Trends Ecol. Evol.* **12**, 188–193.
- Deneubourg, J.-L. & Goss, S. (1989) *Ethol. Ecol. Evol.* **1**, 295–311.
- Beckers, R., Deneubourg, J. L., Goss, S. & Pasteels, J. M. (1990) *Insectes Soc.* **37**, 258.
- Goss, S., Aron, S., Deneubourg, J.-L. & Pasteels, J. M. (1989) *Naturwissenschaften* **76**, 579–581.
- Pasteels, J. M., Deneubourg, J.-L. & Goss, S. (1987) *Experientia*, Suppl. **54**, 155–175.
- Seeley, T. D. (1995) *The Wisdom of the Hive* (Harvard Univ. Press, Cambridge, MA).
- Camazine, S. (1991) *Behav. Ecol. Sociobiol.* **28**, 61–76.
- Stickland, T. R., Britton, N. F. & Franks, N. R. (1995) *Proc. R. Soc. London Ser. B* **260**, 53–58.
- Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Franks, N. R., Rafelsberger, O., Joly, J. N. & Blanco, S. (1998) *Philos. Trans. R. Soc. London B* **353**, 1561–1576.
- Deneubourg, J.-L. & Franks, N. R. (1995) *J. Insect Behav.* **8**, 417–432.
- Franks, N. R. & Deneubourg, J.-L. (1997) *Anim. Behav.* **54**, 779–796.
- Karsai, I. & Penzes, Z. (1993) *J. Theor. Biol.* **161**, 505–525.
- Camazine, S., Visscher, P. K., Finley, J. & Vetter, R. S. (1999) *Insectes Soc.* **46**, 348–362.
- Detrain, C., Deneubourg, J.-L. & Pasteels, J. M. (1999) in *Information Processing in Social Insects*, eds. Detrain, C., Deneubourg, J.-L. & Pasteels, J. M. (Birkhauser, Basel), pp. 331–354.
- Visscher, P. K. & Camazine, S. (1999) *Nature (London)* **397**, 400.
- Prigogine, I. & Stengers, J. (1984) *Order Out of Chaos. Man's New Dialogue with Nature* (Bantam, New York).
- Pasteels, J. M., Deneubourg, J.-L., Verhaeghe, J.-C., Boevé, J.-L. & Quinet, Y. (1986) in *Mechanisms in Insect Olfaction*, eds. Payne, T. & Birch, M. (Oxford Univ. Press, Oxford), pp. 131–138.
- Sudd, J. J. (1960) *Anim. Behav.* **8**, 67–75.
- Hölldobler, B. & Wilson, E. O. (1990) *The Ants* (Belknap, Cambridge, MA).
- Quinet, Y., Biseau de, J. C. & Pasteels, J. M. (1997) *Behav. Proc.* **40**, 75–83.
- Wetterer, J., Shafir, S., Morrison, L., Lips, K., Gilbert, G., Cipollini, M. & Blaney, C. (1992) *J. Entomol. Soc. (Kansas)* **65**, 96–98.
- Fourcassie, V. & Deneubourg, J.-L. (1994) *Physiol. Entomol.* **19**, 291–300.
- Detrain, C., Deneubourg, J. L., Goss, S. & Quinet, Y. (1991) *Psyche* **98**, 21–31.
- Beckers, R., Goss, S., Deneubourg, J.-L. & Pasteels, J. M. (1989) *Psyche* **96**, 239–225.
- Kittel, C. & Kroemer, H. (1980) *Thermal Physics* (Freeman, New York), 2nd Ed., p. 473.
- Sokal, R. R. & Rohlf, F. J. (1995) *Biometry* (Freeman, New York).