Insectes Sociaux, Paris
1990, Volume 37, n° 3, pp. 258-267

COLLECTIVE DECISION MAKING THROUGH FOOD RECRUITMENT

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Reçu le 5 juillet 1989 Accepté le 8 novembre 1989

SUMMARY

A series of experiments shows how the ant *Lasius niger* uses its trail recruitment system to select between two food sources. Simultaneously presented with two 1M sucrose solutions it concentrates on one of them. When offered a 1M solution together with a 0.1M solution it selects the richer source, unless the trail to the 0.1M source had become well-developed before the 1M source was introduced. In the same situation, however, the group/mass recruting ant *Tetramorium caespitum* uses its more individual transmission of information to switch to the 1M source. A mathematical model describes these processes and its dynamics reflect the experimental results.

RESUME

La prise de décision collective à travers le recrutement alimentaire

Nous présentons une série d'expériences qui montrent comment la fourmi *Lasius niger* peut utiliser son système de recrutement par piste afin de sélectionner une des deux sources de nourriture. Si on leur offre simultanément deux solutions 1M de saccharose, la société concentre son activité sur l'une des deux. Si l'on offre deux solutions, une de 1M et l'autre de 0.1M, elle sélectionne la plus riche, à moins que la piste qui mène à la source 0.1M soit déjà bien développée au moment où l'on introduit la source 1M. Face à la même situation, la fourmi *Tetramorium caespitum*, qui recrute par groupe/masse, utilise son mode de transmission d'information plus individuel pour changer son exploitation vers la source 1M. Un modèle mathématique décrit ces processus, dont la dynamique correspond bien aux observations expérimentales.

INTRODUCTION

Sociality provides an opportunity for the exchange of information concerning profitable foraging locations, and numerous food recruitment behaviors, the means by which a number of foragers are directed to a food source, have been described for very different species (Social Insects : WILSON, 1971 ; Ants : HÖLLDOBLER, 1978 ; PASSERA, 1984 ; SUDD and FRANKS, 1987 ; Termites : LEUTHOLD, 1975 ; RICKLI and LEUTHOLD, 1986 ; Honeybees : LINDAUER, 1961 ; VON FRISCH, 1967 ; SEELEY, 1985 ; Gregarious Caterpillars : FITZGERALD and PETERSON, 1983, 1988). In the case of birds, recruitment can either be active or else simply a spying behaviour in which one animal sees another feeding and moves to join in (WARD and ZAHAVI, 1973 ; EMLEN and DEMOMG, 1975 ; BROWN, 1986 ; GOTMARK *et al*, 1986 ; GREENE, 1987). Recruitment, however, is not only a system adapted to the exploitation of a patchy environment or of prey needing cooperative exploitation, but can also be the touchstone of a collective decision-making system developed by animal societies, which we can term the natural selection of food discoveries. The interplay between recruitments to different food sources generates complex social decisions well beyond the capacity of an individual. Small differences in the degree of cooperativity of the recruitment mechanism, as defined by simple individual rules, can lead to totally different social decisions and patterns of food exploitation. These ideas are illustrated for social insects, the most socially integrated of animals, with a series of experiments on ants recruiting to sugar sources and a simple model.

In a typical ant trail recruitment, a scout discovers a food source and returns to the nest, laying a chemical trail. At the nest, other foragers detect the trail (we neglect invitational differences) and follow it to the source (e.g. SUDD, 1960 ; WILSON, 1962 ; WILSON, 1971 ; Ants : HÖLLDOBLER, 1978 ; PASSERA, 1984 ; SUDD and FRANKS, 1987). Those that arrive at the source load food and return to the nest reinforcing the trail. Unsuccessful trail-followers explore the foraging ground before either returning to the nest or finding the food source. As the trail is reinforced, more ants are recruited and less recruits lose the trail, and the recruitment is thus autocatalytic (CORNETZ, 1914 ; PASTEELS *et al.*, 1987). Termite trail recruitment is very similar (LEUTHOLD, 1975 ; RICKLI and LEUTHOLD, 1986).

MATERIALS AND METHODS

In each experiment, a hungry colony of *Lasius niger* was presented with two constantly replenished sucrose solutions, 60 cm apart and both 60 cm from the nest in an 80 × 80 cm arena. The number of ants around each source was counted every minute. The experiments were performed on the trail recruiting ant *Lasius niger* and the group/trail recruiting ant *Tetramorium caespitum*. In this latter species, the number of ants recruited in groups were counted. Also, as it has a smaller natural foraging area, the sources were offered 30 cm apart, 30 cm from the nest.

RESULTS

When a colony was offered two identical sources at the same time, after a short period of equal exploitation, a bifurcation is observed and one of the sources becomes much more exploited than the other (*fig. 1 A*). If a second is discovered after a recruitment is well under away to a first source, the second always remains underexploited. Globally speaking, the colony "decides" to exploit one source fully and to keep the second in reserve, the trail to it being maintained by a low level of exploitation.

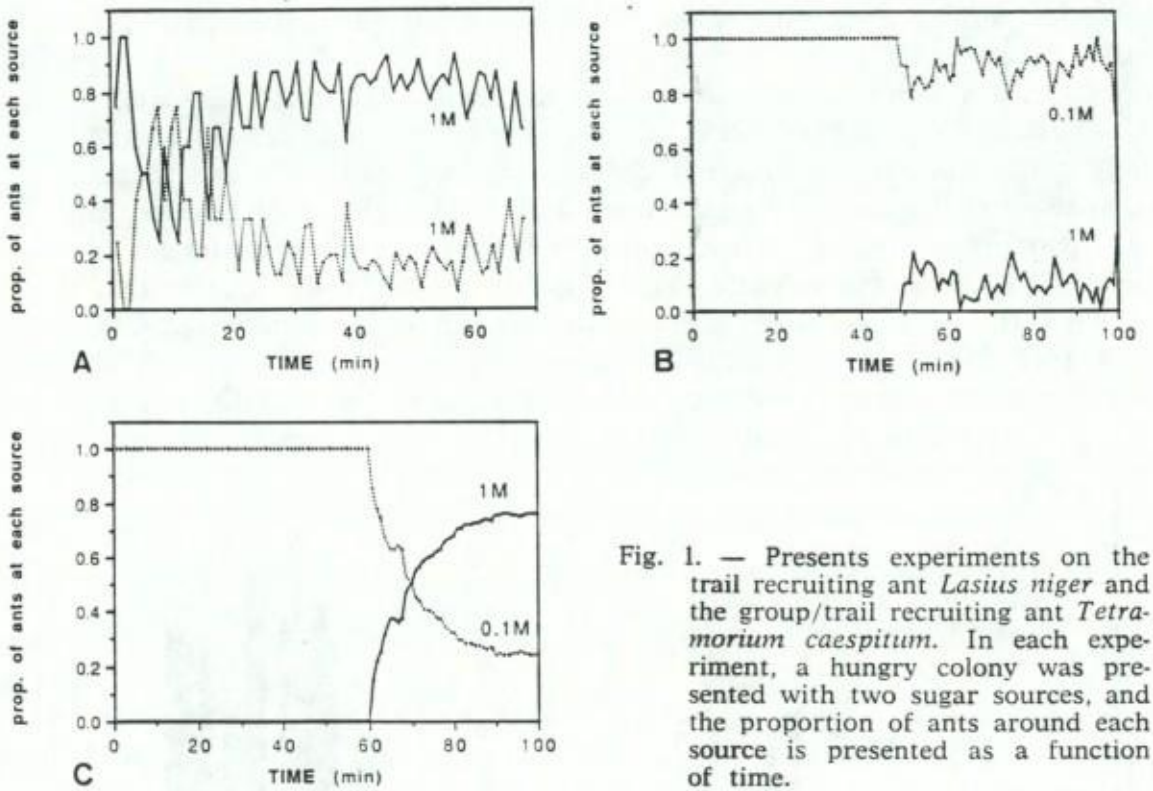

Fig. 1. — Presents experiments on the trail recruiting ant *Lasius niger* and the group/trail recruiting ant *Tetramorium caespitum*. In each experiment, a hungry colony was presented with two sugar sources, and the proportion of ants around each source is presented as a function of time.

A : two 1M sucrose sources introduced simultaneously, with *L. niger*. (7 experiments) ;

B : 1M source introduced 50 mins after a 0.1 M source, with *L. niger* (3 experiments);

C : 1M source introduced 60 mins after a 0.1M source, with *T. caespitum*. (3 experiments).

Fig. 1. — Présente des expériences sur la fourmi *Lasius niger*, qui recrute par piste, et sur la fourmi *Tetramorium caespitum*, qui recrute par groupe/piste. Dans chaque expérience, on présente deux solutions de saccharose à une société affamée, et on mesure la proportion de fourmis autour de chaque source en fonction du temps.

A : deux solutions 1 M introduites simultanément, avec *L. niger* (7 expériences) ;

B : solution 1 M introduite 50 min. après une solution 0.1 M, avec *L. niger* (3 expériences) ;

C : solution 1 M introduite 60 min. après une solution 0.1 M, avec *T. caespitum* (3 expériences).

What happens if the colony is offered two sources of different sugar concentrations ? If the richer source is discovered before or at the same time as the poorer one it is always the more exploited. However, if the richer source is discovered after the poorer one, then it is only weakly exploited (*fig. 1 B*). As before, the colony exploits the first source discovered, even if this means neglecting a richer source for a poorer one. When faced with two simultaneously discovered unequal sources it chooses the richer of the two.

Identical experiments with the trail recruiting ants *Iridomyrmex humilis* and *Pheidole pallidula*, all three having very different life-styles, gave the same qualitative results.

Honeybees use a similar but different recruitment mechanism (LINDAUER, 1961 ; VON FRISCH, 1967 ; SEELEY, 1985). A forager that has found a food source personally transmits the information concerning its location to nestmates by the dance ritual (in ant trail recruitment this information is contained in the trail). Honeybee colonies when confronted with the same decisions as described above choose differently. Whatever the order of discovery, they always select the richer source and exploit two identical sources equally (VELTHUIS, 1977 ; SEELEY and LEVIEN, 1987).

Honeybee recruitment is similar in its logic to group recruitment in ants, in which a successful scout personally guides a small group of nest-

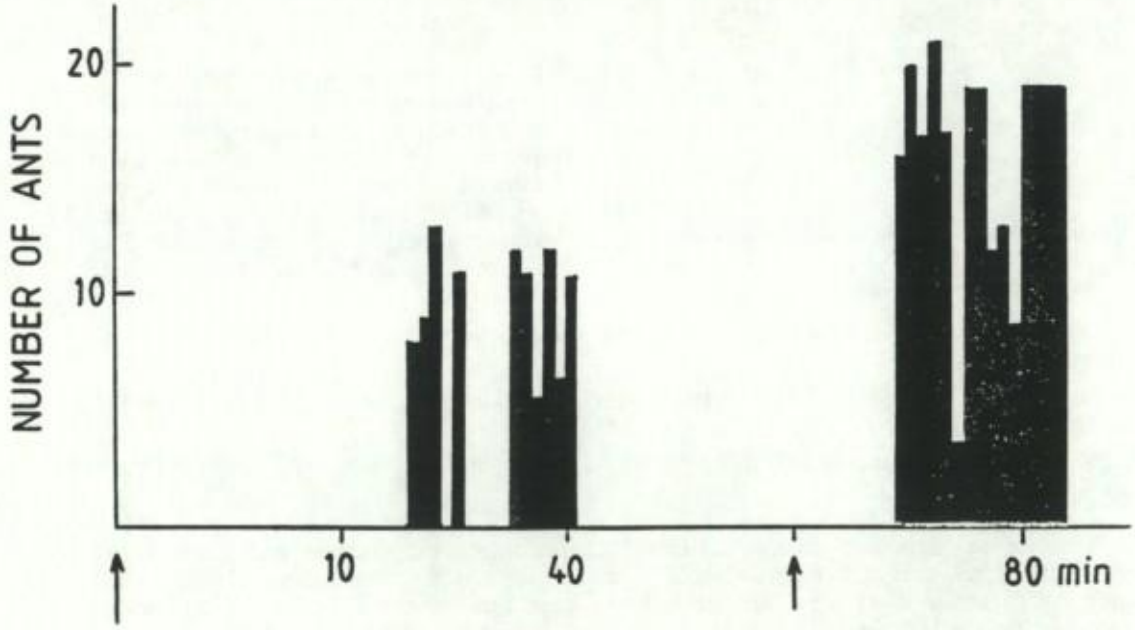

Fig. 2. — Presents the number of *T. caespitum* workers recruited in groups to two sequentially introduced sucrose sources (0.1 M followed by 1 M). The arrows mark the moment in time at which each of the two food sources were introduced.

Fig. 2. — Présente le nombre d'ouvrières de *T. caespitum* recrutées en groupe vers deux sources de saccharose introduites en différé (0.1 M suivie par 1 M). Les flèches indiquent le moment auquel chaque source est introduite.

mates to the source (e.g. WILSON, 1971 ; in tandem recruitment, a third mechanism close to group recruitment, a scout guides, personally and with care, only one recruit - MÖGLICH *et al.*, 1974). One would therefore expect the same set of decisions of choice as found in honeybees. It is, however, impossible to verify this as all the species we know of that practice group recruitment also use trail recruitment. At the beginning of a recruitment, the recruiters lead groups to the food, but also lay a trail between the food and the nest. As this trail becomes stronger, the groups become less frequent and trail recruitment takes over.

These group/trail recruiting species combine the two sets of decisions (PASTEELS *et al.*, 1987). Like honeybees they exploit the richer source, whether discovered first or second, and like trail recruiting ants they exploit two equal sources asymmetrically (*fig. 1 C*) (see also FOWLER, 1987 for the same qualitative results for choice experiments between two different food types in *T. caespitum*). We show in *figure 2* how groups of *T. caespitum* appear at the discovery of each of two sequentially introduced sucrose sources, only to disappear rapidly as mass recruitment takes over.

MATHEMATICAL MODEL AND MONTE-CARLO SIMULATIONS

What is behind these different sets of decisions ? A mathematical model (see also PASTEELS *et al.*, 1987) enables us to link the collective decisions to the individual foragers' behavior which defines the different recruitment systems used and thus the model's kinetics.

Consider a colony of N foragers, of which E are scouts or lost recruits. X_i are at food source i, and $N-E-\Sigma X_i$ are waiting in the nest to be recruited. The autocatlytic nature of the recruitment process can be represented by stating that the number of recruits per unit time to source i is given by the product between a rate constant, a_i, the number of foragers in the nest and the number of foragers actively involved in exploiting that source. Of these recruits, a fraction representing the recruitment accuracy, f_i, reach the source and the complement, $1-f_i$, become lost ants. The scouts/lost ants can return home on average every 1/p time units or can find one of the two sources every 1/c time units. The foragers stay on average 1/b time units at the source before returning to the nest. Thus :

$$dX_i/dt = a_iX_i(N-\Sigma X_i-E) - bX_i + cE \qquad (i = 1,2) \quad (1)$$

$$dE/dt = \Sigma(a_iX_i(1-f_i))\ (N-\Sigma X_i-E) - pE - 2cE \qquad (2)$$

The model's time evolution and stationary states reproduce the competition between the recruitments to the two sources. The difference between the three types of recruitment described lies in the recruitment accuracy, f_i. (Note that the less than perfect accuracy of these recruitment systems may

often lead to the discovery of new sources nearby, especially if the sources are clustered ; DENEUBOURG *et al.*, 1982 ; see also for honeybees and review TOWNE and GOULD, 1988). In ant trail recruitment, the use of the trail to transmit the food location information introduces an element of cooperativity between the recruiters, and the recruitment accuracy increases with the number of recruiters as the trail is reinforced. f_i can be represented by a monotonic increasing function of X_i, $g(X_i)$. In honeybee and ant group recruitment, there is direct (worker-worker) rather than cooperative (worker-trail-worker) transmission of the food location, and the accuracy with which it is transmitted is constant and independent of the number of foragers exploiting the source. f_i can be represented by a constant k. In ant group/trail recruitment both direct and cooperative transmission are present, and f_i may be represented by a linear combination of k and $g(X_i)$.

Both a_i and f_i increase with the source quality. The higher the quality, the greater the quantity of trail pheromone laid per ant trail recruiter (HANGARTNER, 1969), the more intense the dance per honeybee recruiter (LINDAUER, 1961 ; VON FRISCH, 1967 ; SEELEY, 1985), or the more "motivated" the ant group recruiter (PASTEELS *et al.*, in prep.).

With cooperative transmission, the model reproduces the ant trail recruiter's set of decisions, with direct transmission it reproduces the honeybees' set of decisions, and with both it reproduces the ant group/trail recruiters' set of decisions (*fig. 3*). Parameters N, a, b and p were estimated from the analysis of four experimental recruitments to a single 1M source, by relating the number of ants entering and leaving the arena to the numbers at the source, in the arena and in the nest. Parameter c was estimated theoretically from a random walk model.

DISCUSSION

Cooperative transmission is the source of the asymmetrical choice of equal sources. One trail becomes by chance a little stronger than the other, is followed more accurately, and is thus more reinforced and becomes even stronger than the other, and so on. Once a trail is well established, a new and weaker trail to a second, albeit richer source is unable to compete with it. Without cooperative transmission one source cannot dominate an equal or a later one.

Direct transmission enables a recruiter from a newly discovered source to lead recruits to it in spite of a well established recruitment to a previous source, even if this recruitment is cooperative. Without direct transmission, a later source can never be well recruited to. This is clearly seen in the trail recruiting army ants, where a forager must actively invite nestmates on a principal trail to deflect them to a new source (CHADAB and RETTENMEYER, 1975).

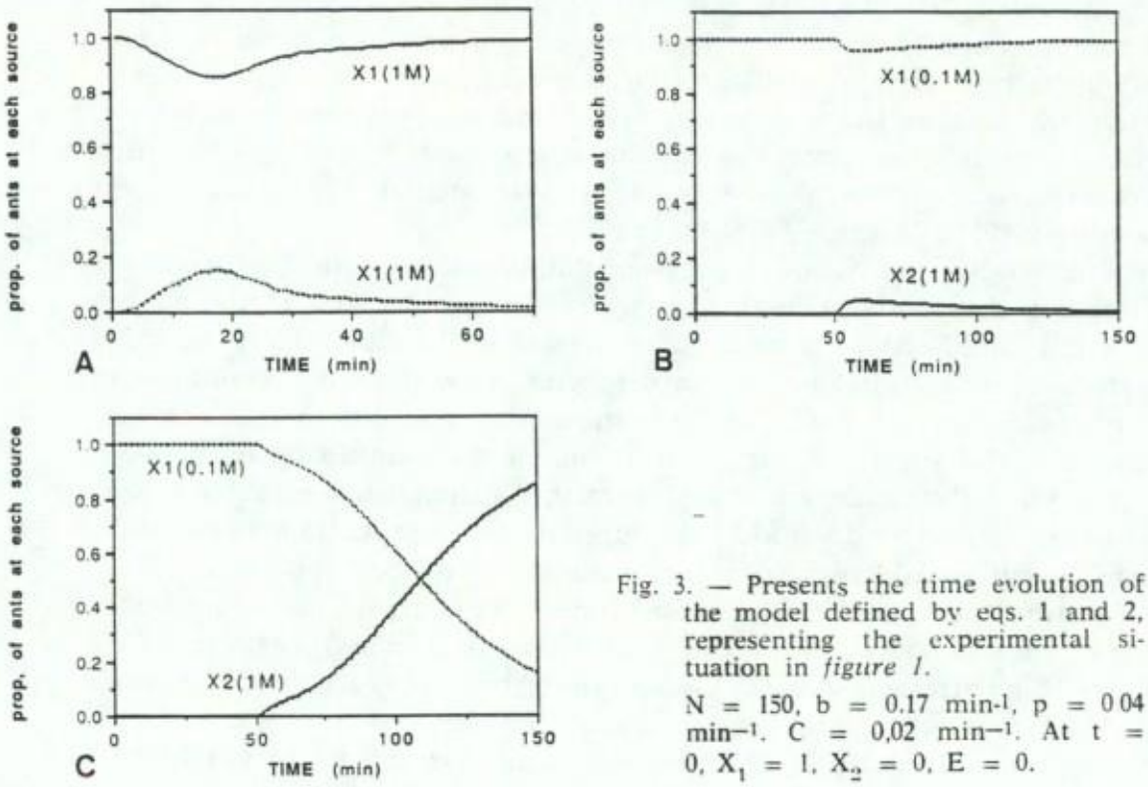

Fig. 3. — Presents the time evolution of the model defined by eqs. 1 and 2, representing the experimental situation in *figure 1*.

N = 150, b = 0.17 min-1, p = 0 04 min−1. C = 0,02 min−1. At t = 0, X_1 = 1, X_2 = 0, E = 0.

A : (*fig. 1a*). $a_1 = a_2 = 0.003$ min−1, $f_i = g(Xi) = (15 + X_i^2) / (30 + X_i^2)$;

B : (*fig. 1b*). $a_1 = 0.0025$, $a_2 = 0.0030$ min−1, $f_1 = g(X_1) = (15 + X_1^2) / (35 + X_1^2)$, $f_2 = g(X_2) = (15 + X_2^2) / (30 + X_2^2)$. Source 2 available after 50 min. ;

C : (*fig. 1c*). idem fig. 2b except $f_i = 0.3\,k_i + 0.7\,g(X_i)$, where $k_1 = 0.6$, $k_2 = 0.9$.

Fig. 3. — Présente l'évolution du modèle défini par les équations 1 et 2, et qui représente la situation expérimentale de la *figure 1*.

N = 150, b = 0.17 min−1, p = 0.04 min−1, c = 0.02 min−1. Au temps t = 0, $X_1 = 1$, $X_2 = 0$, E = 0.

A : (*fig. 1a*). $a_1 = a_2 = 0.003$ min−1, $f_i = g(Xi) = (15 + X_i^2) / (30 + X_i^2)$;

B : (*fig. 1b*). $a_1 = 0.0025$, $a_2 = 0.0030$ min−1, $f_1 = g(X_1) = (15 + X_1^2) / (35 + X_1^2)$, $f_2 = g(X_2) = (15 + X_2^2) / (30 + X_2^2)$. Source 2 disponible après 50 min. ;

C : (*fig. 1c*). idem fig. 2b excepté que $f_i = 0.3\,k_i + 0.7\,g(X_i)$, où $k_1 = 0.6$, $k_2 = 0.9$.

In terms of the model, the system with cooperative recruitment has more than one stationary state, and the initial conditions (e.g. which source is discovered first) and random events can determine which is finally reached (GLANSDORFF and PRIGOGINE, 1971 ; NICOLIS and PRIGOGINE, 1977 ; EDELSTEIN-KESHET, 1988). For the same set of parameters, the system with direct recruitment has only the symmetrical stationary state.

The recruitments' autocatalytic nature amplifies even small quantitative differences in a_i and f_i in relation to the source's quality, leading to the

selection of the rich source (unless a trail recruitment is well established to the poorer source). Using this logic, we can predict that a nearer food source will be preferred to a distant one (FOWLER, 1987, shows that, for *T. caespitum*, the further the source, the fewer ants are recruited). Similarly, the selection of the best nest-site can be understood in exactly the same terms, nest-moving in social insects being also regulated by recruitment (e.g. LINDAUER, 1955 ; WILSON, 1971).

More generally, these foraging systems illustrate certain organisational characteristics that underlie many sorts of collective activity in animal societies. For example, the information centers described in relation to communal roosting or colonial nesting bird species show a strong analogy with social insect colonies. Without going into the evident and potential differences between birds and social insects, such as individual complexity, or between active or passive recruitment, similar complex decisional patterns have been observed, and can be understood by similar if not identical analyses of the individual kinetics. Weaver birds, for example, have been shown to switch from a poorer food source to a richer one (DEGROOT, 1980), and pigeons concentrate on one source, neglecting nearby identical ones (LEFEBVRE, 1983).

It should be stressed that the choices described above are not the result of individual foragers comparing the quality of the two food sources, nor even the result of recruits in the nest comparing the signals from different recruiters, as suggested by CRAWFORD and RISSING, 1983. Equivalent comparisons by "receiver" honeybees are an important factor in their recruitment (LINDAUER, 1949, 1954 ; VELTHUIS, 1977 ; SEELEY and LEVIEN, 1987). Here we show that while they may exist and be important in ants, they are not essential for the collective decision to appear. Instead the collective decisions appear as an unlooked for by-product of the competition between two rival autocatalytic recruitments. Without perhaps it being initially "intended", recruitment is thus more than just a means of concentrating foragers on sources concentrated in time and space, and its variants are more than just different techniques of achieving the same goal. The selection of one or the other may depend on the adaptative value of the resulting decisions or pattern.

These theoretical ideas contrast strongly with a more functional approach, such as developed in a similar experimental context by TAYLOR (1977, 1978), in which the colony is somehow supposed to maximise some metric of performance. Our results suggest that a simpler mechanistic approach can generate a richer set of collective behaviours, questions and explanations than one in which the experiments performed and explanations reached are dictated by the experimenter's *a priori* hypotheses. By leaving open the reasons for a behaviour, the mechanistic approach in fact raises more questions than it answers, which is the very motor of scientific progress.

ACKNOWLEDGEMENTS. — We would like to thank M. PARRO for conducting the experiments on *T. caespitum*. We thank especially the "Schlumberg Foundation for Education and Research" and the "Erna och Victor Hasselbladt Foundation" for financial support. This work is also supported in part by the Belgian program on interuniversity attraction poles.

References

BROWN C.R., 1986. — Cliff swallow colonies as information centers. *Science, 234*, 83.

CHADAB R., RETTENMEYER C.W., 1975. — Mass recruitment by army ants. *Science, 188*, 1124-1125.

CORNETZ V., 1914 — *Les Explorations et les Voyages des Fourmis*. Flammarion, Paris.

CRAWFORD D.L., RISSING S.W., 1983. — Regulation of recruitment by individual scouts in *Formica oreas* Wheeler (Hymenoptera ; Formicidae) *Soc. Ins., 30*, 177-183.

DEGRCOT P., 1980. — Information transfer in a socially roosting weaver bird (*Quelea quelea*) : Ploceinae) : an experimental study. *Anim. Behav., 28*, 1249-1258.

DENEUBOURG J.L., PASTEELS J.M., VERHAEGHE J.-C., 1982. — Probabilistic behaviour in ants : a strategy of errors ? *J. Theor. Biol. 105*, 259-271.

EDELSTEIN-KESHET L., 1988. — *Mathematical Models in Biology*. Random House/Birkaüser.

EMLEN S.T., DEMONG N.J., 1975. — Adaptive significance of synchronised breeding in a colonial bird. *Science, 188*, 1029.

FITZGERALD T.D., PETERSON S.C., 1983. — Elective recruitment communication by the eastern tent caterpillar (*Malacosoma americanum*). *Anim. Behav., 31*, 417-423.

FITZGERALD T.D., PETERSON S.C., 1988. — Cooperative foraging and communication in caterpillars. *Bioscience, 38*, 20-25.

FOWLER H.G., 1987. — Communication and optimal foraging in the ant Tetramorium caespitum (Hymenoptera : Formicidae). *Ciencia y Cultura, 39*, 301-303.

GLANSDORFF P., PRIGOGINE I., 1971. — *Thermodynamics of Structure, Stability and Fluctuations*. Wiley-Interscience, New York.

GOTMARK F., WINKLER D.W., ANDERSSON M., 1986. — Flock-feeding on fish schools increases individual success in gulls. *Nature, 319*, 589.

GREENE E., 1987. — Individuals in an osprey colony discriminate between high and low quality information. *Nature, 329*, 239.

HANGARTNER W., 1969. — Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). *Zeit. Vergl. Physiol., 62*, 111-120.

HÖLLBOBLER B., 1978. — Ethological aspects of chemical communication in ants. In : Rosenblatt J.S., Hinde R.A., Beer C., Bushnel M. (eds.) *Advances in the study of Animal Behavior*. Academic Press, New-York, pp. 75-115.

LEFEBVRE L., 1983. — Equilibrium distribution of feral pigeons at multiple food sources. *Behav. Ecol. Sociobiol., 12*, 11-17.

LEUTHOLD R.H., 1975. — Orientation mediated by pheromones in social insects. In : Noirot P., Howse P., Le Masne G. (eds.), *Pheromones and defensive secretions in social insects*. Proc. symp. IUSSI, Université de Dijon.

LINDAUER M., 1949. — *Uber die Einwirkung von Duft-und-Geschmacksstoffen so wie andere Faktoren auf die Tänze der Bienen. Zeit. für Vergl. Physiol., 31*, 348-412.

LINDAUER M., 1954. — Temperaturregulierung und Wasserhaushalt im Bienenstaat. *Zeit. für Vergl. Physiol., 36*, 391-432.

LINDAUER M., 1955. — Schwarmbienen auf Wohnungssuche. *Zeits. Verg. Physiol., 37*, 263.

LINDAUER M., 1961. — *Communication Among Social Bees*. Harvard University Press, Cambridge, Mass., 143 pp.

MÖGLICH M., MASCHWITZ U., HÖLLDOBLER B., 1974. — Tandem calling : a new kind of signal in ant recruitment. *Science, 186*, 1046.

NICOLIS G., PRIGOGINE I., 1977. — *Self-Organisation in Non-equilibrium Systems*. Wiley-Interscience, New York, 491 pp.

PASSERA L., 1984. — *L'Organisation Sociale des Fourmis*. Privat, Toulouse, 360 pp.

PASTEELS J.M., DENEUBOURG J.L., GOSS S., 1987. — Self-organization mechanisms in ant societies (I) : Trail recruitment to newly discovered food sources. In : Pasteels J.M., Deneubourg J.L. (eds), *From Individual to Collective Behavior in Social Insects. Experientia Supplementum 54*, Birkhäuser Verlag, Basel, pp. 155-175.

PASTEELS J.M., PARRO M., DENEUBOURG J.L., GOSS S., in prep. Flexibility of food recruitment in the ant *Tetramorium caespitum*.

RICKLI M., LEUTHOLD R.H., 1986. — Spatial organisation during exploration and foraging in he harvester termite, *Trinevitermes geminatus*, *Rev. suisse Zool.*, *94*, 545.

SEELEY T.D., 1985. — *Honeybee Ecology*. Princeton University Press, Princeton.

SEELEY T.D., LEVIEN R.A., 1987. — Social foraging in honeybees : how a colony tracks rich sources of nectar. In : Menzel R., Mercer A. (eds.) *Neurobiology and Behavior of the Honeybee*. Springer Verlag, Berlin.

SUDD J.H., 1960. — The foraging method of Pharaoh's ant, *Monomorium pharaonis* (L.). *Anim. Behav.*, *8*, 67-75.

SUDD J.H., FRANKS N.R., 1987. — *The Behavioural Ecology of Ants*. Blackie, Glasgow.

TAYLOR F., 1977. — Foraging behavior of ants : Experiments with two species of Myrmicine ants. *Behav. Ecol. Sociobiol.*, *2*, 147-167.

TAYLOR F., 1978. — Foraging behavior of ants : Theoretical considerations. *J. Theor. Biol.*, *71*, 541-565.

TOWNE W.F., COULD J.L., 1988. — The spatial precision of the honeybees' dance communication. *J. Ins. Behav.*, *1*, 129-155.

VELTHUIS H.H.W., 1977. — Population dynamic aspects and communication in a bee flight room. *Insectes Soc.*, *24*, 293.

VON FRISCH K., 1967. — *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, Mass.

WARD P., ZAHAVI A., 1973. — The importance of certain assemblages of birds as 'information centres' for food finding. *Ibis*, *115*, 517-534.

WILSON E.O., 1962. — Chemical communication among workers of the fire ant *Solenopsis* saevisima (Fr. Smith) : I. The organization of mass foraging. *Anim. Behav.*, *10*, 134.

WILSON E.O., 1971. — *The Insect Societies*. Harvard University Press, Cambridge, Mass., 548 pp.