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THE SELF-ORGANISING CLOCK PATTERN OF *MESSOR PERGANDEI* (FORMICIDAE, MYRMICINAE)

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SUMMARY

A simple model is described wherein ant foragers choose a foraging sector as a function of the pheromone concentration associated with each sector. The choice is autocatalytic, as foragers that find food in a sector add to its pheromone. As a sector's food runs out, the foragers spontaneously switch to the adjacent sector. With increasing food abundance, the model passes from random foraging to the formation of a trail that rotates about the nest. The greater the abundance the more slowly the trail rotates until it finally becomes fixed on one sector. These results agree with experimental observations made on the harvester ant *Messor pergandei* by BERNSTEIN (1975) and RISSING and WHEELER (1976), and reconcile an apparent contradiction between them.

RESUME

L'auto-organisation d'une piste rotative chez Messor pergandei

On présente un modèle simple de choix du secteur de fourragement par des fourmis. Ce choix se fait en fonction de la quantité de phéromone associée à chaque secteur, et est autocatalytique puisque les fourrageuses qui trouvent de la nourriture dans un secteur y ajoutent de la phéromone. Quand la nourriture d'un secteur est épuisée, les fourrageuses transfèrent spontanément leur activité vers le secteur adjacent. Si la richesse en nourriture augmente, le modèle passe d'un fourragement aléatoire à la formation d'une piste qui tourne autour du nid. Plus la richesse est élevée, plus la piste tourne lentement, jusqu'à devenir figée en un secteur. Ces résultats correspondent aux observations faites sur la fourmi *Messor pergandei* par BERNSTEIN (1975), RISSING et WHEELER (1976), y reconcilient une apparente contradiction entre eux.

INTRODUCTION

Oscillations, waves and spatial patterns are now classical phenomena in the domain of population dynamics (e.g. MAY, 1973 ; OKUBO, 1980 ; DEANGELIS *et al.*, 1986), not to speak of physico-chemical systems (NICOLIS and PRIGOGINE, 1977 ; HAKEN, 1983). Recently, however, the techniques and logic related to the understanding of such non-linear phenomena have begun to be applied to the dynamic interactions in animal societies or group living organisms (e.g. KELLER and SEGEL, 1970 ; DENEUBOURG, 1977 ; OKUBO, 1980 ; FOCARDI *et al.*, 1985 ; BELIC *et al.*, 1986 ; PASTEELS *et al.*, 1987 ; DENEUBOURG *et al.*, 1987 ; review in MARTIEL and GOLDBETER, 1987 ; GOSS and DENEUBOURG, 1988 ; DENEUBOURG *et al.*, 1989a).

BERNSTEIN (1975) and RISSING and WHEELER (1976) described a spatial oscillation in *Messor pergandei* (ex-*Veromessor*). Briefly, a concentrated trail of foragers develops to a sector of the foraging area, and with a period of several days to three weeks or so rotates, *grosso modo*, like the hand of a clock around the nest. When BERNSTEIN (1975) artificially increased the seed density near the nest, the hand seemed to widen and then disintegrate followed by uncoordinated random exploitation of the foraging area. RISSING and WHEELER (1976), however, reported that such random foraging, while sometimes observed when food was scarce, was very rare in years of high seed density. Both reported that the columns changed direction more slowly in years or regions when food was abundant.

In this article we will present a mathematical model showing how this pattern may be generated from a simple trail-laying and trail-following behaviour, and the forager/food interactions, without needing to invoke spatial memory, complicated systems of coordination or any change of individual behaviour with food density. The model reproduces the different experimental observations, and reconciles the contradictory observations with high food density.

THE MODEL AND SIMULATIONS

The circular foraging area, with the nest in the centre, is divided into b sectors. Φ_i seeds arrive per time in each sector, each of which contains S_i seeds. A fraction, r, disappear per unit time by competition, decay, etc.

A trail leads to each sector, characterised by C pheromone units, of which a fraction, e, evaporate per unit time. N foragers leave the nest per unit time. A fraction, f_i, choose sector i, according to a non-linear function of the trail pheromone associated with each sector, as determined experimentally for *Iridomyrmex humilis* (DENEUBOURG *et al.*, 1989b). Of this fraction, a small fraction, q, diffuse into each of the two adjacent sectors (note that the sectors adjacent to sector b are sectors 1 and b-1).

The number of seeds found in a sector is given by the product between a constant, g, the number of foragers, F_i, and a function of the number of seeds in that sector, $S_i / (a + S_i)$, which increases monotonically from 0 to 1 with S_i, a being a constant. At the end of each step, all the foragers return to the nest. Those that have found a seed add one pheromone unit to the trail leading to the corresponding sector. Those that find no seeds return without marking. The average equations for this process are thus :

$$\begin{aligned} dS_i/dt &= \text{arrivals} - \text{finds} - \text{disappearences} \\ &= \Phi_i - gF_iS_i / (a + S_i) - rS_i \qquad (i = 1, ..., b) \qquad (1) \\ dC_i/dt &= \text{finds} - \text{evaporation} \\ &= gF_iS_i / (a + S_i) - eC_i \qquad (2) \\ f_i &= (20 + C_i)^2 / \Sigma (20 + C_i)^2 \qquad (\Sigma f_i = 1) \qquad (3) \\ F_i &= N ((1 - 2q) f_i + qf_{i+1} + qf_{i-1}) \qquad (4) \end{aligned}$$

Figure 1 shows a typical Monte Carlo simulation with 4 sectors. At time 0, each sector contains Φ_i/r seeds (the equilibrium value in the absence of ants), and there are no pheromone marks. Initially, the number of foragers choosing each sector is more or less random. By chance one sector is more chosen than the others, in this case sector 2. More food is therefore found in sector 2, and the trail leading to it becomes stronger than that leading to the other sectors. Even more foragers thus choose it at the next step, and so on. This autocatalytic process rapidly leads to the foragers concentrating on sector 2· and corresponds to the formation of a recruitment trail in real space. The foragers may be said to have collectively selected sector 2.

Thereafter, the number of seeds in sector 2 diminishes through the foragers' activity, while they accumulate in the other unfrequented sectors. Eventually, the foragers have difficulty in finding seeds in sector 2, and so the trail to it is no longer reinforced and diminishes by evaporation. At this point, the trails to its two neighbouring sectors 1 and 3 have a higher concentration than sector 4's trail, as they have been exploited at a low rate by foragers diffusing from sector 2. Thus rather than collectively selecting at random between the three (b-1) remaining sectors, the foragers collectively choose between sectors 1 and 3, in this case sector 3. When sector 3 is nearly empty, again there are weak trails leading to the two adjacent sectors 2 and 4. However· sector 2 is still more or less empty, not having had enough time to restock. The foragers collectively choose sector 4, by finding seeds more easily there and therefore reinforcing the trail leading to it. Thereafter, they continue to choose the next sector in the same direction as before, and the trail rotates around the nest. By the time it has gone a full circle, the sectors originally exploited have been restocked, and the rotation continues indefinitely.

A preliminary analysis of the model's stationary states, confirmed by

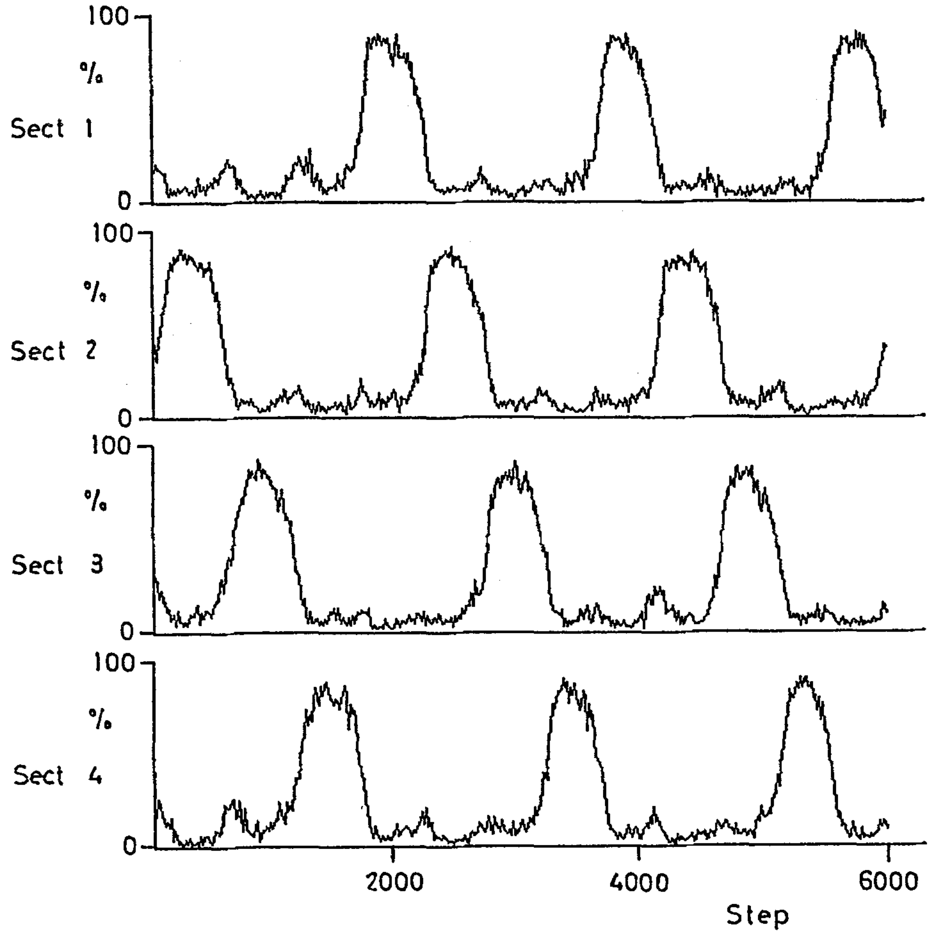

Fig. 1. — Monte Carlo simulation of the model with 4 sectors, showing the percentage of foragers in each sector as a function of time. The foragers clearly form a trail that starts in sector 2 and rotates clockwise to sectors 3, 4, 1, 2, 3, etc., with a regular period.

$N = 100$; $e = 0.03$; $g = 0.1$; $r = 0.001$; $q = 0.05$; $\Phi_i = 2$ $(i = 1, ..., 4)$; $a = 1000$; $S_0 = \Phi/r$.

Fig. 1 — Une simulation Monte Carlo du modèle avec 4 secteurs, montrant le pourcentage de fourrageuses dans chaque secteur en fonction du temps. Les fourrageuses forment clairement une piste qui commence dans le secteur 2 et qui passe aux secteurs 3, 4, 1, 2, 3, etc., avec une périodicité régulière.

$N = 100$; $e = 0.03$; $g = 0.1$; $r = 0.001$; $q = 0.05$; $\Phi_i = 2$ $(i = 1, ..., 4)$; $a = 1000$; $S_0 = \Phi/r$.

simulations, shows that it generates three different patterns depending on the parameter values, notably the food abundance per forager. For a given number of foragers, when the food abundance is very low no columns develop and foraging is random and statistically equal in each sector. When it is greater than a threshold value the column develops and rotates (note that the individual ants have no threshold value, but collectively they do). As the abundance increases, the column rotates more and more slowly, becoming fixed on one sector when food arrives there faster than the ants remove it.

For a given food abundance, with very few foragers the colony is unable to create a trail, and foraging is random. As the number of foragers increases, a column appears but remains fixed on one sector as there are not enough foragers to deplete it. With more foragers, the sector is exhausted, the ants switch to the neighbouring sector, and the column starts to rotate, all the faster as there are more foragers. For very large colonies, the food supply is rapidly exhausted in all the sectors, and foraging again becomes random with the foragers spread all over the foraging area collecting the food as it arrives.

If the leakage (q) between adjacent sectors is very small, the column is formed but switches between different sectors in a random sequence. As q increases, the column rotates. With high leakage, the trail widens and the foraging eventually becomes random.

Finally, the Φ varies from sector to sector (as under natural conditions, especially when food is scarce), the less regular the rotation. Short periods of random foraging while the foragers collectively select a new direction are more frequent, for example when the column rotates towards an empty sector. The columns may "backstep" or even change directions randomly rather than continue in the same clockwise (or anti-clock-wise) direction.

DISCUSSION

The model is extremely simple, and ignores all problems of explicit distance, memory, specialisation and recruitment dynamics, and yet the sequence of patterns random foraging/rotating colums/fixed columns obtained with increasing food abundance closely corresponds to the field observations described in the introduction.

Other observations further support the model's dynamics of the collective selection of one foraging direction. Rissing and Wheeler (1976) observed that double columns may develop at the time of a major change of direction, one leading to the new direction, the other leading to the old direction being progressively abandoned. At other times, two columns may develop together, but within several minutes, one "fails" (Rissing, pers. comm.). Also, Rissing and Wheeler (1976) only observed infrequent periods of random foraging when food was scarce, and therefore when spatial heterogeneity was high.

The only apparent disagreement is with Bernstein's (1975) observation that an artificial increase in food abundance leads to random foraging. However, she dispersed seeds very close to the nest (within 3 m radius), whereas a typical column can be 20 m long or more. This we interpret as sharply reducing the active foraging area, and thus greatly increasing the leakage between the correspondingly smaller adjacent segments, which as shown by the model leads to the trail widening and the foraging becoming random. We predict that if she had equivalently enriched the foraging area in a band say 15 m from the nest, she would have slowed the column's rotation, in accordance with her other observations and those of Rissing and Wheeler (1976), and not elicited random foraging (also suggested by Davidson, 1977). This is indirectly supported by Rissing's (1981) study of seed preference, in which he added and replenished seeds accross the path of a foraging column 12, 24 and 36 m from the nest, and observed that the foraging direction and length remained constant throughout the six consecutive foraging periods of his study. Similarly, Bernstein (1975) reported that during the week or so of maximum seed production, *M. pergandei* used random foraging, although Rissing and Wheeler (1976) appear to contradict this. Again if the seeds were highly abundant very close to the nest during this period, then the model would show random foraging for a short period until the seeds nearest the nest were all gathered, and normal long-distance structured foraging takes over.

Of course in natural conditions, heterogeneity is the rule, and the rotations are not as neatly periodic as in *fig. 1*. For example, the restocking of sectors can be somewhat irregular, especially in desert conditions, contributing to irregularities in the foraging column's rotation. This, however, is compensated for by the fact that *M. pergandei* (Rissing and Wheeler, 1976) switches to less preferable seeds and vegetable matter when top-quality grains are scarce, and by the fact that the rotation is "driven" by the relative abundance of neighbouring sectors, rather than by the absolute abundance. Also, the workers are not necessarily as simple and identical as in the model. For example, Rissing (1988) suggests that there is some degree of worker specialisation, those marked at the head of foraging colums often being found at the head of subsequent columns. Some individual idiosyncrasy is not, however, incompatible with the model's minimalist tenets.

It should be stressed that the *collective* foraging pattern is seen here as an automatic consequence or even a side-effect of just two rules of *individual* forager behaviour: firstly, a forager lays trail when returning to the nest, secondly foragers leaving the nest tend to choose the more highly marked direction. While collective foraging trails have obvious and well-documented advantages that easily justify the pheromonal "expense" incurred, the fact that the *M. pergandei's* column rotates need not *per se* have any functional value, although it probably contributes to the species' territoriality (RISSING, 1987, 1988).

Similarly, the same simple individual behaviour generates different collective patterns under different conditions, these different "side-effects" resulting from the combined interactions between foragers and between foragers and environment. In this light, while the ant colonies certainly benefit from the collective patterns, it would perhaps be a mistake to think that these collective behaviours initially developed as the result of some sort of selective pressure.

Consider a theoretical case. Two sympatric ant species have exactly the same individual behaviour as decribed in the model. The only difference between them is that one harvests a seed that is evenly scattered with a lowish density and the other harvests a seed that is found in patches of high densiy. The model shows that, as a result, the first would exhibit a rotating column, while the second would exhibit a trunk trail. If you didn't know that the individual ants behaved the same, it would be easy to fall into the optimal foraging trap of thinking that the two species had evolved different foraging behaviour closely adapted to their preferred seed's distribution.

It is, however, probable that, starting from the same individual trail lying/following behaviour, different species would add certain refinements that render one of the possible collective patterns predominant, and therefore genuinely species specific, instead of only apparently so. Possible means would include a quantitative adjustment of the individual foragers' trail following (parameters f_i and q) and/or trail laying (amount of pheromone laid per forager, rate of evaporation/decay). For example increasing the trail following capability, the amount of pheromone laid, or using a pheromonal mixture that evaporates less (or foraging more when the temperature is lower or even at night) would change rotating columns to more stable trunk trails.

Some harvester ant species develop trunk trails (e.g. *Pheidole militicida* - HÖLLDOBLER and MÖGLICH, 1980; *Pogonomyrmex rugosus, P. barbatus.* HÖLLDOBLER, 1974), while others forage randomly (*Pogonomyrmex maricopa* - HÖLLDOBLER, 1974; *P. californicus*, even though these can form trails - RISSING, pers. comm.) and *M. pergandei* develops rotating columns. The best way to demonstrate to what extent these differences are based on the same individual behaviour and to what extent on species specific differences would be to perform rigourously controlled experiments on each species with different and even unnatural seed distributions, abundance and colony sizes, and to see whether they stick to their pattern or not.

Meanwhile, certain field observations suggest that there is perhaps a common basis, while others suggest that there is a certain degree of species specificity (RISSING pers. comm.). For example, there is a correlation between colony size and foraging pattern in harvester ants as predicted by the model.

M. pergandei has larger colonies than *P. rugosus* which has larger colonies than *P. californicus*. On the other hand *P. rugosus* and *M. pergandei* exhibit trunk-trails and rotating columns repectively in exactly the same territory. Young, small *M. pergandei* colonies form rotating columns. Even though all *M. pergandei's* columns rotate much slower in years of higher abundance, they still rotate. However, all these points could be explained by the model in terms of colony size or food preference, but until controlled experiments untangle the different factors involved, such evidence remains inconclusive.

Finally, the logic behind the model is not necessarily restricted to trail-laying social insects. Any group-living central-placed foragers that have a mechanism to synchronise the direction of their foraging trips could interact with the food supply to generate a rotating collective foraging direction. Honeybee foragers, for example, select between the different directions "offered" in recruiters' danses. Communal nesting birds are also thought to be capable of recognising when other members of the colony return from a successful foraging flight and to choose their next flight direction accordingly (see work on information centres, e.g. WARD and ZAHAVI, 1973).

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