

"collectors", or the effort required to collect the discovered resources, is not a simple one. The collectors remain inactive for long periods, ready to go to newly discovered resources as soon as the information from the scouts reaches the society. However, the more scouts there are engaged in searching for the resources, the fewer collectors are available at critical moments, and newly discovered food sources may therefore be lost to competitors (Johnson et al., 1987).

In order to find the optimum scout-collector proportion in an ideal society, a numerical model, equivalent to that of Johnson et al. (1987), was developed. This model focused on territorial defense of food patches, finding that species with territorial defense of resources should preferentially visit large patches, and have comparatively large colony sizes and relatively few scouts. Our model focuses on the efficiency of different recruitment systems in food retrieval, allowing the study of the effect on food retrieval of the following variables: total amount of resources collected by a given society, proportion of scouts, recruitment systems, resource density and resource size. As a respectable amount of theoretical knowledge and experimental data has been accumulated on foraging strategies and recruitment systems of ant societies (e.g. Taylor, 1978; Jaffe, 1980, 1984; Jaffe et al., 1985; Gross et al., 1989; Deneubourg and Gross, 1989), the model was developed for food retrieval in ants, but it is thought to apply, with the correspondent modifications, to any eusocial colony where the effort made to search for a resource directly affects the available force for its eventual retrieval.

Model

A numerical model, equivalent to that of Johnson et al. (1987) but developed independently, simulated an ant colony foraging for resources. A society displaying central-place foraging in a finite area with 200 foragers was assumed for all cases where not stated otherwise. Each ant foraged independently, and was randomly assigned as a scout or a collector according to a fixed proportion. Each ant was randomly assigned two thresholds: one for responding to trails or recruiters, and another which regulated the initiation of recruitment according to food quality or quantity (Jaffe, 1980).

A two-dimensional concentric space with 500 possible sites was modelled. The nest was located at the center of the space. Each scout was able to walk randomly to any site to the front or to either side, one space at each time interval. Each food patch was located at one single site, independent of the size of the resource, and any number of ants could share a single space. Although these assumptions are unrealistic, since they imply that large resources are as difficult to find as small ones, they simplify the model, and stress the fact that, relative to the size of the ants, the foraging area is enormous, and that the space occupied by resources (including the area surrounding from which the resource may be detected by the ant) is negligible compared to the size of the foraging area.

Food was randomly distributed in a given environment. Different densities of resource occurrence in the environment (D) were tested; the resource size (RS) at each locality could vary.

Numerical variables used

- N = Number of foragers in the colony (scouts + collectors)
S = Percent of scout ants in a colony, where $100-S$ = collectors (%)
OS = Optimum percentage of scouts, i.e. percentage of scouts by which the maximum amount of food was collected during a fixed period.
D = Resource density: mean food patch density (sites occupied with food (%))
R = Absolute amount of collected resources during a given period
RS = Resource size: mean food patch size (in equivalents of number of collectors required to retrieve it)
GS = Group Size for GR and initial GS for DMR (number of recruited collectors)

Functional variables programmed

- GR = Group recruitment
DMR = Democratic mass recruitment (snowball effect)
AMR = Autocratic mass recruitment

Searching behavior and recruitment

Scouts were programmed to have a sequence of five behaviors:

- 1: Random searching for food
- 2: After finding food, returning to the "nest" following the shortest route
- 3: Recruiting collectors
- 4: Returning straight back to the food source with the recruited collectors
- 5: Returning to the nest with the recruited collectors, carrying food.

Three different recruitment techniques were modeled:

Group recruitment (GR): scouts always recruited a fixed number of collectors, who followed the scout back to the food after being recruited.

Autocratic mass recruitment (AMR): scouts recruited the exact number of collectors required to retrieve the discovered resource, by using a pheromone trail leading from the food to the nest (Jaffe, 1980; Jaffe et al., 1985). Scouts assessed the amount of food to be collected with a given error up to $\pm 95\%$ of the resource size.

Democratic mass recruitment (DMR): scouts recruited collectors by using a pheromone trail leading to the food. The more scouts or collectors returned to the nests from the food, the stronger the odor trail. The stronger the trail, the more collectors were recruited.

Variables measured

The simulated workers were left to move randomly in the modeled foraging area to find the food, recruit collectors and retrieve the food until resources were exhausted. The output of the model was the amount of resources collected during fixed periods for different proportions of scouts/collectors (S). Each value was the mean of the results from 5 runs, using 5 different sets of random variables defining the movement of the workers and the distribution of the resources, which were the same for all curves reported, making qualitative comparisons between curves possible. The optimum proportion of scouts (OS) for each set of parameters was estimated graphically, by finding the value of S giving the maximum value of R (Fig. 1).

Limitations of the models

Our models assumed a given distribution of resources which was not affected by external factors, i.e. the distribution was assumed constant in time, and only the collectors of the modeled society were able to remove the resources. However, since we studied the models only during the initial phase of the resource-discovering and -collecting process, the results can be considered to be general, as a certain mean resource distribution pattern will exist even in very dynamic situations with fast-changing resources.

In nature, the division between scouts and collectors is probably not constant in time, while in our models it was. This should not be a strong handicap, since the actual proportion of scouts to collectors at a given time is related to the discovering abilities for the same period. For the initial phase of a resource-discovering-collecting process, the initial proportion of scouts is probably the dominant feature, giving validity to the results of our models. Foraging models normally and explicitly consider the long-term outcome, but for the long-term phase of recruitment, it is known that scouts eventually start retrieving food, becoming "foragers" (Jaffe and Howse, 1979; Jaffe 1980).

Worker size and resource distribution

Worker size was tested indirectly, i.e. worker size was related to the amount of food that can be retrieved by a single worker. This parameter, in our model, has a relative value which is related to resource size. Hence, variations in resource size in our model produce the opposite but symmetrical effect of variations in worker size. Similarly, large food size is equivalent to a clumped resource distribution, whereas small resource size is equivalent to a uniform resource distribution.

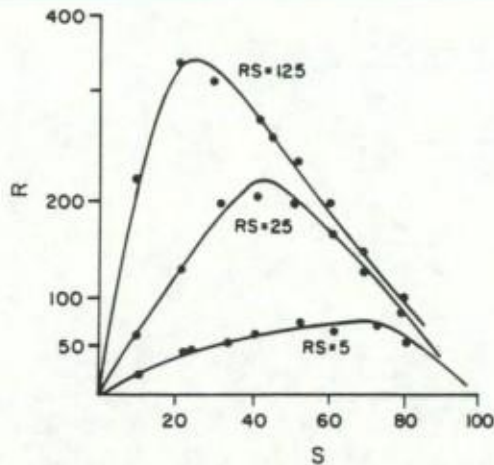


Figure 1. Amount of resources collected (R) by society for different scout-collector proportion given as percentage of scouts (S) in the colony. Conditions were: AMR system, $D = 0.7$ (points indicate the actual means from the 5 "runs" of the model; standard deviations were a maximum of 20% of the means; curves were fitted by eye)

Results

Fig. 1 shows a typical example of the relation between the amount of resources collected by the colony during a fixed period, and the scout/collector proportion given as the percentage of scouts of the whole foraging force (S). Here we see that with small resource sizes, the curves tended to be broader and the amount of collected resources lower, but always an optimum percentage of scouts, i.e. the proportion of scouts by whom the maximum amount of resources was collected (OS), could be deduced from each curve.

Figs. 2 to 4 show the effect of the size of the resource, for each of the three recruitment systems, on the optimal proportion of scouts. Different resource densities in the environment were represented in each figure. It is clear that for the three recruitment systems tested, the OS was smaller at large individual resource sizes, whereas for small resource sizes, the OS tended to reach 100%. Large groups of recruited collectors with group recruitment, or large initial group sizes of recruited collectors with democratic mass recruitment, diminished OS .

The effect of resource density on the OS is such that for high densities of resources, the OS values dropped. It is interesting to note that for group recruitment, the relationship between OS and D was independent of RS and only dependent on GS (Fig. 5). For mass recruitment, OS dropped very fast with increasing D for large RS values (Fig. 6-7).

Fig. 8 shows the relationship between total population (N) and OS for a given set of RS and D values for the AMR system. We observed that the OS dropped at higher values of N . This situation was identical for GR and DMR, since in all cases increased values of N implied a greater absolute number of scouts at a given proportion of scouts for the same environment.

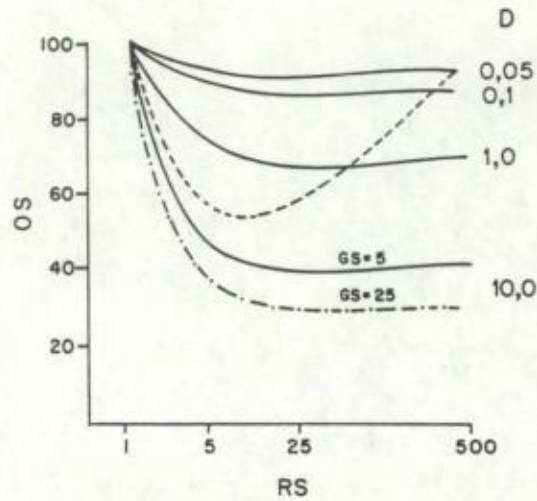


Figure 2. Optimum proportion of scouts (OS) for different resource sizes (RS) for societies using group recruitment (GR). Values for different resource densities (D) are given. The discontinuous line represents the situation at the constant total amount of resources situation where $RS \times D = 50$. Group size (GS) was 5, except in one case (dash-dotted line) where it was 25

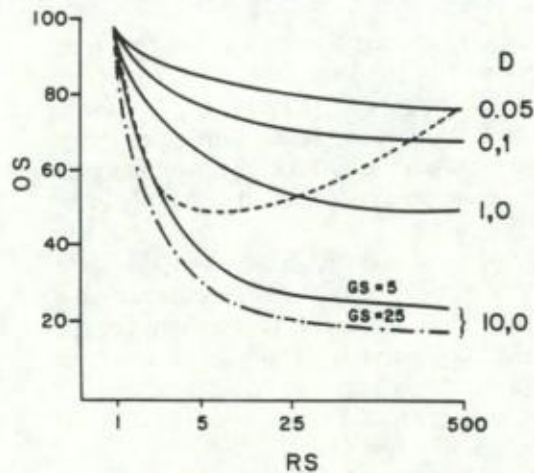


Figure 3. The same as Fig. 2, but using democratic mass recruitment (DMR)

Figs. 9 and 10 compare the efficiency of the different recruitment systems in retrieving resources. Here we see the total amount of resources collected during a period (equivalent to 50 movement decisions for each worker), in which scouts could discover on average two different resource sources. R is given for each recruitment system and for various RS or D. We observe that group recruitment and autocratic mass recruitment were equivalently efficient for small RS and low D. Autocratic mass

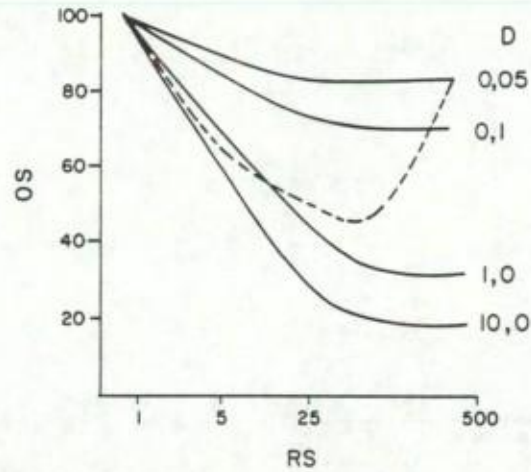


Figure 4. The same as Fig. 2, but using autocratic mass recruitment (AMR). Group sizes were automatically fixed according to RS in this case

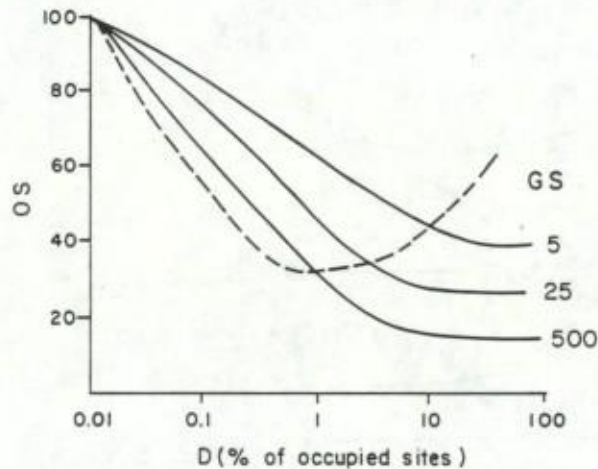


Figure 5. OS for different resource densities (D) for societies using group recruitment (GR). RS coincides with GS. The discontinuous line represents the situation where $RS \times D = 50$

recruitment and democratic mass recruitment were equally efficient at low D or very large RS. Democratic mass recruitment was very inefficient compared to autocratic mass recruitment or group recruitment for small RS.

The differences between the three recruitment systems regarding OS can be appreciated in Figs. 9–11. We see that autocratic mass recruitment required the lowest amount of scouts, except for very high D and very small RS.

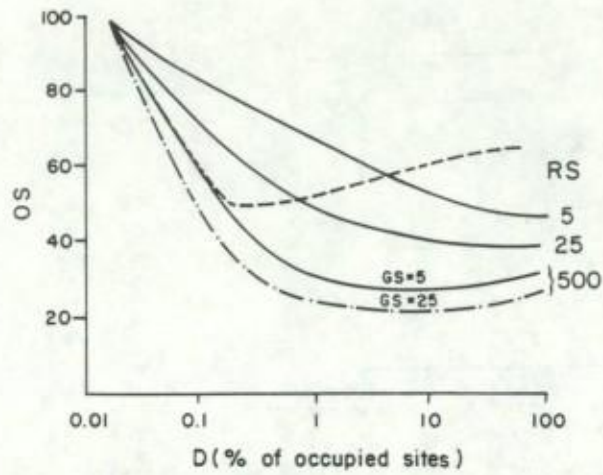


Figure 6. OS for different D for societies using DMR. Curves are for $GS = 5$, except the discontinuous line which represents $GS = 25$. Discontinuous line represents $RS \times D = 50$

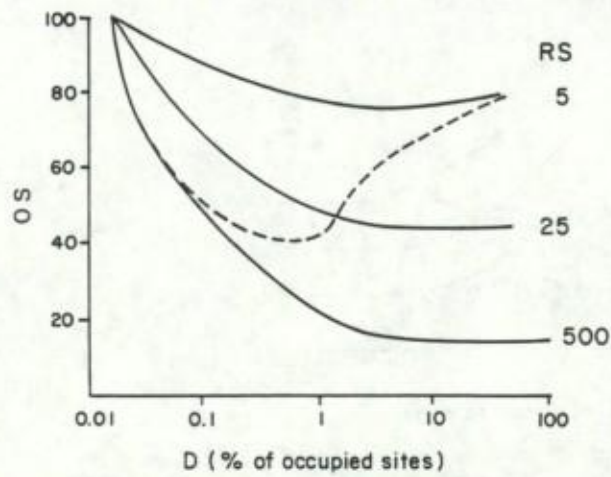


Figure 7. OS for different D for societies using AMR. Discontinuous line represents $RS \times D = 50$

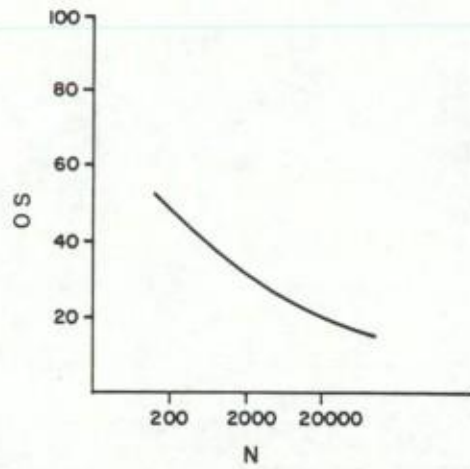


Figure 8. Relation between OS and total number of individuals in the society (N) for AMR. RS = 25, D = 1%

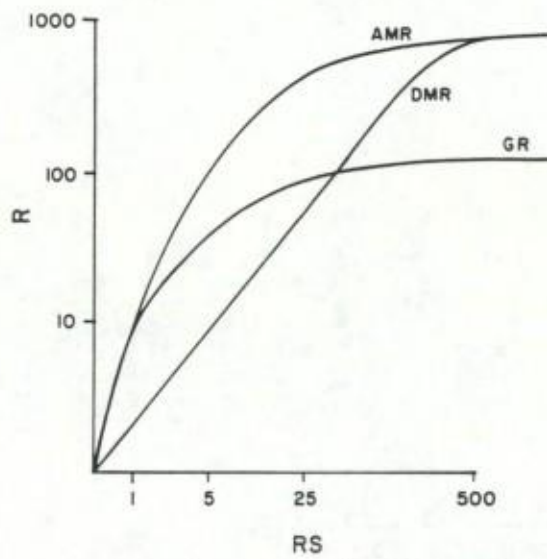


Figure 9. Relation between the amount of resources (R) collected during a fixed period (50 iterations) and resource size (RS) for the different recruitment systems at D = 1

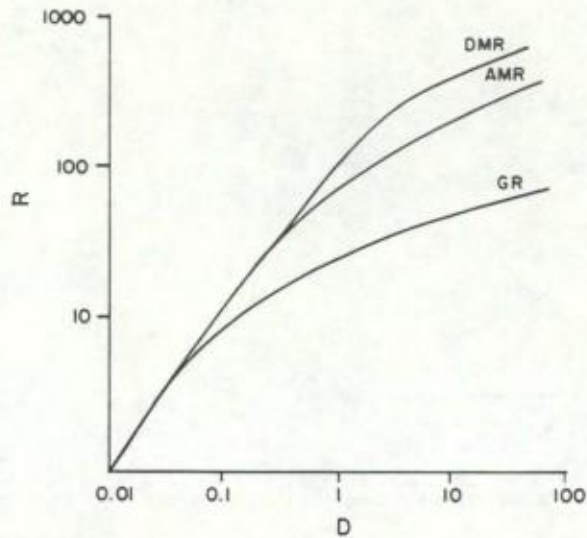


Figure 10. Relation between the amount of resources (R) collected and the resource density (D) for different recruitment systems. $RS = 25$

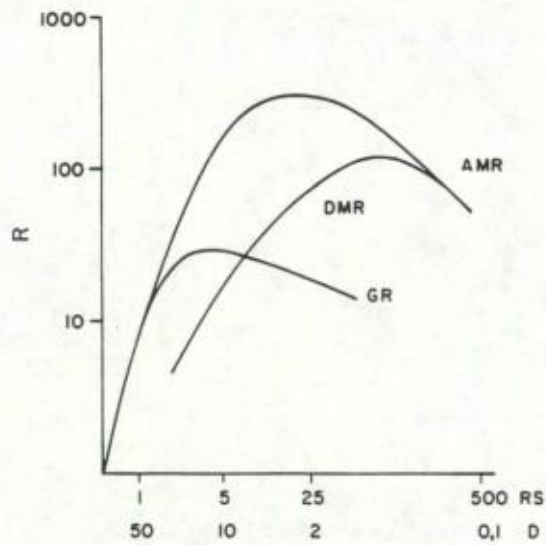


Figure 11. Amount of resources collected (R) by societies using different recruitment systems for different values of RS and D so that $RS \times D = 50$

Discussion

Despite the limitations of this model discussed before, some of the results seem so obvious and are so recurrent that we can conclude the following:

Optimum percentage of scouts

It is interesting to note that for every specific distribution of resources, there is an optimum scout percentage (OS) for each recruitment system employed. For situations requiring high OS values the curves tend to be broad-humped, indicating that small variations in the number of scouts would not affect substantially the collecting ability of the society. It might therefore be expected that selection pressure on S would be stronger (i.e. we might expect small variations in the proportion of scouts among colonies) in situations where optimums are sharper, i.e. in conditions where the OS is small.

Worker size and individual foraging vs recruitment

The individual foraging strategies turned out to be optimal for societies (or species) collecting resources of small size, which can be handled by single individuals, and which are not found in large clusters. Every individual is then both a scout and a forager, and the society maximizes the rate of discovery of resources without affecting the speed of collection of the discovered resources. For colonies foraging on resources of large size, the optimum percentage of scouts tends to be small. From these results we predict that ant species will be either mass recruiters or individual foragers, and that pure group recruitment for food retrieval is rare. Group recruitment should be more a feature of societies using individual foraging strategies, occasionally collecting resources of large size. This prediction might explain the findings of Beckers et al. (1989: Fig. 1), who showed that group recruitment is the less common of the recruitment systems of the 98 species studied by them.

Small workers cost less to produce and maintain than large ones (entomological formulation of the first law of thermodynamics); the loss of larger workers is therefore costlier than that of small ones. This means that, in the absence of specific environmental pressures selecting for large workers, social insects should prefer to produce small workers. On the other hand, it is reasonable to suppose that food sizes in natural environments are very variable. Hence, the maximum amount of food that can be retrieved by an ant or by a colony limits the range of foods that can be used by a given species. These assumptions lead to the following testable prediction: ant species foraging singly for food should have foragers with a relatively greater size, allowing for efficient food collection, whereas for mass recruiters, worker size is of minor importance, since collective food retrieval allows for exploitation of large resources. If these assumptions are correct, the size distribution of foragers of different ant species in a given environment should not follow a normal distribution, but all species using mass recruitment systems should have small foragers, minimizing forager production costs and eventual loss due to predation. Species (r

using individual foraging systems should have larger foragers, depending on the size distribution of the food they are retrieving. This prediction is again in agreement with Beckers et al. (1989) who found that large colonies tend to be mass recruiters, whereas small colonies tend to be individual foragers or recruit via tandem running. This finding helps us to reformulate our supposition in the following way: large workers should be more common among species with small colonies, and small workers among species with large colonies.

The efficiency of the different recruitment systems

Autocratic mass recruitment, although the more complex of the mass recruitment systems studied (Jaffe, 1984), is not the most efficient regarding resource retrieval in situations where several small resources are collected. Only at low D and large RS are these societies more efficient. We might expect species (societies) using autocratic mass recruitment to forage on relatively large resources. This would explain the finding that among ants, only leaf-cutters (Attini), which forage for plants relatively large in relation to individual ants, use the autocratic mass recruitment system. All other species tested used the democratic mass recruitment system (Jaffe et al., 1985). The democratic mass recruitment system is the most efficient for foraging for high-density resources. Hence, the recruitment system used by a society depends on the ecological behavior of the resources used by the society. This would imply that ecological knowledge could be derived by studying the recruitment system of a given society and by measuring the actual percentage of scouts used by the society when foraging for a given resource.

Food retrieval and defense of food patches

Comparing our results to those of Johnson et al. (1987), we confirmed that the optimum percentage of scouts is more sensitive to changes in food patch size than patch density. Johnson et al. found that large colonies were more efficient in retrieving large food patches, whereas we found that mass recruiters were the more efficient. These results complement each other, since Beckers et al. (1989) found that large colonies are normally mass recruiters.

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