Without memory the optimal net benefit is given when the food sources are equal in size to the ants' carrying capacity and smaller ants are more efficient than larger ants in poorer environments. With memory smaller ants are more efficient with small food-sources and larger ants with very large food-sources.

Under certain intermediary conditions being the right size is more important than having a memory and under others the reverse is true.

**INTRODUCTION**

The seven thousand or so known ant species are all characterised by their social organisation, living in colonies of a few to several million individuals who communicate, interact and co-operate, though certain of their activities may be performed individually.

One of the most fundamental aspects of a colony's existence, its foraging activity, is also one which offers a great diversity (Carroll & Janzen, 1973) and which may be analysed quantitatively.

Three levels of diversity may be distinguished, concerning the kind of food taken (live/dead, immobile/mobile,
animal/vegetable..., the level of variety of the food (certain ants being monophagous, others being polyphagous and opportunist) and finally the techniques and strategies involved in finding and bringing back the food. This latter may be organised on a purely individual basis (e.g. certain ponerine ants, Fresnau, 1984), may be essentially collective involving group or mass recruitment (e.g. Tetramorium caespitum, Tapinoma erraticum, Solenopsis invicta, Wilson, 1962; Verhaeghe & Deneubourg, 1983) or may even be strictly collective (e.g. the army ants, Ragniér & Van Boven, 1955).

Modelling the different food-collecting strategies not only enables a quantitative comparison of their efficiency, but also throws some light upon the relationship between the individuals' behaviour and the colony's behaviour, and upon the different ways in which different ants species may have adapted their ethological and physiological characteristics to different environmental conditions. Taylor (1978) proposes a model of foraging behaviour in which the society tends to maximise its net energy intake as a function of the characteristics of the trophic area. This paper presents two models of individual food collecting, with and without memory of the food-source location, and investigates the quantitative advantage of possessing this memory for ants of different sizes in environments of different richness. The model concerning ants without memory is intended as a basic for comparison with the model with memory and with future models involving the different forms of recruitment. At present numerous ants species have been described as possessing memory but little information exists about the quality of this memory or about species that do not possess such a memory.

Of the many parameters that may influence a colony's energetical budget, only the ants' length, number and the surface they exploit and the food-sources' original size and rates of appearance and disappearance are allowed to vary. Otherwise the ants and their environment are considered as being strictly uniform.

This choice reflects the point of view that these are the six most important parameters necessary to determine a colony's energetical budget. All other heterogeneity (such as, within a colony, different sized ants moving at different speeds, carrying different sized loads of different sorts of food found in different parts of a heterogenous foraging area) is considered here to be of secondary importance, and moreover at present could only be represented arbitrarily as a result of lack of data on the one hand and the extreme variability both within any one colony's local environment and between different local environments on the other hand.
1. THE MODELS

i) The Food-Sources

The food-sources considered are inactive, immobile, liquid and spherical, and are nutritionally balanced, with an energy content (G) equivalent to a 1/4 M glucose solution. They are uniform (original weight $w_0$, original diameter $D_0$), falling randomly into the circular foraging area (surface $S$, radius $r$) at a rate of $A_n$ sources per minute ($A_n = 2.5/S$, where $2$ is the food flow estimated at more or less $10^{-5}$ g m$^{-2}$ min$^{-1}$). (A glossary terms is provided at the end of the article)

In the absence of discovery by the ant colony, a food-source disappears naturally by decomposition, discovery by other colonies or species, etc., at a rate of $q$ min$^{-1}$ ($= 10^{-2} - 10^{-5}$ min$^{-1}$). A high value of $q$ therefore implies short-lived food-sources, high competition and a poor environment. Only food-sources of whole number multiples (or fractions) of the ants' carrying capacity ($w_a$) are considered here. $F_n$ represents the number of sources containing $n$ loads ($n = w_0/w_a$ for $w_0 > w_a$; $n = 1, 2, 3, ...$; for $w_0 < w_a$, $n = 1$) present at any moment in the foraging area.

$D_0$ is assumed to remain constant for any one source no matter how many loads have been removed by ants from that source, as long as the source is not totally exhausted.

ii) The Foraging Ants

The foraging ants, $A$, are of uniform size: length $l$, weight $w_a$, perceptive width $D_0$ and speed of travel $v = 0.6$ m min$^{-1}$, for all $l$ (see table I, the relationships between $l$ and $w_0$, $D_0$, $C_0$, $C_1$, $C_2$ and $C_3$ will be presented elsewhere). Each ant can carry its own weight of liquid food, one load containing $y = 0.5$ W$_a$G effective Joules. $0.5$ represents the ants' metabolic efficiency with respect to Joules.

They are divided into two categories. $F$ ants are searching for food-sources and $F_0$ ants are occupied transporting discovered food ($A = F + F_0$). The searching ants are randomly distributed throughout the foraging area (with a constant density) and search at random. They become occupied ants when they meet a source, which happens $bF(P_1 + P_2 + ... + P_n)$ times per minute where, $b = v(D_0 + D_0)/S$, a constant derived from the random search pattern (Laing, 1938).

On average the sources are discovered at $t/1.41$ from the nest. The ant remains occupied for 1 minutes, being the
time required to absorb the liquid (6 min), return directly to the nest (on average r/v 1.41 min), deposit the food (6 min) and return to the foraging area (it is assumed that the ants travel directly a certain distance, on average r/1.41, before starting to search for food sources once more).

Without memory an occupied ant does not return to the food source it discovered, and thus automatically becomes a searching ant again. With memory it returns directly to its food source. If any food remains it repeats the cycle of 7 minutes; if not then it becomes a searching ant again.

A moving unloaded ant consumes \( C_1 \, J \, \text{min}^{-1} \); a moving loaded ant consumes \( C_2 = C_1(1 + \frac{W_{\text{load}}}{W_a}) \) where \( W_{\text{load}} \ll W_a \); a non-foraging ant in the nest consumes \( C_3 = \frac{C_4}{4.15} \); a resting ant consumes \( C_0 = \frac{C_4}{8.3} \).

(Estimations are made from Jensen and Holm-Jensen, 1980 and Nielsen et al, 1982).

The model thus gives larger ants a larger carrying capacity and perceptive width, and a higher energetic consumption.

Table I gives the values of \( 1, D_a, w_a, C_0 \) and \( C_1 \) used in the models.

<table>
<thead>
<tr>
<th>Length</th>
<th>Perceptive</th>
<th>Resting</th>
<th>Moving Unloaded</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 mm</td>
<td>D_a mm</td>
<td>( w_a ) mg</td>
<td>( C_0 ) J min(^{-1} )</td>
</tr>
<tr>
<td>2</td>
<td>1.9</td>
<td>0.2</td>
<td>0.31 \times 10^{-5}</td>
</tr>
<tr>
<td>4</td>
<td>3.4</td>
<td>1.7</td>
<td>1.26 \times 10^{-5}</td>
</tr>
<tr>
<td>6</td>
<td>4.7</td>
<td>5.9</td>
<td>2.83 \times 10^{-5}</td>
</tr>
<tr>
<td>8</td>
<td>5.8</td>
<td>13.9</td>
<td>4.95 \times 10^{-5}</td>
</tr>
</tbody>
</table>

iii) Interaction Between the Foraging Ants and the Food-Sources.

Without memory the dynamics of the interactions between the foraging ants and the food sources are given by:

\[
P_n = A_n - (q + bF) P_n
\]

\[
P_{n-1} = bF P_{n-1} + 1 - (q + bF) P_{n-1} \quad i = 1, \ldots, n-1
\]

\[
F_0 = \sum_{i=0}^{n-1} b F P_{n-1} - F_0/T
\]
where \( P_{n-1} \) is the number of food-sources of size \( n-i \).

Without memory a source disappears at the rate of its successive discoveries \( (b F) \).

With memory, once a source has been discovered it disappears at a rate of one load every \( T \) minutes. If discovered twice it disappears at a rate of two loads every \( T \) minutes. The system (I) thus becomes:

\[
P_n = A_n - (q + b F) P_n
\]

\[
P_{n-1,j} = b F P_{n-1,i,j-1} + j T^{-1} P_{n-1,j} - (q + b F + j T^{-1}) P_{n-1,j}
\]

\( i = 1, \ldots, n-1; j = 1, \ldots, i-1 \) with \( i \geq j, i-1 \geq j \), \( i-1 \geq j-1 \)

Rem.: \( P_{0,j} \equiv P_n \)

\[
F_0 = b F P_n + \sum_{i=1}^{n-1} \sum_{j=1}^{i} (b F + j T^{-1}) P_{n-1,j} - F_0 T^{-1}
\]

where \( P_{n-1,j} \) represents the number of sources containing \( n-i \) loads that have been discovered and are being exploited by \( j \) ants. (For this type of description in physics, chemistry, ..., see Nicolis & Prigogine, 1977)

iv) The Benefit

The gross benefit per minute is given by the caloric content of the \( F_0 T^{-1} \) loads that reach the nest per minute \( = y F_0 T^{-1} \).

The searching ants, \( F \), consume \( F C_1 J \) min\(^{-1} \) and the occupied ants, \( F_0 \), consume on average \( F_0 (C_1 + C_2)/2 \). Furthermore the ants, \( F + F_0 \), consume \( (F + F_0)C_0 J \) min\(^{-1} \) at night. If one considers days of 12 hr. day and 12 hours night, then the net benefit, \( B \), is given by

\[
B = y F_0 T^{-1} - F (C_0 + C_1) - F_0 (C_0 + (C_1 + C_2)/2)
\]

However one Joule is not as useful to a colony of large ants as it is to a colony of small ants. In order to compare the benefits of nests of different sized ants the net benefit, \( B \), is divided by \( C_3 \) (the consumption of non-foraging ants), thereby expressing the net number of non-foraging adult ants (or adult ants and larvae) that the foraging ants support.

Thus in order to be considered equally successful by
the models, a colony of large ants must collect a higher number of Joules min\(^{-1}\) than a colony of small ants.

v) **Optimisation of the Net Benefit.**

In the case of individual foraging as investigated here, the most efficient exploitation of the environment would be achieved by dispersed solitary ants. However this solution is incompatible with the social organisation of their life-cycle, as imposed in these models. The optima must therefore be found with respect to the principal characteristics of the colony, namely the number of foraging ants (A), their size, characterised by their length (l) and the surface they exploit (S).

For a given A, increasing S will at first, by reducing the competition between the searching ants, increase the colony’s net benefit, B/C3, to a maximum after which the increasing distances involved will reduce the benefit. Similarly for a given S, increasing A will at first increase the benefit to a maximum after which the increasing competition between the searching ants will reduce the benefit.

The computation proceeds as follows. The parameters \(l, q, l\) and \(w_{e}\) are fixed, the value of \(l\) determining the ants' weight, perceptive width and their different energetic consumptions. The values of \(S\) and \(A\) are then floated so as to find the maximum values of the net benefit (\(B^{*}/C_{3}\)). This would correspond to a colony adapting its foraging area and the number of foraging ants so as to optimise its net benefit. This optimal net benefit is found for different values of \(q, l\) and \(w_{e}\), albeit under the constraint that \(B^{*}/C_{3} \geq 10 \ A\).

This constraint derives from the ants’ social organisation, characterised by their division of labour, such that the foraging ants must feed the larvae and those ants which work in the nest. Adult ants forage for only about the last tenth of their life, and must thus support at least 10 adult ants at the nest, whereas the optimum total net benefit of the nest may be shown by the model to be given when each foraging ant contributes less than 10 times a non-foraging ant’s consumption \(C_{3}\). Furthermore if one takes into account the larvae’s high metabolic consumption each foraging ant should probably contribute more than 10 \(C_{3}\).

The Results.

The results summarised here must be considered with a certain reserve. Firstly the model analyses the system only at the steady-state, whereas “reality” is anything but that.
Secondly the optimum benefit is calculated without restriction to $S$, whereas an ant can only stray so far from its nest without risking to be unable to find its way back.

Thirdly food-sources of one original size only are considered at any time, whereas ants are often opportunist in their foraging. Fourthly no spatial clustering of food-sources is allowed for. Further models will attempt to limit these reserves.

The figs. 1 and 2 summarise the results obtained without memory, presenting the optimal net benefit, $B^* / C_3$, as a function of the weight of the food source, for ants of two different sizes, in poorer conditions (fig. 1, high $q$) and in richer conditions (fig. 2, small $q$). For convenience the curves are presented as continuous functions of $n$, whereas only sources of whole number multiples (or fractions) of the ants' weight are considered.

It is recalled that the richness of the environment is characterised by $q$, a measure of the level of competition for the food-sources. A low value of $q$ implies long-lived sources and thus a richer environment. A high value of $q$ implies short-lived sources and thus a poor environment.

For ants of a given size (weight $w_a$) the maximum net benefit is given by exploiting food sources whose size is equal to their carrying capacity (i.e. $w_a = w_S$, $n = 1$).

Comparing the different maxima for ants of different sizes shows that their relative value depends upon the richness of the environment. In poorer conditions smaller ants show a higher optimum net benefit, whereas in richer conditions the larger ants show a higher optimum net benefit.

The same relationship is observed for ants with memory (figs. 3 and 4). The benefit is however much less dependent upon the source being the same size as the ants' carrying capacity ($n=1$), particularly with smaller $q$, for which the optimal benefit is achieved with $n \gg 1$, and near-optimal benefits within a large range of values of $n$.

Without memory it is essential to adjust one's size to that of the food source or to specialise in food-sources close to one's carrying capacity. With memory the ant has a greater "freedom of choice" of its size, particularly with smaller values of $q$. With food-sources of variable size (greater than the ants' carrying capacity) it is of great advantage to have a memory. Memory allows a greater freedom of action of factors other than the food-source size on the ants' size.
Food-collection without memory. \( l = 2 \text{ mm and } 4 \text{ mm}, \text{Fig. 1 } q = 10^{-3.4} \text{ and } q = 10^{-4} \text{ for Fig. 2} \)

For other parameters see text and table I.

Food-collection with memory. \( l = 2 \text{ mm and } 4 \text{ mm}, \text{Fig. 1 } q = 10^{-3.4} \text{ and for Fig. 2 } q = 10^{-4} \).

For other parameters see text and table I.
Note that with food sources of \( n < 1 \) and with no spatial clustering, having a memory confers no advantage whatever as the source is exhausted in one trip.

The relative benefit of having a memory, presented in Fig. 5 for \( 1 = 4 \) mm, and defined as

\[
\frac{B^+ \text{with memory} - B^+ \text{without memory}}{B^+ \text{with memory}} = 1
\]

is highest in poor environments, though decreases rapidly as \( n \) increases. With richer environments, smaller relative benefits are obtained, though under a much wider range of values of \( n \).

![Graph](image)

**Fig. 5:** The Relative Benefit of Memory

- \( q = 10^{-3} \)
- \( q = 10^{-3.4} \)
- \( q = 10^{-4.4} \)

With higher competition for food sources, it is of greater advantage to be able to return directly to a food source by memory, i.e. before it disappears.

Finally, Fig. 6 divides the space \( (n, q) \) into different zones depending upon which of the ants of two sizes (1 = 2, 4 mm), with or without memory has the highest optimum net benefit, \( B^+/C_3 \). \( L^+ \) and \( L^- \) symbolize large and small ants, \( M^+ \) and \( M^- \) symbolize with or without memory.

Briefly in zones 1 and 2a (small food sources) the smaller ant is the more efficient whatever the values of \( q \) and \( n \) chosen (\( n < 0.5 \) for the large ant, \( n < 4 \) for the small ant, \( L-M^+ \Rightarrow L-M^- \Rightarrow L^+M^+ = L^+M^- \)).

If \( n > 100 \) for the small ant (\( n > 12 \) for the large ant) the larger ant is the most effective as long as it has a memory, \( (L-M^+ \Rightarrow L-M^- \Rightarrow L^+M^- \Rightarrow L^+M^+ ) \), see right hand of Zone 3, whatever the values of \( n \) and \( q \) chosen.

Between these two limits whether the bigger or the smaller ant is the most effective depends upon the values of \( q \) and \( n \) chosen. Roughly speaking if \( q \) is large the smaller ant is the most effective as long as it has a memory (zones \( 2_b \) and \( 3_a : L-M^+ \Rightarrow L^+M^+ \Rightarrow L^+M^- \Rightarrow L-M^- \)). If \( q \) is small
the larger ant is the more efficient (if \( n > 7 \) for the small ant) even if the larger ant has no memory and the smaller ant does. (Zones \( 2_c \) and \( 3_c \): \( L^+M^+ > L^+M^- > L^-M^+ > L^-M^- \)).

In these zones \( 2_c \) and \( 3_c \) it would thus seem more important from a foraging point of view to adapt one's size to the size of the food source, or to specialise in food-sources close to one's carrying capacity, than to develop a memory, as is also true for zones 1 and 2. In zones 2 and 3 the opposite is true.

Acknowledgements

We would like to thank Profs. E. Cotton, G. Joosens and J. Prigogine for their encouragement and their open-mindedness which made possible the present work. We also thank Drs. Champagne and Verhaeghe for their fruitful discussions.
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$ (m$^2$)</td>
<td>The foraging area</td>
</tr>
<tr>
<td>$Z$ (g m$^{-2}$ min$^{-1}$)</td>
<td>The food flow in the foraging area</td>
</tr>
<tr>
<td>$A_n$ (min$^{-1}$)</td>
<td>The number of food-sources arriving in the foraging area per unit time</td>
</tr>
<tr>
<td>$q$ (min$^{-1}$)</td>
<td>The rate of disappearance of food-sources by competition, decomposition,...</td>
</tr>
<tr>
<td>$P_i$</td>
<td>The number of food-sources present in the foraging area, of size $i$, i.e. consisting of $i$ full loads.</td>
</tr>
<tr>
<td>$A$</td>
<td>The number of foraging ants</td>
</tr>
<tr>
<td>$F$</td>
<td>The number of foraging ants that are searching for food.</td>
</tr>
<tr>
<td>$F_0$</td>
<td>The number of foraging ants that are occupied in loading, transporting, and unloading food, and in returning to the foraging area.</td>
</tr>
<tr>
<td>$v$ (m min$^{-1}$)</td>
<td>The ants' speed</td>
</tr>
<tr>
<td>$r$ (m)</td>
<td>The radius of the foraging area</td>
</tr>
<tr>
<td>$D_a$ (m)</td>
<td>The food-source diameter</td>
</tr>
<tr>
<td>$D_q$ (m)</td>
<td>The ants' perceptive width</td>
</tr>
<tr>
<td>$l$ (m)</td>
<td>The ants' length</td>
</tr>
<tr>
<td>$b$ (min$^{-1}$)</td>
<td>The rate of discovery per searching ant and per source</td>
</tr>
<tr>
<td>$w_s$ (g)</td>
<td>The source weight</td>
</tr>
<tr>
<td>$T$ (min)</td>
<td>The time taken to load the food at the source, return to the nest with the food, unload the food at the nest and return to the foraging area from the nest</td>
</tr>
<tr>
<td>$y$ (J)</td>
<td>The number of useful calories transported in one full load</td>
</tr>
<tr>
<td>$w_a$ (g)</td>
<td>The ants' weight</td>
</tr>
<tr>
<td>$C_0$ (J min$^{-1}$)</td>
<td>The energetic cost of one inactive foraging ant</td>
</tr>
<tr>
<td>$C_1$ (J min$^{-1}$)</td>
<td>The energetic cost of one active unloaded foraging ant</td>
</tr>
<tr>
<td>$C_2$ (J min$^{-1}$)</td>
<td>The energetic cost of one active loaded foraging ant</td>
</tr>
<tr>
<td>$C_3$ (J min$^{-1}$)</td>
<td>The average energetic cost of one non-foraging ant</td>
</tr>
<tr>
<td>$B$ (J min$^{-1}$)</td>
<td>The net energetic benefit of the colony</td>
</tr>
<tr>
<td>$g^{-}$ (J min$^{-1}$)</td>
<td>The optimum net benefit, for a given $w_a$, $I$, $Z$ and $q$</td>
</tr>
<tr>
<td>$n$</td>
<td>The number of loads contained in an undiscovered food-source</td>
</tr>
</tbody>
</table>
REFERENCES


NONEQUILIBRIUM SENSITIVITY AND THRESHOLD PHENOMENA IN BIOLOGICAL SYSTEMS

A. Goldbeter
Faculté des Sciences, Université Libre de Bruxelles, Campus Plaine, C.P. 231, B-1050 Brussels, Belgium

1. Introduction

Living systems have evolved the property of amplifying internal and external stimuli. Although this property is manifested in a variety of ways, it belongs to either one of two types (1,2). Magnitude amplification permits a system to produce a large number of output molecules in response to a few input units. Such process is well exemplified by the response of retinal rod outer segments to light (3). There, each photolyzed molecule of the photoreceptor rhodopsin, through coupling to a protein intermediate, transducin, can activate hundreds of phosphodiesterase molecules, each of which hydrolyzes about $10^2$ molecules of cyclic GMP. As a result of this reaction chain, the photolysis of a single rhodopsin molecule produces the hydrolysis of more than $10^5$ molecules of cyclic GMP (3). Another example is the triggering of large metabolic responses by small hormonal signals through an increase in intracellular cyclic AMP followed by the activation of protein kinases (1).

Rather than being linked to the ratios of absolute sizes of sensory input and physiological response, sensitivity amplification measures the relative changes in stimulus and response (1,2). This measure is most appropriate when characterizing the capability of a system to respond to a step increase in stimulus given a background stimulation. Sensitivity amplification obtains when the % increase in response exceeds the % increase in stimulation. Such amplification is directly associated with the existence