A MODEL OF NONCOOPERATIVE FORAGING IN SOCIAL INSECTS

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Social insects use a number of foraging strategies whose components vary notably in their degree of cooperation (see, e.g., Traniello 1989). The model presented describes noncooperative foraging, that is, foraging with no recruitment, cooperation, or communication in the search for or retrieval of food. Also referred to as individual or diffuse foraging, this type of foraging is characteristic of a significant minority of ant species. Although the model is discussed principally with reference to these ants, it is equally applicable to all bumblebees and to wasps that forage noncooperatively (see, e.g., Oster and Wilson 1978; Passera 1984). Moreover, although a majority of social insects are capable of one or another form of recruitment to enhance the retrieval of larger or more-stable food sources, they rely to a great extent on noncooperative foraging for the discovery of food and the retrieval of the smaller food items.

Few models incorporating single-prey loading (in the sense of Orians and Pearson 1979) and central-place foraging are devoted to social insects. Of these, some optimize an isolated individual’s foraging efficiency with respect to size and load but neglect their essentially social character (see, e.g., Schmid-Hempel et al. 1985; Reyes Lópe 1987). Others consider the simultaneous activity of a group of foragers from the same nest but are more concerned with search patterns or long-term memory (e.g., Harkness and Maroudas 1985; Deneubourg et al. 1987).

The model presented here consists of a series of differential equations that describe the food-source dynamics, the forager activity, and the interactions between forager and source, simulating an entire colony’s foraging activity. We use these simulations to examine how the colony’s foraging benefit varies in relation to two levels of parameters.

At the colonial level, we see the effect of the size of the foraging area and the number of foragers and how the fact that a small number of foragers must feed a much larger number of nonforagers can greatly limit the colony’s foraging benefit.

At the foragers’ level, we examine the influence of two characteristics: (1) body size, the parameter to which most other forager characteristics are linked; and (2) the forager’s ability to remember a food-source location or, more precisely, to return directly to a food source that it cannot transport to the nest in one trip. Although all social insects that we know of have such a memory (see, e.g., Schmid-Hempel 1984; Peeters and Crewe 1987; Traniello 1987), we have used our
freedom as modelers to create foragers without memory as a reference point for quantifying its influence on the colony’s foraging. We see how the effects of forager size and memory vary in relation to the food sources’ size and the duration of availability.

THE MODEL

The foraging area is flat, circular, uniform, and of fixed size, with 12 h of light, 12 h of darkness, and constant environment. The nest has one centrally situated exit.

The food sources arriving are of uniform size and quality and are easily divisible. They are randomly distributed throughout the foraging area, with a constant rate of arrival and disappearance per source. We generally refer to the inverse of their rate of disappearance, which we term the average duration of availability. We refer to a source’s size both in grams and in terms of the number of forager loads it contains. This latter measurement depends, of course, on the foragers’ load-carrying capacity (see below).

The foragers are of uniform length, weight, speed, perceptual width, metabolic consumption, and load-carrying capacity. The model distinguishes the foragers that are searching for food from those that have found food. The searching foragers are distributed randomly throughout the foraging area, independently of their distance from the nest. Each searches randomly until it encounters a food source. It then becomes an occupied forager that loads the food, transports it to the nest, unloads, and returns into the foraging area. With memory of the food-source location, it returns to the place where it found the food. If any food remains, it repeats this transport cycle until the source is exhausted, after which it once more becomes a searching forager. Without this memory, it returns to a random point in the foraging area before once more becoming a searching forager.

In our notation, variables are indicated by capitals and parameters by lowercase letters.

\[ B \] the society’s net foraging benefit, expressed as the number of non-foragers that can be fed by the foragers

\[ B^* \] the maximal socially compatible benefit, that is, the maximum \( B \) with respect to \( f \) and \( z \) for which \( B \geq 10f^*; f^*, z^* \) are its coordinates

\[ P_k \] the number of food sources of \( k \) forager loads (model without memory)

\[ P_{k,j} \] the number of food sources of \( k \) forager loads that have been discovered by \( j \) searching foragers (model with memory)

\[ O \] the number of occupied foragers

\[ S \] the number of searching foragers

\[ a \] the number of new food sources arriving (min\(^{-1}\))

\[ b \] the discovery rate per searching forager per source (min\(^{-1}\))

\[ c_s, c_o, c_x \] the metabolic consumptions of a searching or occupied forager or of a nonforager (j/min)

\[ f \] the number of foragers ( = \( S + O \))
\( l \)  the length of the forager (m)
\( n \)  the number of forager loads in an undiscovered food source
\( q \)  the sources’ average duration of availability (min)
\( t \)  the average duration of one transport cycle (min)
\( u \)  the useful caloric content of one forager load (j)
\( w \)  the weight of a new food source (g)
\( z \)  the foraging area (m²)

We first consider the case of foragers without memory of food-source location.
The sources all contain \( n \) forager loads when they arrive in the foraging area.
They become one size smaller after each discovery. This generates a cascade
situation, in which the discovery of a source of size \( k \) “creates” a source of size
\( k - 1 \), at a rate given by the product of their number \( (P_k) \), the number of searching
foragers \( (S) \), and a coefficient of discovery \( (b) \) (see, e.g., Hollings 1966; Curio
1976). Independent of the discovery process, a source may disappear at any stage
of its exploitation, at a rate given by the quotient of its number \( (P_k) \) and average
duration of availability \( (q) \). These hypotheses were confirmed when tested in the
field on the noncooperative foraging ant *Pachycondyla (= Neoponera) apicalis*
(Goss et al., in press).

The rate of transformation of searching foragers \( (S) \) to occupied foragers \( (O) \) is
determined by the overall rate of discovery in the foraging area. The inverse
transformation is given by the quotient of the number of occupied foragers and the
average duration of one transport cycle, \( t \ (S + O = f) \).

One may represent these events by the following system of differential equations:

\[
P_n = \text{arrival} - \text{disappearance} - \text{discovery} \tag{1}
\]

\[
= a - P_n/q - bSP_n ;
\]

\[
P_k = \text{discovery of } P_{k+1} - \text{disappearance} - \text{discovery of } P_k \tag{2}
\]

\[
= bSP_{k+1} - P_k/q - bSP_k \quad (0 < k < n) ;
\]

\[
O = \text{discoveries} - \text{completed cycles} \quad (= - \dot{S}) = bS \sum_{i=1}^{n} P_i - O/t . \tag{3}
\]

The introduction of a memory of food-source location modifies the sequence of
events. Without memory, a source has to be discovered independently \( n \) times
before becoming exhausted. With memory, a source need be discovered only
once, allowing the forager to return every \( t \) minutes to transport another load.
The cascade now has two pathways. For example, consider a source of five loads
(referred to here as size 5) arriving in the foraging area. With the first discovery it
becomes a source of four loads (or of size 4) discovered once. Should it be
discovered by a second forager before the first one returns, it becomes a source of
size 3 discovered twice. Alternatively, should the first discoverer return before
anyone else finds the source, it will become a source of size 3 discovered once.
The source of size 3 discovered once may similarly become a source of size 2
discovered once or twice. The source of size 3 discovered twice may become a source of size 2 discovered twice or three times, and so on.

Generally, a source of size \( k \) discovered \( j \) times (of which there are \( P_{k,j} \), with \( 0 < j \leq n - k \)) may be created either by the discovery of a source of size \( k + 1 \) discovered \( j - 1 \) times or by the return of an occupied forager to a source of size \( k + 1 \) discovered \( j \) times. It may be transformed by discovery into a source of size \( k - 1 \) discovered \( j + 1 \) times or by the return of one of its discoverers into a source of size \( k - 1 \) discovered \( j \) times (every \( t/j \) minutes). Thus,

\[
\dot{P}_{n,0} = a - (1/q + bS)P_{n,0} ;
\]

\[
\dot{P}_{k,j} = bSP_{k+1,j-1} + (j/t)P_{k+1,j} - (1/q + bS + j/t)P_{k,j} \quad (0 < k < n; \ 0 < j \leq n - k) ;
\]

\[
\dot{O} = bSP_{n,0} + \sum_{k=1}^{n-1} \sum_{j=1}^{n-k} (bS + j/t)P_{k,j} - O/t .
\]

Note that for \( n = 1 \) the model with memory is identical to that without memory. There is, of course, no advantage in returning to a food source that may be transported in one load, nor any disadvantage since the sources are randomly distributed. The foraging systems with and without memory are assumed to function at their steady state (i.e., eqs. 1–6 are set to zero). Having fixed all the parameter values, one may calculate all the variables \((P, S, O)\) and thus the colony’s corresponding foraging benefit, which we now discuss.

With or without memory, the number of loads unloaded per minute is given by the quotient of the number of occupied foragers \((O)\) and the average length of one transport cycle \((t)\). Multiplying this by the useful caloric content of one load \((u)\) gives the gross benefit \((j/min)\). The foraging cost \((j/min)\) is given by the number of searching and occupied foragers multiplied by their respective average energetic consumption \((c_s \ and \ c_o)\). We do not consider the cost related to their foraging-dependent mortality.

However, one joule may be considered to have a greater value to a species of small social insects than it would to a species of large ones. We therefore express the net benefit in terms of the number of nonforagers that the foragers can feed, by dividing the net benefit by the average consumption of a nonforager \((c_x)\). The model considers a benefit of 1000 nonforagers in a large species equal to the same benefit in a small one, even though the latter collects fewer joules per minute. Thus,

\[
B = (\text{gross benefit} - \text{foraging cost})/\text{one nonforager’s cost}
\]

\[
= (uO/t - Oc_o - Sc_s)c_x .
\]

**PARAMETER VALUES**

Our parameter values are based on data available for many different ant species, including noncooperative and collective foragers, and on empirical laws that cover the ant and other animal families. The conclusions from our model have
been shown to be robust with respect to the choice of numerical parameter values, in the sense that different values give, of course, different benefits but do not change the qualitative results. This specifically concerns forager speed and loading time, food flow, and useful caloric content per gram of food (see below).

Length (l).—All the forager parameters (excluding speed) are estimated from their length. Implicitly, we are considering an archetypal forager, the same "model" in different sizes, so to speak, rather than particular known species of different sizes, whose characteristics may be related differently. This is in keeping with our wish to examine the general, qualitative effect of forager size on foraging. We limit our presentation here to the results obtained for three sizes, 2, 4, and 6 mm in overall length, a range that covers some 85% of European species (Bernard 1968; Kutter 1977).

Forager weight.—We relate weight to length with the following formula, based on a cylindrical ant of a length about five times its diameter, of specific gravity equal to 1: weight equals 27000 l^3 (length in meters, weight in grams). This gives results comparable to Sage's (1982) empirical formula for Formicidae.

Forager load-carrying capacity.—The maximum size of loads transported by any given species is rather variable (see, e.g., Traniello 1989), although in many cases it only rarely exceeds the forager's weight (Levieux 1972; Hennault-Riche et al. 1979; Lynch et al. 1980; Wehner et al. 1983; Verhaeghe and Deneubourg 1983). We use the following approximation: forager load-carrying capacity equals forager weight.

Speed.—Allometric relations between speed of locomotion and mass give exponents varying from 0.12 for African mammals to 0.36 for lamellicorn beetles (see review in Peters 1983). However, plotting Bernard's (1981, 1983) data for the speed of ant species against their length gave no discernibly consistent relation. Furthermore, a forager's speed depends greatly on temperature, the nature of the terrain, the frequency of their rests, etc. Because the foragers' form is the same for different sizes, both the power available and the power required to move the forager are proportional to its mass (Alexander 1971). We therefore choose to consider speed independent of body length, within the ants' size range. The results presented here were obtained with a speed of 1 cm per second, for both loaded and unloaded foragers.

Metabolic consumption \((c_s, c_o, c_x)\).—Jensen and Holme-Jensen (1980) obtained a general relation between the net cost of locomotion and body weight (see also Lighton et al. 1987; Bartholomew et al. 1988). Adapting this to take into account the forager speed and the basic metabolic cost \((\approx 0.15 \text{ net cost})\) yields an unloaded cost equal to 0.12 weight^{2/3} (cost in joules per minute, weight in grams). Nielsen et al. (1982), Lighton et al. (1987), and Bartholomew et al. (1988) showed that for loads smaller than or equal to forager weight, loaded cost equals unloaded cost times \((1 + \text{load weight}/\text{forager weight})\). Assuming that, for this load range, a loaded forager moves at the same speed as an unloaded one and that an occupied forager is loaded roughly half the time and unloaded half the time, an occupied forager's consumption will equal the average of a loaded and an unloaded forager's consumption.

The consumption of an average nonforager is the average of larval, sexual, and domestic-worker consumptions, weighted according to their somewhat variable
relative frequency. (Other sources of variability include temperature, degree of
domestic-worker inactivity, and larval weight.) We chose to use a minimal value,
such that nonforager consumption equals worker basal metabolic consumption.
Finally, one must add to these consumptions, which are calculated per minute of
active period, the cost pertaining to one minute of the 12-h inactive nocturnal
period, in which we assume that all ants consume at their basal metabolic level.
Thus, for the searching and occupied foragers and for the nonforagers,
\[ c_s = 0.14 \text{ weight}^{2/3} \text{ (j/min)}; \]
\[ c_o = (0.14 + 0.06 \text{ load/weight})\text{weight}^{2/3}; \]
\[ c_x = 0.034 \text{ weight}^{2/3}. \]

**Duration of one transport cycle (t).**—This is the time taken to load and trans-
port the food to the nest, unload, and return into the foraging area. The loading
and unloading times may vary from a few seconds to many minutes, depending on
the size and nature of the food source and especially on whether it is liquid or solid
and, if solid, whether easily divisible. The results presented here were obtained
with a loading time of 6 min (corresponding more to a liquid food or a solid food
needing to be divided before transport). The unloading time, or more precisely the
time taken before the forager leaves the nest again, was taken as equal to the
loading time.

The time moving to and from the nest depends on the forager’s speed and the
source’s distance from the nest. The average distance of a point in a circle from
the circle’s center is equal to \( \frac{z}{2} \) of the radius. Thus,
\[ t = (\text{load} + \text{unload}) + (\text{come} + \text{go}) = 12 + 1.25(z)^{1/2} \text{ (min)}. \]

**Food flow.**—The results presented here were obtained with a food flow (i.e.,
the rate of arrival of food in the foraging area) of \( 10^{-5} \text{ g m}^{-2} \text{ min}^{-1} \).

**Number of sources arriving in the foraging area (a).**—For a given food flow and
unique source size, \( a \) is inversely proportional to the source’s weight (\( w \)). This
relation corresponds to the direct inverse proportionality between population
density and body weight found for the animal kingdom (Peters 1983). Thus,
\[ a = 10^{-5} \frac{z}{w} \text{ (min}^{-1}). \]

**The number of forager loads per source (n).**—The number of loads in a source,
\( n \), is the source’s weight, \( w \), divided by the foragers’ load-carrying capacity. For
convenience, we chose values of \( w \) that gave integral values of \( n \). Foragers thus
always transport full loads, except when we consider sources that are smaller than
their load capacity. In this case, \( n \) equals one, and the loads are integral fractions
(\( \frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \ldots \) ) of a full load.

**The useful caloric content of one forager load (u).**—This value depends on
whether the source is animal or vegetable, liquid or solid, with respect to both
the energy content of the source and the efficiency with which the ants can digest and
metabolize it (the product of these two factors determines the value of \( u \)). The
results presented here were obtained with a value corresponding to a liquid
carbohydrate food source, with \( u = 376 \) load weight (in joules).

**The rate of encounter per source per forager (b).**—We use Laing’s (1938)
Fig. 1.—The net foraging benefit ($B$) is presented as a function of the number of foragers ($f$) and the foraging area ($z$). $B$, expressed in terms of the number of nonforagers that the foragers can feed, is represented by solid, isometric curves corresponding to values of 50, 250, 450, . . . , 3850 (the maximum of 9300 is marked by a dot). The dashed curve joins the points at which $B = 10f$. The star on this curve indicates the maximum socially compatible benefit ($B^*$), that is, the maximum benefit with $B \geq 10f$ ($l = 2$ mm, $n = 1$, $q = 2800$ min).

formula for a random searcher, relating $b$ to the searcher’s speed, perceptual width, the source’s width, and the foraging area ($z$). When tested in a field study of Pachycondyla apicalis, Laing’s formula gave encounter rates close to those observed (Goss et al., in press). A source’s width is deduced from its weight (spherical form, specific gravity of 1) and is assumed to remain constant whatever the number of loads removed by foragers. Since ants generally need to stumble across food to notice it, the width of the perceptual corridor swept by a forager is closely related to the gap between the two antennae’s extremities, linked to body length by an empirical formula. Thus,

$$b = \text{speed (perceptual width + source width)/area}$$
$$= 0.6[0.018 l / (0.017 + l)] + 1.24 w^{1/3} / z \quad (\text{min}^{-1}).$$

NUMBER OF FORAGERS, FORAGING AREA, FORAGER-TO-NONFORAGER RATIO, AND FORAGING BENEFIT

We consider here the influence of two of the most important factors at the colonial level, namely, the number of foragers ($f = S + O$) and the foraging area ($z$). Figure 1 presents $B$ as a function of $f$ and $z$, calculated from the steady-state solutions of equations (1)–(7).

For a given $z$, $B$ first increases with $f$ to a maximum, after which it decreases. Similarly, there is a maximum value with respect to $z$ for a given $f$. These two
tendencies combine to give a unique maximum with respect to \( f \) and \( z \) and may be understood as follows. For a given foraging area, two foragers are able to find more food per minute than is one forager, but not twice as much. By their activity, the two foragers reduce the number of sources in the foraging area more than does a single forager and thus spend correspondingly more time searching. The gross benefit increases more and more slowly with \( f \), whereas the cost increases linearly.

Similarly, for a given number of foragers, a small foraging area would contain so few sources per forager that they would be snatching the food from under each other’s mandibles. Increasing the area increases the number of sources available and thus the benefit. With large areas, however, the increasing distances increase the transport cost, thus decreasing the benefit.

Their social nature and their division of labor impose one highly important constraint on the foraging benefit. If every worker spent its whole time foraging, the gross foraging benefit would be maximal but other essential tasks such as nursing, nest defense, etc., would be neglected. On the average, each forager must feed about 10 nonforagers (Baroni-Urbani et al. 1978; Goss et al., in press). In terms of the model,

\[
B \geq 10f.
\]

(8)

Remembering that \( B \) is expressed in terms of the number of nonforaging ants that may be fed by the \( f \) foragers, one may divide figure 1 into a “socially compatible” zone, for which \( B > 10f \), and an “incompatible” zone, for which \( B < 10f \) (see dashed curve, obtained by calculating, for a given \( z \), the value of \( f \) such that \( B = 10f \)). The maximum benefit falls well into the incompatible zone, varying more or less between \( f \) and \( 2f \) for the range of values studied here.

The maximum “socially compatible” benefit (\( B^* \)) is the maximum value of \( B \) obeying relation (8) and is obtained with \( f^* \) foragers and a foraging area of size \( z^* \). In figure 1 and for all the results presented here, \( B^* \) is on the dashed frontier (\( B = 10f \)). In figure 1, \( B^* \) is only one-third of the maximum \( B \), and the corresponding \( f^* \) and \( z^* \) are even smaller. The quantitative effect of this social constraint is thus considerable.

\( B^* \) is a unique value in the \( z, f \) space, representative of noncooperative foraging's best performance, and in the following sections we use it as such in analyzing the influence of forager or environmental parameters. Bearing in mind that other factors may limit a foraging area (e.g., navigational ability) or the number of foragers (e.g., colony age), we presume that a colony is able within its lifetime to adapt to local conditions by changing \( z \) or \( f \) so as to reach its \( B^* \). Changing a forager character, such as size, would generally require an evolutionary length of time.

FORAGER SIZE AND MEMORY, FOOD-SOURCE SIZE AND DURATION OF AVAILABILITY, AND MAXIMUM SOCIALLY COMPATIBLE BENEFIT

Figure 2 presents \( B^* \) as a function of the arriving food-source size, for the 2-, 4-, and 6-mm foragers, with and without memory of food-source location. Figure 2a corresponds to a shorter duration of availability than figure 2b.
Fig. 2.—The maximum socially compatible benefit ($B^*$) is presented as a function of the food sources' weight ($w$), for 2-, 4-, and 6-mm foragers. Solid curves, Foragers without memory; dashed curves, foragers with memory. The arrows on the horizontal axis indicate the points at which the source weights are equal to the different-sized foragers' load-carrying capacity. Duration of availability: $a$, 2800 min; $b$, 10,000 min. The curves were formed by extrapolating between the values of $B^*$ calculated for sources that were integral multiples or fractions of the foragers' load-carrying capacity.
Let us first consider the foragers without memory (solid curves). Two important results may be seen. First, the highest benefits are obtained when the food sources and the forager’s load capacity are equal (n = 1, see arrows); the benefit decreases sharply as these two parameters differ. Second, there is always one size at which the forager’s highest benefit is greater than that of foragers of other sizes (the 2-mm foragers in fig. 2a, the 4-mm ones in fig. 2b). The longer the duration of availability of the sources (fig. 2b vs. fig. 2a), the larger the optimal forager size and, of course, the greater the benefits for all forager sizes (the area’s richness is proportional to the duration of availability).

With memory (dashed curves), the maximum benefit is obtained when n > 1, and the sharp peak seen without memory becomes a plateau allowing nearly maximum benefits to be obtained with a wide range of source sizes. The plateau’s width and height increase with the duration of availability. Memory increases the range of source sizes for which a given smaller forager has a greater benefit than a given larger forager; and although there is still an optimal forager size for every source size, its edge over the other sizes is not so marked. Memory thus removes to a large extent the strong necessity for forager size to correspond to food-source size, insofar as similar benefits may be obtained by one size of forager exploiting a wide range of different-sized sources or by a wide range of different-sized foragers exploiting one size of sources. (Within a simulation, the foragers and the arriving sources are uniform.) Other factors (e.g., predator avoidance) may thus be freer to influence the forager size.

Note that when food sources are smaller than or equal to the foragers’ load-carrying capacity (n = 1), memory provides no advantage whatsoever because the randomly distributed sources are exhausted in one trip.

For a given duration of availability, larger foragers, with or without memory, have a higher maximum z* with respect to food-source size and a lower corresponding foraging density (f*/z*) than smaller foragers (see the discussion).

Finally, increasing the rate of arrival of sources and decreasing the duration of their availability in the same proportion (the same richness with a higher turnover) increases, for each food size, the value of B* in the same proportion, while z* remains the same.

THE COMPARATIVE INFLUENCE OF SIZE AND MEMORY

In figure 3 we compare the relative values of B* for four forager types, small and large (2 and 4 mm) and with and without memory (black and white).

Zone I.—The sources are smaller than the small foragers’ load-carrying capacity. There is thus no difference between those with memory and those without memory. The small foragers are more effective in this zone.

Zone II.—The sources are larger than the load capacity of the small foragers and smaller than that of the large foragers. Memory thus confers an advantage to the small foragers but not to the large ones. In zone IIa, the small foragers are more effective than the large ones. As the source size approaches the large foragers’ load capacity, the large foragers become more effective than the small one without memory (zone IIb); and with longer availability, they become more effective than the small forager with memory (zone IIc).
Fig. 3.—The space defined by the duration of availability and the weight of the food source \(q, w\) is divided into zones according to the ranking of the maximum compatible foraging benefit of 2- and 4-mm foragers (small and large ants) with and without memory (black and white ants). The ranking decreases from top to bottom. The small forager without memory is omitted from the ranking in zones IIc and III (large sources), since it is unable to achieve a positive \(B^*\). The vertical dashed lines correspond to the small and large foragers' load-carrying capacities.

Zone III.—The sources are larger than the large foragers' load capacity. The foragers with memory thus perform better than those of the same size without memory. In zone IIIb, the large forager with memory is more effective than the small forager with memory, which is more effective than the large forager without memory. As the sources' size increases, this ranking becomes predominant, whatever the duration of availability. However, for the smaller sources in zone III, a change in the duration of availability may reverse the ranking. With long availability, the large forager without memory is more effective than the small one with memory (zone IIIc, continuing zone IIc) and being the right size is more important than possessing a memory. With short availability, the small forager with memory is better than both the large forager without memory and the large one with memory (zone IIIa, continuing IIb) and possessing a memory is more important than being the right size. Thus, as the duration of availability decreases in zone III, the small ant with memory moves up from third place (zone IIIc) to second place (zone IIIb) to first place (zone IIIa).

CONCLUSIONS AND DISCUSSION

Our model is basically an accounting system, adapted to noncooperative foraging, that keeps track of the foragers, the food sources, and their interactions in the foraging area. Associated with it are a number of parameters whose influence has been investigated, namely, the number of foragers and the foraging area, forager size and memory, and food-source size and duration of availability. With the
appropriate reservations in mind, these comparisons offer some interesting insights.

As one might expect, the model predicts an optimal-foraging benefit with respect to the number of foragers and the size of the foraging area, but it also shows the quantitative importance that the social constraint (each forager must feed a number of nonforagers) can have on this optimum. The model may be used to situate a given colony in a given environment with respect to its theoretical maximum foraging capacity and to pinpoint the factors that may be limiting its foraging potential. As such, it provides an interesting means for examining the extent to which optimal-foraging criteria determine a colony’s characteristics, as well as a practical framework for identifying and quantifying the basic parameters and variables that determine a colony’s energy budget for foraging (Goss et al., in press).

The model may help us understand why different colonies of the same species in different environments (e.g., with respect to competition) or colonies of different-sized species in the same environment have different foraging areas or numbers of workers. For example, Wehner et al.’s (1983) study of the noncooperative foraging ant Cataglyphis bicolor in Greek and Tunisian sites gave excellent quantitative data. In Tunisia, the foragers and their prey are significantly larger than in Greece (27 vs. 9 mg; 40 vs. 6 mg). The authors attribute this to the presence in Tunisia of the competitive species C. albicans, similar in size to the Greek C. bicolor. The competition for the smaller prey would thus have pushed C. bicolor to exploit the larger, albeit numerically less abundant, prey and thus to increase the size of their foragers. Our model shows that, all things being equal, larger foragers reach their maximum compatible benefit with larger foraging areas and lower foraging densities than smaller foragers. This is indeed what is observed. In Tunisia, the mean foraging distance and the distance between nests are both larger (20 vs. 8 m; 45 vs. 11 m), and the foraging density is lower (7000 vs. 46,500/ha).

One may also apply these notions to territoriality, which, among other things, has the effect of reducing competition within the foraging area, that is, of increasing the sources’ duration of availability. The model predicts that this would favor larger colonies of larger foragers. Aggressive, territorial behavior could then be associated simultaneously with large foragers, colonies, prey, and foraging areas and with low densities. Indeed, larger foragers would perhaps find it easier to be territorial than would smaller ones. This tendency would be reinforced if the relative cost of territorial defense decreased with the size of the foraging area, as suggested by Hölldobler and Lumsden (1980) for Oecophylla species. An increase with body size in the accuracy of memory of nest and food-source location, as suggested by the learning experiments of Bernstein and Bernstein (1969), would again reinforce the large-forager association. The statistical bimodality of noncooperative foraging species thus predicted between this association and its converse (small colonies of small, nonaggressive foragers, small prey and foraging area, and high foraging density) corresponds to Hunt’s (1983) observations and hypotheses concerning two antipredator strategies for noncooperative foraging ants (large, stinging, biting foragers vs. small, cryptic, nocturnal ones).
The model’s use of a forager without memory of food-source location enables a quantification of this memory’s effect on the colony’s foraging and on its interaction with forager size, food-source size, and duration of availability. Foragers without memory, for example, can efficiently exploit only food sources that are more or less equal in size to their load-carrying capacity. They must accordingly adapt their choice of sources or their own size, necessarily becoming specialists with respect to the size of the sources exploited. The foragers with memory may, by contrast, become opportunists, efficiently exploiting a wide range of source sizes.

Apart from its obvious adaptive value, this effect has other implications. Memory of food-source location may be seen as conferring a large plasticity in the choice of food sizes that would reduce the need for size polymorphism, following Oster and Wilson’s (1978) discussion. By diminishing this foraging constraint on forager size, especially with longer availability, memory may allow other selective factors to act on size. Conversely, exploiting sources that may be transported in one load may render memory less important. Finally, the relative influences of size and memory on the colony’s foraging benefit also depend on the sources’ size and the degree of competition for them. For example, in the case of moderately large food sources, with low competition it is better to be a large forager without memory than a small one with memory, whereas with high competition the reverse is true.

SUMMARY

We present a model of foraging that applies to social insects foraging without recruitment, cooperation, or communication in the search for or retrieval of food. It simulates a colony’s foraging via a series of differential equations that quantify the forager activity, the food-source dynamics, the interactions of foragers and food sources, and the colony’s energy budget for foraging, defined as the number of nonforagers that the foragers can feed. At the colonial level, the influence of the number of foragers and the size of the foraging area is examined; the colony’s social structure, in which only a small proportion of workers forage, greatly limits its potential benefit, leading to the definition of a maximum socially compatible foraging benefit. This is measured in relation to forager characteristics (size and the possession or lack of a memory of food-source location) and to food-source characteristics (size and duration of availability). Foragers without memory obtain their highest benefit when the food sources equal in size their load-carrying capacity, but those with memory can exploit sources several times larger with nearly maximum benefit. There is always one forager size that achieves a maximum benefit greater than that of other sizes. Increasing the sources’ duration of availability, or decreasing the competition for them, increases this size. Larger foragers achieve their maximum benefit with larger foraging areas and lower foraging densities. For sources of intermediate size and long availability, a large forager without memory has a higher benefit than a small one with memory; with short availability, the reverse is true. It is predicted that social insects foraging
without recruitment or cooperation tend to group into two classes. One is charac-
terized by large colonies, foragers, foraging areas, and prey, low foraging densi-
ties, and aggressive territorial behavior; the other class is the inverse.

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LITERATURE CITED

carriage, and emigration in the column-raiding army ant Ecton hamatum. Physiol. Zool.
61:57–68.
—. 1981. Recherche sur les vitesses de locomotion des fourmis. Pages 23–24 in French section of
the International Union for the Study of Social Insects, Toulouse, France.
—. 1983. Recherche sur la vitesse des fourmis. Pages 151–160 in French section of the Interna-
tional Union for the Study of Social Insects, Les Eyzies, France.
Bernstein, S., and R. A. Bernstein. 1969. Relationship between foraging efficiency and the size of the
head and component brain and sensory structures in the red wood ant. Brain Res. 16:85–104.
mechanisms in ant societies (II): learning in foraging and division of labor. Exper. Suppl.
(Basel) 154:177–196.
Individual foraging in the ant Pachycondyla apicalis. Oecologia (Berl.).
Harkness, R. D., and N. G. Maroudas. 1985. Central place foraging by an ant (Cataglyphis bicolor
fuliginosus: piste, cycles d’activité et spécialisation territoriale des ouvrières. Pages 71–78 in
French section of the International Union for the Study of Social Insects, Lausanne.
732–739.
Hunt, J. H. 1983. Foraging and morphology in ants: the role of vertebrate predators as agents of
natural selection. Pages 83–104 in P. Jaisslin, ed. Social insects in the tropics. Université de
Formica fusca L., Formica rufa L. and Camponotus herculaneus (Hymenoptera, Formi-
Laing, J. 1938. Host finding by insect parasites. II. The chance of Trichogramma evanesens finding


