Individual foraging in the ant *Pachycondyla apicalis*

S. Goss 1, D. Fresneau 2, J.L. Deneubourg 1, J.-P. Lachaud 2, and J. Valenzuela-Gonzalez 3

1 Unit of Theoretical Behavioural Ecology, Université Libre de Bruxelles, CP 231, Bld. du Triomphe, B-1050 Bruxelles, Belgium
2 UA CNRS 667, Université de Paris XIII, F-9430 Villeurbanne, France
3 Centro de Investigaciones Ecologicas del Sureste, 30700 Tapachula, Chiapas, Mexico

Summary. A model of individual foraging in social insects is presented that formalises the dynamics of foraging and concentrates on the collective rather than the individual benefit, quantifying the relationships between a colony's foraging area, number of foragers and foraging energy budget and the food sources' rate of arrival, disappearance and capture. A series of experiments, in which a number of prey were offered to colonies of the individually foraging ant *Pachycondyla (ex-Neoponera) apicalis* confirm the hypotheses implicit in the model and measured the rates of capture and competition. 60 days observation of 3 *P. apicalis* colonies' foraging activity are summarised and used in conjunction with the model to obtain estimations of the density and rate of arrival of available prey in the foraging area. We examine how a colony's foraging benefit may be influenced by its foraging area, the number of foragers, and the forager/non-forager ratio and show that a colony's social structure strongly limits its potential foraging benefit. Within these limits, *P. apicalis* does not appear to be an optimal forager.

Key words: Foraging benefit – Capture rate – Competition rate – Food flow – Foraging area

While kinetics occupy a central role in the study of population dynamics and predator-prey relationships (e.g. May 1973; Hassell 1978), they have been largely ignored in behavioural ecology. This is particularly true in the studies of foraging in social insects, which focus their attention mostly on the foraging patterns or the type and quantity of food captured. The object of the model and experiments performed was to formalise the dynamic nature of foraging and the capture/competition process, in the simplest way possible that takes into the account the constraints specific to eusociality. Rather than considering the individual foragers’ benefit, we concentrate on the collective benefit and the food-sharing between the foragers and the much greater number of non-foragers. This, together with the high degree of liberty with respect to the number of foragers, distinguishes our approach from the few other central place foraging models devoted to social insects (e.g. Harkness and Maroudas 1985; Schmid-Hempel et al. 1985; Deneubourg et al. 1987).

The model is specifically adapted to individual foraging, i.e. foraging with no cooperation in the discovery or retrieval of food items. This is not only the simplest of social insect foraging strategies, used by a significant minority of ant species (Oster and Wilson 1978; Passera 1984), bumblebees and certain wasps, but is also fundamental to the more widespread foraging with recruitment, which relies to a great extent on individual foraging for the collection of small food sources and the discovery of large ones. The model has, therefore, a number of analogies with that developed by Johnson et al. (1987) to estimate the optimal fraction of scouts in species using recruitment. We present the model, test its mechanisms and quantify its parameters for the individually foraging ant *Pachycondyla (ex-Neoponera) apicalis*, and examine this species’ foraging efficiency.

Materials and methods

The model. This model is applicable to individually foraging social insects whose food items are transported in one load (single prey-loading, sensu Orians and Pearson 1979; see also Goss et al. 1989 for general model).

The food items are uniform and arrive randomly (without clustering) in the uniform circular foraging area, the nest being in the center. They may be captured by the colony’s foragers or may disappear for reasons other than the colony’s activity, such as competition from other colonies or species, decay, etc. (we lump these processes under the term competition).

The colony’s foragers are uniform. They search randomly throughout the foraging area, without spatial specialisation. When a searching forager encounters a food item, it becomes an occupied forager, which transports the food item to the nest and returns into the foraging area, becoming a searching forager once more.

The variables (in capitals) and parameters are:

- $B$: the society’s net foraging benefit ($J/min$)
- $B_c$: the society’s net foraging benefit, expressed as the number of non-foragers that can be fed by the foragers ($B = B_c/c_o$)
- $P$: the number of food items in the foraging area
- $S$: the number of searching foragers
- $O$: the number of occupied foragers

Offprint requests to: S. Goss
The number of food items arriving (min⁻¹)  

the discovery rate per searching forager per food item (min⁻¹)  

cₜ, cₒ, cₙ the metabolic consumptions of a searching, occupied or non-forager (J/min)  

the rate of competition per food item (min⁻¹)  

the total number of foragers (searching + occupied) (= S + 0)  

the average time an occupied forager remains occupied (transport of food item to the nest and return into the foraging area) (min) (tₜ, α ʃ t)  

the useful energy content of one food item (J)  

the foraging area (m²)  

The following differential equations may be established:
\[
\frac{dP}{dt} = \text{arrival} - \text{competition} - \text{captures} = a - eP - bSP \\
\frac{dO}{dt} = \text{captures} - \text{completed transports} = -dS/dt = bSP - O/tₜ \quad [1] \\
B = \text{gross benefit} - \text{foraging cost} = ubSP - cₙS - cₒO \quad [3]
\]

Capture/competition experiments. Equation [1] assumes that both capture and competition are independent processes. It quantifies the capture by the product between the number of sources, the number of searching foragers and a rate constant, and quantifies the competition by the product of the number of sources and a rate constant. To test these hypotheses, frequently used in ecological models (e.g. Holling 1966; Curio 1976), and to measure their rates (b and e), the following series of experiments were performed.

*P. apicalis* was studied in traditional coffee-cocoa plantations in Tapachula, Chiapas, Mexico. The workers are large (30 mg, n = 771), and the colonies typically range from 30 to 200 adults. They forage individually in the daytime, on and in the litter and dead branches, their prey being 80% arthropods, of which roughly half are larvae and half adults (Lachaud et al. 1984). Approximately 3/4 of the prey are transported in one load.

A total of 14 experiments were performed on 4 nests. In each experiment a dead fly (*Anastrepha ludens* or *Ceratitis capitata*, typical prey) was placed every 30 cm on 3 concentric circles (1 m, 3 m, 6 m, covering the essential part of the colonies’ foraging areas) around the nest entrance at dawn. The prey were color marked according to which circle they were on. Every 15 min, for 5 h, a note was taken of which prey remained on which circle. Simultaneously, a continuous record was kept of the traffic at the nest entrance (exits, entry with marked prey, entry with unmarked prey, entry without prey).

Foraging activity. 3 *P. apicalis* colonies were intensively studied. Table 1 gives the nests’ composition. The foragers were individually marked and the nest entrance was observed from dawn to mid-day, a period covering approximately 3/4 of the foraging activity. All entrances and exits with or without prey were noted, a number of prey being collected for sampling. At the same time, as many foragers as possible were followed around the foraging area.

### Results

**Capture/competition experiments**

As the flies were not replaced, and as only the foraging activity with respect to these flies was considered, the food flow parameter *a* in equation [1] is zero, and the solution for this equation is given by:

\[
\ln P/P₀ = -(e + bS)t \quad [4]
\]

Plotting ln *P/P₀* (where *P₀* represents the number of flies at the beginning of the experiment) against *t* should therefore give a straight line (e.g. Fig. 1), the slope of which is -(e + bS). This was confirmed for each experiment, both overall and for each circle (0.85 < *r*² <0.99).

The ratio between the number of prey captured by the colony and the total number of prey that disappeared by capture or competition provides an estimation of the proportion of prey captured by the colony (bS + eS). Knowing (e + bS) from the semilog regressions above, one may calculate bS and e.

The average rate of competition (e ± se = 0.5 ± 0.02 h⁻¹) was much higher than the average rate of capture by the colonies (bS ± se = 0.1 ± 0.02 h⁻¹). As hypothesised, e did not vary significantly with the distance from the nest (0.4, 0.5, 0.6 h⁻¹ for 1, 3, 6 m). On the other hand, bS decreased markedly, suggesting naturally enough that the no. of foragers per m² is higher nearer the nest, assuming b to be independent of the distance from the nest. Dividing the values of bS at 3 m and 6 m by that at 1 m estimates the foraging density at these distances relative to that at 1 m (= 0.4, 0.2 for 3 m, 6 m). With more circles one would be able to deduce an empirical law relating the foraging density to the distance from the nest. Note that the model assumes the foraging density to be uniform throughout the foraging area, and the number of foragers to be constant.

Dividing bS by S, the number of searching foragers, measured in 7 of the 14 experiments, gives an estimation of the rate of capture per forager per prey (b ± se = 0.014 ± 0.005 h⁻¹). This value must be considered with caution when applied outside the context of these experiments. Firstly the number of foragers (*f*), i.e. the number of workers outside the nest at any moment, was not always constant and they were all assumed to be searching foragers.

![Fig. 1 presents the ln of the proportion of prey remaining on the 3 circles of a capture/competition experiment (see text) as a function of time (dois), together with the fitted regression line (r² = 0.99)](image)

**Table 1. Nest composition**

<table>
<thead>
<tr>
<th>Nest</th>
<th>Eggs</th>
<th>Larvae</th>
<th>Pupae</th>
<th>Workers</th>
<th>Sexuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3</td>
<td>25</td>
<td>43</td>
<td>62</td>
<td>2</td>
</tr>
<tr>
<td>B</td>
<td>34</td>
<td>59</td>
<td>50</td>
<td>174</td>
<td>1</td>
</tr>
<tr>
<td>C</td>
<td>–</td>
<td>48</td>
<td>172</td>
<td>122</td>
<td>27</td>
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</tbody>
</table>