

Individual foraging in the ant *Pachycondyla apicalis*S. Goss¹, D. Fresneau², J.L. Deneubourg¹, J.-P. Lachaud², and J. Valenzuela-Gonzalez³¹ Unit of Theoretical Behavioural Ecology, Université Libre de Bruxelles, CP 231, Bld. du Triomphe, B-1050 Bruxelles, Belgium² UA CNRS 667, Université de Paris XIII, F-9430 Villetaneuse, France³ Centro de Investigaciones Ecológicas 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 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_j	the society's net foraging benefit (J/min)
B	the society's net foraging benefit, expressed as the number of non-foragers that can be fed by the foragers ($B = B_j/c_n$)
P	the number of food items in the foraging area
S	the number of searching foragers
O	the number of occupied foragers

- a the number of food items arriving (min^{-1})
 b the discovery rate per searching forager per food item (min^{-1})
 c_s, c_o, c_n the metabolic consumptions of a searching, occupied or non-forager (J/min)
 e the rate of competition per food item (min^{-1})
 f the total number of foragers (searching + occupied) ($= S + O$)
 t_o the average time an occupied forager remains occupied (transport of food item to the nest and return into the foraging area) (min) ($t_o \propto 1/\sqrt{z}$)
 u the useful energy content of one food item (J)
 z the foraging area (m^2)

The following differential equations may be established:

$$\begin{aligned} dP/dt &= \text{arrival} - \text{competition} - \text{captures} \\ &= a - eP - bSP \end{aligned} \quad [1]$$

$$\begin{aligned} dO/dt &= \text{captures} - \text{completed transports} (= -dS/dt) \\ &= bSP - O/t_o \end{aligned} \quad [2]$$

$$\begin{aligned} B &= \text{gross benefit} - \text{foraging cost} \\ &= ubSP - c_s S - c_o O \end{aligned} \quad [3]$$

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 ob-

served 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:

$$\ln P/P_0 = -(e + bS)t \quad [4]$$

Plotting $\ln P/P_0$ (where P_0 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 ratio between bS and $(e + bS)$. Knowing $(e + bS)$ from the semi-log regressions above, one may calculate bS and e .

The average rate of competition ($e \pm \text{se} = 0.5 \pm 0.02 \text{ h}^{-1}$) was much higher than the average rate of capture by the colonies ($bS \pm \text{se} = 0.1 \pm 0.02 \text{ h}^{-1}$). 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 m^2 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 ($b \pm \text{se} = 0.014 \pm 0.005 \text{ h}^{-1}$). 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

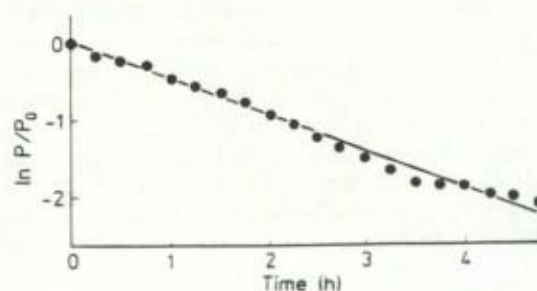


Fig. 1 presents the \ln of the proportion of prey remaining on the 3 circles of a capture/competition experiment (see text) as a function of time (dots), together with the fitted regression line ($r^2 = 0.99$)

Table 1. Nest composition

Nest	Eggs	Larvae	Pupae	Workers	Sexuals
A	3	25	43	62	2
B	34	59	50	174	1
C	-	48	172	122	27

(*S*) and none occupied foragers (*O*), the transport time (t_o) in these experiments being small compared to the time taken to discover a source. Secondly, the prey offered were dead and on top of a leaf, and thus possibly easier to find and capture than under more natural conditions. Thirdly, the rate of capture is necessarily linked to a given surface area. In these experiments the foragers were considered to search essentially within a 7 m radius ($\approx 150 \text{ m}^2$). The value of b for a foraging area of $z \text{ m}^2$ would be 0.014 multiplied by $150/z$.

It is interesting to compare the value 0.014 h^{-1} with that of 0.006 h^{-1} estimated theoretically for the *P. apicalis* foragers in these experiments from Laing's (1938) random search formula ($=v(d_s+d_f)/z$; with v , the forager's speed $\approx 1 \text{ m/min}$; d_s , the width of the corridor swept by the forager $\approx 7 \text{ mm}$; d_f , the preys' diameter $\approx 8 \text{ mm}$; z , the foraging area $\approx 150 \text{ m}^2$). The two values are in relatively close agreement, considering the non-random distribution of both prey and foragers, suggesting that the model's radical simplifications are acceptable.

Foraging activity

Table 2 summarizes the data obtained from 256 hours' observation. The number of foragers is defined as being the average number of workers outside the nest at any one moment, and is not to be confused with the total number of different individuals that have been known to leave the nest and which are sometimes inside and sometimes outside.

The foraging benefit is calculated in the following manner. The average prey weighed 5.1 mg dry weight ($se = 0.54 \text{ mg}$, $n=98$). Assuming a calorific content of 23 J/mg dry mass (Peakin 1972; Randolph et al. 1975; Baroni-Urbani et al. 1978; Mackay 1978) and an assimilation efficiency of 80% (Petrusewicz and Macfayden 1970), gives a useful energy content (u) of 94 J per prey. The gross benefit is given by multiplying this value by the number of prey captured per hour. The foraging cost is given by multiplying the number of foragers by their energy consumption, estimated at 1.3 J/h from Jensen and Holme-Jensen's empirical formula (1980) (Lighton et al.'s 1987 study of *Atta columbica*'s energetic consumption gives a not too different value of 0.8 J/h when adjusted for *P. apicalis*' weight and speed). The cost, ignoring foraging-related mortality, is in any case only some 6% of the gross benefit, underlining ants' eusociality. The 8 foragers of nest A, for example, must not only feed themselves but also 56 adults and 25 larvae. The importance of this factor on their foraging is seen below. Finally, mapping together all the observations of the different foragers' foraging trips, it was possible to obtain a rough estimation of the colonies' foraging area, z .

The number of prey and the food-flow

The model and experimental data allow an indirect estimation of two important environmental parameters that are

otherwise difficult to measure, namely the number of prey and the food flow in the foraging area.

The capture/competition experiments confirmed that one may estimate the number of food items captured per hour by bSP . Thus, dividing the items captured per hour (observed for the 3 colonies) by b and S one may estimate P , the number of prey present in the foraging area (Table 2). Note that this assumes the b measured in these experiments (weighted according to the 3 colonies' foraging areas) to be applicable for normal foraging, and that all the foragers were searching foragers ($S \approx f$). Dividing the values of P thus obtained by the foraging area gives the food density (Table 2).

The steady state solution of equation [1] gives:

$$a = P(e + bS) \quad [5]$$

As we now have estimations for P , e , b and S we may estimate a , the rate of arrival of the food items in the foraging area. Dividing a by z gives the rate of arrival $\text{m}^{-2} \text{ h}^{-1}$, and multiplying by the food items' average energy content gives the rate of arrival in $\text{J m}^{-2} \text{ h}^{-1}$ (Table 2).

An important consideration of these estimations is that they are derived directly from the ants' own activity and not from human activity. A field biologist using a quadrat sample and a sieve is estimating the number of prey potentially available, in that he is likely to count a number of food items that the ants themselves would not be able to find or capture, or else would not choose, and which are thus "not available" to the foragers. The number of prey actually available would certainly be much lower. To estimate the latter from the former, one would have to perform an exhaustive study of the foragers' prey preferences, with regard to species, age and location, how much time they spend on or in the litter, how far into the litter they search, their chances of finding and capturing the different prey under different conditions, and so on. Using the model leaves most of the work to the ants and provides acceptable first order estimations for these environmental parameters.

Is *P. apicalis* an optimal forager?

Now that the model's parameters have all been estimated, we may see the effect on the benefit of changing the foraging area, the number of foragers and the forager/non-forager ratio.

In this section we shall express the benefit in terms of the number of non-foragers the foragers can feed, by dividing the benefit in J/h by an average non-foragers' metabolic consumption ($B = B_f/c_n$). In this context, the non-foragers are the larvae, the nest-workers and reproductives.

c_n is estimated from the data in Tables 1 and 2 by dividing the net benefit by the number of larvae and nest workers, giving an average value of 1.6 Joules per h of foraging. This assumes that an average sized larva (13 mg , $n=216$) consumes as much as a nest worker (30 mg), and

Table 2. Foraging activity

Nest	h obs	For Area m^2	No of Foragers	Prey Capt h^{-1}	Gr Ben J/h	Cost J/h	Net Ben J/h	No of Prey	Prey m^{-2}	Prey Arrival $\text{m}^{-2} \text{ h}^{-1}$	Prey Arrival $\text{Jm}^{-2} \text{ h}^{-1}$
A	67	180	8	1.7	160	10	150	19	0.10	32.10^{-5}	73.10^{-4}
B	89	420	11	3.1	291	15	276	47	0.11	33.10^{-5}	76.10^{-4}
C	100	330	18	3.3	310	24	286	28	0.09	27.10^{-5}	63.10^{-4}

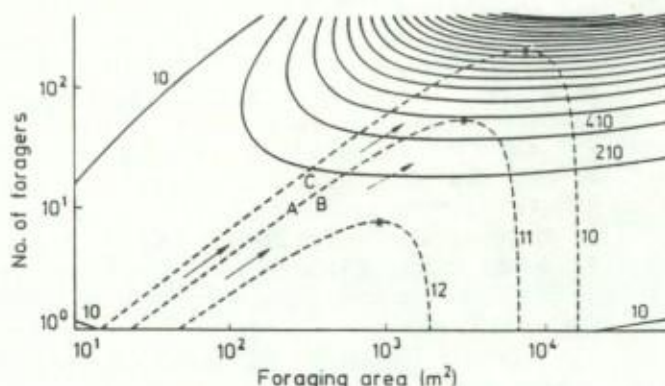


Fig. 2 presents the models' calculations of a *P. apicalis* colony's net foraging benefit as a function of the number of foragers and the foraging area. The benefit, expressed in terms of the number of non-foragers the foragers can feed, is represented by iso-benefit (solid) curves of 10, 210, 410, ..., 3810. The 3 dotted curves mark the points at which one forager may feed 10, 11 or 12 non-foragers. The asterisk on each of these curves marks its point of maximum benefit. The experimentally determined positions of the 3 colonies are marked A, B and C.

includes possible food wastage in the consumption. The consumption per circadian hour is probably only one half as much, as foraging occurs in daylight while the ants metabolise throughout the 24 h day. By way of comparison, extrapolating from Nielsen's (1972) measurement of *Lasius alienus* larval consumption of $56 \text{ J g}^{-1} \text{ h}^{-1}$ would give 0.7 J/h for an average *P. apicalis* larva. The value used earlier in this paper for an active forager was 1.3 J/h .

Figure 2 presents isometric curves for different values of B as a function of the number of foragers and the foraging area, the curves being calculated from the steady-state solutions of equations [1]–[3].

For a given foraging area, increasing the number of foragers increases the colony's gross benefit to a maximum where all the arising sources are immediately captured. The foraging cost, however, increases more or less linearly with the number of foragers. The net benefit thus increases to a maximum then decreases. Similarly, for a given number of foragers, increasing the foraging area increases the number of sources available, and thus the benefit. However, the increasing distances involved increase the transport time and costs and eventually the benefit, which thus increases to a maximum and then decreases. Note that whereas the number of occupied foragers is small enough to be neglected under natural conditions, this is not so with larger foraging areas. They were thus taken into consideration in these calculations, using values of t_0 calculated from the foraging area and an average transport speed of 1.5 m/min .

The overall picture is that of a hill whose peak lies beyond the top right hand corner of Fig. 2, with a height of ≈ 100000 non-foragers. It is evident that *P. apicalis* colonies never get to anything like this size, the largest having perhaps 200 adults. From this point of view they are definitely not optimal foragers.

Perhaps the single most important reason lies in ants' social organisation. Just as in any militarized society only a small proportion of the population can be front-line soldiers, the rest providing supplies of else too young or too old, so with insect societies only something like one tenth of the individuals that eat are foragers. For example, in

the three colonies studied each forager fed 11, 20 and 10 non-foragers (the value of 20 for various reasons related to a wave of larval emergence may be considered as exceptionally high). In other species similar values are obtained (Baroni-Urbani et al. 1978; Wehner et al. 1983). How does this "social" constraint affect the foraging benefit?

The 3 dashed curves in Fig. 2 mark the points at which one forager may feed exactly 10, 11, or 12 non-foragers, i.e. the points at which $B/f = 10, 11$ or 12 . Assuming that 10 is a minimum value for ant societies, only the area enclosed within the corresponding dashed curve is socially acceptable. Most of the foraging area/forager number space, and particularly that part giving the highest benefit, is unreachable in that the non-forager/forager ratio is less than 10. A limit of 11 or 12 restricts the colony's possibilities even more severely.

There is still, however, a maximum "socially acceptable" benefit possible, that is to say the point on each dashed curve furthest up the hill, marked in Fig. 2 with an asterisk. Its value depends greatly upon the minimum required non-forager/forager ratio, being 2100, 600 and 100, for ratios of 10, 11 and 12, with corresponding foraging areas of 8100, 3400 and 1000 m^2 . One might imagine that a young colony would start with a low number of foragers and a small foraging area, and increase both proportionately so as to follow the arrows marked on Fig. 2, up to the asterisks representing the theoretical maxima. This assumes that a colony is unlimited with respect to the choice of its size and foraging area, whereas many factors may intervene to limit this choice. For example, the foragers' capacity for orientation or competition from other nests may restrict the foraging area, and the colony's capacity for organisation or its reproductive strategy may limit its size.

How are the 3 *P. apicalis* colonies placed with respect to this path? They are marked A, B and C on Fig. 2, according to their number of foragers and foraging area, and, although on the pathway, are a long way from the "optimal" asterisks. Theoretically, they could increase their foraging area by a factor of 10, i.e. move to the right on the graph, and increase their benefit slightly, increasing correspondingly their benefit per forager from 10–11 to 11–12. Increasing their number of foragers by a factor of 10, i.e. moving upwards on the graph, would increase their benefit to something like 400 non-foragers, but would place their non-forager/forager ratio outside the limit of 10. To increase the benefit while remaining within the social limits would require a more or less proportional increase in both parameters, i.e. moving up and to the right on the graph.

Discussion

The model is basically an accounting system, adapted to non-cooperative foraging, that keeps track of the foragers and food items and their interactions in the foraging area. Keeping in mind the reserve appropriate to all mathematical descriptions of living processes, it is of practical use, and its experimentally confirmed simplicity, far from being a drawback, constitutes its greatest strength. We have seen how it can help a field worker understand the basic events involved in foraging, and thereby to see which parameters are the most pertinent to an analysis of foraging, how they may be measured, and how they may fit together to define and explain some of the quantitative and qualitative aspects

of a colony's foraging activity. More specifically, the model and experimental data allow an indirect estimation of two important environmental parameters that are otherwise difficult to measure, namely the number of prey and the food flow in the foraging area.

Finally the model shows how a colony's social organisation, i.e. the necessity for each forager to feed a large number of non-foragers, can severely limit their foraging potential. The large number of nest workers is related to the division of labour within the society, which includes a reserve of unspecialised and often inactive replacement workers (e.g. Abraham and Pasteels 1980; Lachaud and Fresneau 1987; Schmid-Hempel unpublished work). It should not be confused with the need of recruiting social insects to keep a large number of their foragers waiting in the nest to be recruited (see e.g. Johnson et al. 1987; Deneubourg et al. 1989). Allowing for this division of labour, and within the limits of the criteria applied, the data obtained seem to indicate that *P. apicalis* is far from being an optimal forager with respect to the number of foragers and the foraging area.

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