Decision-making in foraging by social insects

Claire Detrain, Jean-Louis Deneubourg and Jacques M. Pasteels

Summary

How are foraging decisions determined in social insects? Investigations implemented within the framework of the optimal foraging theory bring evolutionary and functional answers. In this respect, decisions of solitary foragers like bumblebees seem to be ruled by an optimization of the energy (and time) invested among different feeding sites. Similarly, in insects which can forage collectively, like ants or honeybees, decisions have been interpreted in terms of energetic reward assigned to single workers without any reference to recruitment. Evidence, however, supports the idea that (time and energy) investments in recruitment of nestmates can also alter foraging decisions of the individual. Additional questions arise as to how an insect processes information about food resources and environmental constraints and decides whether or not to recruit nestmates. In ants, adaptive collective decisions emerge from numerous interactions among individuals which use local information and follow simple decisional algorithms to modulate their recruiting behavior. The environment itself contributes to the emergence of foraging decisions by altering the dynamics of recruitment and trail reinforcement. Several experimental and theoretical findings will lead us to re-consider the level of complexity of information processing and coding needed for the emergence of adaptive foraging patterns.

Introduction

As argued by Tinbergen [1], behavioral studies should aim to answer four major questions about the causation, current function, development and phylogenetic history of a particular behavior. Most research effort on foraging behavior in
social insects has concentrated (i) on the functional significance and (ii) on the mechanisms which underlie decision-making processes.

In the present chapter, we aim to synthesize major issues brought by these functional and mechanistic approaches to foraging decisions. The first section will provide an overview of foraging decisions evidenced in social insects exploiting food solitarily and interpreted in the light of the optimal foraging theory. Decision making is here analyzed through cognitive models which often assume, either implicitly or explicitly, that the insect possesses a relatively great capacity to process information. Such individual complexity remains, however, speculative without direct ethological and neurophysiological evidence.

The following sections will refer to insects which can forage collectively. As cooperation and recruitment occurs, additional questions arise as to how foragers decide (or not) to communicate information to nestmates. At first, we will summarize the contribution of the optimization concept to the understanding of recruitment decision in ant and honeybee societies (e.g. how the energy and time costs of recruitment alter the behavior of foragers). Thereafter, we will focus on the proximate mechanisms of decision making evidenced in ants. Indeed, these societies provide us with a system open to analytic studies of the mechanisms involved in foraging. By altering colony components or environmental constraints and by quantifying the individual’s response, it is possible (i) to identify cues used by the foragers to take their decisions whether or not to recruit nestmates and (ii) to follow how information is transferred. Bottom-up investigations and simulations on foraging patterns will be reviewed since they enable to link individual decisions to collective ones. We will identify which information on food and environmental constraints are “measured” by scouts and are coded to nestmates by scent trails. In addition, we will ask whether the environment itself might alter the dynamic properties of recruitment and therefore might contribute to the emergence of collective decisions. We will demonstrate that simple decision-making algorithms and local processing of information may account for most foraging strategies of the insect society. The level of complexity in information processing and coding needed for optimal foraging will be discussed.
Decision making in social insects foraging solitarily

When dealing with foraging by solitary insects, investigators questioned how the individual invests energy (and time) among different feeding sites in order to harvest food in the most efficient way. In the ant species known to forage solitarily (e.g. Cataglyphis spp. [2, 3] or Pachycondyla apicalis [4]), workers leave the nest in the sectors pointing towards food sites and concentrate their effort on rewarding areas. While deciding to exit the nest in a particular direction, each forager relies on reward expectation, which is set by the food availability of the environment.

Similar questions on foraging decisions have arisen in bumblebees. Each insect may visit thousands of flowers, and after each flower visit it has to decide whether to depart from the plant or to stay and visit another flower on the plant. These decisions were often analyzed in the light of optimal foraging theory. This concept was initially developed from studies on vertebrates [5–7] and was extended to encompass social insects as bumblebees which carry food items back to a central place where food is eaten or stored [8]. As regards bumblebees [9, 18], three food parameters susceptible to altering foraging decisions attracted the attention of researchers: the amount of food available, the variability in availability (risk) and the spatial distribution of food resources.

Concerning the amount of available food, bumblebees capitalize on the most rewarding flowers by altering their foraging behavior. Forager's responses to increased amount of pollen [9] or nectar [10] include a decreased likelihood of departure from plants, reduced distances of movements within and between plants, and longer-lasting or more frequent visits to flowers.

As regards the variability in food supply, there is evidence that some bumblebee species are sensitive to risk (variability) in the amount of nectar rewarded [11–13], while others are risk-indifferent [14]. When risk-sensitive bumblebees are faced with two patches of flowers, one of which provides a constant nectar volume and the other a variable volume (with a same average amount), foragers often show preference for the constant type (risk-averse). However, they can become "risk-prone" as the amount of food stored within the nest decreases [15].

The spatial distribution of food resources also influences the foraging behavior of bumblebees. On plants that are characterized by a gradient of nectar amount decreasing from bottom towards the top of inflorescence, the insect moves systematically from one flower to the adjacent upper flower. Hence, the
nectar received from the current flower is an accurate predictor of the reward in as-yet unvisited flowers and affects the forager's decision to leave the plant [16–18]. When neither flower arrangement nor nectar distribution show any consistent pattern, bees seem to integrate information from more than a single flower in making departure decisions [19]. Foraging decision rules in bumblebees appear to be straightforward adaptations to patterns of nectar availabilities.

The energetic optimization concept proved to be a stimulating framework to analyze decisions of solitary foragers within an evolutionary perspective. This ultimate approach, however, provides little insight into the mechanisms by which adaptive foraging behavior is achieved. In this respect, one can assume that, in order to forage optimally, each bumblebee has to monitor pollen and nectar availabilities, to attend to the colony needs and possibly to assess the presence of competitors, predators or disturbances. Only theoretical descriptions of information processing can be found in literature which all suggest that bumblebees use complex departure rules and computational algorithms [18, 20, 21]. Experimental evidence is, however, lacking on the capabilities and limitations of insect cognitive machinery.

**Decision making in insects foraging collectively: an optimization approach**

**The impact of individual energetic balance on foraging decisions**

When applied to insects which can forage collectively, the optimization approach often dealt with the individual, outside any context of recruitment. In this respect, honeybee foraging behavior (e.g. number of flower visits, flight patterns, handling time on the flower or crop loading) was analyzed exclusively in terms of individual energetic efficiency [22–24] without any reference to cooperation and information sharing between nestmates. Similarly in ants, optimality in prey choices under different food availabilities and external conditions (e.g. temperature) was interpreted in terms of cost and benefit, only for the individual forager [25, 26].

Since ants and honeybees are central place foragers, the impact of food distance on foraging optimization deserved special attention from the investigators. When single honeybees are faced with food patches at different distances from the hive, they seem to fill their crop with a nectar load which maximizes the
energetic efficiency \((\text{benefit} - \text{cost})/\text{cost}\) in an average foraging excursion [22, 23]. The use of energetic efficiency as the food profitability criterion might be appropriate for those flying animals in which the foraging success seems more limited by energy expenditure than by time availability [27]. Constraints on foraging decisions are different for terrestrial insects in which the cost of walking per unit of time is much lower than the cost of flight and in which foraging decisions seem less influenced by energetic expenses. Hence, the energetic gain rate \((\text{benefit} - \text{cost})/\text{time}\) appears to be a more important currency than energetic efficiency for foraging ants. This was demonstrated for harvester ants [28], but seems less evident for nectar-feeding species with lower benefit/cost ratios (Paraponera clavata, [29]). Besides, the optimal foraging theory predicts that feeding selectivity increases as a function of the distance to a forage site. Though this trend was confirmed in some studies on seed harvesting [30] and leaf-cutting ants [31], similar tests showed no significant change in the range size of seeds collected at different foraging distances [32, 33].

The next section will raise questions about how recruitment and associated energetic/time constraints might influence foraging decisions at both the individual and collective level.

The impact of recruitment costs on foraging decisions

In the case of insects foraging solitarily, one assumes that their decisions take origin in the energetic balance of the forager itself. However, as sociality proceeds in ants or honeybees, foragers become a part of a large, integrated unit composed of related workers: the decision to recruit taken at the individual level ultimately leads the colony to a mean feeding rate higher than in foraging without any communication. One would expect that the individual energetic gain of those foragers that decide to recruit nestmates would be reduced owing to food sharing with nestmates, to the metabolic cost invested in recruitment signals (e.g. bee dances or trail deposits) and to the time spent in recruitment activities. Hence, foraging decisions appear as a trade-off between immediate maximization of the individual energetic reward and prospective higher returns due to collective food exploitation. Evidence for such a trade-off might be found in bees where foragers return from flowers with partially filled crops. Similarly, leaf-cutting ants sacrifice individual food delivery rate to recruit nestmates earlier to higher quality
leaves. These seemingly suboptimal behavior might be explained by the long-term advantages of maximizing social efficiency through the exchange of information with nestmates [34–36].

Studies are lacking on recruitment costs, but several observations support the idea that time spent in recruitment of nestmates matters in decision making since it represents a substantial portion of each foraging cycle. In honeybees, large time investments in recruitment, through long-lasting dances, are restricted to food sources with a high profitability [37]. In ants, less frequent and weaker recruitments lead to food sources requiring higher energetic and time investments (e.g. to food further from the nest [38] or connected to the nest by routes with high vegetational cover [28]). Several foraging patterns also appear as a means to reduce the time costs of recruitment. For instance, temporary recruitments are directed towards the permanent network of trails in aphid-tending ants [39] or towards the raid column in army ants [40], which allows a quicker recruitment of extranidal foragers to newly discovered food. Similarly, P. clavata foragers match recruiting effort to increase in distances via two mechanisms (i) a reduction in the relative number of foragers that recruit to long-distance resources, and (ii) an extranidal recruitment (and hence reduced recruitment times) of specialized workers that concentrate their foraging on remote resources [41].

All these studies devoted a great deal of attention to the economics and to the functional significance of decision making. Within this perspective, the insect is assumed to balance global properties of food resources and to “measure” the payoff of a foraging behavior by using the adequate energetic currency. Such an assumption raises questions as to how such a complex and flexible processing of information operates within insects whose cognitive capabilities may be limited. The aim of the next section is to review individual decision rules during food recruitment as well as their consequences on collective foraging behavior.

Decision making in ants' recruitment: a proximate approach

Collective decisions in ants

Foraging decisions in ants are intimately linked to recruitment mechanisms which enable the colony to focus foragers on top-quality sources and to readjust
the work allocation when the environment and food profitability change [42, 43]. Key factors which may alter foraging patterns are listed in Tables 1 and 2, while collective decisions and recruitment behaviors reported in literature are briefly summarized. Special emphasis is put on bottom-up studies which try to link individual decision rules and recruitment processes to collective decisions.

Most quoted studies refer to a subset of food and environmental factors (e.g. food quality), whereas data are crucially lacking for other parameters (e.g. for the dynamics of food availability). Collective decisions reported in Tables 1 and 2 always appear as efficient choices which tend either to maximize the energetic return (e.g. selection of the richest source) or to minimize the costs due to foragers’ movements (e.g. selection of the shortest route) or due to competitors’ pressure (selection of safe sources). However, such conclusions about the adaptive value of foraging decisions are more frequently supported by common sense and intuition than by actual energetic data.

While most studies discuss the ultimate issues of collective decisions, fewer investigate recruitment mechanisms which lead to their emergence. Two main recruiting behaviors which differ in whether they provide directional information deserve attention from investigators (i) invitation displays (body jerking or antennation) to nestmates which stimulate them to leave the nest without directional information, and (ii) behaviors such as trail recruitment which stimulate workers to leave the nest and lead them to food sources.

Recruitment dynamics are then shown to closely depend on the percentages of ants laying a trail (TLA) or inviting congener in the nest (IA), and on the intensities of invitation behavior (IIB) or chemical trail marking (ICM) performed per recruiting ant.

Most frequently, experiments show that higher rates of foragers mobilized (RMF) to a food source are essentially due to higher percentages of inviting and/or trail-laying ants (Tab. 1). Additional modulation may occur at the individual level (e.g. in the amount of pheromone laid per recruiter), but seems restricted to the coding of some parameters such as the quality of food.

The two following sections will identify parameters measured by the foragers and criteria used to modulate their recruiting behavior. This review of recruitment decision rules should not, however, shade the influence of other factors on the emergence of collective decisions such as the evaporation rate of scent trails. In this respect, assumptions on how the environment itself might contribute to the emergence of adaptive foraging patterns will be presented.
<table>
<thead>
<tr>
<th>Food variables</th>
<th>Collective decision</th>
<th>Individual recruitment behavior</th>
<th>Decision criteria</th>
<th>Species [reference]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food quality</td>
<td></td>
<td>Trail-laying</td>
<td>Invitation</td>
<td>sucrose concentration</td>
</tr>
<tr>
<td>Concentration of</td>
<td>higher RMF to rich food</td>
<td>higher percentage of TLA</td>
<td>higher percentage</td>
<td>Acanthomyops interjectus [44]</td>
</tr>
<tr>
<td>sucrose solution</td>
<td>sources</td>
<td></td>
<td>of IA to rich food</td>
<td>Formica oreas [45]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>sources</td>
<td>Lasius niger [46]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Monomorium spp, Tapinoma spp. [47]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Myrmica sabuleti [48]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Paraponera clavata [49]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Solenopsis geminata</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S. saevissima [38, 50, 51]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Tetramorium impurum [52]</td>
</tr>
<tr>
<td>Food weight</td>
<td>higher RMF to heavy prey</td>
<td>higher percentage of TLA to heavy prey</td>
<td></td>
<td>Lasius neoniger [53]</td>
</tr>
<tr>
<td>Food Volume</td>
<td></td>
<td></td>
<td></td>
<td>Myrmica spp [54, 55, 56]</td>
</tr>
<tr>
<td>Droplet below the</td>
<td>higher RMF to large food</td>
<td>higher percentage of TLA but same</td>
<td>higher percentage</td>
<td>Paraponera clavata [29]</td>
</tr>
<tr>
<td>volume of the ant</td>
<td>droplets</td>
<td>intensity of ICM to large droplets</td>
<td>of IA but same</td>
<td>Pheidole pallidula [57, 58, 59]</td>
</tr>
<tr>
<td>crop</td>
<td></td>
<td></td>
<td>intensity of IIB to</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>large droplets</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>ability to fill</td>
<td>Lasius niger [60]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>the crop to a</td>
<td>Myrmica sabuleti [56]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>desired volume</td>
<td>Paraponera clavata [49]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Solenopsis geminata [38]</td>
</tr>
<tr>
<td>Droplet above the</td>
<td>higher RMF to large food</td>
<td>same percentage of TLA and intensity</td>
<td>same percentage</td>
<td>Lasius niger [60]</td>
</tr>
<tr>
<td>volume of the crop</td>
<td>droplets</td>
<td>of ICM (excepted for Paraponera clavata)</td>
<td>of IA and same</td>
<td>Paraponera clavata [29]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>intensity of IIB</td>
<td>Solenopsis geminata [51]</td>
</tr>
<tr>
<td>Food variables</td>
<td>Collective decision</td>
<td>Individual recruitment behavior</td>
<td>Species (reference)</td>
<td></td>
</tr>
<tr>
<td>--------------------------------</td>
<td>---------------------</td>
<td>---------------------------------</td>
<td>---------------------</td>
<td></td>
</tr>
<tr>
<td>Number of food items</td>
<td>higher RMF to numerous food items</td>
<td>same percentage of IIB</td>
<td>Myrmica sabuleti [56]</td>
<td></td>
</tr>
<tr>
<td>Spatial and temporal distribution of food</td>
<td>higher RMF to dense and/or persistent food patches</td>
<td>—</td>
<td>Messor rufitarsis [61] Pogonomyrmex occidentalis [38]</td>
<td></td>
</tr>
</tbody>
</table>

Collective decisions are related to the recruitment behavior of individuals. Trail-laying behavior, invitation displays within the nest and decision criteria actually used by the individual forager are summarized. Recruitment mechanisms and decision criteria are mentioned if they were evidenced in at least one (but not necessarily all) quoted ant species. Blank cells mean that no data are available on the topic. RMF, rate of mobilized foragers; TLA, trail-laying ants; ICM, individual chemical marking; IA, inviting ants; IIB, individual invitation behavior.
Table 2 Review of ants foraging responses to environmental constraints

<table>
<thead>
<tr>
<th>Environmental constraints</th>
<th>Collective decision</th>
<th>Individual recruitment behavior</th>
<th>Species (reference)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trail-laying</td>
<td>Invitation</td>
<td></td>
</tr>
<tr>
<td>Number of predators/competitors</td>
<td>higher RMF at the safe food source</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Deviation from the nest-food axis</td>
<td>higher RMF on routes leading straightfully to food</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Light exposure</td>
<td>higher RMF on routes with low trail degradation by UV</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Nature of the substrate</td>
<td>higher RMF on substrate with same percentage of TLA and same intensity of ICM</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>adsorption/evaporation rate of the trail pheromone</td>
<td>higher RMF on low evaporation rate of ICM</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

For meaning of abbreviations see Table 1 captions.
Individual assessments of food and recruitment decision rules

Though one might suspect that the “correct” assessment of both the environment and available resources would be a matter of importance for colony fitness, the pertinent criteria used by the insect in mediating an adaptive behavior remain largely uninvestigated. Since chemical trails in ants act as stimulating signals increasing the exit of nestmates as well as orientation cues channeling them to feeding areas, each scout can influence the global foraging strategy by deciding whether or not to lay a trail and by modulating the rate of pheromone emission. The present section will review how decision rules and coding of information through chemical trails are implemented in ants.

Coding of food quality

For food droplets differing in sucrose molarity, the intensity of individual recruitment behavior (and hence the amount of trail pheromone laid by each recruiter) increases as a function of the concentration perceived by the forager [38, 44–52]. Though this recruitment decision rule seems trivial, not in terms of physiological abilities of ants but in logical terms, it appears to be an efficient means for the colony to select energetically valuable food sources.

Coding of prey weight

In Pheidole pallidula [57–59], for a pile of small prey (e.g. fruit flies), the mobilization of foragers is very slow, whereas a large prey item (e.g. a cockroach) induces a strong recruitment. These foraging patterns can be generated using the following individual rules of thumb. Success in prey-carrying encourages the forager to move on and to lay a weak trail on its way back to the nest. This can possibly lead to slow monopolization of the source when small items are numerous. A failure by the forager to retrieve the prey results in a shortened stay at the food source followed by intense trail recruitment. Recruited ants then gather around the prey, suck its hemolymph or dissect it on the spot into smaller pieces which are retrieved by individual or collective transport. It was demonstrated that the individual decision to recruit depends on a key parameter used by the forager to
estimate prey size: prey resistance to retrieval. Though crude in appearance, this tractive resistance is a decision criterion of higher functional value than any sophisticated measure of prey size or weight. Indeed, it provides indirect information at every moment about not only prey size but also prey vitality, current force of cooperating carriers or any factors affecting resistance to retrieval such as microtopography.

**Coding of food volume**

Several ant species are known to increase their foraging activity to large food sources by increasing the proportion of scouts laying a trail [49, 60] and/or recruiting workers within the nest [49, 56]. Experiments on *Lasius niger* showed that scouts make no absolute measure of food volume. Indeed, when they are faced with sugar droplets of different sizes, their decision to recruit depends simply on their ability to fill their crop to a desired volume [60]. When the source is too small to provide such a volume at once, the ant returns to the nest without laying a trail or goes on exploring for additional droplets. The well-known statement that an unfed ant does not recruit [50] thus appears as one extreme case of a more general decision rule. This simple individual decision rule generates many adaptive responses at the collective level: (i) the dynamics of food recruitment (e.g. the rate of trail reinforcement) is expected to fit to the patch size of droplets (e.g. to the number of aphids) and to be synchronized to their renewal rate (e.g. rate of honeydew production). (ii) As first highlighted by Wilson [50], no overcrowding of foragers will occur at one large food source. As recruitment proceeds, the increasing difficulty (or even inability) of newcomers foragers to reach food and to ingest a desired volume will lead them to delay (or even to suppress) their recruiting activity.

These experimental findings on decision rules lead us to reconsider the idea that collective foraging patterns find their roots in behavioral complexity and extensive cognitive abilities of the individual. Adaptive strategies can emerge from numerous interactions among individuals which use local information and follow simple rules of thumb to modulate their recruiting behavior. The next section will show that the coding itself of information may be unnecessary and that the environment can directly influence recruitment dynamics.
Environment as an agent of the decision making process

The following models will demonstrate that environmental constraints which alter the dynamics of trail reinforcement may contribute to the emergence of adaptive foraging decisions without any explicit measure or coding of information by the foragers.

The distance effect

In theoretical simulations, ants are given the choice between two paths of different lengths leading to two food sources of equal quality. A major assumption of the model is that no modulation of trail laying nor of any other recruiting displays occurs according to distance to the food source (for more details about the model, see legend, Fig. 1). Simulations show that, for a low flow of 0.03 ant/s and for one source placed at a distance twice as long as the nearest food (e.g. \(dr = 30\) cm and \(dn = 15\) cm), this nearest source is preferred in less than 60% of simulations. For a same distance ratio but longer absolute distances (e.g. \(dr = 120\) cm, \(dn = 60\) cm), higher percentages of simulations end with the choice of the nearest source. The choice of the nearest source is also facilitated by high flows of foragers (0.2 ant/s). In this case, even very small differences in distances between sources (e.g. 10%, 17 versus 15 cm) lead to a marked selection of the nearest source (in around 80% of the simulations).

As demonstrated by these simulations, the distance by itself can determine collective choices as far as this parameter significantly alters traveling times and hence rates of trail reinforcement. Evidence for a decrease in the percentage of trail-laying behavior with increasing distances of food from the nest [29, 51] appears more as an improvement rather than a prerequisite for the selection of near food sources by the colony. One could suspect that this trail modulation would be most useful to discriminate between food sources with small or medium distance differences.
Figure 1 Results of 1000 simulations describing choices of ant colonies between two food sources of equal quality but offered at different distances from the nest.

The x-axis gives the distance ratio between the remote (dr) and the nearest food source (dn). A value (15, 30, 45 or 60 cm) is associated to each curve and gives the absolute distance from the nest to the nearest source (dn). The y-axis gives the proportion of simulations where the nearest source is chosen. For each simulation, a food source is considered as chosen when, after 2 h, the corresponding branch bears more than 50% of the ant traffic. These simulations rely on the following model. The probability that an ant will choose the path leading to the nearest source (Pn) is ruled by the equation $Pn = \frac{(k + Cn)^n}{(k + Cn)^n + (k + Cr)^n}$ where Cn and Cr are the trail concentration on the shorter and longer paths respectively. k is a constant standing for all factors other than the trail pheromone (e.g. thigmotaxis), which might influence the choice made by foragers. Except for the distance to food, the following parameters were kept fixed with values drawn out of empirical data on Lasius Niger: $k = 6$, $n = 2$, the time spent at the food source (100 s), ant velocity (1 cm/s), the lifetime of trail pheromone (1 h). No recruitment of foragers occurs but only a constant input flow of 0.2 or 0.03 foragers.

The effect of risk and competition

As described for *L. palliariensis*, food associated with high risk is neglected, and foraging decisions are affected by encounters with a competitor or a predator [62, 63]. Similarly, in *L. neoniger* [67] and *Pogonomyrmex* spp. [68], confrontations between workers of adjacent colonies in a common foraging area will result in their segregation on two newly established trails and in their partitioning on distinct areas.
Figure 2 Results of 1000 simulations describing the choices of ant colonies between two food sources of equal quality but exposed to different competition risks.

The x-axis gives the probability for each ant to fight with an enemy during food exploitation. The y-axis gives the percentage of simulations in which the safest source was chosen. The model equation is the same as in Figure 1. The probability that an ant will choose the safe source is $P_s = (k + Cs)^n / (k + Cs)^n + (k + Cd)^n$ where Cs and Cd are the trail concentration on paths leading to the safe and dangerous sources, respectively.

Simulations (Fig. 2) demonstrate that this adaptive selection of the safest food might occur without any coding of risk. In this model, ants choose between food sources of equal quality exposed to different probabilities of enemy encounters. Each hostile confrontation is assumed to result in physical blocking: each fighting forager will stay 300 s longer around the food than a nonfighting one before returning to the nest. For a low flow of foragers (0.03 ant/s), the safest side is preferred as the risk associated to the other food increases. A higher flow (0.2 ant/s) induces a more marked selection of the safest food: all simulations end up with a unanimous choice of this source, when the probability of enemy encounters reaches 0.5.

Although the desertion of dangerous food sources occurs simply due to delays in the return of fighting foragers to the nest, the ant society may refine this basic response both on short and long time scales, by achieving defensive recruitments,
by mobilizing specialized castes of soldiers [69] or by adapting demography (e.g. by increasing the colony production of soldiers [70]).

**Integration of multiple information and complex decision making**

In nature, ant foragers encounter complex situations where it may be advantageous to assess a wide array of variables. For instance, as the quality of a food source improves, its attractiveness and hence the occurrence of competitive interactions increases. In these conflict situations, foraging choices may demand the sacrifice of some amount of foraging success in order to achieve other goals as well. In *L. pallitarsis* and *Myrmica incompleta* colonies [71, 72], the use of the higher-quality patch is depressed as an associated mortality risk increases. The authors assume that this trade-off is related to an integrated balance between nutritive returns and losses of workers due to predation. However, they give no idea how sensory inputs about quality and risk may be processed by the forager and how collective decisions may emerge. On the one hand, one can speculate about a recruitment trail which might be a complex blend of attractive and repulsive signals (see contribution of Stickland et al., this volume) and which reflect both the quality and the danger of feeding in the patch perceived by the forager. An alternative way to explore trade-offs in ants is through models based on the minimalist assumption that no sophisticated coding of information occurs at the individual level. (Fig. 3, J.C. Romond et al., unpublished data). Simulated ant colonies are faced with two food sources which differ in quality (sucrose concentration of S1 > concentration of S2) as well as in the risk of fatal encounters at the richest one (Pm: probability of mortality at S1). The model assumes that the amount of pheromone laid per recruiter (Q1,Q2) is modulated according to sucrose concentration only and that no additional coding of danger occurs. For a given ratio of pheromone quantities laid from the poorest and the richest food (e.g. Q2/Q1 = 0.6), the most profitable (in terms of energetic return) source S1 remains preferentially exploited as long as predation pressure is low (Pm < 0.4, Fig. 3a). As the mortality risk increases, less than half of colonies forage at the source S1 and even completely abandon this rich but dangerous source (Pm > 0.7). It should be stressed that the desertion of the most profitable food S1 shifts to higher predation pressure as the difference increases between the energetic returns expected from the rich and poor sources (to Pm values >0.9 for

346
Figure 3
(a) Results of 1000 simulations describing the choices of ant colonies between two food sources (S1 and S2) which differ in both quality (sucrose concentration of S1 > concentration of S2) and associated predation risks (no risk at source 2, probability of mortality Pm at source 1 between 0 and 1). The pheromone quantities laid from the poorest and the richest food source are, respectively, Q2 and Q1. The x-axis stands for the mortality risks (Pm) at the richest food S1. The y-axis gives the proportion of simulations in which the safest source was chosen. Values (1, 0.6 or 0.2) associated with each curve give the ratio Q2/Q1, Q1 being kept constant (= 1). The model underlying these simulations is basically the same as in Figure 2. (b) Same as in (a). The y-axis gives the mean number of dead ants found at the end of simulations.
Q2/Q1 = 0.2). As regards the number of dead foragers, it does not simply increase with risk but shows a maximum value followed by a decrease in mortality when ants undergo severe predation (Fig. 3B). This counterintuitive result can be explained as follows: when the higher trail-laying intensity to the rich but dangerous food source no longer makes up for the loss of recruiters, it becomes deserted, resulting in a decrease in global mortality. Peak values of foragers’ death are observed when despite a high predation pressure, the colony is “trapped” in its first choice of the most profitable source and is unable to shift its activity to the safest one. As the difference in profitabilities (and hence in the amounts of trail pheromone laid per recruiter) between the two sources increases, mortality peak value shifts to higher predation pressures, resulting in higher loss of foragers (e.g. for Q2/Q1 = 0.2, maximum number of dead foragers = 300 versus 100 for Q2/Q1 = 0.6, Fig. 3B).

In the foregoing sections, foraging decisions were studied in the laboratory on a limited subset of food parameters while trade-offs were investigated by theoretical simulations dealing with two parameters only. However, under natural conditions, a colony frequently has to choose between multiple (more than two) food sources, whereas recruitments may be altered by several factors such as by food reserves stored within the nest or by the network of preexisting trails. Hence, we might wonder whether the simplicity in behavioral mechanisms evidenced so far is compatible with the complexity and flexibility of foraging patterns shown by ants in nature. We believe this to be the case due to the property of chemical trails which is to convey information, dynamic in both time and space. Spatiotemporal plasticity in foraging trails is due to the fact that increased amounts of pheromone induce not only higher rates of nest exits but also a higher directionality of recruited nestmates. As a result, either the succession of trail reinforcements to long-lasting food sources or the spatial proximity of individual trails to clumped food items will elicit an adaptive shift from nondirectional foraging to oriented recruitment and will allocate more foragers to areas where the expectancy for food is higher. Even more complex spatial patterns like the highly coordinated swarms of army ants or the rotation of trails in harvester ants may theoretically arise without any centralized control of foraging from simple decision rules and autocatalytic trail reinforcements [42, 73, 74].
Conclusion: is foraging optimization dependent on complexity of decision-making?

One can examine foraging in social insects without investigating mechanisms by which optimal decisions are achieved. However, the advantages of a proximate approach is that it helps: to clarify the pertinent variables used by the insect to modulate its behavior, and to determine what level of physiological and cognitive complexity is required at the individual level to achieve adaptive strategies. Researchers brought, either implicitly or explicitly, several answers which vary greatly in the level of complexity assumed.

At first sight, the integration of all pertinent variables by the animal might be seen as a prerequisite for optimal foraging strategy. In the case of social insects foraging collectively, an exhaustive and precise coding of information might be favored by natural selection, since it increases colony efficiency in recruitment and task performance. However, several constraints might limit this behavioral complexity as for example:

1) The physical, physiological and cognitive abilities of the insect. The individual has an experience limited in time and space which cannot follow all fluctuations of an unpredictable environment. Each forager is biologically limited in its perception of environmental cues as well as in its integrative power of multiple signals at high neuronal networks.

2) The time costs spent in assessing food or environmental features. One might suspect that the more precise the assessment of food, the more careful its inspection carried out by foragers. Hence, complex individual assessments which are time-consuming might expose foragers to higher predation risks, delay nestmates’ recruitment and prevent food monopolization against competing species.

3) The risk for erroneous transmission of information to nestmates, which potentially increases with the complexity of individual assessment and the multiplicity of coding vectors.

An alternative scheme to behavioral complexity is that individual decisions rely on a small set of simple and functional criteria. Instead of assessing multiple parameters, foragers measure and hence communicate to nestmates only a few cues (e.g. prey resistance to traction) which most pertinently summarize food
properties (e.g. weight) and environmental constraints (e.g. microtopography). All cues evidenced so far were indirect measures of energetic benefit and/or expenses: they allow the individual to make optimal decisions and to save time during food exploitation due to limited processing of information. Moreover, any parameter (e.g. food distance from the nest) which influences the dynamic properties of recruitment can be an intimate part of the decision-making process and hence does not need to be specifically measured or coded by foragers, at least in theory.

Though we do not deny the possible existence of more sophisticated decision making, we point out that adaptive foraging strategies can emerge out of simple decision rules through the iterative processes of recruitment and trail reinforcement. As they have been determined by their particular evolutionary history, the decision rules evidenced in ants do not apply in their details to any other group-living animals, but analogous mechanisms underlie the functioning of societies like honeybees [37, 75], tent caterpillars (see Fitzgerald and Costa, this volume) or even mole and Norway rats [76, 77]. From the examples described above, we believe it will be possible to conciliate some “panglossian” view of foraging optimization with simplicity in the decision-making processes of social insects.

Acknowledgments

We would like to thank S. Camazine for his critical reading of the manuscript. This work was supported by the Belgian Fund for Joint Basic Research (grant no. 2451393F). C. Detrain and J. L. Deneubourg are research associates from the Belgian National Fund for Scientific Research.

References

1 Tinbergen N (1951) *The study of instinct*. Oxford University Press, Oxford
4 Fresneau D (1985) Individual foraging and patch fidelity in a ponerine ant. *Insect Soc*
31 Roces E (1990) Leaf-cutting ants cut fragment sizes in relation to distance from the nest. Anim Behav 40: 1181–1183
50 Wilson EO (1962) Chemical communication among workers of the fire ant Solenopsis saevissima (Fr Smith): the organization of mass foraging. Anim Behav 10: 134–147
53 Traniello JFA (1983) Social organization and foraging success in Lasius neoniger


66 Natan C (1997) Rôle de l’exploration et du substrat dans l’organisation du réseau de pistes chez *Lasius niger*. *Mémoire de licence-Université Libre de Bruxelles*


74 Goss S, Deneubourg JL (1989) The self-

