Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants

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Abstract. The usual evolutionary and ecological approaches to foraging in social insects often lack an investigation at the level of both individual behavioural complexity and social mechanisms ruling the emergence of adaptive collective strategies. The prey scavenging behaviour of the dimorphic ant *Pheidole pallidula* was used in this study to investigate (1) how individuals estimate the size of prey, (2) how they modulate their behaviour and communication and (3) how these modulations generate the diversity of collective foraging patterns. For a pile of small prey (fruit flies), the recruitment of foragers was slow because of the weak intensity of individual trail-laying behaviour and the long time spent by ants wandering around the food. In contrast, for a large prey item (a cockroach), strong recruitment was induced by ants that dashed back to the nest laying a more continuous chemical trail. Experiments with small immovable prey showed that the tractive resistance of prey was the key parameter the foragers used to estimate prey size and that it ruled their trail-laying intensity. These data allow us to generate a model about decision making in scavenging. The rules leading to collective choice in a foraging or an agonistic context are discussed. On the basis of these findings, some theoretical stances in sociobiology and some shortcomings in current approaches to cooperation in social insects are considered.
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An ant colony can demonstrate a wide range of strategies from solitary foraging to mass recruitment (see review by Passera 1984; Hölldobler & Wilson 1990). Foraging responses change depending on the type of food, for example insect versus seed or sugared water (Cammaerts 1980; Cammaerts & Cammaerts 1980; Breed et al. 1987), the food size (Wilson 1962; Traniello 1987), or the spatio-temporal distribution of available food (Hölldobler & Wilson 1970; Itzkowitz & Haley 1983; Hahn & Maschwitz 1985; Breed et al. 1987; Sundström 1993).

Behavioural ecology provides a framework for describing and predicting these strategies in terms of Darwinian fitness. According to optimality theory, each selected foraging strategy represents the best achievable balance of costs and benefits that maximizes the net energetic yield to the colony. Many field and laboratory studies aim to

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assess these costs and benefits in terms of food intake, size of body reserves, energy expenditure of retrieving food, mortality risks from predators or competing species, and so on. However, this usual approach to foraging and other types of cooperation in social insects often remains at a rather theoretical level, describing the outcome of behaviour but not the mechanisms by which the outcome is achieved. Preoccupied with the adaptive value of the 'chosen' foraging strategy, sociobiology has more or less forgotten to investigate how an ant 'measures' complex parameters at the food source, 'calculates' costs and benefits of actions and 'chooses' one kind of recruitment system over another. Answering these questions needs a close interplay between optimality studies and analyses of behavioural mechanisms. Currently, we have little idea about the behavioural complexity needed at either an individual or a collective level, for an ant colony to achieve the best foraging pattern. In this respect, possibly the best known ants' foraging behaviour is trail recruitment to a sucrose solution: faced with two

food sources of different concentrations, a larger and more rapid recruitment is directed to the richer one (Pasteels et al. 1987; Beckers et al. 1990, 1993; for similar results with bees see Camazine & Sneyd 1991; Seeley et al. 1991). The resulting recruitment curves emerge from an interplay between positive feedbacks (trail laying) and from limiting factors such as the number of potential foragers and crowding around the food source (a non-feeding ant does not recruit, Wilson 1962). The intensity of trail-laying behaviour is modified according to the sucrose concentration perceived by the recruiting ant (Wilson 1962; Hantgartner 1969, 1970; Cammaerts 1977; Verhaeghe 1982; Pasteels et al. 1987; Beckers et al. 1990, 1993). The highest sucrose concentration results in the strongest trail reinforcement. These behavioural rules and social constraints can lead the colony to choose collectively to exploit the more energetically valuable food. In this case, we do know which information (here the sucrose concentration) causes the ants to alter their trail-laying behaviour and hence induces, at the colony level, the best response. This is one example in which an adaptive foraging pattern can be fully linked to behaviour and food assessment by the scouts.

A wide array of foraging responses is also observed during prey scavenging but the mechanisms governing their emergence remain unclear. The scavenging patterns also range from individual exploitation of small items to strong trail recruitment for heavy prey. In *Myrmica* spp. (Cammaerts 1980; Cammaerts & Cammaerts 1980; de Biseau & Pasteels 1994) and *Pheidole pallidula* (Detrain & Pasteels 1991), the scavenging pattern is regulated through the use of chemical trails and recruitment displays in the nest, more intense for large cockroaches than for small fruit flies. These differences in recruiting behaviour result from a decision-making system that remains poorly understood. To fill this gap, we have studied the scavenging behaviour of the European ant *P. pallidula*. More precisely, we investigated how the *P. pallidula* colony 'measures' the size of food items and then 'chooses' a suitable scavenging pattern.

The sterile caste of *P. pallidula* is dimorphic, majors accounting for 2–15% of the whole population. This species is a generalist and opportunistic ant, in terms of diet which varies in quality and size. Retrieved insects vary from 0.3 to 10 mg. One minor can carry small items while medium-sized prey or cumbersome body parts (such as legs) are retrieved by groups of cooperating minors. On average most scavenged insects individually retrieved weigh 0.86 mg. Larger prey (mean 3.5 mg) are carried back to the nest by the ants collectively (Detrain 1990). A very large food item induces a massive recruitment of both minors and majors which dissect the prey directly at the food site. Food discovery and trail recruitment is done exclusively by the minors, whose poison gland contains trail pheromone. Majors perceive and follow these trails but cannot produce the pheromone (Ali et al. 1988; Detrain & Pasteels 1991). The majors' caste is only involved in recruitment for heavy prey which they cut into pieces.

Scavenging in *Pheidole* species provides a good model for understanding how dead prey of different sizes induce different global foraging patterns and different levels of cooperation in the ant colony. It also raises several questions about the information content of the food itself, the relevant criteria and the measurement methods used by the forager at the food source. We also question how precisely the ant conveys information about the discovered food to the nest, and how the adaptive foraging response can emerge at the society level. The ultimate goal is to incorporate into the same framework this deeper understanding of decision-making systems in social insects and the more usual evolutionary and ecological approach to foraging.

METHODS

Study Species

Pheidole pallidula is widespread in the Mediterranean. Nests are often dug under stones in arid areas on sunny slopes facing south or west. Up to 6000 individuals can be found per nest. This opportunistic ant feeds upon dead insects, seeds, fruit or even flower nectar. It occasionally hunts larvae or imagoes of small living insects. More details about prey scavenging in nature are given in Detrain (1990).

Rearing in the Laboratory

Colonies (one queen, 2000–3000 minors, 70–100 majors) were collected in southwest France

(Pyrénées Orientales) and reared in plaster nests (20 × 20 × 2.5 cm). The humidity was maintained by regular moistening of the plaster. Artificial lighting was timed on a 12:12 h light:dark regime. Room temperature remained constant at 22° ± 1°C. Ants were fed three times per week with brown sugar solution (1 M), water and dead cockroaches.

Prey of Different Sizes

In the laboratory, we studied scavenging by *P. pallidula* workers with prey differing in size. We compared exploitation of individually retrievable fruit flies, *Drosophila melanogaster*, with recruitment for large cockroaches, *Periplaneta americana*. Fruit flies were chosen because their weight (around 1 mg) is close to the mean weight of natural prey (0.86 mg) which are individually retrieved by *P. pallidula* in the field (Detrain 1990). On the other hand, cockroaches (weighing about 1 g) are too heavy to be retrieved even by collective transport. Each tested colony was offered either one cockroach or 600 fruit flies put in a pile on a 3-cm-diameter plate. For both prey, we compared recruitment dynamics and individual behaviour with the observation procedure described below. We aimed to confirm previous observations of foraging done in the laboratory (Detrain & Pasteels 1991) and the field (Detrain 1990). We repeated the experiments five and eight times respectively, for cockroaches and a pile of fruit flies, on the same two colonies. Repeat experiments were separated by at least 1 week.

Prey of Altered Retrievability

As the difference in foraging strategy could be linked to a food preference, we set up experiments using the same prey whose retrievability was artificially altered. Flies identical in quality but differing in their retrievability were successively offered to the same two colonies.

The first prey type were 600 fruit flies put in a 3-cm-diameter pile. An ant could pick up any fly in the pile and carry it directly back to the nest on its own.

In the second experimental set-up, the same pile of 600 fruit flies was covered by a 1-mm-mesh wire-net which allowed minors access to the flies but prevented them from taking away any prey. The whole food pile was not retrievable even by

several foragers. In this respect, the wired pile of small fruit flies can be compared to an immovable large insect. As with cockroaches and individual fruit flies, we observed recruitment dynamics and trail-laying behaviour during five replicates of the experiment separated by at least 1 week.

Flies with free access and those kept under a net are at the extremes of the prey retrievability scale. To test prey of intermediate retrievability we pinned single flies by their wings to the substrate. A single ant could retrieve a pinned fly but only with sustained effort. Each ant had to pull the fly for some time before it could tear away its wings. The trail-laying behaviour of these ants returning from the food was analysed. We carried out the experiment three times on the same colony.

Dynamics of Food Exploitation

Before each experiment, colonies were food-deprived for 3 days. Each nest was connected to a foraging area (1 × 1 m) by a narrow bridge. Food was placed 60 cm away from the end of the bridge in the foraging area. Each colony was followed for 2 h. At 1-min intervals we counted ants crossing the bridge, thus allowing us to follow recruitment dynamics. We measured the time spent by workers at the food source by carefully following individuals from their arrival until their departure from the food. We did this during the first 30 min of the experiment when no overcrowding occurred around the prey. We compared the mean duration of stay at the food source for the different prey.

Quantification of Trail-laying Intensity

The trail is laid exclusively by the minors' caste. During the first 30 min of recruitment, we focused a camera with a magnifying lens (× 8) on the bridge to record ants walking to and from the food source. Only individuals recorded with satisfactory definition over a distance of 5 cm were included (5–13 ants per experiment). Observed from side on, trail-laying minors were easily recognizable by changes in their locomotory behaviour. Their gaster was bent downwards and the tip dragged on the ground allowing them to lay spots of trail pheromone. Video recordings were analysed frame by frame (every 1/25 s). Intensity of trail-laying by one recruiter was given by the percentage of frames where this ant was seen dragging its abdominal tip on the bridge. We

assessed this trail-laying behaviour for the following prey: cockroaches, free fruit flies and flies kept under a net.

Trail-laying Intensity and Prey Retrievability

We designed a final experiment to ascertain how the trail-laying behaviour of an ant could be influenced by the effort it had experienced in the extraction of the prey. In the same colony, three recruitments were launched to flies pinned down by their wings to the substrate. For each observed forager carrying back a fly during the first 30 min of the experiment, we recorded the time spent on the fly's extraction and the intensity of its further trail-laying behaviour. Extraction effort was assessed by the time spent by each individual at the food, from its first bite to when it tore a fly away. Occasionally, foragers interrupted their biting to explore the food source; we excluded this time from our measurement. The trail-laying behaviour was assessed as previously stated.

RESULTS

Prey of Different Sizes

Dynamics of food exploitation

Although a similar number of scouts (3–4% of the total colony) were present on the experimental area before we introduced the food, recruitment dynamics differed strongly depending on whether a pile of 600 fruit flies or a cockroach was being exploited. When fruit flies were given, the ants' population gradually increased over the foraging area especially in a spindle-shaped zone centred along the bridge–food axis. However, it never led to a clear-cut trail, even 1 h after food introduction. Figure 1a shows the development of the population of minors and majors on the foraging area. The number of foraging minors increased fairly slowly without any clear division between the growing phase and the plateau value. Considering all experiments ($N=8$), during the first hour, the mean growth rate on the area $\pm$ SD was $7 \times 10^{-4} \pm 3 \times 10^{-4}$ minors/(min $\times$ total colony population). The mean plateau value, reached after 2 h, was $10 \times 10^{-2} \pm 3 \times 10^{-2}$ of the total colony population. Only a few majors (nine individuals maximum) were recruited.

Cockroaches were exploited in a completely different way. They induced a strong recruitment, the dynamics of which fit a steep logistical curve and reach a plateau value (Fig. 1b). Considering all experiments ($N=5$), during the first hour, the mean growth rate on the area was $21 \times 10^{-4} \pm 9 \times 10^{-4}$ minors/(min $\times$ total colony population). The mean plateau value was $17 \times 10^{-2} \pm 4 \times 10^{-2}$ of the total colony population. In less than 30 min, a well-defined trail linking the nest to the food source was followed by numerous foragers. Nearly all foragers belonged to the minor caste but majors were also recruited although their number never exceeded 20 individuals. These majors were involved in cutting the prey's sclerites into pieces. Thereafter, minors filled their crops with the haemolymph coming out of the cut sclerites. In the present experiments, no collective transport of prey body parts was observed, although such cooperative behaviour can occur in *P. pallidula* (Detrain 1990).

Minors stayed for less time around cockroaches ($\bar{X}=324$ s, $N=17$) than around fruit flies ($\bar{X}=720$ s, $N=34$). In both cases, some of this time was devoted to inspecting and wandering around the prey. The shorter stay at the cockroach should result in fewer minors around the food source than with fruit flies. However, we observed that the total number of minors on the area was higher for cockroaches (around 0.17 of the total population of minors) than for fruit flies (around 0.1 of the total population of minors) at the end of the experiment. Additionally, the growth rate of recruited minors was three times higher for cockroaches than for fruit flies. These differences in recruitment dynamics should be related to differences in trail-laying intensity.

Quantification of trail-laying intensity

When a pile of fruit flies was discovered, most ants took one prey in their mandibles and carried it back to the nest. A few ants returned unloaded having spent a long time around the pile. About 40% of returning ants laid a continuous trail (Fig. 2a). Many foragers marked the ground discontinuously or did not even lay a trail. Some ants (50%) leaving the nest again were also seen laying a trail up to the food source.
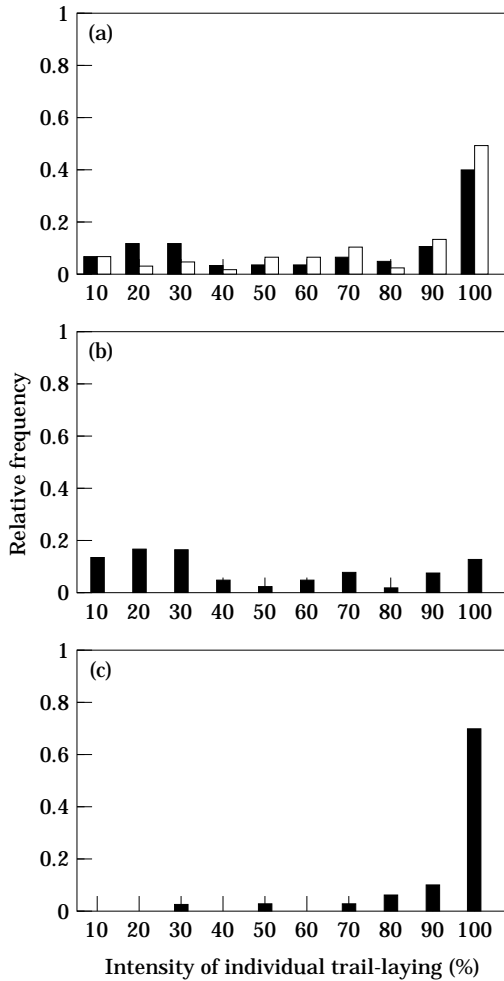
When cockroaches were offered, trail-laying intensity was higher: 80% of the recruiters had
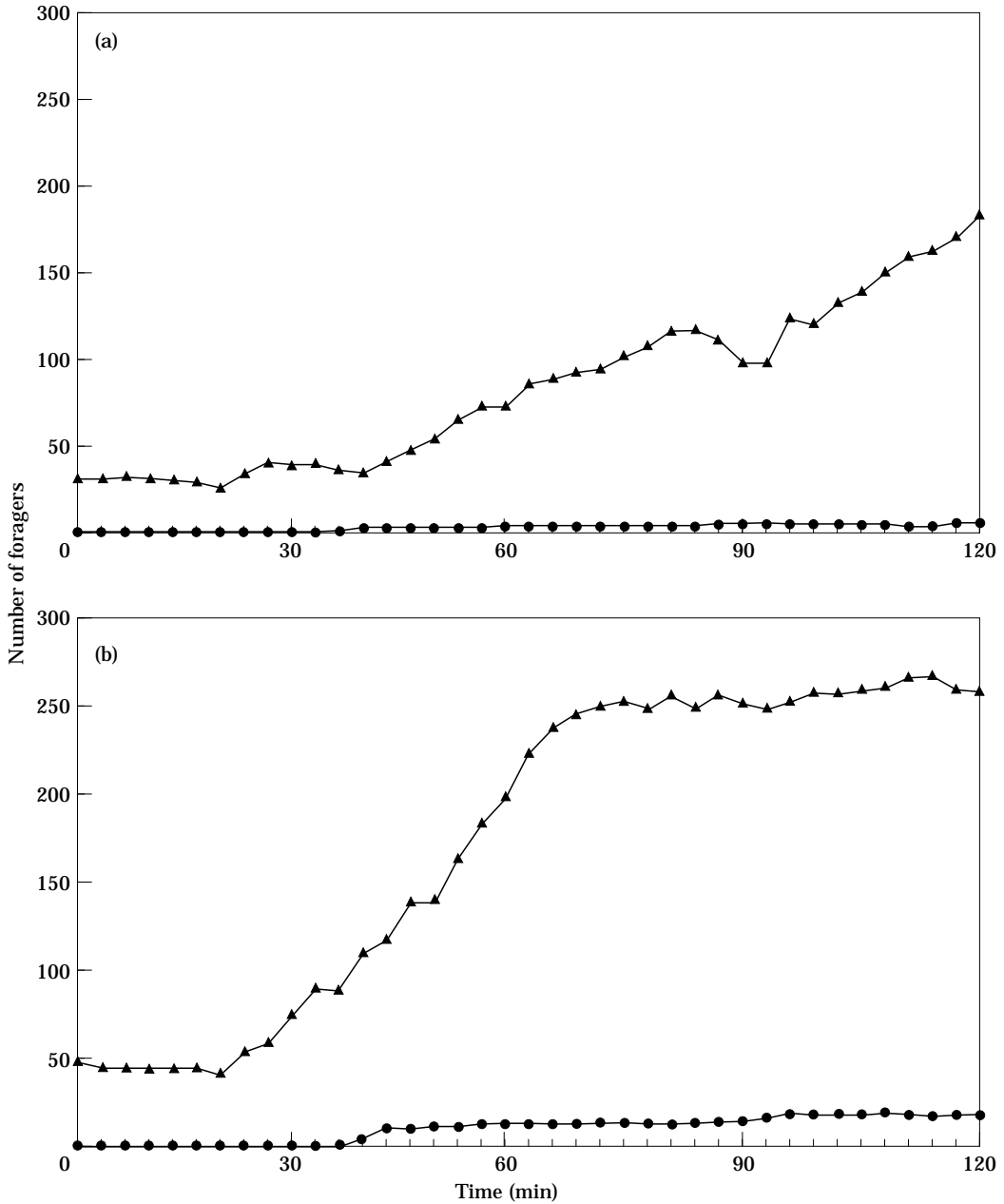
Figure 1. Recruitment of ants to (a) a pile of fruit flies and (b) a cockroach. Minors (▲) and majors (●) present in the foraging area are shown.
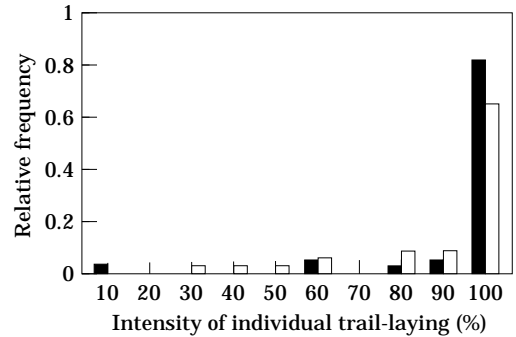
their abdomen permanently on the ground during their way back to the nest (Fig. 3). All video frames showed the gaster bent downwards close to the bridge. After the scouts' entrance, several nestmates streamed out and followed the track laid to the food source. Additionally, many ants (more than 60%) leaving the nest were also seen laying a continuous trail. Most probably these

Figure 3. Trail-laying behaviour of ants returning to the nest (■, $N=33$) or going to a cockroach (□, $N=28$). The relative frequency of each category of trail intensity is shown as in Fig. 2. The observed minors are always non-retrieving ants.
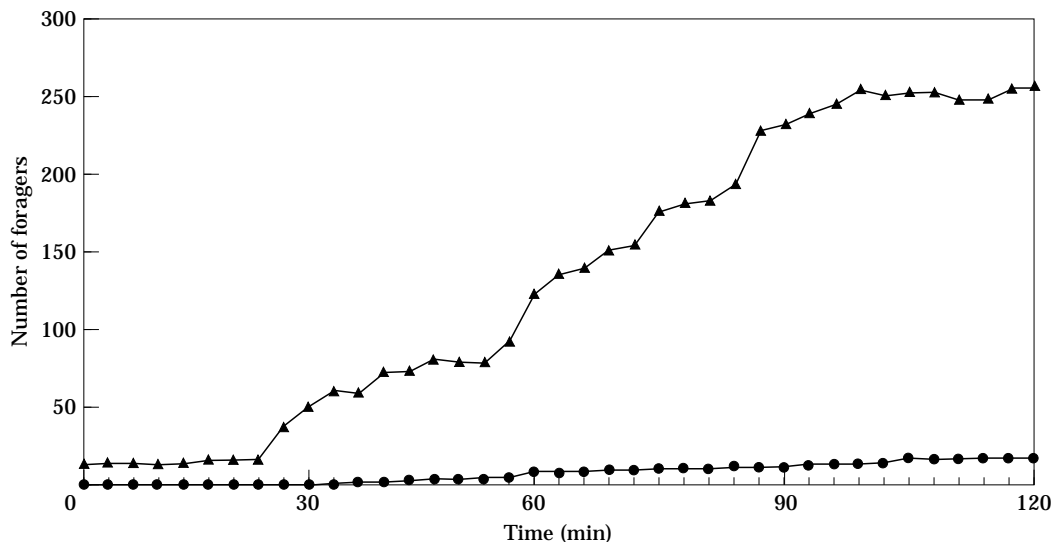
Prey of Altered Retrievability

Recruitment dynamics

When fruit flies were free to be retrieved (Fig. 1a), recruitment of minors was weak and most ants carried a prey to the nest. When the same flies were offered under a wire net and could not be retrieved by individual foragers (Fig. 4), recruitment was strong. The recruitment dynamics were similar to that observed with cockroaches (Fig. 1b). For all experiments ($N=5$), during the first hour, the population in the foraging area increased at a mean rate of $21 \times 10^{-4} \pm 9 \times 10^{-4}$ minors/(min $\times$ total population of the colony). The plateau value was $18 \times 10^{-2} \pm 4 \times 10^{-2}$ of the total population of the colony. The number of majors never exceeded 20 individuals.

Foragers stayed only a short time around the net with a mean duration of 249 s ($N=19$) before returning unloaded to the nest. This duration is close to that observed for cockroaches and is markedly lower than the time spent by foragers around movable flies. All these results show a striking similarity between the exploitation of large cockroaches and that of small flies kept under a net.

Quantification of trail-laying intensity

Trail-laying behaviour was often discontinuous when workers had free access to fruit flies (Fig. 2a). However, when flies were kept under a net (Fig. 5), 80% of the minors laid a continuous

Figure 2. Trail-laying behaviour of ants exploiting a pile of fruit flies. For each observed ant, its trail-laying intensity was measured by the percentage of video frames in which its gaster was seen touching the substrate. (a) The relative frequency of each category of trail intensity for all the observed minors, either returning to the nest (■, $N=62$) or going to the food (□, $N=51$). Among minors returning to the nest, the relative frequency of each trail-laying intensity is given for (b) minors retrieving a prey ($N=34$) and for (c) non-retrieving minors ($N=28$).

were scouts returning to the food source after having invited nestmates to follow them. A continuous trail was thus laid by the majority of foragers, this behaviour accounting for the higher recruitment to large cockroaches.

Figure 4. Recruitment to a pile of fruit flies kept under a net. Minors (▲) and majors (●) present in the foraging area are shown.

trail to the nest after several unsuccessful attempts to extract the prey. Another 60% of minors, from among the ants leaving the nest and going to the net filled with flies, showed continuous trail-laying behaviour. It appears that the individual recruiting behaviour was similar for a large prey and a small item that could not be retrieved. This suggests that the 'choice' of a scavenging pattern is not guided by the size of the prey but rather by its functional correlates: the prey retrievability.

Trail-laying Intensity and Prey Retrievability

When movable fruit flies were offered, two subpopulations of foragers could be distinguished: carrying and non-carrying individuals. Ants loaded with one fly (Fig. 2b) demonstrated all intermediate stages between no trail and a continuous trail-laying behaviour. Most carrying ants scarcely bent their gaster to the ground and laid only a weak chemical trail. However, considering non-carrying ants (Fig. 2c), a return without prey makes the ant more likely to lay a continuous trail. This decision-making rule also accounted for the higher frequencies of ants that laid a continuous trail when food was naturally (cockroach, Fig. 3) or artificially (flies under a net, Fig. 5) not retrievable.

As a further step, we tried to define more accurately the relationship between the tractive resistance experienced by the ant and its trail-laying behaviour. There was no correlation ($r^2 = 0.045$) between the time spent by an ant pulling at a pinned fly and its trail-laying activity (Fig. 6). There was no finely tuned trail-laying behaviour, only a greater tendency to lay a continuous trail when the prey was not retrievable.

DISCUSSION

The majority of studies devoted to scavenging patterns state that unsuccessful attempts to retrieve a prey item are responsible for the behavioural change of the scout that rushes towards the nest and recruits nestmates. However, this assertion often remains experimentally unproven since experiments usually compare prey differing not only in size but in quality as well. Thus, food preference could never be excluded as a possible explanation for the observed foraging differences. In the present study, we avoided such a bias by comparing recruitment dynamics for the same type of prey either retrievable or made experimentally not retrievable (flies under net, pinned flies). By simply preventing ants from taking a small
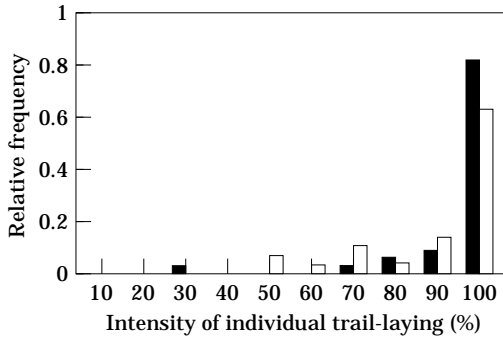
Figure 5. Trail-laying behaviour of ants returning to the nest (■, *N*=33) or going to food (□, *N*=29), a pile of flies kept under a net. The observed minors were always non-retrieving ants.
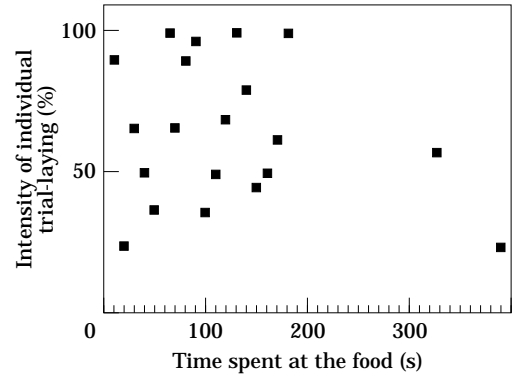
Figure 6. Relation between the intensity of individual trail-laying of 20 observed minors and the time they spent at the food source (fruit flies pinned down on the substrate).

prey item away we simulated the situation of a prey item that is too large to be retrieved in a single homeward trip. Although unquantified, similar observations were made on *Tetramorium caespitum* (Dobrzanski & Dobrzanska 1975) and *Messor* species (quoted as *Novomessor* in Hölldobler et al. 1978; Hahn & Maschwitz 1985) which were offered identical prey either pinned down or free.
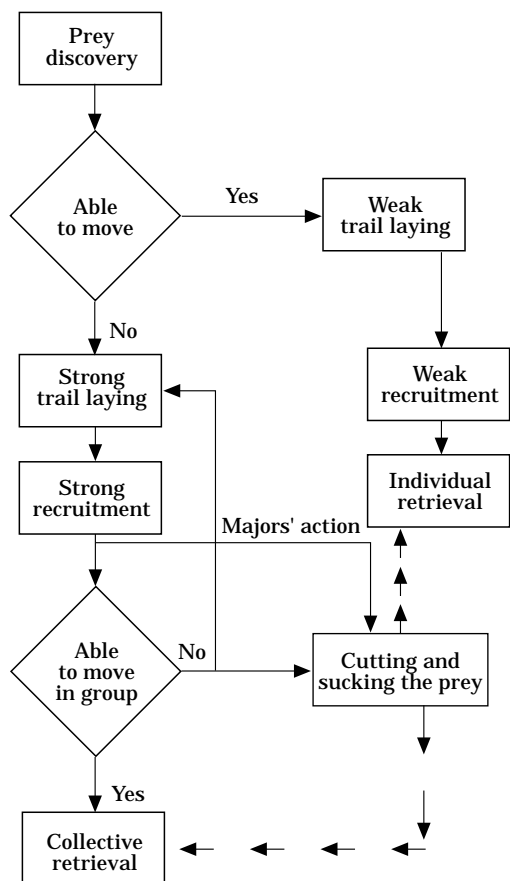
In *P. pallidula*, at least two key parameters of recruitment kinetics changed according to prey retrievability: the time spent by foragers at the food source and their trail-laying intensity.

As far as the time parameter is concerned, *P. crassinoda* workers are known to decrease the time they spend in pulling prey when the tractive resistance of the food item is experimentally increased (Sudd 1960). Similarly, the time spent by *P. pallidula* foragers wandering around the food was shorter for heavy cockroaches or flies under a net than for retrievable flies. We believe that the decision of the scout as to when to stop food inspection does not rely on complex behavioural mechanisms. The shorter stay around large prey is the mere by-product of a rule of thumb that could be expressed as follows: stop dragging the food item if no movement is initiated. Such a shorter stay of scouts around a cockroach decreased the time between food discovery and potential recruitment of nestmates. This shortened time for transmission of information would account for the quicker and steeper kinetics observed for large prey that could not be retrieved.

The second parameter, the trail-laying intensity, was modulated according to prey tractive resistance. When an item could not be retrieved by one scout, it headed straight to the nest, touching the ground with its gaster. Such frequent and often continuous trail-laying behaviour enhanced the intensity and speed of recruitment to large prey that could not be retrieved. On the other hand, the trail-laying behaviour to small food items was always weaker and more discontinuous, making recruitment slower. So, both parameters (time at the food and trail-laying) synergistically contributed to the build-up of foraging strategies changing according to prey retrievability.

Our experimental set-up shows that the tractive resistance of the prey experienced by the ant is a major element in the 'choice' of a scavenging pattern. Although crude in appearance, this tractive resistance is an assessment of higher functional value than any absolute measure of prey size or weight. Indeed, for workers involved in collective transport, it provides indirect information at every moment about both the prey size and the current force of cooperating carriers. As a result, through the tractive resistance experienced, scouts can efficiently adapt their recruitment behaviour if there is a need for helpers. As the shift from individual to collective scavenging is related to the prey resistance experienced, this behavioural change should occur at a critical size of prey for each ant species. This could explain why critical sizes of prey (where social retrieval occurs) seems specific and related to the workers'

Figure 7. Algorithm and decision-making processes followed by the ants during prey scavenging.

the colony level of the best suited scavenging patterns results from crude estimates of prey size and simple decision rules at the individual level. We have demonstrated here that ants do not accurately 'measure' prey size/weight but rather shape their recruiting behaviour according to a simple key criterion: the prey tractive resistance. In the case of sugar solution, the comparison of experiments on *Paraponera clavata* (Breed et al. 1987) and *Myrmica sabuleti* (de Biseau & Pasteels 1994) also suggest that some crude 'estimate' of food size does occur: a large drop induces strong recruitment whereas ants are unlikely to recruit after feeding on a small drop. In both species, the probability that a scout returns to the nest and recruits nestmates increases dramatically at a critical volume of the sugar solution close to the loading capacity of a worker. The ability to fill its crop seems to be another simple criterion used by the forager to 'decide' whether to recruit.

Much current theoretical thinking in sociobiology is based upon assumptions about 'risk assessments, estimate of food energetic nutritive return, optimisation of foraging behaviour . . .' (Oster & Wilson 1978) that have little basis in empirical fact. Unexpectedly, very few studies have been devoted to understanding how relevant information (size, number of food items) is assessed by the ants at the food source and acts as the touchstone of the decision-making process either at the individual or colony level. Usually, it is assumed (either explicitly or implicitly) that complex global responses arise from complex individual behaviour. For instance, when exploiting small food items (e.g. seed, fruit flies) in patches of different sizes, each *Messor rufitarsis* scout begins to recruit nestmates only after several successful foraging trips to one seed patch (Hahn & Maschwitz 1985). Such a decision-making process implies some behavioural complexity of each individual scout which measures patch size through the number of its rewarding trips. An alternative to this rather complex individual assessment is the collective measure of patch size by *P. pallidula* foragers. Indeed, when small prey items are locally abundant, the weak trails laid by *P. pallidula* minors are superimposed: these trails progressively concentrate workers near the food and provide the colony with some collective measure of prey abundance. There is no need to evoke any sophisticated measure of patch size by each scout. Although these two species show the

size in several north temperate ant species (from data in Traniello 1987).

By way of summary, all major scavenging patterns in ants can be generated from the following algorithm (Fig. 7). Success in prey-carrying encourages the forager to move on and lay a weak trail on its way back to the nest. This could lead to a slow and progressive monopolization of the source when small food items are numerous. Failure to retrieve the prey item results in a shortened stay at the food source followed by an intense trail recruitment. Recruited ants then gather around the food and try to retrieve it collectively. If they are unsuccessful, they tear up the large prey item and suck its haemolymph. Large insects can be dissected on the spot into smaller pieces which are taken back home on an individual or collective basis. According to this algorithm, the outcome at

same collective foraging pattern (recruitment to large food patches versus individual foraging to small ones), their decision-making system differs deeply in the assumed behavioural complexity of individual scouts.

These findings lead us to reconsider some usual evolutionary and ecological statements concerning foraging and other types of cooperation in social insects. When foraging for food is associated with mortality risks from predators or competitors, according to Nonacs & Dill (1988, 1990), the foraging responses of *Lasius pallitarsis* ants should result from complicated decisions which involve trade-offs between risks and nutritive return. Each forager is assumed to possess the behavioural complexity and sophisticated means of communication needed to handle complex information about food and risk. However, such an assumption remains experimentally unproven. Moreover, without implying complex individual assessment, factors such as a higher mortality rate of foragers and physical blocking by competitors could explain the weaker trail deposition to the risky food source than to the safe one. Only further investigations about specific responses of individuals to experimentally controlled stimuli will reveal the mechanisms by which foragers assess, communicate about and respond to both food and risk.

Cooperative defence of *Myrmecocystus* ants is a final example that perfectly illustrates this major alternative now existing in sociobiology: is complexity of global behaviour a by-product of complex individual assessments or the expression of simpler behavioural rules, limiting factors and amplification processes. Several decision-making systems have been suggested to account for *Myrmecocystus*' ritualized fights (Hölldobler 1982; Lumsden & Hölldobler 1983). On the one hand, the first two models hypothesize behavioural complexity of the individual ant able to census the number of aggressive encounters ('head counting model') and the caste of opponents ('caste polling'). *Myrmecocystus*' tournaments are seen as sites for global harvesting of information and integrative sampling to tally colony strength. The ant 'measures', by some analogical counting, the colony size and even gets an image of the opponent colony's caste system. On the other hand, in the third model ('queue flooding'), requirement for information storage and processing by individual ants is less demanding. In this case, the mere detection of a supply of unengaged nestmates is in itself sufficient to release recruitment behaviour and to result in a raid on the weaker colony. This implies that ants are not engaged in some accurate sampling procedure but are locally reacting to simple behavioural rules.

These few examples lead the way to a deeper understanding of collective behaviour which investigates decision processes in social insects. Which information is 'measured' by the ant and allows the forager, through its recruitment, to modulate the global response of the colony? Which level of behavioural complexity, at the individual or collective level, allows colonies to track their environment and to modulate their cooperative response? As demonstrated in our experiments on scavenging, ants are likely to make quick decisions triggered by simple stimuli. Complex foraging or defensive strategies could result simply from the interplay between rules of thumb and self-organizing processes. We have the feeling that, in most cases, there is no need to evoke any choice at the individual or society level based on sophisticated assessments of environmental conditions. This assumption could trigger new critical reading of existing literature.

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