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Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*

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Abstract According to the weight and size of their prey, *Ectatomma ruidum* workers can employ different recruitment systems (solitary hunting, cooperative hunting and group hunting with recruitment) when mastering and retrieving prey items from short distances from the nest. Prey size determined the backwards entry typically adopted by this species, while prey weight determined the predatory strategy selected. After a common initial sequence (search for prey, detection, localization), predatory sequences varied in terms of the type of approach, the site of seizure, the reaction after stinging and the type of transport. Nevertheless, irrespective of prey weight and size, seizure was preferentially oriented towards the head and prey were always stung. Short-range recruitment and mass recruitment without trail laying were elicited by a large range of heavy prey (> 2.5 times the weight of an individual worker). According to the mortality risk associated with each prey, hunters exhibited a “prudent” stinging posture associated with an increase in the duration of the subsequent phase of waiting for prey immobilization. The overall time of capture was positively correlated with the weight of the prey. When collective hunting strategies were involved, *E. ruidum* colonies matched the number of recruited hunters to the size and weight of the prey. Compared to solitary hunting strategies, for short food–nest distances, this graded recruitment appeared to enhance the energetic benefits derived by this species from the use of recruitment systems: the higher the number of workers involved in the recruitment process, the greater the energetic benefits obtained. The exhibition or absence of trail laying behavior in the recruitment responses dis-

played by *E. ruidum* workers is discussed in relation to their involvement in scavenging or predatory behavior.

Key words Predation · Behavioral flexibility · Graded recruitment · Ponerine ants · *Ectatomma*

Introduction

For all animals, regardless of whether they are solitary or social, the search for and retrieval of food items constitute the major part of their time-budget and energy expenditure. However, in social vertebrates, such as lions, wolves or hyenas (Curio 1976; Alcock 1993), as well as in social insects (Wilson 1971; Oster and Wilson 1978; Franks 1986; Moffett 1988; Schmid-Hempel 1991; Duncan and Crewe 1993), cooperative food source mastering and/or recovery may greatly enhance the efficiency of the foraging by reducing total energy costs.

In the course of their evolution, ants have developed a variety of foraging strategies depending on their species-specific behavioral repertoire and communication systems, and on various parameters related to the food sources (e.g., nature, size, weight, quality, availability, accessibility) and to the intrinsic characteristics of the foragers (e.g., size and strength, level of internal energetic reserves, prior experience, nutritional status of the colony) (Traniello 1989a; Hölldobler and Wilson 1990; Schmid-Hempel 1991). From an adaptive perspective, the more flexible the foraging behavior, the more readily colonies may adjust to environmental changes. Bernstein (1975) found that the shifts in foraging strategies recorded in the seed harvesting ants *Pogonomyrmex* spp. and *Messor* (= *Veromessor*) *pergandei*, were related to seed density. At high densities, these species exhibited individual foraging. At medium densities, scout ants were used to locate food and to recruit a column of ants. At the lowest densities, group foraging without a scout ant occurred along defined trunk trails. A similar relation between the relative food abundance and the for-

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aging strategy adopted by the large African ponerine ant *Megaponera foetens*, was proposed by Longhurst and Howse (1979) to account for the regional differences in foraging and recruitment systems reported for this termitophagous species. For a given species, the existence of a multiple strategy of foraging is mainly attributable to its ability to recruit nestmates to food sources and to the variety of the recruitment systems employed (Wilson 1971; Oster and Wilson 1978; Hölldobler and Wilson 1990). Such flexibility in foraging techniques may permit the utilization of alternative food sources by specialized species (Dejean 1982; Masuko 1984; Lachaud and Dejean 1994) or the exploitation of a wider range of food items by generalist species (Hölldobler 1984; Dejean et al. 1993).

The ponerine ant *Ectatomma ruidum* Roger is one of these generalist species. This terricolous medium sized ant (7–9 mm in length; 5–12 mg in weight, mean = 8 mg) is widespread in disturbed habitats as well as in damp rain-forests (Brown 1958). Very common in Central and northern South America (Weber 1946; Kugler and Brown 1982; Levings and Franks 1982; Young 1986), it is the dominant ant species in some habitats like tropical thorn forest in Colombia (Kugler and Hincapié 1983) or coffee and cocoa plantations in southeastern Mexico, where its density can vary between 2 700 and 11 200 nests per hectare (Lachaud et al. 1996). Its efficiency as a predator and its ecological impact on insect pests had already been noted and various authors have proposed this species as a potential agent for biological control in coffee/cocoa plantations in Panama and Mexico (Weber 1946; Lachaud 1990), and in maize cultures in Nicaragua (Perfecto 1990, 1991). Whereas a substantial body of information exists concerning various aspects of its foraging activity, social behavior and intraspecific relationships (Lachaud et al. 1984; Jaffe and Marquez 1987; Lachaud and Fresneau 1987; Corbara et al. 1989; Pratt 1989; Breed et al. 1990, 1992; Lachaud 1990; Schatz et al. 1994), little information is available on its predatory behavior. In the laboratory, foragers of *E. ruidum* were observed to fall into one of five specialized categories: hunters, sugar collectors, unspecialized intermediates, patrollers, and nest-maintenance workers (Schatz et al. 1995). There is an even more subtle within-caste specialization between stingers and transporters within the hunters (Schatz et al. 1996). While this species has been described as a solitary hunting ant (Levings and Franks 1982; Lachaud et al. 1984), recruitment may occur in some instances (Lachaud 1985; Pratt 1989) and some degree of cooperation between stingers and transporters has been reported (Schatz et al. 1996). However, the available information dealing with recruitment behavior appears somewhat contradictory (see Lachaud 1985; Pratt 1989; Bestmann et al. 1995), and the factors which provoke the exhibition of trail-laying behavior or its absence remain unclear.

To determine the predatory repertoire of this species and to analyze the cooperative strategies used and the

conditions under which they are induced, we studied the flexibility of the workers' predatory behavior when faced with prey of different sizes and weights. These factors, as well as the distance of the food source from the nest, appear to be the key parameters responsible for the energy cost related to food retrieving and determining the choice of predatory strategy, especially in species generally considered as solitary foragers (see Dejean 1982, 1991; Dejean et al. 1993; Lachaud and Dejean 1994).

Methods

Five queenright colonies of *E. ruidum*, ranging from 70 to 350 workers, were reared in plaster nests placed in an experimental room under controlled conditions (temperature at $25\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$, $60\% \pm 5\%$ humidity and a 12/12 L/D photoperiod). For each colony, a 35×35 cm box, connected to the nest, was used as a foraging area. Ants had access to a permanent supply of honey and water, in addition to fresh prey (crickets, cockroaches, or *Tenebrio* larvae) given twice a week. In this study, we examined in laboratory conditions the predation sequence exhibited by the hunters when offered larvae of *Tenebrio molitor* as prey. In order to avoid predatory specialization or preference associated with a particular type of prey, instead of several types of prey with different sizes, we chose to use only one type of prey showing large differences in size. Prey ($n = 274$) differing in size and weight (respectively 7–27 mm in length, 4–204 mg in weight) were offered randomly. Prior to each experiment, the prey offered was measured and weighted, and the observation of the predation sequence began when the prey was placed at the center of the foraging area (about 20 cm from the nest entrance). A significant positive logarithmic correlation was detected between prey size and weight ($r = 0.977$; $P \leq 0.0001$).

The duration of predation tests was fixed at 30 min for all experiments. In all cases, the exact behavioral sequence and its duration were recorded. A squared paper, placed under the transparent floor of the foraging arena, allowed us to estimate the distance of detection of the prey (as determined by a change in the motility and orientation of the ants to the prey, see Dejean 1982). The orientation of the hunter towards the prey during the approach and the part of the body prey seized during the attack were also analyzed. In the case of strategies for which several hunters had been involved, only the behavior of the first hunter was considered.

In order to discriminate between weight and size effects, the weight of 44 additional larvae of *T. molitor*, belonging to a given size category (12.5–14 mm in length), was reduced by removing a certain amount of their haemolymph with a syringe needle. Immediately after the wounded larvae ceased to bleed, it was placed in the foraging area. Treated larvae were alive and moving at the moment of attack by *E. ruidum* workers.

Observations were sorted *a posteriori*, according to the strategy employed by the ants towards prey of different weight and size. For each predatory strategy, a flow diagram was devised from observational data. For each sequence, percentages were calculated based on the overall number of transitions between each individual behavioral act. For strategies involving recruitment, two parts were considered for the calculation of the transition frequency between each behavioral act: (i) one hunter only, and (ii) all hunters participating in the predatory sequence. During cooperative hunting, recruited individuals were involved in different steps of this sequence. Therefore in the calculation of transition frequencies, we considered the total number of individuals starting at the beginning of the recruitment phase.

Complementary field observations were made at the beginning of the rainy season, in the same coffee plantation from where the colonies studied in the laboratory had been collected. This plantation was located in the Rosario Izapa Experimental Station of the

Instituto Nacional de Investigaciones Forestales y Agropecuarias, in the Cacahuatan District, Chiapas State, Mexico, at 420–440 m elevation. In order to estimate cooperative foraging in this species, six nests of *E. ruidum* were observed over 6 h every day, for 4 consecutive days. Observations were made between 0830 and 1430 hours, a period which includes nearly 60% of the daily activity in the rainy season (Lachaud 1990). We recorded the type and the number of prey brought back to the nest by solitary ants or groups working collectively. The range and distribution of prey weights and sizes was estimated by measuring a sample of prey (earthworms) showing cylindrical-shape analogies with the *T. molitor* larvae used in the laboratory experiments.

Results

Three main types of predatory strategy were defined depending on prey weight and size: solitary hunting, cooperative hunting involving only short-range recruitment, and group hunting with recruitment from the nest. On the basis of qualitative changes in the behavioral sequence, it was possible to distinguish some variants both in the solitary hunting strategy (according to the frequency of the lifting, stinging and “let go and re-seize” phases, and to the mode of entry into the nest) and in the recruitment strategy (according to the number of “givings-up” and the whether or not the prey was cut). However, in all cases, a certain flexibility was encountered in the choice of the strategy adopted. The range of prey weights corresponding to each strategy was not strict: two prey items with the same weight could trigger different responses. For this reason, the median weights and the 10–90% ranges were determined for each strategy.

Solitary hunting involved a small range of prey weights (Fig. 1). For solitary hunting type 1, the median

prey weight was 8 mg (10–90% range: 4.9–11 mg), and for type 2, the median weight was 15 mg (10.5–19.5 mg). The differences in median weight and range of prey weights for each of the three remaining strategies were much greater: 39 mg (17.6–79.0 mg) for the cooperative hunting, 115 mg (72–157 mg) for type 1 group hunting with recruitment, and 175 mg (159–199 mg) for type 2 group hunting with recruitment. In the latter case, however, the possibility of a more extensive range of prey weights could not be ruled out since observational data were limited by the size/weight characteristics of the experimental prey.

Common behavioral phases

In this study, as far as the succession of the main behavioral phases is concerned, the first part of the behavioral sequence (search for prey – detection/localization – approach/antennation – seizure) was essentially the same for all the strategies. Nevertheless, some aspects can vary, namely those related to the orientation of hunters towards the prey and the part of the body prey seized.

Search for prey – detection/localization

During the search for prey, the worker moved slowly and sinuously, antennae spread apart and mandibles closed. For all cases, detection occurred as soon as the prey appeared to enter the field of visual perception of the ant. Immediately, the hunter oriented its antennae towards the prey and opened its mandibles. Prey were detected at a distance of 1–2 cm, a figure similar to that found in the field (Lachaud 1990). However, the movement of the prey was apparently necessary for its detection and localization, since various workers passed by a motionless prey at this same distance of 1–2 cm without locating it.

Approach/antennation – Seizure

The solitary strategy type 1 differed from all other strategies: it was the only situation for which no preferential direction was detected during the approach, although hunters clearly chose to seize the prey in the middle part of its body. For all other strategies, during the approach, the middle part of the body of the prey was significantly preferred, but the head was also chosen preferentially to the tail. Moreover, for the site of the seizure, a highly significant preference was shown for the head or, to a lesser extent, for the tail; hunters avoided the central part of the body prey (Fig. 2). During the seizure phase, the hunter displayed a forward movement of the whole body. With the exception of the solitary strategy type 1, the seizure behavior normally occurred according to the following sequence. When its antennae

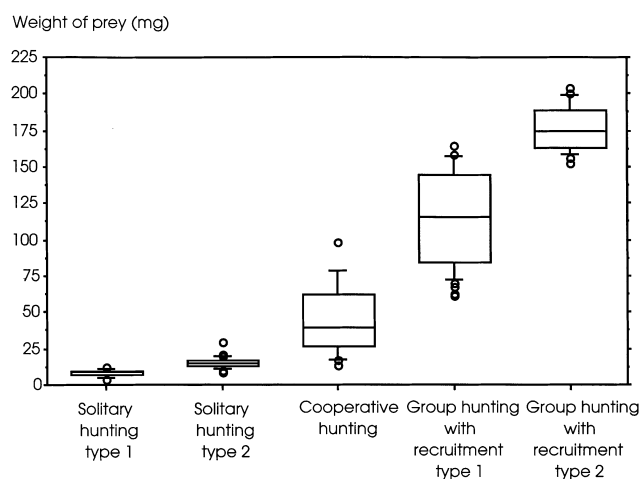


Fig. 1 Hunting strategy adopted by *Ectatomma ruidum* workers according to prey weight. Whisker box representation with median weight of the *Tenebrio molitor* larvae offered as prey (middle bar) and 20–80% range values (extremities of the whisker box); open circles indicate the observed minimal and maximal values; bars indicate the 10–90% range values. There is some overlap at the division between adjacent categories of prey weights: two pieces of prey with the same weight can trigger two different predatory responses

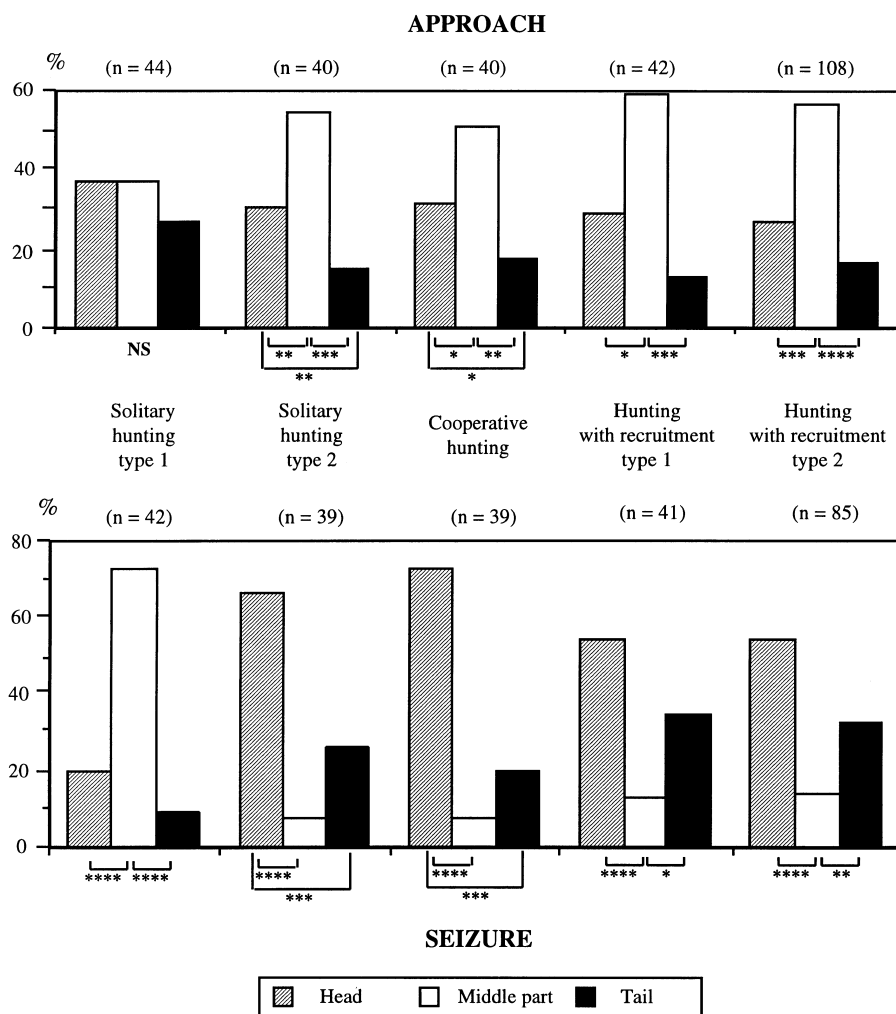


Fig. 2 Part of prey body used as target during approach and seizure phases for the different hunting strategies. Chi-square comparison with a theoretical random approach or seizure (* $0.01 < P < 0.05$,

** $0.001 < P < 0.01$, *** $0.0001 < P < 0.001$; **** $P < 0.00001$; n = number of individual approaches or seizures)

came in contact with a motionless prey, the hunter positioned its body above that of the prey in order to align its body axis with that of the prey, and always oriented its head towards the head of the prey. Once this posture was secured, the hunter opened widely its mandibles, placed its antennae on each side of the body of the prey, and went up until the head where the seizure abruptly occurred. This particular behavior strongly suggested that the preference exhibited by the hunter to seize its prey by the head, really corresponded to an active choice. This sequence was the most common (121 times out of 204). However, other sequences were also observed. For instance, various hunters were observed (32 times) running over the body of the prey while walking by its side and, when several hunters were involved in the attack, while the first hunter seized the prey by the head, the second hunter seized it by the middle part of its body (2 cases) or by the tail (16 cases) (comparison with a random seizure: $\chi^2 = 19.6$; $P \leq 0.0001$). This suggests that hunters prefer to seize the prey by their extremities and more particularly by the head.

Solitary hunting

Two variants of solitary hunting sequences, related to an increase in the weight and size of the prey, were distinguished: type 1 and 2 (Fig. 3a, b). Solitary hunting type 1 occurred with the smallest prey, ranging from 4 to 12 mg in weight and 7 to 12 mm in length. The total time of capture lasted from 10 to 160 s, with a mean time of 77.6 ± 40.5 s ($n = 44$). Solitary hunting type 2 occurred with prey ranging from 9 to 30 mg in weight and 11 to 17 mm in length. The total time of capture lasted from 40 to 220 s, with a mean time of 141.2 ± 40.5 s ($n = 40$). For both types, most abandoned prey (77%, $n = 13$) were encountered during the "let go and re-seize" phase. When the prey did not struggle after being stung, it was directly transported to the nest. If the prey struggled, the hunter stung it repeatedly and waited for its immobilization for at least 20 s before transporting it to the nest.

Differences between both types were qualitative and quantitative. Aside from the duration of the total se-

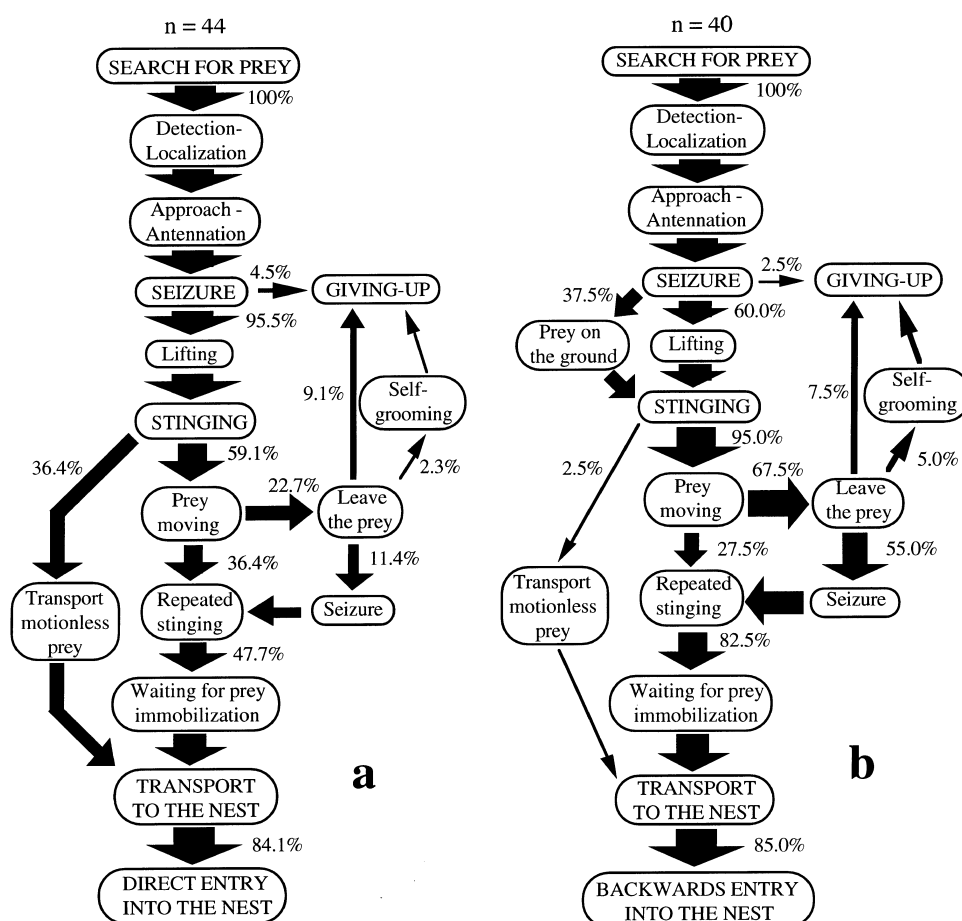


Fig. 3 Flow diagrams for the solitary hunting strategy: **a** solitary hunting type 1 ($n = 44$ sequences); **b** solitary hunting type 2 ($n = 40$ sequences). For each sequence, percentage values were calculated

based on the overall number of transitions between each individual behavioral act

quence, the main differences concerned the lifting and stinging phases, of which the occurrence was less frequent for solitary hunting type 2, and the “let go and re-seize” phase which was much more frequent in this case. Besides, while for solitary hunting type 1 the entry into the plastic tube connected to the nest was always direct, for type 2, after several attempts to enter directly, the hunter always turned round and entered backwards, pulling its load.

In order to distinguish between the effects of the size of the prey and its weight in the choice of the solitary strategy to adopt, we experimentally manipulated the weight of similar size prey (see Methods). A total of 44 larvae of *T. molitor* were chosen within a given range of intermediate sizes (between 12.5 and 14 mm) corresponding to a median of 15 mg (range of weights: 13–17 mg), for which hunters regularly adopted solitary hunting type 2. By extraction of haemolymph, prey weight was reduced to a median of 8.5 mg (range of weights: 7.5–9.25 mg), for which hunters normally adopted solitary hunting type 1. Faced with these experimental prey, we predicted that hunters would adopt solitary strategy type 1 if they were more sensitive to the

weight of the prey, or solitary hunting type 2 if they were more sensitive to the size of the prey. The predatory strategy adopted by hunters faced with experimentally modified prey corresponded to solitary hunting type 1, except for entry into the nest (Table 1). In all cases, this latter behavior was performed backwards as in solitary hunting type 2. These data strongly suggest that prey weight determines the solitary hunting strategy for *E. ruidum*, except for the way in which the hunters enter the nest, which is determined by the size of the prey item (probably for mechanical reasons, Lachaud 1985).

Cooperative hunting

Retrieval of heavier and larger prey (approximately ≥ 20 mg in weight and 15 mm in length) appeared to be difficult for a solitary individual. In these cases, the cooperation of several workers was generally necessary and was triggered by the scout ant.

Cooperative hunting (Fig. 4) occurred for prey of a range of weights and sizes from 13 to 98 mg and 13 to 22.5 mm, respectively. The total time of capture lasted

Table 1 Comparative importance of size against weight of prey in the choice of predatory strategy to adopt by solitary hunters of *Ectatomma ruidum*. Treated prey refer to 44 larvae of *Tenebrio molitor* (12.5–14 mm in length) in which mean weight was reduced

from about 15 mg to 8.5 mg by removal of haemolymph. Prey size determined the backwards entry into the nest while prey weight determined the choice of predatory strategy (chi-square comparisons)

Behavioral acts	Number of behavioral acts performed			Statistical comparison (χ^2 test)	
	With treated prey ($n = 44$) (A)	During solitary hunting type 1 ($n = 44$) (B)	During the solitary hunting type 2 ($n = 40$) (C)	Between A-B	Between A-C
Lifting of prey	42	42	24	NS	$\chi^2 = 15.6$ $P = 0.0001$
Direct transport of motionless prey	18	16	1	NS	$\chi^2 = 17.7$ $P < 0.0001$
Leaving moving prey	9	10	27	NS	$\chi^2 = 18.9$ $P = 0.0001$
Stinging moving prey	15	16	11	NS	NS
Backwards entry into the nest	38	0	38	$\chi^2 = 66.9$ $P < 0.0001$	NS

from 80 to 990 s, with a mean time of capture of 418.2 ± 273.3 s ($n = 39$). By contrast with both strategies of group hunting with recruitment described below, the recruited workers involved in the cooperative

strategy were never recruited directly from the nest by the scout ant, but were attracted from the surroundings of the prey. The scout ant, after the first attempt at seizure, engaged in repeated, aggressive stinging. The

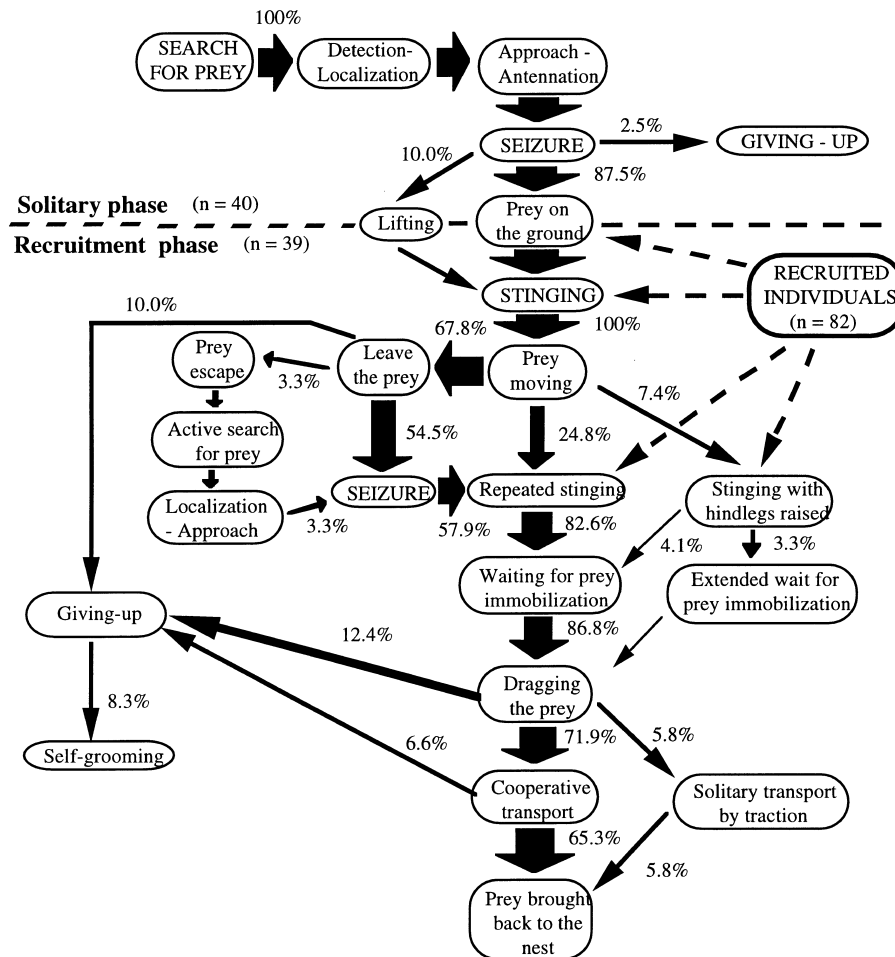


Fig. 4 Flow diagram for the cooperative hunting strategy ($n = 40$ sequences)

nearby nestmates (within a radius of about 10 cm) appeared to be attracted and readily joined the scout ant and began to attack the prey and sting it. Although no evidence of any chemical communication was detected, the release of an alarm pheromone originating from the mandibular glands or the poison gland (Pratt 1989) may have occurred. Visual and acoustical information could also be responsible for the attraction observed.

Of a total of 39 prey which triggered local recruitment, all were successfully transported to the nest. Nevertheless, only 71.1% of the hunters (of a total of 121 involved in the cooperative hunting) participated in all the phases of the killing and transport of the prey to the nest.

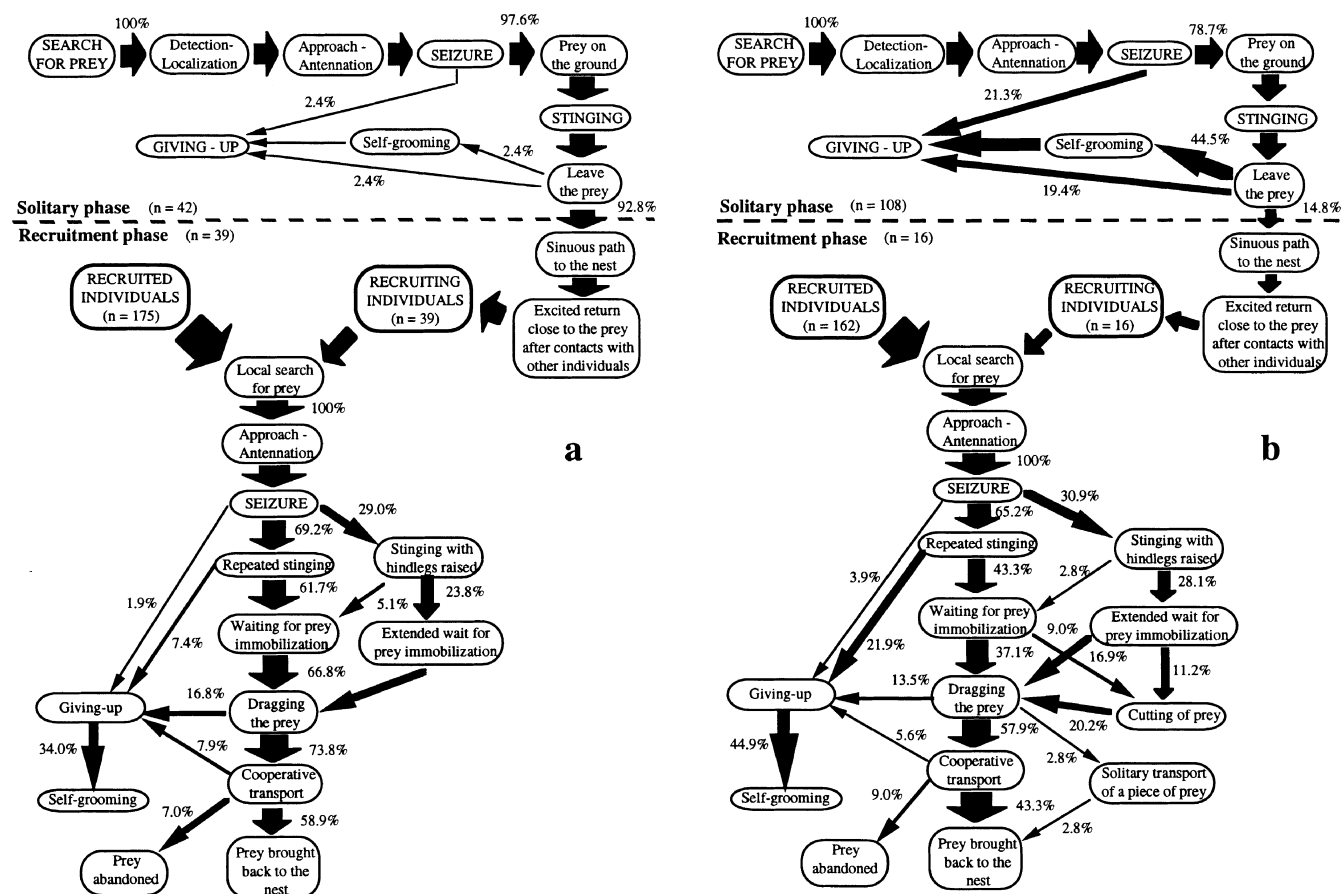
Group hunting with recruitment

Two variants of group hunting with recruitment were distinguished following an increase in prey weight and size (for prey approximately ≥ 79 mg and 21.5 mm). Both were characterized by a similar behavioral sequence performed by the recruiter. Once the prey was

discovered, the typical succession of behavioral acts (detection, localization, approach, antennation, seizure, stinging, and dropping) was observed. Heavy prey were never lifted. A rudimentary mass recruitment without trail laying was then triggered by the scout ant which performed a very excited return path back to the nest in order to activate other hunters prior to returning to the prey (see Lachaud 1985; Pratt 1989). The orientation of the recruited ants towards the prey was not related either to the presence of a leader nor with a chemical trail, but appeared to be directed by signals originating from the prey (odors, movements, visual or acoustic information). Evidence for this was supported by the fact that each recruited ant followed a different individual path between the nest and the position of the prey which, nevertheless, came together at the prey. Ants recruited by the scout ant never engaged in recruitment behavior.

Subsequently to this first recruitment phase, two different behavioral sequences were exhibited according to the weight of the prey (Fig. 5a, b). Group hunting with recruitment type 1 occurred with prey ranging from 61 to 165 mg in weight and 20.5 to 25.5 mm in length. The total time of capture lasted from 670 s to more than 30 min. Of a total of 39 prey which triggered this strategy, 36 (92.3%) were successfully retrieved. Nevertheless, only 58.9% of the hunters (of a total of 214 involved in the recruitment) participated in all the

Fig. 5 Flow diagrams for the group hunting strategy with recruitment: **a** group hunting with recruitment type 1 ($n = 42$ sequences); **b** group hunting with recruitment type 2 ($n = 108$ sequences)



phases of the killing and transport to the nest. Group hunting with recruitment type 2 occurred with prey ranging from 152 to 201 mg in weight and 24.5 to 27 mm in length. The upper limits of 201 mg and 27 mm resulted from the limits in the weights and sizes of available *T. molitor* larvae in our studies. Nevertheless, the great increase in both the number of giving-up behaviors before recruitment (85.2%) and the total duration of the capture (which in all cases lasted more than 30 min) suggested that a prey weight of 200 mg actually constituted a limit for the hunters of *E. ruidum* to complete the predatory sequence. The main characteristic of this sequence was the frequent cutting of the prey (28.1%), always performed between two segments of the *Tenebrio* larva. A total amount of 162 individuals was recruited, i.e. an average of 10.1 recruited ants per recruiting worker, significantly different ($\chi^2 = 6.87$; $P \leq 0.01$) from the average of 4.5 recruited ants per recruiting worker reached in the previous type of group hunting with recruitment. Of 16 prey which triggered group hunting with recruitment type 2, 13 (81.3%) were successfully brought back to the nest. Only 46.1% of the recruited hunters (of a total of 178 hunters involved in the recruitment) participated in all the phases of the killing and transport to the nest.

Comparative analysis of some characteristics

Lifting of the prey and stinging behavior

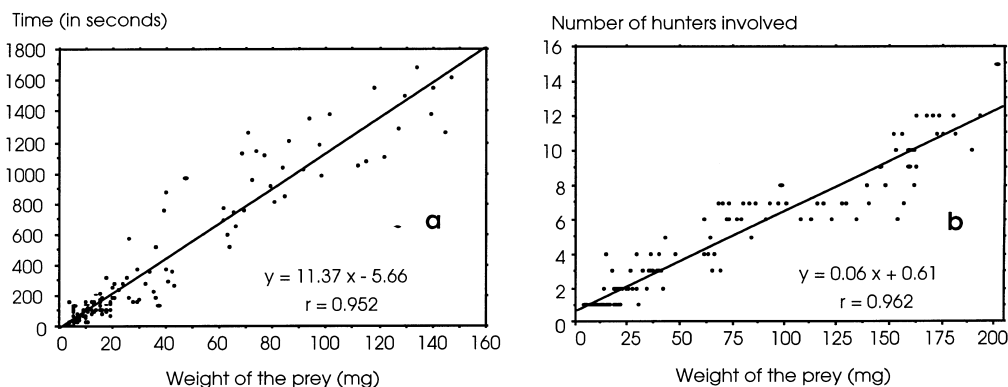
In both types of solitary hunting, the small and light prey were lifted, in most cases, and rapidly stung by the hunters. Nevertheless, in the subsequent collective strategies, this behavior rapidly disappeared with the increase of the weight and size of the prey. When the prey were larger and heavier (> 15 mm in length and 20 mg in weight), hunters of *E. ruidum* began to adopt a particular posture during the stinging behavior (Figs. 4

and 5): their hindlegs were raised high above the gaster in an apparently defensive posture. The use of this “prudent” stinging by the hunter was clearly associated with an increase in the duration of the subsequent phase of waiting for prey immobilization (from 20–40 s to more than 150 s). A total of 126 cases (out of 420 stinging behaviors) were recorded over the three collective strategies (23.1%, 29.5%, and 32.2% of the stings, respectively), for which the “prudent” stinging posture was exhibited by the hunters: a subsequent phase of extended wait for prey immobilization occurred in 83.3% of these cases, while such an extended wait was never observed after “normal” stinging. Moreover, the increase in the percentage of “prudent” stinging followed by an extended wait for prey immobilization according to the increase in the weight of the prey (44.4% for cooperative hunting, 82.3% for group hunting with recruitment type 1, and 90.9% for group hunting with recruitment type 2) suggested that hunters adjusted their behavioral response, perhaps related to a “mortality risk” associated with each prey.

Duration of capture and number of hunters involved

The time needed to capture a prey item and transport it to the nest was positively correlated with its weight ($r = 0.952$; $P < 0.0001$; $n = 140$) (Fig. 6a). The hunters demonstrated an important ability to adjust the number of recruited nestmates according to the weight of the prey. In spite of the variability in the defense behavior performed by the prey triggering the different strategies, a highly significant positive correlation was encountered between prey weight and number of hunters involved in the predatory sequence ($r = 0.962$; $P < 0.0001$; $n = 94$) (Fig. 6b). Moreover, this positive correlation persisted within each one of the collective strategies: the number of hunters involved varied from 2 to 8 individuals for cooperative hunting ($r = 0.821$; $P < 0.001$; $n = 39$), from 6 to 11 individuals for the group hunting with recruitment type 1 ($r = 0.522$; $P < 0.05$; $n = 39$), and from 8 to 15 individuals for the group hunting with recruitment type 2 ($r = 0.686$; $P < 0.01$; $n = 16$).

Fig. 6 Relationship between prey weight and **a** duration of the predatory sequence or **b** number of workers involved in the predatory sequence



Efficiency of the predatory strategy adopted

According to the prey weight, the predatory efficiency of *E. ruidum*, as measured by the ratio of actual captures per hunting attempt was relatively high (84.1–92.3%) and only the very large prey (weight between 20 and 25 times that of an individual ant) induced frequent giving-up by the hunters (efficiency of retrieval 12%), which occurred essentially during the solitary phase prior to any recruitment. In the case of the collective hunting techniques, however, considering only the attempts which actually triggered recruitment behavior, it is obvious that all three collective strategies used according to the increase in prey weight were highly efficient, with a subdue-and-retrieval efficiency varying from 81.3% to 100%.

This efficiency of the collective hunting techniques was accompanied by an increase in the net energetic benefit derived from the cooperative prey retrieval. Considering the mean number of workers involved in prey retrieval and the mean weight of prey retrieved successfully to the nest, the overall mean energetic benefit (Table 2) was greater for collective strategies than for solitary ones, given a distance of only 20 cm from nest entrance. Furthermore, if we consider that only a part of the total workers recruited in each one of the collective strategies actually completed all the steps of the predatory behavior involved in the transport of large prey to the nest, it may be argued that the coarse estimates of energetic benefits indicated here are underestimates of the actual benefits derived from the use of recruitment systems by *E. ruidum*. Overall, these estimates suggest that the mean weight of prey retrieved per individual worker actually increased according to the mean number of hunters recruited by the scout ant.

Field observations

During the 24 h of observation dedicated to each nest, 419 prey were collected belonging to 50 families and 19 orders of arthropods (insects, arachnids, crustaceans, diplopods, chilopods), annelids (earthworms) and mollusks (snails, slugs). During this survey of predatory hunting in field conditions, *E. ruidum* hunters exhibited

all the hunting strategies described above. While different types of prey were involved, the five strategies observed in laboratory studies with larvae of *Tenebrio molitor* could be easily extrapolated to the diversity of natural prey. However, the frequency of collective prey recovery was very low: 96.4% of prey were brought back to the nest by solitary ants. Moreover, the range and distribution of the weights and sizes of 84 earthworms (Halotaxida, Lombricidae) separated from the collected prey, showed that though 15.5% of this type of prey were larger than 20 mm in length, only 1.2% (1 case) was heavier than 20 mg. This result confirms that the range of weights and sizes of the prey collected in field conditions corresponds to that triggering the solitary hunting strategy in laboratory conditions.

Discussion

Behavioral sequences

Although, in field conditions, *E. ruidum* workers appear to forage individually for the most part, they can employ different recruitment systems when mastering and retrieving large prey items. The behavioral analysis of these infrequent collective retrieval strategies appears worthwhile considering the possibly strong adaptive value of such flexibility in the predatory behavior of this species. According to the increasing weight and size of the prey, five sequences of predatory behavior, clustered into three main strategies, were distinguished: solitary hunting, with two variants, for small prey (weight < 2.5 times that of an individual worker), cooperative hunting for medium prey (weight between 2.5 and 9 times that of the ant) and group hunting with recruitment, also with two variants, for large prey (weight > 9 times that of the ant).

For predatory species, which are not equipped with long mandibles, as is the case for *E. ruidum*, the first behavioral phases of the predatory sequence are always very short and consist in a rapid approach and antenation, followed by the seizure and the stinging of the prey (Dejean and Bashingwa 1985). In *E. ruidum*, whatever the size of the prey, the initial sequence was

Table 2 Estimation of the energetic benefits derived by *E. ruidum* from the use of five different hunting strategies (solitary hunting type 1 and 2, cooperative hunting, collective hunting with recruitment type 1 and 2). The number of workers considered for this

estimate (*n*) was either the total number of workers involved in all cases corresponding to each strategy (minimum estimate) or only the number of workers involved in all successful prey retrieving (maximum estimate)

Median prey weight triggering each strategy (mg)	Total weight retrieved (mg)	Energetic benefits (in mg of retrieved prey per individual)	
		Minimum estimates	Maximum estimates
8	284	6.45 (<i>n</i> = 44)	7.68 (<i>n</i> = 37)
15	515	12.88 (<i>n</i> = 40)	15.15 (<i>n</i> = 34)
39	1465	12.01 (<i>n</i> = 122)	17.03 (<i>n</i> = 86)
115	4102	18.90 (<i>n</i> = 217)	32.56 (<i>n</i> = 126)
175	2196	8.13 (<i>n</i> = 270)	26.78 (<i>n</i> = 82)

always observed according to the same succession of behavioral acts: search for prey, detection and localization. The position of the antennae during this ultimate phase, suggests that olfaction could be important during the localization of the prey (Dejean and Bashingwa 1985). Moreover, in *E. ruidum* visual information is likely to be influential since, as for *Myrmecia nigriceps* (Via 1977; Eriksson 1985) and *Odontomachus troglodytes* (Dejean and Bashingwa 1985), prey movements appear necessary to achieve localization by hunters. Such prey movements are also likely to be involved in the short-range recruitment triggered by medium weight prey. Considering the importance of visual information in other aspects of its foraging behavior, like the orientation towards food sources or the spatial specialization of honey-collectors (see Jaffe et al. 1990; Schatz et al. 1994, 1995; Beugnon et al. 1996), the use of such information in the predatory behavior of this species is not surprising. Finally, another factor, the nutritional state of the hunter, is known to possibly affect the distance of detection of the prey (Holling 1966; Hardman and Turnbull 1980; Dejean 1987), and such a situation could not be ruled out in our experiments. Nevertheless, food was provided regularly to the colonies in small quantities and a possible effect of repletion or starvation was not considered as highly probable.

During the approach, the hunter moves very slowly in order to place itself in a favorable position for the attack. Such an approach, very common in ants, is thought to allow the hunter to avoid a subsequent attack from the prey (Dejean 1982). The high preference shown by the hunters of *E. ruidum* for the head of the prey as site of seizure, is very similar to what occurs for other predatory ant species and, according to Dejean (1982), can be interpreted as an attempt to destroy the nervous system of the prey.

According to the type of strategy, qualitatively important changes occur in the behavioral sequence after the phase of the seizure of the prey. It may be argued that this phase is essential for the hunter to estimate the size and weight of the prey and to determine the subsequent strategy to adopt. For prey which are not too heavy (< 20 mg, i.e., with a weight < 2.5 times that of the hunter) the vigorous struggle of the prey releases the lifting and stinging behaviors of the hunter, as described for *Myrmecia gulosa* (Robertson 1971), *O. troglodytes* (Dejean and Bashingwa 1985), *Pachycondyla soror* (Dejean 1991), *Paltothyreus tarsatus* (Hölldobler 1984; Dejean et al. 1993) and various dacetine ants (Dejean 1982; Masuko 1984). Moreover, in *E. ruidum*, the rapid first part of the predatory sequence (approach and antennation) is always followed by the stinging of the prey, as in *Hypoponera* sp., *Ponera coarctata*, *Pachycondyla* (= *Mesoponera*) *caffraria*, *Aphaenogaster senilis* and *A. subterranea* (Agbogba 1982). The stinging is always associated with a waiting phase of at least 20 s, except for very small larvae of *T. molitor* which are immediately transported to the nest by the hunter. In the case of the collective strategies, and whatever the strategy con-

cerned, the duration of the waiting phase is significantly longer when it occurs after the stinging behavior with hindlegs raised. A similar behavior has been described for *Pachycondyla villosa* (Dejean et al. 1990) and *Paltothyreus tarsatus* (Dejean et al. 1993). According to these authors, it corresponds to a "prudent" posture, in order to avoid the defensive kicks of the prey which may injure the ant. This behavioral response suggests that, when faced with vigorous large and heavy prey, scout ants of *E. ruidum* are able to perceive the presence of a danger and to associate a mortality risk to this kind of prey. The perception of a mortality risk associated with the access to a food source has been demonstrated for some ant species (Nonacs and Dill 1988, 1990, 1991) and was shown to affect their foraging patterns (Traniello 1989b; Nonacs 1990). In the case of *E. ruidum*, the fact that large and heavy prey may be associated with a mortality risk seems to be confirmed by the clear increase in the duration of the subsequent phase of waiting for the immobilization of the prey (4–8 times greater).

Recruitment systems and graded recruitment

The factor that determined the strategy adopted by a scout ant of *E. ruidum* appeared to be prey weight. Prey size essentially affects the forward or backward entrance of the hunter carrying its load, in a mechanistic way. Moreover, for the type of prey used in our study, taking into account the positive logarithmic correlation between size and weight, for large prey the range of variation of prey weights is much greater than that of prey sizes, making prey weight a more useful parameter to estimate the energetic cost associated to a given prey item.

Two types of recruitment were involved during our experiments: a local, short-range recruitment which attracted only the nearby nestmates and a rudimentary mass recruitment performed in the nest without trail laying. It is currently assumed (Sudd and Franks 1987) that any recruitment system which reduces the number of ants returning without a load to their nest would be an advantage. Nevertheless, the more the recruitment system could adjust the response levels to additional labor needs, the more efficient this recruitment would prove to be (Taylor 1978; Oster and Wilson 1978). In some species, the reinforcement of the chemical trail between the food source and the nest is proportional to the food quality (i.e., the richer the food source, the more pheromone is laid per returning forager), allowing an adaptive response to food sources of differing quality (Hangartner 1970; Verhaeghe 1982; Crawford and Rissing 1983; Beckers et al. 1993; de Biseau and Pasteels 1994). In a previous study on recruitment behavior in *E. ruidum* Pratt (1989) concluded that colonies did not appear to match numbers of recruited workers to the size of baits. On the contrary, our data demonstrate that when collective strategies are used for the mastering and retrieving of large prey, and whatever the recruitment system involved (short-range or mass recruitment), the number of nestmates recruited by the scout ant is posi-

tively correlated with the weight of the prey. Furthermore, for short-range recruitment, the number of ants attracted may be progressively regulated in the course of the process by a possible feed-back mechanism: the vigorous prey movements triggered by the stinging (kicks, twists, starts) probably enhance the ability of workers to detect the prey. Moreover, as shown in *Aphaenogaster* (= *Novomessor*) *albisetosus* and *cockerelli* (Markl and Hölldobler 1978), the emission of stridulations, known to occur mainly in the ultrasonic range in *E. ruidum* (Pavan et al. 1996), is likely to be involved as a modulatory signal (see Hölldobler 1995) enhancing the behavioral response of nestmates to this recruitment. For mass recruitment, however, the number of recruited ants has to be finely adjusted at the start since a unique foraging team (constituted of all recruited workers) occurs in each case. Such a modulated response of an individual hunter which, according to some characteristics of the food source, is able to determine whether to recruit and, if this recruitment occurs, the number of recruited foragers requested (Taylor 1978), constitutes a typical example of graded recruitment.

The only other case of graded recruitment in a ponerine ant was reported by Breed et al. (1987) for another species of the Ectatommini tribe, the giant tropical ant *Paraponera clavata*. Individual workers of *P. clavata* encountering prey items, gauge the size and/or unwieldiness of the item regardless of its weight when determining whether to recruit. Nevertheless, as pointed out by these authors, the prey used in their study were presented pinned to the substrate and weight was not considered as a parameter in this experiment since none of the prey could be moved. By contrast, in the case of *E. ruidum*, this parameter appears to be the key-factor allowing individual hunters to gauge the feasibility of prey loading and, if recruitment is needed, to match the number of recruited workers.

In our experiments, chemical trail laying never occurred though it has been clearly demonstrated that such trail laying from the Dufour's gland is involved in mass recruitment to rich or difficult food sources (Pratt 1989; Bestmann et al. 1995). The differences in the experimental procedure used by these authors may have a bearing both on our failure to obtain mass recruitment with chemical trail-laying (Lachaud 1985; Schatz et al. 1996; and this study) and on Pratt's failure to find graded recruitment in *E. ruidum*. The same procedure as that used for *P. clavata* (Breed et al. 1987) was employed by Pratt (1989) and Bestmann et al. (1995) to trigger recruitment (i.e., large, unwieldy, freshly killed prey, pinned to the ground). Consequently, the prey were "infinitely" heavy to the scout ant which probably adopted a maximal response in its recruitment and so displayed the more efficient trail-laying behavior. In the same way, though two sizes of protein bait (whole beetles, *Pelidnota* sp., versus beetle pronota only) were compared by Pratt in order to test the ability of *E. ruidum* to match numbers of recruited workers to the sizes of baits, both prey were of similar unwieldiness and both probably triggered the same un-

differentiated maximal response. Moreover, in our experiments, aside from being free to be moved, *T. molitor* larvae were vigorous living prey which were associated with a mortality risk, which was unlikely to be the case for a dead prey item. Such a difference might explain why, for scavenging behavior, large prey trigger trail laying even when the prey is located at an unusually long distance (up to 7 m, see Pratt, 1989), while this form of recruitment is not performed for predatory behavior and merely relayed by short-range recruitment or rudimentary mass recruitment by incitement to leave the nest. Additional evidence suggesting that *E. ruidum* workers do not show the same behavioral response for scavenging and predatory behavior sequences is the difference observed between the exploitation of either a source of 50–100 freshly killed termites (Pratt 1989) or a source of 20–100 living *Drosophila* flies (Schatz et al. 1996). In the first case, when only scavenging behavior is concerned, the scout ant returns to the nest to recruit nestmates laying a chemical trail while in the second case, dealing with predatory behavior, a collective strategy occurs with a division of labor between the hunters, some individuals specializing as killers, the others as transporters. Thus, the range of modulated behavioral responses available for *E. ruidum* foragers, according to the situation, appears very impressive and the trail laying behavior described by Pratt should in fact correspond to the highest level in the graded series of mass recruitment used by this species.

The benefits derived by *E. ruidum* from the use of this finely graded recruitment give an undeniable adaptive value to the expression of such a strategy and probably account both for the ecological success of this species in the Neotropics and for its predatory impact on arthropod populations (see Lachaud et al. 1996). Searching for food is an energetically costly activity (Nielsen et al. 1982; Lighton et al. 1987) and the cost of maintaining many workers out foraging is important. Nevertheless, such a disadvantage may be outweighed by a sufficiently increased probability that food items are successfully retrieved (Moffett 1988). This is what occurs in *E. ruidum*, which is able to secure a high probability of provisioning success using different ways. When solitary strategies are involved, they can adopt an efficient cleptobiotic behavior, either using the foraging trail laid by other species to take food items from them when they are returning to their nest (Perfecto and Vandermeer 1991) or entering nearby colonies of the same species to steal their stores (Breed et al. 1990, 1992). When collective strategies are involved (this study), their efficiency is obvious since the majority of prey which trigger recruitment are brought back to the nest (88 out of 94 prey). In collective strategies, the cooperative retrieving of the prey apparently does not imply a reduction in transport costs, which may even be increased by interference between ants and inefficiency in group transport (Sudd and Franks 1987). As reported by Pratt (1989), when two or more *E. ruidum* workers cooperate in retrieving a large prey item, they often worked at cross-

purposes and generally proceed very slowly. However, Duncan and Crewe (1993) suggested that the extra energy needed for more foragers is probably compensated by the energy obtained from the larger food, an hypothesis confirmed by our laboratory results. For short food–nest distances, the energetic benefits (expressed in mean weight of prey retrieved per individual) derived by *E. ruidum* from the use of recruitment systems are enhanced in comparison with the solitary hunting. Furthermore, the higher the number of workers involved in the recruitment process, the higher the energetic benefits obtained.

Various additional laboratory observations suggest, however, that aside from prey weight and size some other parameters like the number of nestmates present in the foraging area nearby the food source and/or the distance of this food source to the nest (B. Schatz, unpublished data), may also be important for the choice of the strategy to adopt and might explain the apparent indecisiveness in strategies adopted for prey weights falling between two categories that trigger different predatory responses (cf. Fig. 1). Even though *E. ruidum* appears to be more efficient in retrieving large food items (approximately 115 mg in weight) in relatively small groups (5.5 workers on average), such factors could also explain why, in nature, this species relies more on solitary foraging and hunting. As suggested by Beckers et al. (1989) and Jaffe and Deneubourg (1992), the foraging and food retrieval strategies may be more influenced by the effort made to discover new resources than by the effort required to collect the discovered resources (i.e. the efficiency of food retrieval). Although the range of sizes of the foraging area intensively exploited by this species is very reduced (between 0.5 and 8.4 m², see Lachaud et al. 1984, 1990; Breed et al. 1990), the experiments in the laboratory had a much smaller food–nest distance (only 20 cm) than that intuitively expected in a natural situation. Moreover, in this case, intraspecific competition was absent. In natural conditions, given the extremely high density of *E. ruidum* colonies (up to 11 200 nests/ha) and the resulting level of intraspecific competition, at larger distances (> 20 cm) from the nest, it would appear too costly for *E. ruidum* to engage in the collective strategies. Even if the lack of a distance factor in the laboratory study does not permit the testing of this hypothesis, this is supported by the fact that, in field conditions, the food–nest distances for which the mass recruitment used by this species is efficient are shorter than 1.5 m, and the impact of a given nest on the exploitation of a food source is virtually absent at a distance of 2 m from the nest (Lachaud et al. 1990). The differences between the foraging behavior observed in nature and in the laboratory suggest a high degree of flexibility in the foraging strategy adopted by *E. ruidum* according to the level of competition.

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