Predatory behavior of a seed-eating ant: *Brachyponera senaarensis*

Jean-Paul Lachaud[1] & Alain Déjean[2]

[1]*Centre de Recherche en Biologie du Comportement, URA CNRS 1837, Université Paul-Sabatier, 118 route de Narbonne, F-31062 Toulouse Cedex, France*

[2]*Laboratoire d'Ethologie Expérimentale et Comparée Paris XIII, URA CNRS 667 Avenue J.-B.-Clément, F-93430 Villetaneuse, France*

Abstract

The great flexibility of the feeding strategies exhibited by the ponerine ant *Brachyponera senaarensis* (Mayr) allows it to exploit either seeds or animal prey items as food resources. Predation is generally limited to small prey and is very similar to scavenging behavior. In laboratory conditions, the predatory behavior of *B. senaarensis* is not different in structure from that known in other carnivorous ants species. The workers forage individually and return to the nest using a series of cues involving light, a chemical graduated marking system near the nest entrance, and memory. During nest-moving, recruitment by tandem running was observed. However, in colonies where the food supply is regular, workers that discover food do not recruit nestmates, but make repeated trips between the nest and the food source. On the contrary, in starved colonies, the introduction of prey may produce a massive exit of foragers, corresponding to a primitive form of mass recruitment similar to that observed in some other ant species.

Introduction

Different aspects of the biology and behavior of *Brachyponera senaarensis* have previously been studied in the dry tropical climate of the Sudanes savannas (Lévieux & Diomandé, 1978; Lévieux, 1979), and in two humid tropical regions of Zaire (Déjean & Lachaud, 1994). These studies showed that this species is active throughout the year, and has a highly flexible opportunistic feeding strategy that allows it to adapt to environmental changes.

One of the most striking traits of *B. senaarensis* is its ability to use seeds as food source. The transition from a strictly carnivorous diet, typical of the majority of ponerine ants, to a partially or even totally granivorous one, depending on the environmental conditions, is supposed to have played a prime role in the dispersal of this species across the African continent ensuring its ecological success (Déjean & Lachaud, 1994). As suggested by Fewell (1990) for *Pogonomyrmex occidentalis*, an other seed-eating ant, such a specialization on the same kind of food limits the behavioral flexibil-

ity of individuals and therefore can strongly constrain their foraging strategies at the individual level. In the case of *B. senaarensis*, however, as for all other known ponerine species, animal prey are also brought back to the nest and represent a not insignificant part of its diet (Lévieux & Diomandé, 1978; Déjean & Lachaud, 1994). In order to verify if the predatory behavior of *B. senaarensis* is typical of the ponerines or integrates some degenerative patterns we investigate, under laboratory conditions, this behavior in terms of its four characteristic elements (see Déjean, 1991): searching for food, return to the nest, recruitment of nestmates and prey capture.

Materials and methods

Data were recorded between January and June 1985 from nine experimental colonies, each initially composed of a queen, 50 workers, 20 pupae and 25 larvae. The ratio of one larva for two workers was maintained at a constant level. Each colony was placed in an arti-

ficial nest consisting of a test tube (2.5×20 cm). A ball of humid cotton wool placed in the end acted as a water reservoir. Each tube, covered with a cardboard, was placed in a 110×110 cm foraging arena. The floor of the arena was covered with squared paper and the whole apparatus was covered with a glass lid. Each nest received a daily diet of honey, banana and prey. Two kinds of prey were used: small prey items (fresh bread pieces and *Cubitermes* workers 2–4 mm in length) and large prey items (locusts 6–10 mm in length).

The foraging trips made by each worker were recorded in felt pen on the glass lid. Every 60 s, a mark was added on the line corresponding to the worker's trajectory in order to provide a time base for data analysis. Each trajectory was copied onto tracing paper and its length calculated with a flexi-curve. The speed for each trip was also measured. By calculating the ratio between the straight-line distance between the beginning and end of the trip, and the actual distance travelled, we were able to establish a measure of the 'directness' of the trip. This 'mean index of directness' (m.i.d.) was used in comparing different kinds of trips (prey-searching trips, return trips, and the repeated trips in the presence of abundant food). Each ant was individually marked by paint on the head, gaster or thorax.

Results

Searching for food and returning to the nest

Small prey items. While searching for prey, workers tend to move slowly and follow a highly curved trajectory (Table 1 and Fig. 1). On the return trip, the speed is always greater, and the trajectory much more direct. In eight out of the 22 cases studied (36%), the return trip was virtually a straight line (m.i.d. <1.1). No ant was observed to drag its sting or gaster along the ground during the return trip and it seems unlikely that a chemical trail was deposited.

When food is abundant, there are repeated return trips between the food source and the nest. In such cases, the foragers merely leave the food at the entrance to the nest, rather than entering and distributing the food amongst the other workers, as they do with honey. From the second return trip onward, the nest-bound ants take increasingly direct routes. On the first trip, only eight out of 15 cases showed an index of directness of less than 1.2; on the second and third trips, 13 out of 15 workers showed such a low value. The

differences in speed and index of directness between the second and third trips are not significant χ^2 for the Yates correction=0.25 and 2.54 respectively for speed and index of directness; df=1, N.S. in both cases) but the differences between the second and third and the first trips are highly significant (P<0.01).

Large prey items. Outward trips were not significantly different from those reported above (speed: x=1.35±0.25 cm/s; m.i.d.=4.12). For return trips there were two variants:

a) Those ants which seized the prey in such a fashion that they could walk forward (18 cases). A large variability was observed in these cases. Some return trips were very direct (m.i.d.<1.1 in eight cases); others were very erratic (m.i.d. up to 9), as if the worker could not find the route back to the nest.

b) Those ants which seized the prey by an appendage or by the end of the abdomen and dragged the prey by walking backwards (14 cases). Whenever a worker departed too much from the route to the nest, they would drop the prey, circle around (during which they would sometimes find the nest), correct their orientation and pick up the prey again. This could take place several times during a given trip (up to four times in the trips recorded here).

Orientation

The role of substrate chemical marking. In three of the colonies studied, we placed a removable strip of paper (15×40 cm) on the floor of the arena. This paper was exactly the same in composition as that used to make up the surface of the arena. After a week, a series of small brown marks were observed. These marks consisted of fecal deposits left by workers, and were most dense around the nest entrance.

To verify if this marking may act as a chemical gradient to orientate the foragers toward the nest, the strip of paper was initially placed in the centre of the arena, midway between the nest entrance and the location where prey were placed. We carried out the following experiment 30 times. When a worker reached the prey, we removed the strip and observed the worker's reactions when it arrived at the zone previously covered by the strip, and now free of marking.

In 22 cases (73%), the worker crossed the marking-free zone with no difficulty, showing only a slight initial perturbation, shown by a slight decrease in
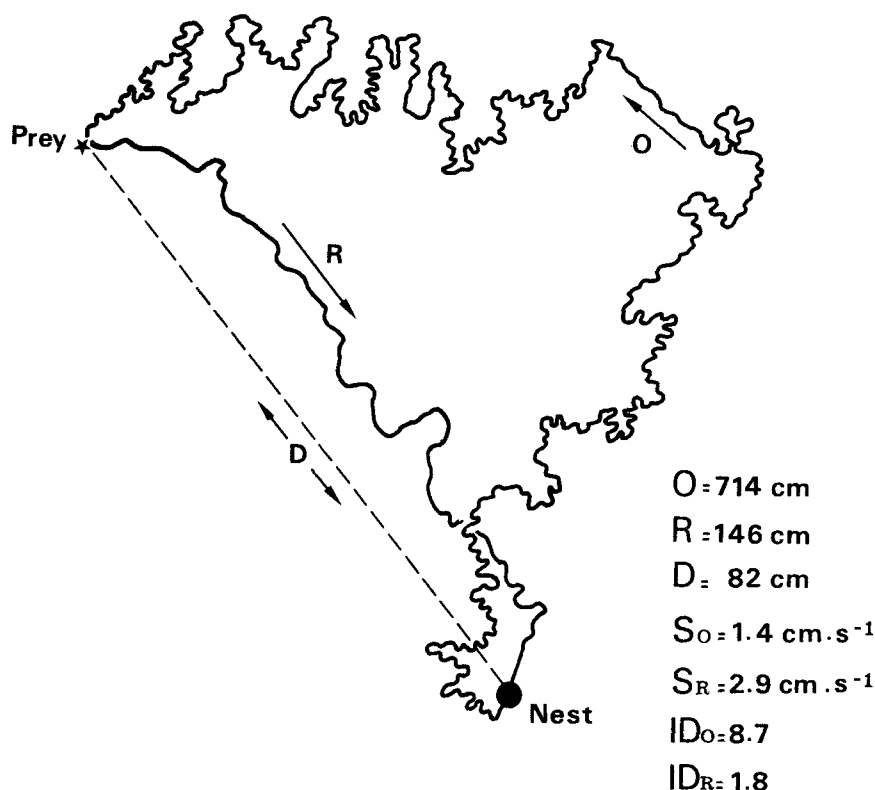
Fig. 1. Example of a forager's trip. O: outward trip; R: return trip; D: straight line distance between nest and prey; So and Sr: speed during outward and return trips; IDo and IDr: index of directness for outward and return trips.

Table 1. Characteristics of foraging trips (N = 22) in *Brachyponera senaarensis* when small prey items are introduced

Forager's trip	Length (in cm)	Speed (in cm/s)	Mean index of directness	Range
Outward trip	from 63.5 to 809	1.23±0.22	3.97	1.49–14.36
Return trip	from 40.2 to 199	2.38±0.83	1.46	1.02–3.38
Difference*	$\chi^2 = 20.4 > 10.82$ $P<0.001$	$\chi^2 = 26.2 > 10.82$ $P<0.001$	$\chi^2 = 15.3 > 10.82$ $P<0.001$	

*All the statistics were performed with the χ^2 test for Yates correction.

the directness of the route. However, in the other eight cases (27%), the importance of some form of chemical marking for orientating the return to the nest seems to be greater taking into account the strength of the released perturbation. Having covered a few centimeters of the marking-free zone, the worker turned around, found the edge of the marked zone, and followed an extremely tortuous path around the edge of the zone until it found the nest.

The role of memory. In order to test this factor, two experiments were carried out.

a) While a worker was exploring or feeding at a new food source, we placed a 35 cm long aluminium tube perpendicularly across the direct prey-nest route. In all cases (N=20), the worker turned either to the right or the left, continued along the length of the obstacle until the end, and then went virtually

straight to the nest, without returning to the direct prey-nest route. The lateral trip seems to have been integrated.

b) While a worker captured a prey, we moved the nest. In all cases (N=10), the worker returned to the previous site of the nest and began a highly erratic path. Each worker finally dropped the prey and continued its circuitous route, each time returning to where the prey had been left. By making a series of loops the worker would find the nest and return directly to the prey. In four cases the worker made a foraging trip soon afterwards: it returned to the food-source without difficulty from the new nest location.

The influence of the light-source. The room where the nests were kept had one large window. All nest-prey routes were perpendicular to the window. In ten cases, while a worker discovered a small prey (a termite) placed in the centre of the foraging arena, we turned the whole apparatus through 180°.

Having captured the prey, the worker returned in the direction of the previous location of the nest. When it had travelled a distance more or less corresponding to that of the prey-nest distance, it either began an erratic course (four cases), or dropped the prey and began an extremely circuitous trip (six cases). In eight cases the worker returned to the food-source site, in the other two they followed the edges of the arena. In the case of the eight workers that returned to the food-source site, the nest was found after a search which appeared, at the beginning at least, to be stochastic.

Recruitment

Recruitment during nest moving. In this experiment we stimulated the ants to move their nest (N=16). The contents of the nests were tipped into the centre of the arena, at the periphery of which a new nest had previously been placed. Enormous confusion resulted, followed by a regrouping of the whole colony. Some workers explored the foraging arena and discovered the new nest. They then returned to the other workers and recruited nestmates involved in activities outside the nest by tandem running, guiding them to the new tube (the role of these individually marked workers had been previously defined during a study of polyethism, Déjean & Lachaud, 1994 and unpubl.). Recruiting and recruited ants then returned to the rest of the colony either to recruit new nestmates by tandem running or to transport workers of the 'interior service' and brood.

Foraging recruitment. The results of tests carried out in the laboratory suggest that the nutritional state of the colony has a very important effect on the type of behavioral response shown when a rich food source is discovered.

a) *Colonies fed regularly (N=30 colonies, with 3 to 4 repetitions for each colony).* A worker that has discovered a large source of honey, of fresh bread or a group of small prey, returns to the nest with a part of the food and then makes a series of return trips until all the food has been transported. When several workers find the food, each continues to make its return trips without any recruitment taking place. We did notice a tendency for more foragers to leave the nest after a worker returned with food, but this difference was not significant.

b) *Colonies starved for nine days (3 colonies).* After the fifth or sixth day without food, few foragers left the nest (in general, in these experimental colonies, we rarely saw more than two workers in the arena at one time). On the tenth day we introduced into the centre of the arena five locusts, each 6–10 mm long, together with fresh bread. The worker who was foraging at the time eventually found the prey, and took a part of the food back to the nest. Upon arrival, many workers exchanged antennal contacts with the forager and touched the prey. Shortly afterwards, the successful forager returned directly to the prey to remove another part, while 10–15 other workers (hunters and honey collectors, Déjean & Lachaud, unpubl.), left the nest to forage in the arena. In general they ended up finding the prey and the bread, having followed a very erratic path (similar to outward trip shown in Fig. 1). This type of recruitment, which we can describe as 'incitement to leave the nest' (Lachaud, 1985) or 'social facilitation' (Peeters & Crewe, 1987), corresponds to a very elementary form of mass recruitment that is only seen in a few other ponerine species.

Prey capture

To study predation, we observed foragers capturing prey of varying sizes, either live, freshly killed, or killed one hour previously. The prey used were worker termites (*Cubitermes* sp. and *Macrotermes* sp.: 2–4 mm long; *Macrotermes* sp.: 6–10 mm long; locusts (without tibia of hind legs): 6–10 and 15–18 mm long; caterpillars: 17–25 mm long).
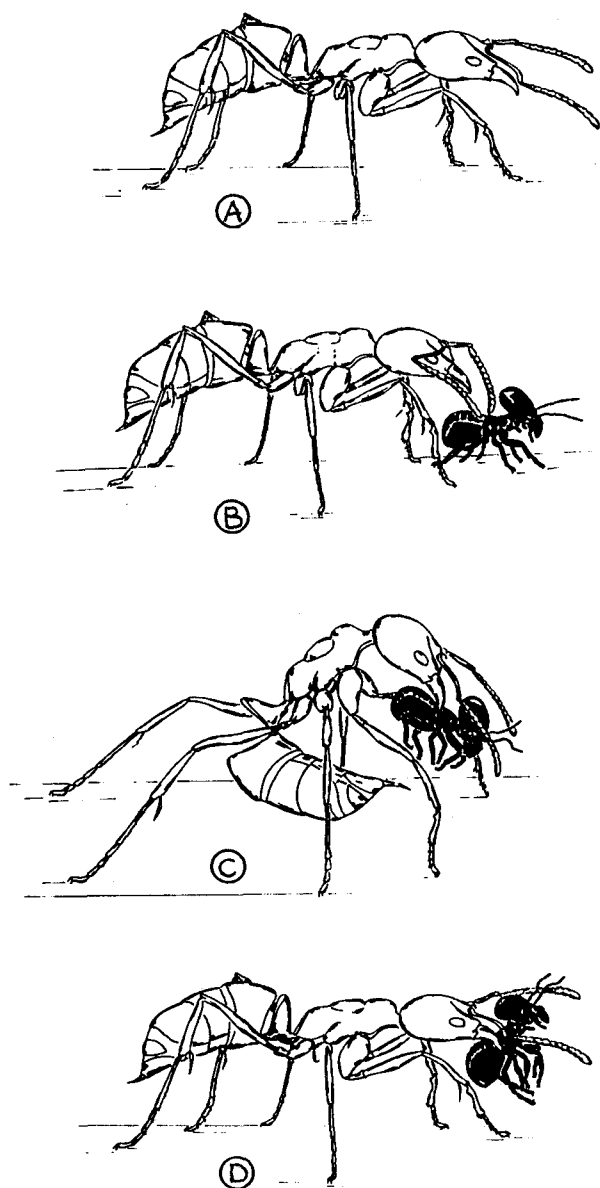
Fig. 2. Behavioral sequence for the capture of small prey items (termites). A: searching for prey, mandibles closed and antennae separated; B: antennal palpation; C: keeping hold of the prey and curving of the gaster before stinging; D: transport to the nest.

In general, while searching for prey, the worker moves slowly (x=1.23±0.22 cm/s), while keeping its antennae separated, the funicular segment of the antennae touching the ground (Fig. 2a) and the mandibles closed.

Live and active prey

a) Cubitermes *workers, 2–4 mm long (N=60: Fig. 2 and 3a).* In 16.7% of cases prey were detected by contact. For the remaining 83.3% of cases, the worker passed very close to the prey (maximum of 1–2 mm between the apexes of the antennae and the prey), changed the position of its antennae, pointing them forwards, the two apexes nearly touching each other (Fig. 2b). We called this reaction 'localisation', because it was followed by an approach to and a brief palpation of the prey (1–3 s in duration). Prey detected by contact were also briefly palpated (1–3 s), long palpation (10–12 s) being exceptional (1.8%).

Opening of the mandibles followed palpation. The prey was then seized by a rapid closing of the mandibles, accompanied by a rapid forward movement of the ant's body. This movement was termed an attack. In 75% of cases, the prey was seized by the thorax, 25% by the abdomen. In the case of prey seized by the thorax, the worker returned rapidly to the nest (Fig. 2d). In the case of prey seized by the abdomen, the ant's grip seemed less efficient, and the struggling of the live prey provoked a reaction in the worker. The ant moved backwards for about 1 cm, and changed the position of the mandibles on the prey's body, while keeping hold of the prey with the anterior legs. The mandibles were then closed ever-tighter until the prey stopped struggling and it was taken to the nest. Although we observed curving of the gaster on several occasions (Fig. 2c), we did not observe, under these conditions, any prey being stung. Capture duration varied between 3 and 15 s.

b) Macrotermes *workers, 2–4 mm long (N=50: Fig. 3b).* Ten percent of the prey were detected by contact (there is no significant difference between this level and that reported above; χ^2=0.9, df=1, N.S.). In the other 90% of cases, we observed localisation at short distance (1–2 mm) followed by approaching. Brief palpation (1-4 s) was followed by attack, the prey being seized by the thorax (82%) or the abdomen (18%). All prey seized by the abdomen were stung, as against only nine out of 41 seized by the thorax. In all, 36% of prey were stung. Of the others, 60% were taken directly to the nest, and 4% were abandoned. Capture duration varied between 5 and 18 s.

c) Macrotermes *workers, 6–10 mm long (N=63: Fig. 3c).* Prey were localised at short distance (1–4 mm between the prey and the apex of the closest anten-

na). All the prey were abandoned, either following localisation (41%), approaching (30%) or palpation (29%).

d) *Locusts, 6–10 mm long, introduced into colonies fed regularly (N=30: Fig. 3d).* As in the preceding example, the prey was localised at a distance varying from 1 to 4 mm, and was abandoned following localisation (33%), approach (40%) or palpation (27%).

e) *Locusts, 6–10 mm long, introduced into colonies following nine days without food (N=15: Fig. 3e).* The prey was detected by contact (13%) or localised at a distance varying from 2 to 4 mm, and in all cases was then quickly attacked (rapid approach, simple antennal contact). This rapid attack was immediately followed by a retreat, the curving of the gaster, and the beginning of a phase of stinging.

The prey was either taken whole to the nest (14 cases), either transported or pulled backwards, or in one case was cut into pieces, the worker making a series of return trips.

f) *Locusts, 15–18 mm long (N=35).* The prey was localised at a distance varying from 1 to 5 mm. Following a rather timid approach, the prey was abandoned in 29% of cases. In the remaining 71% of cases, approach was followed by palpation, generally followed by the prey being abandoned (66% of cases). However, we did observe two cases of attack (6%), following which the prey was abandoned.

Freshly-killed prey

a) Macrotermes *workers, 2–4 mm long (N=36: Fig. 4a).* Apart from two cases where detection was by contact, prey localisation took place at short distance (1–3 mm). Palpation, which lasted 3–12 seconds, took place following a slow approach. The prey was subsequently either abandoned (6%), or seized by a slow closing of the mandibles and transported to the nest (89%). Lifting followed by stinging were exceptional (6%). Capture duration varied from 7 to 20 s. There was no significant difference in capture duration between live and freshly-killed prey of this kind ($\chi^2=1.24$, df=1, N.S.).

b) Macrotermes *workers, 6–10 mm long (N=42: Fig. 4b).* The frequency of prey being abandoned is high: 55% following localisation, 2% following approach, 17% during palpation and 2% following seizing. In 24% of cases the prey was transported to the nest. Stinging took place in only three cases. Capture durations varied between 2 and 22 s.

c) *Locusts, 6–10 mm long (N=20: Fig. 4c).* Capture duration varied from 12 to 19 s. In this case, prey were also frequently abandoned: 15% following localisation, 40% during palpation, 30% after seizing; only 15% were taken to the nest. In one case, a 'relay' phenomenon (Agbogba, 1982) was observed: one worker, having captured the prey, leaves the prey to a nestmate encountered on the route back to the nest, and continues foraging.

d) *Locusts, 15–18 mm long (N=30; Fig. 4d).* The level of prey being abandoned was very high: 43% following the antennal contact which precedes attack, 53% following palpation. Only one prey (3%) was taken back to the nest.

e) *Caterpillars, 17–25 mm long (N=26: Fig. 4e).* The level of prey being abandoned was significantly lower than in the previous examples ($\chi^2=13.7$, df=1, P<0.01): 19% of prey were abandoned after localisation, 31% after palpation. Of the remaining 50%, the prey was seized after a long bout of antennal palpation and pulled backwards (27%), or was lifted and carried forwards to the nest (23%).

Prey killed one hour before. The prey (locust, 6–10 mm long; N=40) was abandoned in only eight cases (20%), following a long bout of palpation. There is a significant difference with freshly-killed prey ($\chi^2=20.5$, df=1, P<0.001). In this case, 70% of prey were pulled to the nest, 10% were cut up before transportation, the worker making a series of return trips. Capture duration for those locusts dragged to the nest was between 6 and 18 s. For those prey that were cut up, the period from discovery to the removal of the last piece of the prey lasted from 20 s to over 3 min.

Discussion

Prey capture. In terms of its characteristics, the predation behavior shown by *Brachyponera senaarensis* in laboratory conditions is very similar to simple scavenging behavior as described for other ponerine species like *Ectatomma tuberculatum* (Déjean & Lachaud, 1992) or *Paltothyreus tarsatus* (Déjean et al., 1993b). We have never observed a fight between a worker and prey, as is frequently reported for other carnivorous ants (Robertson, 1971; Agbogba, 1985; Déjean & Bashingwa, 1985). Stinging is also rare. For small prey, it is notable that the 'handling time'
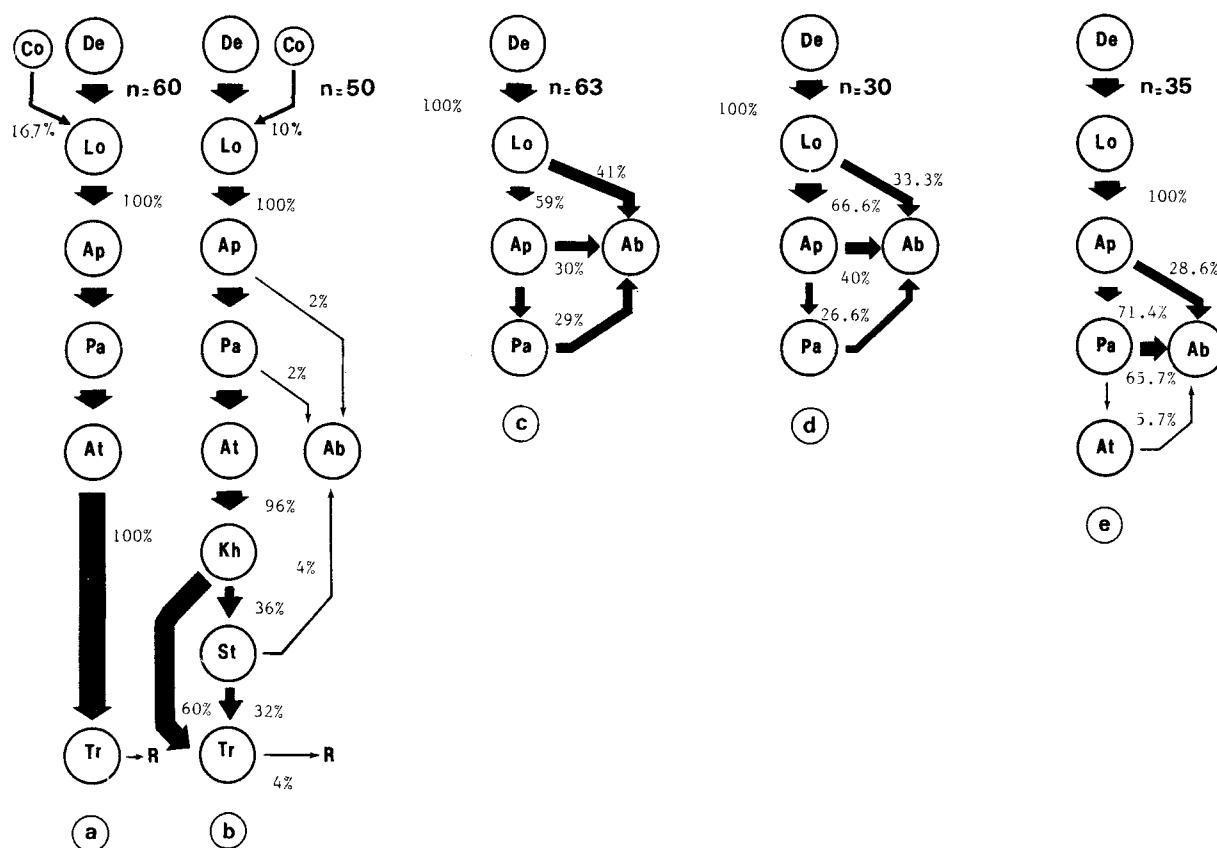
Fig. 3. Behavioral diagrams for predation on various live and active prey. Percents are calculated on the base of the overall number of cases for each category. Ab: abandon of prey; Ap: approach; At: attack; Ca: catching of prey; Co: detection by contact; De: detection at short distance; Kh: keeping hold of the prey; Lo: localisation; Pa: palpation; R: retray; St: stinging; Tr: transport to the nest. (a) *Cubitermes* workers 2–4 mm long; (b) *Macrotermes* workers 2–4 mm long; (c) *Macrotermes* workers 6–10 mm long; (d) Locusts 6–10 mm long; (e) Locusts 15–18 mm long.

(Holling, 1966) in this species is not significantly different for predation or scavenging behavior. In the case of prey longer than 15 mm, only scavenging behavior was observed.

Experimental and field observations suggest that *B. senaarensis* generally attacks only small live prey, whereas 6–10 mm long locusts (which cannot really be considered as 'large prey', given that workers are about 8 mm long) are only attacked by the colony which has been without food for some time. This kind of strategy is also found in other ants: either *Camponotus maculatus* (Déjean, 1988) or *Paltothyreus tarsatus* (Déjean et al., 1993b) workers will attack and capture large living prey when the colony has been without food for several days, while they avoid such prey when the colony is regularly fed.

Foraging behavior can also be modified when the nutritional needs of the colony are altered, for example when the number of larvae to be fed changes, as we could verify in complementary experiments (Déjean, unpubl.). Thus, if the larvae are removed, the number of foragers leaving the nest rapidly drops to a very low level. Foragers were rarely seen in the arena, and on the second day after removal of the larvae, no prey capture was recorded. On the other hand, if the brood is doubled in number rather than being eliminated (workers:larvae ratio=1:1), the number of captured prey tends to increase, although there is no significant difference from the number of prey normally captured when the workers:larvae ratio is 2:1. Under conditions of increased number of brood, the most important change is a better use of the captured prey, with little rejection from the nest by cleaning ants.

Hunger is, however, not the only factor which influences prey capture, and it is probable that certain olfactory elements, specific to the prey, may also be
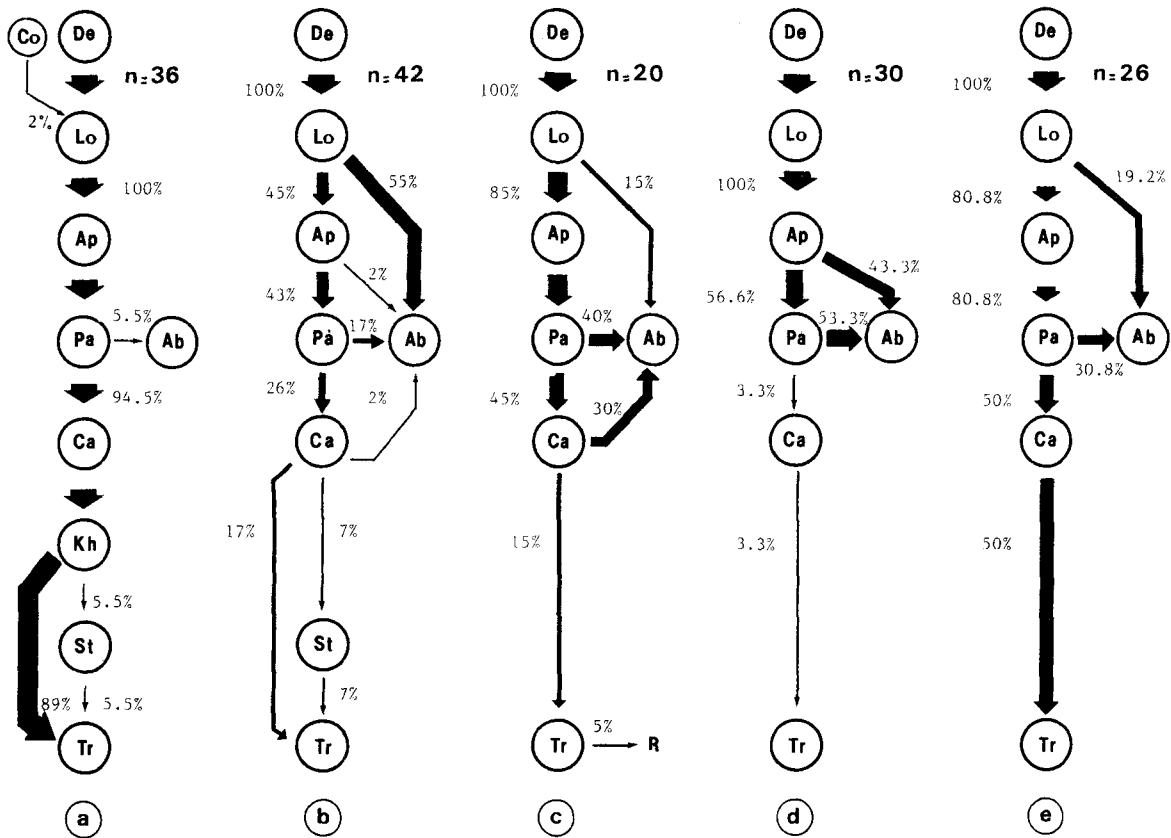
152

Fig. 4. Behavioral diagrams for predation on freshly-killed prey (see Fig. 3 legend). (a) *Macrotermes* workers 2–4 mm long; (b) *Macrotermes* workers 6–10 mm long; (c) Locusts 6–10 mm long; (d) Locusts 15–18 mm long; (e) Caterpillars 17–25 mm long.

involved. For example, the small *Macrotermes* workers were stung in 26% cases, whereas *Cubitermes* workers, of the same size, were never stung. Similarly, among the dead prey, 15–18 mm long freshly-killed locusts were only exceptionally palpated (once out of 30 prey), while 50% of the slightly larger caterpillars were accepted, and 80% of locusts killed one hour before. The fact that slight differences in olfactory cues may be involved in the differential behavioral patterns exhibited by *B. senaarensis* workers is supported by the observations made during nest moving. These observations suggest the existence of a difference between workers involved in activities 'inside' or 'outside' the nest, which the workers can perceive. This difference could be expressed through differences in the performance of certain behaviors, or, more probably, through differences in the odour of the behavioral subcaste to which the workers belong, as was demonstrated in *Camponotus vagus* nurses and foragers (Bonavita-Cougourdan *et al.*, 1987) at the level

of their cuticular pheromones.

Orientation during homing. The disturbance in orientation recorded when foragers were returning to the nest with large prey items, in particular when workers were walking backwards, was shown by the dropping of the prey and the 'reorientation' circuit. Such a disturbance during homing is apparently relatively common in foraging ants loaded with large prey and has been reported in other species like *Ectatomma ruidum* (Lachaud, 1985) or *Paltothyreus tarsatus* (Hölldobler, 1984; Déjean *et al.*, 1993a). As Hölldobler (1984) proposed in the case of this latter species, the most probable explanation is a disturbance of visual orientation. However, we cannot completely rule out the possibility of a disturbance of chemical orientation due to an interference by the prey odour, as seems to be the case in *Ectatomma ruidum* (Lachaud, 1985).

In laboratory conditions, such a chemical orientation in *B. senaarensis* appears to be mainly involved

near the nest entrance where small fecal deposits are left by workers, with the density of these guideposts decreasing when the distance to the nest increases. These fecal deposits may correspond to a form of territorial marking that has previously been described in the formicine *Oecophylla longinoda* (Hölldobler & Wilson, 1977; Déjean & Beugnon, 1991; Beugnon & Déjean, 1992), which mark leaves where prey search occurs, and in the ponerine *Rhytidoponera metallica* (Haskins & Haskins, 1983). Nevertheless, explicit marking behavior was not observed in *B. senaarensis* and it is more likely that these small olfactive guideposts may represent a chemical and incidental nest entrance marking similar to that reported for the ponerine ants *Pachycondyla soror* (Déjean, 1991) and *Paltothyreus tarsatus* (Déjean *et al.*, 1993a) or for the formicine *Cataglyphis cursor* (Mayade, 1992).

Foraging strategies. The workers of *B. senaarensis* forage and hunt alone. This form of foraging has been reported for various species like *Diacamma rugosum* (Uezu, 1977), *Cataglyphis bicolor* (Wehner *et al.*, 1983), *Ectatomma ruidum* (Lachaud *et al.*, 1984), *Pachycondyla (=Neoponera) apicalis* (Fresneau, 1985; Goss *et al.*, 1989), *Ophthalmopone berthoudi* (Peeters & Crewe, 1987), *Formica schaufussi* (Traniello, 1988), *F. cunicularia* (Deffernez *et al.*, 1991) and *Paltothyreus tarsatus* (Déjean *et al.*, 1993b). However, unlike these species, where the workers forage in a clearly predictable fashion and have individual foraging territories in the foraging area around the nest, *B. senaarensis* workers show an individual stochastic search path, even though they may show a certain degree of concentration on one physical area (Déjean & Lachaud, 1994). This strategy, found in a number of vertebrates and invertebrates, and notably in ants (see Harkness & Maroudas, 1985), seems to be very efficient for central place foragers, because it enables them to explore a large area of ground at a minimal distance from the nest. According to Bovet (1983) and Bovet *et al.* (1989), the efficiency of this strategy is within 5% of a theoretical maximum, in which the animal would trace a perfect Archimedes spiral, the centre of which would be the nest, and the track the width of the band of ground explored (that is, in the case of a ground-exploring insect: the distance between the antennal apexes+the possibilities of detection). The ideal return to the nest consists of a straight line. The trips made by *B. senaarensis*, with a food-searching strategy that appears to be stochastic and a return to the nest which is often virtually direct, seems to fit this description.

The combination of mechanisms involved in guiding the return to the nest (chemical marking, light-guided orientation and memory) tend to emphasise the behavioral flexibility abilities of this species allowing a more efficient adaptation to fluctuating environment conditions. Such high flexibility abilities are also illustrated by the use made of recruitment in the foraging strategies. As reported for *Pachycondyla obscuricornis* (Hölldobler & Traniello, 1980) and *P. (=Neoponera) apicalis* (Fresneau, 1985), *Brachyponera senaarensis*, while showing recruitment during nest-moving, and then only in the simple form of tandem running, does not use foraging recruitment in normal conditions. Nevertheless, taking into account the strategy of niche exploitation shown by *B. senaarensis* colonies, the use of such a foraging recruitment does not appear indispensable in terms of foraging benefits. This strategy involves the exploitation of secondary foraging zones, which may be situated up to 16 m from the centre of the nest, and linked to it by a network of radiating galleries (Lévieux & Diomandé, 1978; Déjean & Lachaud, 1994). These satellite zones are of a limited surface area; the foragers do not venture far from the gallery exits (Déjean & Lachaud, 1994). A worker that has discovered a food source of intermediate importance and which moves at the mean speed of 2.4 cm/s (overall value for outward+inward trips) will remove all the food much quicker if it simply leaves the food at the entrance to the gallery than if it returns to the nest and recruits a nestmate by tandem running, which involves a large amount of time in terms of both recruitment and the time taken to make the trip (see Fewell, 1988), given that movement under these circumstances is much slower.

On the other hand, the benefits derived from the use of foraging recruitment may increase under certain environmental constraints and give a further undeniable adaptative value to the expression of such a strategy. This is what happen in *B. senaarensis* when prey provisioning is unsufficient. By starving the colony for a few days, we have been able to show the existence of a primitive kind of mass recruitment in the form of a mass incitement to leave the nest, a phenomenon known in some other ponerine species such as *Odontomachus chelifer* (Fowler, 1980), *O. troglodytes* (Lachaud & Déjean, 1991), *Ectatomma ruidum* (Lachaud, 1985), *Ophthalmopone berthoudi* (Peeters & Crewe, 1987) and *Paraponera clavata* (Breed & Bennet, 1985), which show the same kind of recruitment. Each worker tending to forage in a random fashion, it is possible to go over the surrounding

environment 'with a fine tooth-comb' in a few minutes. In this way, other food sources can be discovered. Even though, in this case, recruitment is not directed and therefore tends to be less efficient, this strategy is nonetheless extremely useful for this species, whose normal food (grain and small prey) are distributed at random or in the form of small groups arranged in a heterogeneous fashion in the foraging area.

Résumé

La grande flexibilité manifestée par la fourmi ponérine *Brachyponera senaarensis* (Mayr) au niveau des stratégies alimentaires utilisées, lui permet d'exploiter aussi bien des graines que des proies animales en tant que sources d'aliments. La prédation, généralement limitée aux petites proies, est très proche du simple comportement nécrophagique. Par sa structure, le comportement prédateur de *B. senaarensis*, en conditions de laboratoire, ne diffère pas de celui rapporté pour d'autres espèces de fourmis prédatrices. Les ouvrières fourragent de façon individuelle et sont capables de rentrer directement au nid grâce à une orientation où peut intervenir l'influence de la source lumineuse, d'un marquage chimique présentant un gradient à proximité de l'entrée du nid, et de la mémoire. Lors de déménagements de nids, les ouvrières utilisent un recrutement par tandem running, mais aucun recrutement alimentaire n'a pu être observé dans les colonies régulièrement approvisionnées. Dans ce cas, les ouvrières qui découvrent une source importante de nourriture effectuent simplement une série d'allers-retours entre le nid et la source d'aliments. Au contraire, dans les colonies soumises à un jeûne prolongé, l'introduction d'un groupe de proies peut déclencher, chez les ouvrières approvisionneuses, une incitation massive à sortir, correspondant à une forme primitive de recrutement de masse déjà connue chez quelques autres espèces de fourmis.

References

Agbogba, C., 1982. Contribution à l'étude de la prédation et de l'approvisionnement de la société chez des Fourmis carnivores. Unpublished doctoral thesis, Marseille, 132 pp.

Agbogba, C., 1985. Quelques observations sur le comportement de chasse de la ponérine *Mesoponera caffraria* Smith (Hymenoptera, Formicidae). Actes Coll. Insectes Soc. 2: 235–238.

Beugnon, G. & A. Déjean, 1992. Adaptative properties of the chemical trail system of the African weaver ant *Oecophylla longinoda* Latreille (Hymenoptera, Formicidae, Formicinae). Insectes Soc. 39: 341–346.

Bonavita-Cougourdan, A., J.-L. Clément & C. Lange, 1987. Sub-caste discrimination in the ant *Camponotus vagus* Scop. In: J. Eder & H. Rembold (eds), Chemistry and Biology of Social Insects. Verlag J. Peperny, München: p. 475.

Bovet, P., 1983. Optimal randomness in foraging movement: a central place model. In: M. Cosnard, J. Demongeot & A. Lebreton (eds), Rhythm in Biology and Other Fields of Application. Springer Verlag, Berlin: pp. 295–302.

Bovet, P., A. Déjean & M. Granjon, 1989. Trajets d'approvisionnement à partir d'un nid central chez la fourmi *Serrastruma lujae* (Formicidae, Myrmicinae). Insectes Soc. 36: 51–61.

Breed, M. D. & B. Bennett, 1985. Mass recruitment to nectar sources in *Paraponera clavata*: a field study. Insectes Soc. 32: 198–208.

Deffernez, L., J.-C. Verhaeghe & J. M. Pasteels, 1991. Spécialisation spatiale des ouvrières de *Formica cunicularia* (Hymenoptera, Formicidae). Actes Coll. Insectes Soc. 7: 83–90.

Déjean, A., 1988. Prey capture by *Camponotus maculatus* (Formicidae: Formicinae). Biol. Behav. 13: 1–19.

Déjean, A., 1991. Le comportement prédateur de *Pachycondyla soror*. Entomol. exp. appl. 58: 123–135.

Déjean, A. & P. E. Bashingwa, 1985. La prédation chez *Odontomachus troglodytes* Santschi (Formicidae: Ponerinae). Insectes Soc. 32: 23–42.

Déjean, A. & G. Beugnon, 1991. Persistant intercolonial trunkroute-marking in the African weaver ant *Oecophylla longinoda* Latreille (Hymenoptera, Formicinae): Tom Thumb's versus Ariadne's orienting strategies. Ethology 88: 89–98.

Déjean, A., G. Beugnon & J.-P. Lachaud, 1993a. Spatial components of foraging behavior in an African ponerine ant, *Paltothyreus tarsatus*. J. Insect Behav. 6: 271–285.

Déjean, A. & J.-P. Lachaud 1992. Growth-related changes in predation behavior in incipient colonies of the ponerine ant *Ectatomma tuberculatum* (Olivier). Insectes Soc. 39: 129–143.

Déjean, A. & J.-P. Lachaud 1994. Ecology and behavior of the seed-eating ponerine ant: *Brachyponera senaarensis* (Mayr). Insectes Soc. 41: in press.

Déjean, A., J.-P. Lachaud & G. Beugnon, 1993b. Efficiency in the exploitation of patchy environments by the ponerine

ant *Paltothyreus tarsatus*: an ecological consequence of the flexibility of prey capture behavior. J. Ethol. 11: 43–53.

Fewell, J. H., 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behav. Ecol. Sociobiol. 22: 401–408.

Fewell, J. H., 1990. Directional fidelity as a foraging constraint in the harvester ant, *Pogonomyrmex occidentalis*. Oecologia 82: 45–51.

Fowler, H. G., 1980. Populations, prey capture and sharing, and foraging of the paraguayan ponerine *Odontomachus chelifer* Latreille. J. Nat. Hist. 14: 79–84.

Fresneau, D., 1985. Individual foraging and path fidelity in a ponerine ant. Insectes Soc. 32: 109–116.

Goss, S., D. Fresneau, J.-L. Deneubourg, J.-P. Lachaud & J. Valenzuela-Gonzalez, 1989. Individual foraging in the ant *Pachycondyla apicalis*. Oecologia 80: 65–69.

Harkness, R. D. & N. G. Maroudas, 1985. Central place foraging by an ant (*Cataglyphis bicolor* Fabr.): a model of searching. Anim. Behav. 33: 916–928.

Haskins, C. P. & E. F. Haskins, 1983. Situation and location-specific factors in the compatibility response in *Rhytidoponera metallica* (Hymenoptera: Formicidae: Ponerinae). Psyche 90: 163–174.

Hölldobler, B., 1984. Communication during foraging and nest-relocation in the African stink ant, *Paltothyreus tarsatus* Fabr. (Hymenoptera, Formicidae, Ponerinae). Z. Tierpsychol. 65: 40–52.

Hölldobler, B. & J. F. A. Traniello, 1980. Tandem running pheromone in ponerine ants. Naturwiss. 67: 360.

Hölldobler, B. & E. O. Wilson, 1977. Colony-specific territorial pheromone in the African weaver ant, *Oecophylla longinoda* (Latreille). Proc. Nat. Acad. Sci. USA 74: 2072–2075.

Holling, C. S., 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48: 1–86.

Lachaud, J.-P., 1985. Recruitment by selective activation: an archaic type of mass recruitment in a ponerine ant (*Ectatomma ruidum*). Sociobiology 11: 133–142.

Lachaud, J.-P. & A. Déjean, 1991. Food sharing in *Odontomachus troglodytes* (Santschi): a behavioral intermediate stage in the evolution of social food exchange in ants. An. Biol. 17: 53–61.

Lachaud, J.-P., D. Fresneau & J. Garcia Pérez, 1984. Etude des stratégies d'approvisionnement chez trois espèces de fourmis ponérines. Folia Entomol. Mex. 61: 159–177.

Lévieux, J., 1979. La nutrition des fourmis granivores. III. Cycle d'activité et régime alimentaire, en saison des pluies, de *Brachyponera senaarensis* (Hym., Formicidae, Ponerinae). Fluctuations saisonnières. Insectes Soc. 26: 232–239.

Lévieux, J. & T. Diomandé, 1978. La nutrition des fourmis granivores. II. Cycle d'activité et régime alimentaire de *Brachyponera senaarensis* (Mayr) (Hymenoptera: Formicidae). Insectes Soc. 25: 187–196.

Mayade, S., 1992. Le marquage de l'aire extérieure chez *Cataglyphis cursor* (Hymenoptera, Formicidae): corrélats biologiques et éthologiques. Unpublished doctoral thesis, Toulouse, 151 pp.

Peeters, C. & R. Crewe, 1987. Foraging and recruitment in ponerine ants: solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). Psyche 94: 201–214.

Robertson, P. S., 1971. Pheromones involved in aggressive behavior in the ant *Myrmecia gulosa*. J. Insect Physiol. 17: 691–715.

Traniello, J. F. A., 1988. Variation in foraging behavior among workers of the ant *Formica schaufussi*: ecological correlates of search behavior and the modification of search pattern. In: R. L. Jeanne (ed.), Inter-Individual Behavioral Variability in Social Insects. Westview Press, Boulder, Colorado: pp. 91–112.

Uezu, K., 1977. On the foraging activity of *Diacamma rugosum* (Le Guillon). Biol. Mag. Okinawa 15: 5–17.

Wehner, R., R. D. Harkness & P. Schmid-Hempel, 1983. Foraging strategies in individual searching ants *Cataglyphis bicolor* (Hymenoptera: Formicidae). Information Processing in Animals, vol. 1, Gustav Fisher Verlag, New York, 83 pp.