The Hunting Behavior of *Polyrhachis laboriosa*, a Non-Dominant Arboreal Ant of the African Equatorial Forest (Hymenoptera: Formicidae, Formicinae)

by

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ABSTRACT

The results are reported of the first extensive study of the predatory behavior of *Polyrhachis laboriosa*, a non-dominant arboreal formicine ant of the African equatorial forest that sometimes is able to occupy territories "in the manner of the dominants" and so corresponds to the definition of sub-dominant.

Large colonies of *P. laboriosa* show important scavenging and predatory activity, exploiting various arthropod prey, while workers of relatively small colonies do not hunt.

Prey, even relatively large, are captured by solitary hunters. In contrast to dominant arboreal ants, *P. laboriosa* forage mainly individually. However, they employ long-range recruitment to summon nest mates to large prey items which cannot be retrieved by a single worker. This recruitment intervenes after the prey is paralyzed or numbed. Recruitment also intervenes when a worker discovers a group of small prey. A detailed analysis is provided of the sequences of behavioral events observed during the hunting of various insect prey, very large prey being dissected on the spot, each piece being retrieved individually.

The foraging behavior of *P. laboriosa* is compared with that of other *Polyrhachis* and with that of dominant arboreal ants of the same region, in particular, *Oecophylla longinoda*.

Key words: *Polyrhachis laboriosa*, Formicidae, arboreal ants, predatory behavior.

INTRODUCTION

Tropical arboreal ant species are often divided into four status groups: dominants, co-dominants, sub-dominants and non-dominants (Majer, 1972, 1982).

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The dominant ant species are the most abundant; their mature colonies are very large and usually polydomous (i.e., occupying several nests). Workers are highly aggressive toward both conspecific and heterospecific aliens, and their competition for the control of space frequently results in a three-dimensional mosaic distribution of their territories (Leston 1973; Room 1971; Majer 1972, 1982; Hölldobler & Wilson 1990).

All dominant ant species studied in study area show similarities in their predatory behavior. During hunting, numerous workers stalk on the leaves and branches of the supporting tree. When a worker seizes a prey, the emission of an alarm pheromone attracts nest mates situated in the vicinity. Each worker seizes the prey at an appendage or at the body and spreads it apart. Depending on the species, the venom is either utilized as in *Oecophylla longinoda* Latreille (Hölldobler & Wilson, 1978; Dejean 1990) and *Pheidole megacephala* Fabricius (Dejean in prep.) or is utilized as in *Crematogaster* spp. (Tsapi 1990), *Tetramorium aculeatum* Mayr (Owona 1992) and *Atopomyrmex mocquerisi* André (Ngnegueu 1993). This last species also presents a more primitive behavior in carving up the prey on the spot.

The subdominants are species which may reach dominant status when they occur in a favorable environment, for instance in the gaps between adjacent dominant ant territories where the species has its highest density in the proximity of its nest. Lastly, the non-dominants, usually characterized by a relatively small colony size, either occupy free zones separating territories of dominant ants, or are tolerated within these territories (Majer 1972, 1982).

The biology and ecology of dominant ants of tropical ecosystems is relatively well-known, as these insects are often used as agents of biological control for various agricultural pests. Non-dominant ants are much less known. However, it is already known that some of them are important predators of pests that the dominant ants do not attack (Taley 1976; Faeth 1980; Sato & Higashi 1987; Way *et al.* 1989). As pointed out recently by Way & Khoo (1992), the attention given so far to non-dominant ants is inadequate, and further research on that subject remains a challenge for the future.

During numerous ecological studies on the distribution of arboreal ant species made in different tree crop plantations and the natural environment, it appears that the presence of *Polyrhachis laboriosa* F. Smith is frequent (Dejean *et al.* 1991; 1992a & b).

This species which is considered as non-dominant and found mainly in association with *O. longinoda* and various *Crematogaster* according to Room (1971) seems, however, in our samplings to occupy a variable place in arboreal ecosystems. Generally, the workers seem very timid, but sometimes they actively hunt, even other ant species, including dominant.

In this study, through the analysis of predatory behavior, we research arguments pérmitting the classification of *P. laboriosa* among the subdominant or the nondominant.

THE ANT

The ant genus *Polyrhachis* (subfamily Formicinae, tribe Camponotini) contains approximately 700 species and, thus, belongs to the largest ant genera (Bolton 1973; Dorow & Maschwitz 1990); however, the biology of these ants remains surprisingly little known. As stressed recently by Dorow*et al.* (1990), the ants of the genus *Polyrhachis* evolved a broad spectrum of adaptations enabling them to coexist with dominant and subdominant species, and, hence, they are ideal subjects for studies of highly-specialized niches and of complex interactions between ant species coexisting in tropical forests.

P. laboriosa inhabit arboreal nests constructed from various vegetal fibres, small twigs, fungal hyphae, and silk collected from spider webs and the empty cocoons of various Lepidoptera (Wheeler 1922; Collart 1932; Bolton 1973). In contrast to some other species of the genus, *P. laboriosa* do not use their larvae as shuttles to bind together leaves of their nests. They present a semi-claustral mode of colony foundation like primitive ants (Lenoir & Dejean 1994). Colonies of *P. laboriosa* are usually relatively small: most frequently, their size does not exceed several hundred individuals (Mercier 1992). The worker caste is monomorphous, the total body length ranging from 10.2 to 11.6mm (Bolton 1973).

METHOD

Field observations were carried out between January 1988 and February 1991 in Cameroon: Yaoundé, Kala, Matomb and Ndupé (25 km, 70km and 125km, respectively, to the west of Yaoundé).

We first controlled to see if the societies were polydomous, which necessitates a large enough population to be subdominant, by the following observations and experiments.

1) Observations consisted of following workers leaving a nest situated relatively close to others (less than 10m), permitting them to control if they could then enter one of these nests.

2) Taken with smooth forceps 10 workers of 5 nests belonging to 3 supposed groups of 5 to 10 nests and releasing them one by one on another nest of the same group.

3) We then released the workers on nests of another group (distance between groups of more than 500m).

4) In the last experiment, 20 workers from each of the 3 groups of nests were released on 3 isolated nests, and reciprocally, 20 workers from each isolated nest were released on a nest of one of the 3 groups and 20 others were released on another isolated nest.

After collecting field data on arthropods captured by *P. laboriosa*, we controlled the response of foragers to live Tettigoniidae of 10-15 mm length (with tibiae of their posterior legs cut off, to prevent them from jumping) which were released in their hunting area. We distinguished the foragers belonging to 6 isolated nests (installed on isolated trees) from workers belonging to 3 polydomous societies comprising at least 5 nests (the biggest nest, ovoid in shape was 42cm long for 36cm wide).

The predatory behavior of *P. laboriosa* was investigated by means of a method proposed by Dejean (1988a, b) on 9 large nests of *P. laboriosa* kept in semi-captivity in the laboratory. The ants were living in intact leaf nests collected in the field. The branches supporting these nests were each fixed in a neck of a bottle filled with water, to keep the leaves alive as long as possible. The ants stayed in their nests even after the leaves had completely dried up: the only major modification in their behavior consisted in the increased frequency of foraging trips for water. The workers were not confined to any hunting area; they could move freely in the laboratory to forage for food, which was provided, as a rule, daily. They were fed with honey, jam, pieces of various fruits, and small grasshoppers. They were also provided with cotton and the fibres of oil palm to strengthen and/or enlarge their nests.

During each test we noted which elements of the sequence of predatory behavior were present, and in what order. We also noted the successive relative positions of the predator and the prey, successive positions of the antennae, the mandibles and the legs of the ant, and the parts of the body of the prey seized by the ant. We also noted the total duration of all successful capture of prey, from the detection of the prey to the beginning of its transport to the nest. In the case of large prey cut into pieces before being transported to the nest, we noted the latencies from the detection of the prey to the start of the retrieval of its last piece. We used the following insect prey: 1) workers of the termite *Cubitermes fungifaber* Sjöstedt (6-7mm long; 55 tests); 2) workers of the termite *Macrotermes bellicosus* Smeathman (6-7mm long; 54 tests); 3) large soldiers of *M. bellicosus* (15-16 mm long; 34 tests); 4) small larvae (10-13mm long; 54 tests) of an unidentified tettigoniid grasshopper; 5) medium-sized intact larvae (18-22mm long; 45 tests); 6) medium-sized larvae with the tibiae of their posterior legs cut off to prevent them from jumping (18-22mm long; 30 tests); 7) large larvae (27-35mm long), also with the tibiae of their posterior legs cut off (51 tests); the same species of Tettigoniidae was utilized in 4, 5, 6 and 7; 8) groups of small prey: 5 workers of *Macrotermes bellicosus* released simultaneously at the same spot (31 tests).

The prey were offered to the ants at various places in the laboratory, but practically never at the same place twice. Each experimental session was preceded by a two-day period during which the ants were not fed any animal prey. We continued, however, to feed them daily with honey. During each session, we constantly changed the species of prey offered to the ants.

Although we did not study in detail the division of labor employed by *P. laboriosa* during foraging, we can already state that even in large colonies of that species only some foragers act as hunters. Thus, during our laboratory tests some foragers of *P. laboriosa* did not attempt to capture prey; instead, they responded to them either by immediate retreat and/or escape, or displayed the so-called "posture of prudence", opening the mandibles and throwing the antennae backwards, and sometimes also flexing the gaster. In the present study, only the behavior of "true hunters", i.e. ... foragers responding to their potential prey by predatory behavior, have been taken into account.

The statistical analysis of our data was carried out mostly by means of the X^2 test, if necessary with the Yates' correction. The duration of capture for various categories of prey were compared by means of the median test.

RESULTS

Hypothesis of Polydomy

In zones where several nests are situated close to each other, we often observed workers entering a new nest just after leaving another one. On the other hand, we also frequently observed fighting between workers of different societies which encountered each other during foraging far from their nests.

The 150 workers taken from a nest belonging to a group of nests were always accepted when released on another nest of the same group, while the 150 others released on a nest of another group were always heavily attacked and killed.

The 60 workers drawn from nests belonging to a group were always attacked and killed when introduced in the territory of an alien isolated nest. We got the same result when workers of an isolated nest were released on another one or on a nest belonging to a group.

We have therefore arguments permitting us to think that grouped nests belong to the same polydomous society, in this species where the aggressiveness towards alien conspecifics is very strong.

Field Observations on Predation and Scavenging (Table 1).

P. laboriosa are generalist predators and scavengers exploiting numerous species of arthropod prey (insects and spiders). In many cases,

Table 1. Observations of capture and handling of various prey by workers of *Polyrhachis laboriosa* recorded in the field in Cameroon between January 1988 and February 1991

Prey	Number of cases	% of the total number of cases
Aranea	1	0.6
Orthoptera:		
Gryllidae	1	0.6
Acrididae	3	1.8
Tettigonidae	9	5.6
leg of an unidentified grasshopper	7	4.3
Isoptera:		
workers	11	6.8
winged sexuals	9	5.6
Dicyoptera:		
Blattidae	2	1.2
Homoptera:		
Psyllidae	12	7.4
Diptera:		
Calliphoridae	17	10.6
other	4	2.5
Coleoptera:		
larvae	2	1.2
adults	1	0.6
Lepidoptera:		
larvae	11	6.8
adults	1	0.6
Hymenoptera:		
Formicidae - workers	8	4.9
Formicidae - alates	12	7.4
other	2	1.2
Small pieces of unidentified insects	48	29.8
TOTAL	161	

it was impossible to determine whether a particular prey had actually been killed by these ants, or found by them when already dead. Several times we observed groups of workers of *P. laboriosa* engaged in carving up very large prey items (cockroaches and grasshoppers often more than 4cm long).

Relationship Between Society Size and Predation (Table 2).

We distinguished 5 different reactions of the workers that discovered the Tettigoniidae introduced in their field of foraging. Whether the workers belonged to an isolated nest or a polydomous society, when they detected the tettigoniid, they reacted by: 1) escaping; 2) avoiding; 3) attacking then releasing the prey, drawing back and escaping; 4) attacking followed by seizure, bending of the gaster and abandoning the prey.

Only workers of the polydomous societies subdued and retrieved the prey to the nest; the difference between workers of the two kinds of nest is highly significant (P<0.01).

Laboratory Experiments on Hunting Behavior

Capture of various insect prey small enough to be retrieved by a single ant (Fig. 1-2)

We observed two types of prey detection. Frequently, the prey were detected as a consequence of accidental antennal contact "detection by contact". However, relatively often they were also detected from a distance ranging from 3 to 15mm. Such "detection from a distance" manifested itself in a sudden immobilization of the ant. Then, the ant successively oriented its antennae in the direction of the prey, approached it, and, lastly, rapidly touched the prey with its antennae. In

Table 2. Reactions of 35 workers from 6 isolated nests and 35 others from 3 polydomous societies faced with Tettigoniidae larvas (1015 mm long) devoid of the tibiae of their posterior legs.

BEHAVIOUR OF THE WORKERS	SMALL SOCIETIES	LARGE SOCIETIES
1- ESCAPING	13	7
2-AVOIDING	11	9
3-ATTACKING-RELEASING DRAWING BACK- ESCAPING	7	4
4-ATTACKING-SEIZURE ABANDONING/PREY	4	1
5-ATTACKING-SEIZURE RETIEVING	0	14
TOTAL	35	35

Statistics:Comparison between occurences 1, 2, 3. versus occurences 4, 5 in the two kinds of societies: X^2: P<0.01.

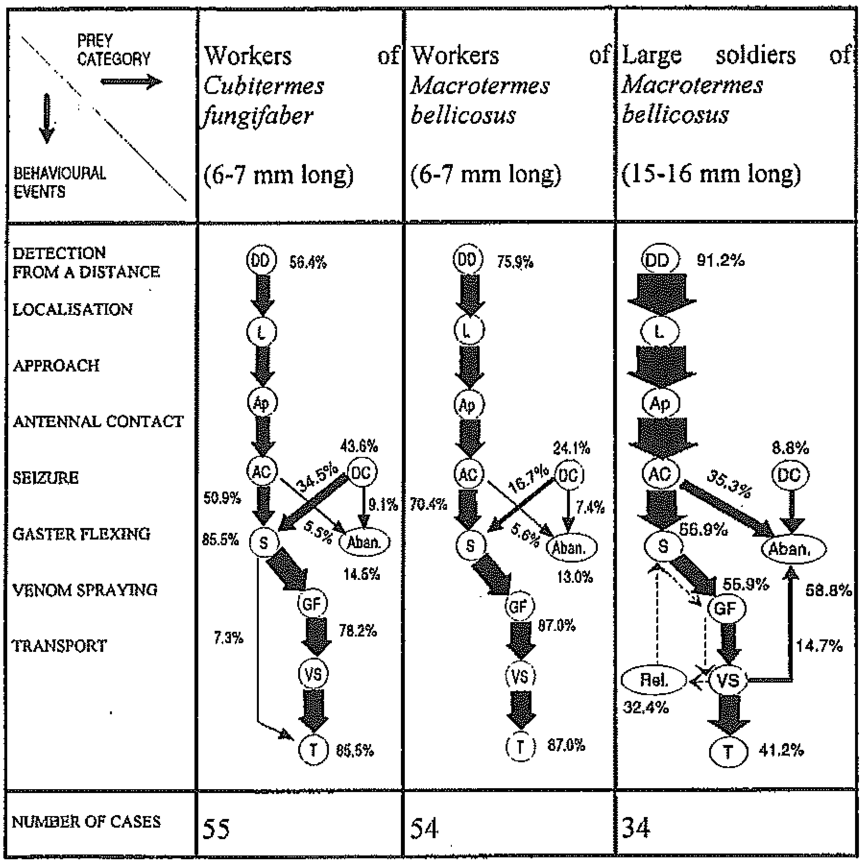


Fig. 1. Sequences of behavioral events observed in *P. laboriosa* during the attempts to capture various termites. Aban. = abandoning of the prey. DC = detection by contact. Rel. = release of the prey.

some cases, the ant was already opening its mandibles while turning its antennae toward the prey, but sometimes it only opened its mandibles after antennal contact with the prey.

The ratio of detections by contact to detections from a distance was apparently influenced by the size of the prey (Table 3). It is illustrated in the case of the Teittigoniidae (same species tested) with significant differences in the ratios of the two kinds of detection between small and large ones (P<0.05) and medium-sized and large ones (P<0.025). There was little difference in the ratios of the kinds of detection between grouped and isolated workers of *M. bellicosus* (P<0.1), while termite workers of the same size but belonging to different species showed

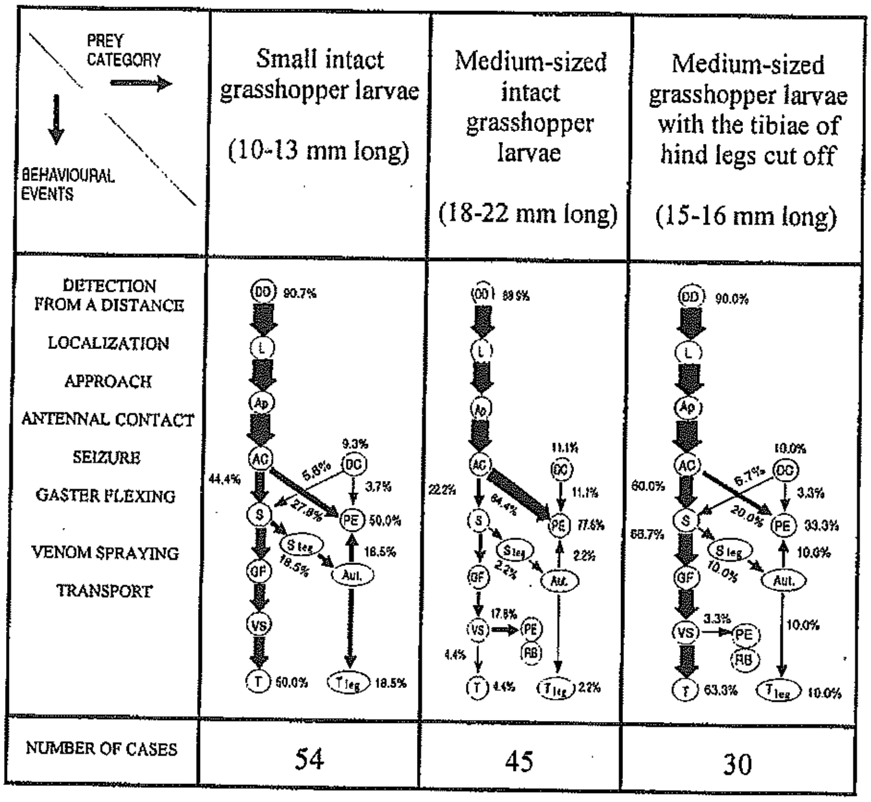


Fig. 2. Sequences of behavioral events observed in *P. laboriosa* during the attempts to capture small and medium-sized grasshopper larvae. Aut. = autotomy of the posterior leg seized by the ant; DC = detection by contact; PE = escape of the prey; RB = reserve behavior; S_{leg} and T_{leg} = seizure and transport of a posterior leg, following its autotomy;

significant differences (P<0.05).

After antennal contact or later after attack, the prey can be abandoned. This was the case for termites with 14.5% and 13% of the cases for the 2 kinds of workers tested, but with 58.8% for the soldiers of *M. bellicosus* (P<0.002 and P<0.001, respectively).

Grasshoppers reacted to the antennal contact by jumping and often escaped (50% for small ones; 77.8% for medium-sized ones; P<0.0001). Individuals seized by a posterior leg reacted by autotomy, a good strategy permitting 18.5% of the small individuals to escape (but the ant, on his end had a reward and retrieved the leg to the nest).

Tettigoniids devoid of the tibiae of the posterior legs, were, of course, captured at a higher rate than intact ones (P<0.00001), the objective of

Table 3. Relative frequency of detection from a distance and detection by contact during encounters of workers of *Polyrhachis laboriosa* with various insect prey. n = number of cases.

Prey	Number of tests	Detection from a distance n (%)	Detection by contact n (%)
1 Workers of *Cubitermes fungifaber*	55	31 (56.4)	24 (43.6)
2. Workers of *Macrotermes bellicosus*	54	41 (75.9)	13 (24.1)
3. Soldiers of *Macrotermes bellicosus*	34	31 (91.2)	3 (8.8)
4. Small (10-13 mm) intact grasshopper larvae	54	49 (90.7)	5 (9.3)
5. Medium-sized (18-22 mm) intact grasshopper larvae	45	40 (88.9)	5 (11.1)
6. Medium-sized (18-22 mm) grasshopper larvae with the tibiae of hind legs cut off	30	27 (90.0)	3 (10.0)
7. Large (27-35 mm) grasshopper larvae with the tibiae of hind legs cut off	51	51 (100.0)	0 (0.0)
8. Groups of 5 workers of *Macrotermes bellicosus*	31	28 (90.3)	3 (9.7)

Statistics:

I. Effect of prey size

1. Workers of *Cubitermes fungifaber* versus grasshoppers of various size: 1 versus 4: X^2: $P<0.0001$; 1 versus 5: X^2: $P<0.001$; 1 versus 6: X^2: $P<0.0025$;1 versus 7: X^2: $P<0.0001$

2. Workers of *Macrotermes bellicosus* versus grasshoppers of various size: 2 versus 4:X^2: $P<0.05$; 2 versus 5: X^2: NS ($P<0.1$); 2 versus 6: X^2: NS; 2 versus 7: X^2: $P<0.001$

3. Workers versus soldiers of *Macrotermes bellicosus*: 2 versus 3: X^2: NS ($P<0.1$)

4. Various groups of grasshoppers: 4 versus 5: X^2: NS; 4 versus 6: X^2: NS; 4 versus 7: X^2: $P<0.05$; 5 versus 6: X^2: NS; 5 versus 7: X^2: $P<0.025$; 6 versus 7: X^2: $P<0.025$

5. Soldiers of *Macrotermes bellicosus* versus grasshoppers of various size: 3 versus 4:X^2: NS; 3 versus 5: X^2: NS; 3 versus 6: X^{22}: NS; 3 versus 7: X^2: $P<0.05$

II. Effect of prey species: workers of *C. fungifaber* versus workers of *M. bellicosus*: 1 versus 2: X^2: $P<0.05$

III. Detection of single versus clustered prey: single workers versus groups of 5 workers of *M. bellicosus*: 2 versus 8: X^2: NS ($P<0.1$)

this last study consisted in obtaining enough data on the duration separating the beginning of the attack from the transport of such seized prey for comparison with other prey. It gives an idea on the utilization of venom, and indirectly on the activity of this venom.

The seizure was accomplished by a forward lunge, very rapid when attacking termite workers, but usually relatively slow and hesitant when attacking soldiers. The part of the body seized by the ant's mandibles varied as a function of the size and nature of the prey (Table 4), termite workers were always seized at the body, while soldiers were seized at an appendage in 21.1% of the cases. Grasshoppers were seized at an appendage in 27.3% to 34.7%. Often workers also used their forelegs to immobilize the small grasshoppers.

Table 4. Parts of the body of the prey seized by workers of *Polyrhachis laboriosa* during their encounters with various insect prey small enough to be retrieved by a single ant.
n = number of cases

Prey	Number of cases	Part of the body of the prey seized by the ant			
		Thorax n (%)	Abdomen n (%)	Anterior & median leg n (%)	Posterior leg n (%)
1 Workers of *Cubitermes fungifaber*	47	20 (42.6)	27 (57.4)	0 (0)	0 (0)
2. Workers of *Macrotermes bellicosus*	47	28 (59.6)	19 (40.4)	0 (0)	0 (0)
3. Soldiers of *Macrotermes bellicosus*	19	7 (36.8)	8 (42.1)	4 (21.1)	0 (0)
4. Small (10-13 mm) intact grasshopper larvae	37	10 (27.0)	15 (40.5)	2 (5.4)	10 (27.0)
5. Medium-sized (18-22 mm) intact grasshopper larvae	11	2(18.2)	6 (54.5)	2 (18.2)	1 (9.1)
6. Medium-sized (18-22 mm) grasshopper larvae with the tibiae of the hind legs cut off	23	4 (17.4)	11 (47.8)	5 (21.7)	3 (13.0)

Statistics:
I. Workers of *C. fungifaber* versus workers of *M. bellicosus*: seizure by the thorax versus by the abdomen: 1 versus 2: X^2: NS ($P<0.1$)
II. Workers versus soldiers of *M. bellicosus*: seizure by the leg versus by the body (thorax + abdomen): 2 versus 3: X^2: $P<0.0025$

The seizure of the prey was usually immediately followed by gaster flexing and probably venom spraying, even in the case of the workers of *C. fungifaber*, 91.5% of which struggled only very little after being caught.

During the encounters with soldiers of *M. bellicosus*, gaster flexing was fairly often (in 32.4% of the tests) followed by the retreat of the attacking ant. In about a half of the observed cases (14.7% of the tests), the prey was then ultimately abandoned.

Grasshoppers seized by a worker of *P. laboriosa* always struggled vigorously to escape. After seizure, small ones were always subdued very rapidly, while 8 of the 9 remaining intact medium-sized ones succeeded in escaping.

We can argue that the bending of the gaster is accompanied by venom spraying. Sometimes, it is obvious since the prey's cuticle becomes bright. After a fight, when a worker or a soldier of *M. bellicosus* has been abandoned, generally, after few a seconds it tilted up on its back. Grasshoppers that escaped after a fight remained immobile in a

Table 5. Duration of capture of various insect prey by workers of *Polyrhachis laboriosa*, measured from the detection of the prey to the start of its transport to the nest (prey categories 1— 6), or to the start of the retrieval of the last piece of the prey (prey category 7)

Prey category	Number of cases	Duration of capture	
		Mean	Range
1 Workers of *Cubitermes fungifaber*	55	6.5"	3" - 22"
2. Workers of *Macrotermes bellicosus*	54	7.7"	5" - 25"
3. Soldiers of *Macrotermes bellicosus*	34	22.3"	7" - 60"
4. Small (10-13 mm) intact grasshopper larvae	54	12.4"	5" - 30"
5. Medium-sized (18-22 mm) intact grasshopper larvae	45	21.5"	11" - 32"
6. Medium-sized (18-22 mm) grasshopper larvae with the tibiae of hind legs cut off	30	13.0"	8" - 35"
7. Large (27-35 mm) grasshopper larvae with the tibiae of hind legs cut off	51	-	35' - 1h40'

Statistics (as distributions of duration of capture were not normal, we used the median test): 1 versus 2: X^2: $P<0.05$; 2 versus 3: X^2: $P<0.005$; 3 versus 4: X^2: NS; 4 versus 6: X^2: NS; 6 versus 7: X^2: $P<0.0001$

"normal position", didn't jumped or jump a very short distance, if excited by repetitive contacts with a pen 10 to 30 seconds after the fight.

The total duration of the capture (Table 5) is also an argument in favor of venom utilization. Bites on the legs of grasshoppers, for instance, cannot explain how such prey can be subdued so quickly.

The workers of both termite species were lifted and transported to the nest immediately after the phase of the gaster bending, while subdued grasshoppers and soldiers of *M. bellicosus* were usually released and then seized again in a manner more suitable for transport. Immobilized grasshoppers were usually bitten repeatedly before being transported. Most often, the hunting ant first bit the abdomen of the prey, and then continued to bite its body while moving towards its head until arriving at the antennae. That behavior probably finally helped to completely subdue the prey. In some cases, in response to violent movements of the prey, the ant again sprayed it with venom.

In all of the observed cases, the workers retrieving the prey returned directly to the nest. Their return trip was always fairly straight, even if the prey was found relatively far from the nest. All of the captured soldiers of *M. bellicosus* were transported to the nests of *P. laboriosa*, but later they were all rejected and thrown out from the nests.

Escape of a prey

Workers of *P. laboriosa* usually responded to the escape of their prey by apparent excitement and by quickly running along a very sinuous path, keeping their mandibles open. That very characteristic pursuit behavior triggered by the escape of the prey has already been described in numerous ant species. Dejean (1988a) termed it the "reserve behavior". We observed several cases of the recapture of prey as a consequence of that alternative hunting tactic. In all of these cases, the prey was attacked immediately after its detection, without new antennal contact. Moreover, the attempt at the seizure of the prey was now preceded, and not followed, by venom spraying, and the ant was using not only its mandibles, but also its anterior legs to seize and immobilize the prey.

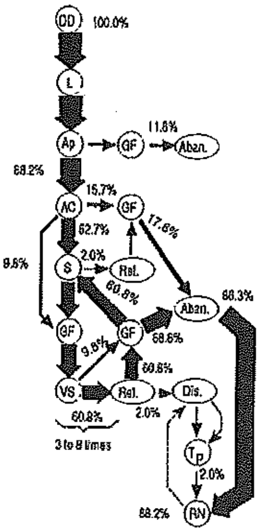
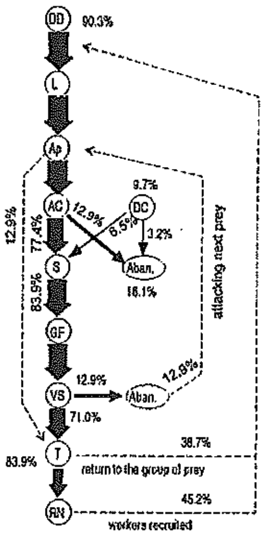
PREY CATEGORY → ↓ BEHAVIOURAL EVENTS	Large grasshopper larvae with the tibiae of hind legs cut off (27-35 mm long)	Groups of 5 workers of *Macrotermes bellicosus* (6-7 mm long)
DETECTION FROM A DISTANCE LOCALISATION APPROACH ANTENNAL CONTACT SEIZURE GASTER FLEXING VENOM SPRAYING TRANSPORT RECRUITMENT OF NESTMATES		
NUMBER OF CASES	51	31

Fig. 3. Sequences of behavioral events observed in *P. laboriosa* during the attempts to capture large grasshopper larvae and during the encounters with groups of termites. Aban. = abandoning of the prey; DC = detection by contact; Dis. = dissection of the prey; Rel. = release of the prey; RN = recruitment of nestmates; T_p = transport of a piece of the dissected prey.

Capture of large prey, too heavy to be retrieved by a single worker (Fig. 3)

Very large grasshopper nymphs were always detected from a distance. The frequency of detections from a distance was significantly higher in their case than in the case of any other prey (Table 3). However, similar to the case of soldiers of *M. bellicosus*, some ants also ultimately abandoned their prey before any attempt to seize it (11.8%; difference with the responses of *P. laboriosa* in front of small and medium-sized grasshoppers was highly significant; X^2: $P<0.0001$). They can also temporarily abandon the prey after the first antennal contact with it and gaster flexing (15.7% of the tests), or, less frequently, its seizure (2% of the tests). The prey seemed thus to be rejected, but in all of these cases the attacking ant returned to the nest to recruit nest mates, and then came back to the prey.

In 9.8% of the cases, the first antennal contact was followed directly by gaster flexing, without any previous attempt to seize the prey. Such behavior was never observed when hunting medium-sized grasshoppers (X^2: $P<0.01$).

After a cycle of 3-8 successive acts of gaster flexing, probably with venom spraying, each followed by a retreat, the ant usually returned to the nest to recruit nest mates (68.6% of the cases). Sometimes, the hunting worker cut off a piece of the prey's body and transported it to the nest where it recruited nest mates (2%). In total, the long-range recruitment of nest mates to a large grasshopper was observed in 88.2% of the cases.

The time separating the detection of the prey and the ant's leaving to recruit nest mates varies from 13 to 45 seconds (mean: 25.4±3.7; 26 cases analyzed) and seems very short. Since the grasshopper remained in place (or sometimes moved only a few centimeters), we suppose the effect of the venom is very efficient.

The grasshoppers were dissected by 6-13 workers, among which 1-2 ants both participated in cutting the prey into pieces, and acting as guards to prevent competitors from stealing it.

As a rule, the legs and the antennae of the prey were cut off first, and immediately afterwards transported to the nest. Then, the remaining part of the body of the prey was dissected into 2-3 pieces. During the dissection of a large grasshopper, *P. laboriosa* employed both cutting and pulling behavior. Frequently, many workers simultaneously pulled in various directions, which helped them to break free a part of the body of the prey. The pulling behavior was intensified after the legs and the antennae of the grasshopper had already been cut off.

In 84.5% of the cases, the pieces of a large grasshopper were transported to the nest by single workers of *P. laboriosa*. In the remaining 15.5% of the cases, we observed the joint transportation of a piece of the prey by two workers, but only along the initial 20-150cm of their return trip; the final retrieval of each piece of the prey was always conducted by a single ant. The workers which did not manage to get a hold of a piece of the prey continued to explore the spot at which the prey had been killed and dissected, walking slowly along a very sinuous path during the next 5-15 minutes, and then also returned one by one to the nest.

Hunting behavior triggered in response to a group of small prey (Fig. 3)

Hunting foragers of *P. laboriosa* detected at distance a single termite almost as well as a group of the termites (Table 3). The sequences of the behavioral acts following the detection of a group of workers of *M. bellicosus* were very similar to those observed during encounters with single workers of that species. In particular, the frequency of abandoning the prey after the first antennal contact with it was closely similar in these two situations (16.1% and 13.0% of the cases, respectively; X^2: NS).

During their encounters with groups of termite workers, *P. laboriosa* behaved in a rather variable way. In 12.9% of the tests, the ant captured its second termite immediately after having subdued the first one, without returning to the nest. However, in the majority of the cases (71%) the ant transported its first prey to the nest. Then, in about half of the cases (38.7% of the total number of the tests), the ant returned alone to the group of prey, captured another termite, and transported it again to the nest. On the other hand, in 45.2% of the total number of tests, the worker laid a chemical trail during its return with the prey to the nest and then returned again, followed by 1—2 nest mates, to the group of termite workers; other nest mates also arrived later at the group of the prey.

Comparison of the overall efficiency of the attempts of *P. laboriosa* to capture various categories of prey.

The termite workers of the two species tested *(Cubitermes fungifaber* and *Macrotermes bellicosus)* were captured with similar efficiency (Fig. 1; X^2: NS). In contrast to that, the successful capture of soldiers of *M. bellicosus* were highly significantly less frequent than those of workers of that species (X^2: $P<0.0001$).

The successful capture of small grasshoppers was significantly more frequent than that of intact medium-sized ones (Fig. 2; X^2: $P<0.001$). Of course, the capture of medium-sized grasshoppers with the tibiae of their hind legs cut off was successful significantly more frequently than in the case of intact grasshoppers of the same size (Fig. 2; X^2: $P<0.001$). The successful capture of the termite workers of any of the two species used was significantly more frequent than that of small and medium-sized intact grasshoppers (Figs. 1 and 2; X^2: $P<0.0001$ in all the cases). The soldiers of *Macrotermes bellicosus* were captured with a similar efficiency as small intact grasshoppers (X^2: NS), but significantly more frequently than medium-sized intact grasshoppers (X^2: $P<0.001$).

The successful capture of large grasshoppers was significantly more frequent than that of medium-sized grasshoppers with the tibiae of their hind legs cut off (X^2: $P<0.01$), most probably because large grasshoppers were sprayed with venom much more intensively than medium-sized ones, and because they were finally killed and cut into pieces by groups of workers recruited from the nest.

DISCUSSION

Although the biology of the ants of the genus *Polyrhachis* is still surprisingly little known, it is already known that these ants are extremely variable in the majority of such aspects of their biology as colony size, mode of colony founding, nesting habits and recruitment behavior (Dorow & Maschwitz 1990). The feeding behavior of these ants also shows great diversity. Thus, *P. dives* F. Smith from East Asia, known to form huge polydomous colonies containing up to one million workers (Yamauchi & Itô 1987), are so strongly predacious that they have been used with success to control the pine defoliator *Dendrolimus punctatus* (Wlk.) in South China (Hsiao 1981). In contrast to that, in *P. arachne* Emery, *P. hodgsoni* Forel and *P. (Myrmhopla) muelleri* Forel, studied by Dorow & Maschwitz (1990) and by Dorow *et al.* (1990) in West Malaysia, predatory behavior was never observed. However, ants of these species accepted pieces of dead insects offered to them as food. *P. lacteipennis* F. Smith (= *P. simplex* Mayr), studied by Ofer (1970) in Israel, were observed to prey only on small chironomid midges, but scavenged for a wide range of dead arthropods. Preying on various arthropods was also observed in the founding queens of *P. laboriosa* and *P. militaris*, investigated in a previous study (Lenoir & Dejean, 1994).

The overall foraging strategies of *Polyrhachis* ants is little known. Bolton (1973) related that workers of *P. militaris*, closely related to *P. laboriosa*, forage individually. Strictly solitary foraging has also been documented in *P. muelleri* (Dorow *et al.* 1990). In contrast, the rapid and efficient recruitment to food was discovered in *P. arachne* and *P. hodgsoni* (Dorow & Maschwitz 1990).

The present results show that societies of *P. laboriosa* have a tendency to be polydomous, and that the reactions of workers in front of prey is correlated to the size of the society. Only large polydomous societies have workers that hunt. Since alien workers are attacked and killed, we can conclude that societies are closed, intraspecific fighting was also frequently observed between foragers. It is possible that the acquisition of dominant status by large, polydomous societies does not need interspecific territoriality, because this species is well known to be tolerated by most of the dominants (Room 1971; Leston 1973; Majer 1972; numerous personal observations). It would be interesting to know the origin of the tolerance by true dominants, such as an allomone (that appeases, or, on the contrary repels) or a powerful venom.

The solitary foraging behavior of *P. laboriosa* is fundamentally different from that of dominant ants of the same community. In particular, the capture of prey, even very large, is almost always carried out by a single worker. Although *P. laboriosa* employ long-range recruitment to summon their nest mates to large prey, only the dissection of large prey items is collective: the transport of pieces of prey to the nest is once again carried out by single ants. However we can note that the possibility of spreading the prey apart (the technique utilized by dominant ants to catch prey) appears in the behavioral repertory of *P. laboriosa*, but it is rarely utilized and then, after long-range recruitment.

The solitary mode of hunting of *P. laboriosa* may be interpreted to some extent in terms of the low density of hunting foragers, making impossible the efficient short-range recruitment of nest mates to the prey. In contrast to that, the density of hunting workers within the territories of dominant arboreal ants of African forests is usually very high, making efficient the short-range recruitment to prey (Hölldobler & Wilson 1978; Dejean 1990a). Actually, in *O. longinoda* predatory behavior and territory defence behavior are difficult to tell apart: usually both conspecific territorial intruders and prey are killed in the same manner, by cooperative stretching, and then transported to the nest and eaten (Hölldobler & Wilson 1978; 1990; Hölldobler 1979; Dejean 1990a, b, c). The importance of the high density of workers as a factor facilitating group hunting has also been suggested in the case of other ant species, such as *Proatta butteli* Forel (Moffet 1986).

P. laboriosa are generalist predators able to capture a wide range of arthropod prey. Their hunting behavior is well-adapted to deal with various categories of prey. The time necessary to subdue the prey, principally large ones seems so short that we suppose that gaster flexing is always followed by venom spraying and that the effect of this venom is particularly powerful. So, we ask the following question: is it only composed of formic acid?

We also observed that the autotomy of posterior legs is a very efficient anti-predator tactic protecting grasshoppers against these ants.

The so-called "reserve behavior", an alternative hunting tactic employed by *P. laboriosa* in response to the escape of the prey, is known in many other ants. This "reserve behavior" mainly involves the increased speed and sinuosity of locomotion. In formicine ants, the escape of the prey often additionally triggers immediate venom spraying. The prey reached by the venom becomes less agile, and may be subdued much more easily after being rediscovered by the ant (Dejean, 1988a, b, 1990a).

The detection of dangerous prey (termite soldiers; large grasshoppers) is usually followed by the quick retreat of the ant, adopting then the so-called "posture of prudence", with open mandibles, antennae thrown backwards, and sometimes also gaster flexing. The tendency to seize the prey by a leg instead of orienting the attack directly towards its body is still another element of prudence behavior shown by *P. laboriosa* while hunting termite soldiers. Strikingly similar postures and modifications of hunting behavior have been observed in several ponerine ants during encounters with termite soldiers (Dejean *et al.* 1990).

During encounters with groups of termites, some workers of *P. laboriosa* were observed successively killing more than one prey before starting to transport the termites to the nest. As termites are usually encountered in groups, such behavior is an important adaptation for termite hunting, well-known in numerous termitophagous ponerines (Mill 1984; Agbogba 1985; Dejean 1991).

The prey capture behavior of *P. laboriosa* present similitudes with that of *Camponotus maculatus* F., another African formicine ant of the tribe Camponotini, but this last species is terrestrial (Dejean 1988b).

The dissection of large prey items into small pieces transported by single ants, as opposed to the cooperative retrieval of whole prey, is considered to be a primitive behavioral trait, as it increases the risk of interference competition with sympatric ant species (Hölldobler *et al.* 1978; Traniello 1983, 1987; Traniello & Beshers 1991). Its occurrence in *P. laboriosa* corroborates precedent results (Lenoir & Dejean 1994) which demonstrate that this species shows a primitive mode of foundation.

In conclusion, even if this species shows primitive traits, it can have large, polydomous societies. In this last case, the societies can reach the status of subdominant even if the behavior of the workers of the external service is very different from that of the dominant species. Majer (1972) mentions a similar case in Ghana where an arboreal *Platythyrea*

(Ponerinae; subfamily considered like primitive) is for reasons unknown a subdominant.

ACKNOWLEDGMENTS

This research was financed by a "Campus" grant (108 CD 90) of the French Ministry of Cooperation, entitled "Impact des fourmis arboricoles sur les essences tropicales d'intérêt économique". The participation of E. J. Godzinska in this research was possible thanks to a grant from EC Tempus for a training course at the Université Paris Nord, and thanks to a Statutable Grant from the State Committee for Scientific Research of the Nencki Institute of Experimental Biology in Warsaw (Poland). We thank C. Djieto-Lordon and P.R. Ngnegueu, Laboratory of Zoology, Faculty of Sciences of Yaoundé, for their field assistance.

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