

Selection and capture of prey in the African ponerine ant *Plectroctena minor* (Hymenoptera: Formicidae)

Bertrand Schatz^{a*}, Jean-Pierre Suzzoni^b, Bruno Corbara^c, Alain Dejean^b

^aLECA, FRE-CNRS 2041, université Paul-Sabatier, 118, route de Narbonne, 31062 Toulouse cedex, France

^bLET, UMR-CNRS 5552, université Paul-Sabatier, 118, route de Narbonne, 31062 Toulouse cedex, France

^cLAPSCO, UPRESA-CNRS 6024, université Blaise-Pascal, 34, avenue Carnot, 63037 Clermont-Ferrand cedex, France

Received 27 January 2000; revised 29 November 2000; accepted 15 December 2000

Abstract – Prey selection by *Plectroctena minor* workers is two-fold. During cafeteria experiments, the workers always selected millipedes, their essential prey, while alternative prey acceptance varied according to the taxa and the situation. Millipedes were seized by the anterior part of their body, stung, and retrieved by single workers that transported them between their legs. They were rarely snapped at, and never abandoned. When *P. minor* workers were confronted with alternative prey they behaved like generalist species: prey acceptance was inversely correlated to prey size. This was not the case vis-à-vis millipedes that they selected and captured although larger than compared alternative prey. The semi-specialised diet of *P. minor* permits the colonies to be easily provisioned by a few foraging workers as millipedes are rarely hunted by other predatory arthropods, while alternative prey abound, resulting in low competition pressure in both cases. Different traits characteristic of an adaptation to hunting millipedes were noted and compared with the capture of alternative prey. We also noted the parsimony of the behavioural phases during their capture compared to the capture of alternative prey. © 2001 Éditions scientifiques et médicales Elsevier SAS

feeding specialisation / millipedes / predation / prey selection

1. INTRODUCTION

In the tropical rainforest ants play an important ecological role due to their abundance and diversity [16]. Most species are generalist predators that accept many kinds of arthropods while others are specialists that capture only prey belonging to a particular order or family [3, 10, 16]. The most specialised ant species are disproportionately concentrated in the subfamily Ponerinae with specialists of earthworms, spider eggs, isopods, centipedes and termites [3, 4, 8–10, 16, 19]. We decided to study species of the ponerine genus *Plectroctena* as the workers have hypertrophied mandibles, a characteristic thought to be associated with prey specialisation. Previous studies concluded that the main food of this genus is composed of millipedes (Iulidae) and beetle larvae, but termites and soft-bodied arthropods are also accepted [1, 17, 18]. Recently we showed that the presence of millipedes in the diet of mature *P. minor* colonies is necessary for

the production of winged females and enhances the production of workers [23]. Millipedes can therefore be considered as ‘essential prey’ for this ant species, as opposed to ‘alternative prey’ or other accepted arthropod taxa that provide energy for colony maintenance (see [12]).

Consequently, *P. minor* workers select and capture millipedes, although several other litter-dwelling arthropod taxa are more frequent (see [5, 16]). Moreover, millipedes are protected by a sclerified body, a defensive secretion (methyl-benzoquinone) and a defensive rolled position [14]. We therefore conducted cafeteria experiments followed by a comparison of the predatory behaviour of hunting workers when confronted with different arthropod prey to verify whether millipedes were captured more efficiently than the other tested arthropods.

2. MATERIALS AND METHODS

Our study was carried out in the region of Yaoundé (Cameroon), where we collected five queenright colonies of *P. minor*. Each contained about seventy work-

*Correspondence and reprints: fax +33 5 61 55 61 54.
E-mail address: schatz@cict.fr (B. Schatz).

ers and abundant brood. *P. minor* workers (15.2–17.6 mm in length) forage in the forest litter beneath the bark of rotting or collapsed logs [1, 2, 17, 18]. They employ a peculiar snap-jaw mechanism in which the closed mandibles cross over in an audible ‘click’ to deliver a sharp blow to an adversary, also observed both in *Mystrium* (Ponerinae), and in termite soldiers (*Termes* and *Capritermes*; [2, 11, 15, 20]).

In the laboratory, the colonies were bred in test tubes (22 × 2 cm) supplied with a watering place and opening into plastic boxes (45 × 35 × 5 cm) covered with a plate of glass that served as hunting areas. The bottom of these boxes was not covered with sand nor leaf litter in order to fully expose the prey items and to standardise the test conditions. As in the field, workers deposited chemical markers around the nest entrances and hunting areas.

2.1. Cafeteria experiment

Prior to the cafeteria experiments, colonies were supplied during 4 d with the same range of prey items as during the tests to avoid the influence of previous meals on their feeding preference. No food was provided the day preceding the tests to induce foraging. In all cases, prey items were introduced while all the workers rested in the artificial nests. The tests were performed when only one worker foraged in the hunting area. During each test, one individual from each of the ten compared prey types was placed inside a plastic ring (3 mm in height; 45 mm in diameter) to prevent them from escaping until they were discovered by a forager. The ring plus prey were placed at different locations in the hunting areas between the different tests.

Prey collected just before the experiments belonged to the most abundant taxa among the ground-dwelling arthropods of the rainforest: termite workers (Isoptera; 5 to 7 mm long *Cubitermes subarquatus* and *Nasutitermes* sp.; 8 to 9 mm long *Macrotermes bellicosus*), 1 and 4 cm long grasshopper larvae (*Homorocoryphus* sp.; Orthoptera), 1 to 1.2 cm long oniscoid isopods (Isopoda), 2.5 cm long Tenebrionidae larvae (Coleoptera), 3.5 to 4 cm long millipedes (Myriapoda, Iulidae), centipedes (Myriapoda, Scolopendromorpha) and 3 to 4 cm long earthworms (Oligochaeta). The tibiae of the posterior legs of both types of grasshoppers were cut off to prevent them from jumping.

The ten prey types were left in the hunting area during a half-hour from the moment of the first capture. We scored ‘1’ for each prey type captured and ‘0’ for each prey type not captured. The tests were repeated 25 times resulting in a score comprised between 0 and 25 for each prey type. We then conducted a second experiment by offering, after a 4-d starvation

period, the prey items that had a score equal or less than 12 out of 25 in the first experiment. We compared the number of prey accepted using Dunnett’s test (Systat 7.0.1. software) and Fisher’s exact tests (StatXact 2.05 software). For the correlation between prey size and percentage of acceptance we used Cricket Graph 1.3.2. software.

2.2. Predatory behaviour

Experiments on predatory behaviour were carried out after a preliminary study where we noted the complete behavioural sequence used by hunting workers (classical procedure; see [9, 22]). We then established data sheets that we used during experimentation to note each behavioural act performed and the part of the prey body seized. Data were compiled on the respective postures of prey and predator for each phase. A flow diagram was established for each type of prey tested. The predatory behaviour of *P. minor* workers was studied with eight prey types from six taxa: *C. subarquatus* workers (5–7 mm long); *M. bellicosus* workers (8–9 mm long), small soldiers (9–10 mm long) and large soldiers (17–18 mm long); 1 to 1.2 cm long oniscoid isopods; 2 to 2.5 cm long grasshopper larvae (*Homorocoryphus* sp.; tibiae of the posterior legs cut off); 2 to 3.5 cm long Tenebrionidae larvae; and 3.5 to 4 cm long millipedes (Iulidae).

Percentages (transition frequency between behavioural acts) were calculated. Raw data were compared using Fisher’s exact test (StatXact 2.05 software) and appropriate probabilities were adjusted for the number of simultaneous tests, using the sequential Bonferroni procedure [21].

3. RESULTS

3.1. Cafeteria experiment

P. minor hunting workers captured prey belonging to eight out of the ten taxa offered, with four of them captured in more than 50 % of the cases (*figure 1A*). Millipedes, captured in all tests, were significantly more often selected than any other prey type (*figure 1A*). In the ‘reduced choice’ situation, workers captured five prey types out of the six offered, four of them in more than 50 % of the cases (*figure 1B*). Except for earthworms, significant differences existed with the previous situation for each taxa (*figure 1*).

A significant correlation existed between prey size and the percentage of acceptance of each prey type when centipedes and millipedes were excluded ($r = 0.907$; 6 df; $P < 0.005$), while no correlation was found when all prey types were considered ($r = 0.518$; 8 df; n.s.; *figure 1C*). This suggests that centipedes,

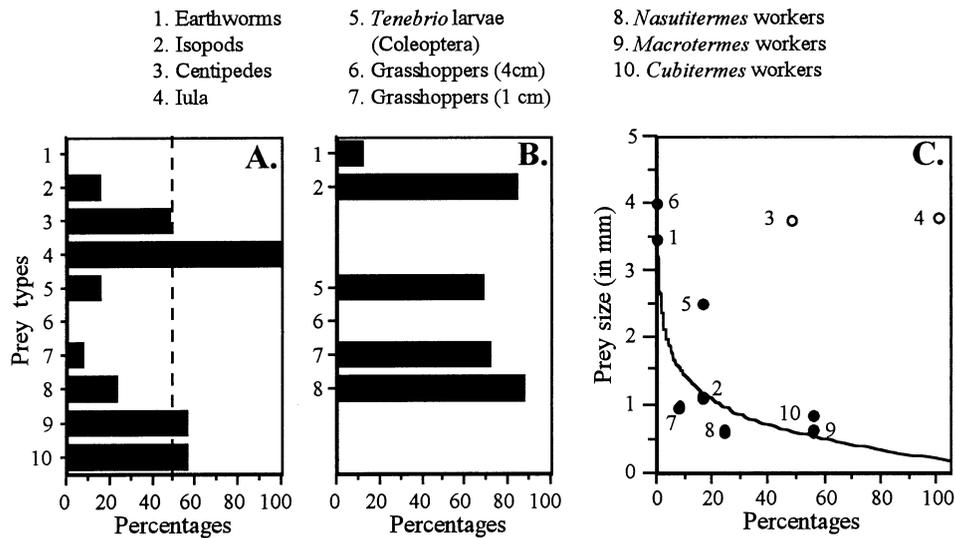


Figure 1. Feeding preferences during a cafeteria experiment conducted with *P. minor* workers. For the first experiment (A), in each of the 25 tests, foraging workers had the choice between ten prey items (one from each taxa). For the second experiment (B), colonies had the choice between the taxa that had a score inferior to 50 % in the previous experiment. (C) Relationship between prey size and the percentage of prey choice in the cafeteria experiments, the curve represents the relationship without prey No. 3 and 4. Statistical comparisons between '4' and other cases in situation A (Dunnett's test): $P < 0.001$ in all cases; comparisons between situations A and B (Fisher's exact tests): (1) $P = 0.23$; n.s.; (2) $P = 2.6 \cdot 10^{-6}$; (5) $P = 4.4 \cdot 10^{-4}$; (7) $P = 6.3 \cdot 10^{-6}$; (8) $P = 9.5 \cdot 10^{-6}$.

and particularly millipedes, were preferentially selected by the hunting workers regardless of size.

3.2. Predatory behaviour

The complete behavioural sequence was composed of the following phases: detection (prey perception), localisation (orientation towards the prey and opening of the mandibles), approach, antennation, snapping, seizure, stinging, long-range recruitment and transport to the nest.

3.2.1. Termites

The first difference in the behavioural sequence appeared for detection: *Cubitermes* and *Macrotermes* termite workers were detected by contact while termite soldiers were rather detected from a distance (table I, figure 2). The distance of localisation varied between 3 and 6 mm and was always characterised by a short antennation phase lasting from 1–4 s. Except for *Cubitermes* workers, the ants' antennae were rapidly retracted after the prey was detected. Termite workers were randomly seized, while soldiers were significantly seized between the head and thorax (figure 3), which allowed the hunting workers to avoid contact with the soldiers' mandibles. The seizure phase was followed by some prey being abandoned for the two

types of termite soldiers (figure 2C, D). Between antennation and seizure, *P. minor* workers occasionally snapped at termite workers and always at termite soldiers (table I), the latter being frequently abandoned. In contrast to the soldiers, termite workers were not always stung before being retrieved (figure 2). The duration of stinging varied from several seconds for termite workers up to 16 min for soldiers. The rate of successful capture was higher for termite workers than for soldiers (table I).

3.2.2. Solitary arthropods

Millipedes were significantly more often detected from a distance than were isopods, Tenebrionidae larvae and grasshoppers (table I, figure 4). The ants' antennae were significantly more often retracted for grasshoppers than for large millipedes when detected from a distance (Fisher's exact test: $P = 2.0 \cdot 10^{-5}$). The ants snapped at Tenebrionidae larvae or a grasshopper significantly more often than at millipedes, while a non-significant difference was noted between millipedes and isopods (table I). Tenebrionidae larvae and grasshoppers were randomly seized while millipedes were significantly more often seized by the anterior parts of their bodies (figure 3). Isopods were always seized dorsally (31.1 % in a normal position and 68.9 % when rolled). Isopods directly retrieved when

Table I. Comparisons of the occurrence of different predatory behaviours displayed by *P. minor* when confronted with different prey taxa. *P*-values were calculated for all possible permutations using Fisher's exact tests in order to apply the sequential Bonferroni procedure: *** $P < 0.001$; * $P < 0.05$; n.s.: non-significant difference. All prey captured were snapped at in the comparison C vs. D. The symbols A to H correspond to those from figures 2 and 4.

		A vs. B	B vs. C	B vs. D	C vs. D	D vs. E	H vs. E	H vs. F	H vs. G
Detection	by contact vs. from a distance	0.063	$3 \cdot 10^{-7}$	$< 10^{-8}$	0.051	$< 10^{-8}$	$< 10^{-8}$	$8 \cdot 10^{-7}$	0.034
		n.s.	***	***	n.s.	***	***	***	*
Snapping	occurred vs. did not occur	0.078	$< 10^{-8}$	$< 10^{-8}$	/	$< 10^{-8}$	0.26	$9 \cdot 10^{-7}$	$< 10^{-8}$
		n.s.	***	***		***	n.s.	***	***
Capture rate	prey captured vs. prey abandoned	0.141	$4 \cdot 10^{-3}$	$4 \cdot 10^{-4}$	0.116	$1 \cdot 10^{-7}$	$5 \cdot 10^{-4}$	$< 10^{-8}$	$< 10^{-8}$
		n.s.	***	***	n.s.	***	***	***	***

rolled (figure 4E) were not always stung. Their defensive posture of rolling into a ball makes them a prey easy to capture due to the large mandibles of the *P. minor* workers. Nestmates were always recruited for the capture of grasshoppers and in 14.8 % of the cases for millipedes larger despite their size (Fisher's exact test: $P < 0.001$; figure 4G, H). The hunting workers returned to their nest by laying a scent trail after the prey was paralysed. They recruited two to five nestmates that co-operatively retrieved the prey. Note that large prey items (and also termite soldiers) were generally transported with their ventral face up preventing the prey from clinging to the ground. The rate of capture of millipedes was maximum (100 %) and significantly higher than all other tested prey (table I).

4. DISCUSSION

During cafeteria experiments, we noted that *P. minor* workers always selected millipedes, their essen-

tial prey, followed by a graded acceptance of alternative prey. When confronted with alternative prey, *P. minor* workers behave like those from generalist predatory ponerine species, showing a strong inverse correlation between prey size and prey acceptance. This is interpreted as greater prey size correlated with better prey defence [6, 7, 22]. The same does not hold true for millipedes that were captured although larger in size than compared alternative prey.

As millipedes are rarely accepted by other ground-dwelling ant species of the same rainforests [10], competition for *P. minor*'s essential prey is low and mostly represented by congeneric species that are infrequent [2]. Competitors for *P. minor*'s alternative prey are numerous and concern a wide range of predatory arthropods, mostly ants, but these prey abound. As a result, the semi-specialist character of *P. minor* permits the colonies to be easily provisioned, even with a few solitary foraging workers.

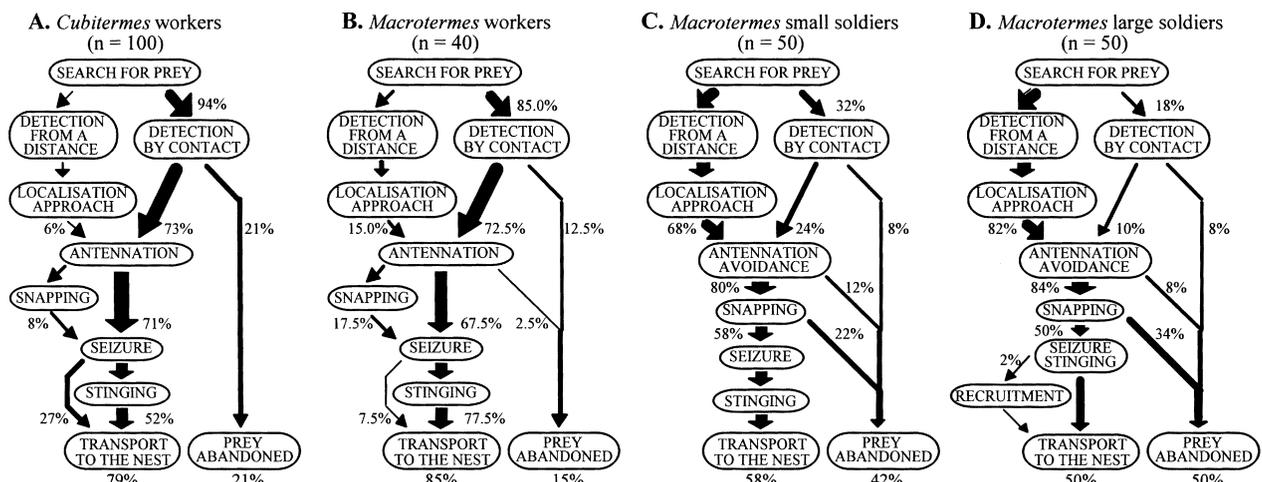
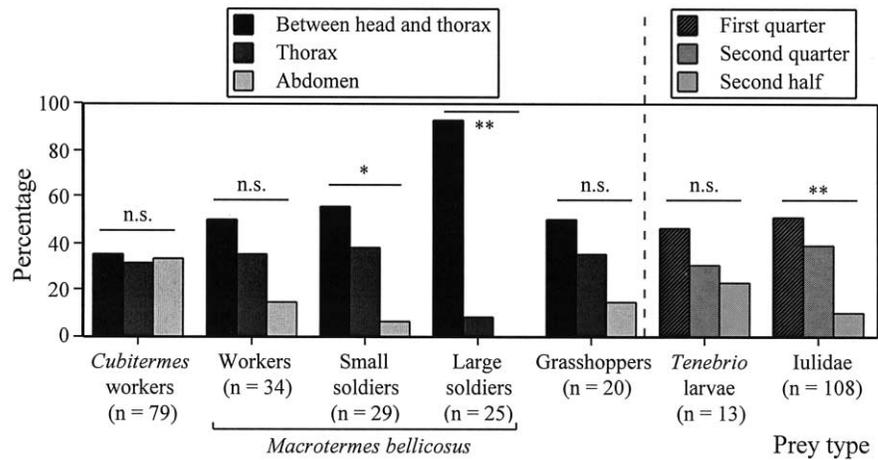


Figure 2. Flow diagram of the predatory strategy used by *P. minor* hunting workers when confronted with termites: *Cubitermes* workers (A); *Macrotermes bellicosus* workers (B); small (C) and large (D) soldiers.

Figure 3. Part of the prey body targeted by *P. minor* workers during seizure of the four types of termites, grasshoppers, Tenebrionidae larvae and millipedes. (Fisher's exact tests; n.s.: non-significant; * $P < 0.05$; ** $P < 0.01$).



A comparative study of the prey capture behaviour of essential and alternative prey permitted us to show different adaptations to the capture of millipedes. Detection (by contact vs. from a distance) depends on prey size (large prey detected from a distance) and on prey type (dangerous termite soldiers were also detected from a distance). Brief antennal palpation vs. bending the antennae backward followed the same pattern, with exceptions concerning millipedes and Tenebrionidae larvae confirming that the type of prey defence could trigger this behaviour. Snapping, known for its defensive role [20], was used frequently against termite soldiers, grasshoppers and Tenebrionidae lar-

vae, but rarely for millipedes although larger in size. This suggests that millipedes were not considered as 'dangerous' by *P. minor* workers whereas they perceived a risk when capturing other large prey, a behaviour also noted in other ponerine ants [6, 7, 22]. Stinging, known to be triggered by prey that struggle [22], is not always used against termite workers and isopods. The retrieval of large prey by single workers vs. co-operation between several workers varied according to prey shape and size. Grasshoppers were always co-operatively retrieved while millipedes were in only 14.8 % of cases, and Tenebrionidae larvae were always retrieved by single workers. Grasshop-

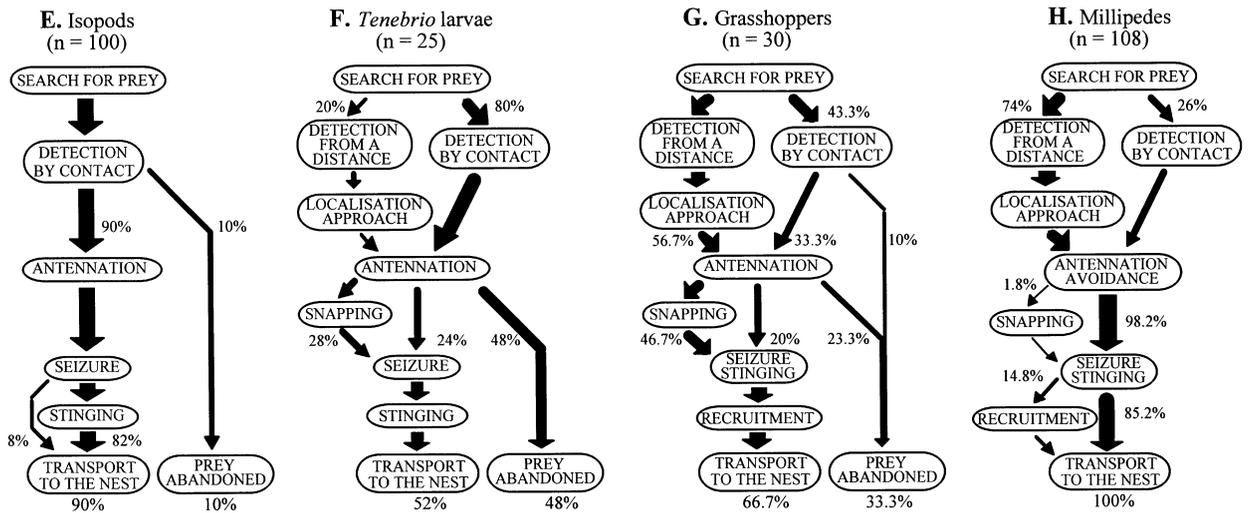


Figure 4. Flow diagram of the predatory strategy used by *P. minor* hunting workers when confronted with isopods (E), Tenebrionidae larvae (F), grasshoppers (G) and millipedes (H).

pers were pulled backwards while the two other tubular-shaped prey were transported between the workers' legs with their ventral face up preventing the prey's legs from clinging to the ground, a behaviour well adapted to tubular-shaped prey retrieval and reminiscent of swarm raider ants [9, 10, 13, 19].

As a result, *P. minor* hunting workers displayed several behaviours well adapted to the capture of tubular-shaped prey that are likely to greatly decrease the cost/benefit ratio associated with the capture of millipedes in comparison with alternative, smaller prey. The resulting savings in time, effort and exposure to competition and predation are potentially of great adaptive value. Millipedes were never abandoned, were seized by the anterior part of their body, rarely snapped at, and retrieved by single workers. We can also note the parsimony of behavioural phases during their capture compared to the capture of alternative prey. This parsimony was noted again during isopod capture, but it only results from the ease for long-mandibulated ants in seizing these prey that roll into a ball, as isopods were rarely selected during the cafeteria experiments, and ant species specialised in their capture displayed specific behaviours [1].

In conclusion, their specialisation in millipede capture limits the competition between *P. minor* and other ground-dwelling ants that are mostly predators of termites [3, 10, 16]. This specialisation is known for all *Plectroctena*, so that their nests can be located by the piles of large sclerified exoskeletal coils of millipedes [1, 2, 17, 18]; pers. obs.). Prey specialisation, considered as a derived condition [16], has permitted this African genus to evolve into a large number of species characterised by a common mandible morphology (presence of small teeth, apex shape, curve, condyle gap) well adapted to the capture of millipedes [2].

Acknowledgments. We are grateful to Dr Barry Bolton (Museum of Natural History, London, where voucher specimens were deposited) for the identification of the ants, and to Andrea Dejean for her review of the English.

REFERENCES

- [1] Arnold G., A monograph of the Formicidae of South Africa, Ann. S. Afr. Mus. 14 (1915) 1–766.
- [2] Bolton B., A revision of the ponerine ant genus *Plectroctena* F. Smith (Hymenoptera: Formicidae), Bull. Brit. Mus. Nat. Hist. 30 (1974) 311–339.
- [3] Corbara B., Dejean A., Adaptive behavioral flexibility of the ant *Pachycondyla analis* (= *Megaponera foetens*) (Formicidae: Ponerinae) during prey capture, Sociobiology 36 (2000) 465–483.
- [4] Dejean A., Evraerts C., Predatory behavior in the genus *Leptogenys*: a comparative study, J. Insect Behav. 10 (1997) 177–191.
- [5] Dejean A., Masens D., Kanika K., Nsudi M., Buka M., Les termites et les fourmis, animaux dominants de la faune du sol de plusieurs formations forestières et herbeuses du Zaïre, Actes Coll. Insectes Soc. 3 (1986) 273–283.
- [6] Dejean A., Corbara B., Oliva-Rivera J., Mise en évidence d'une forme d'apprentissage dans le comportement de capture des proies chez *Pachycondyla* (= *Neoponera*) *villosa* (Formicidae, Ponerinae), Behaviour 115 (1990) 175–187.
- [7] Dejean A., Lachaud J.P., Beugnon G., Efficiency in the exploitation of patchy environments by the ponerine ant *Paltothyreus tarsatus*: an ecological consequence of the flexibility of prey capture behaviour, J. Ethol. 11 (1993) 43–53.
- [8] Dejean A., Grimal A., Malherbe M.C., Suzzoni J.P., From specialization in spider egg predation to an original nesting mode in a 'primitive' ant: a new kind of lestopiosis, Naturwissenschaften 86 (1999) 133–137.
- [9] Dejean A., Schatz B., Orivel J., Beugnon G., Prey capture behaviour of *Psalidomyrmex procerus* (Formicidae: Ponerinae), a specialist predator of earthworms (Hymenoptera: Formicidae), Sociobiology 34 (1999) 545–554.
- [10] Dejean A., Schatz B., Orivel J., Beugnon G., Lachaud J.P., Corbara B., Feeding preferences on African ponerine ants: a cafeteria experiment, Sociobiology 34 (1999) 555–568.
- [11] Deligne J., Quennedy A., Blum M.S., The enemies and defense mechanisms of termites, in: Social Insects, vol. 2, Academic Press, London, pp. 1–76.
- [12] Evans E.W., Stevenson A.T., Richards D.R., Essential versus alternative foods of insect predators: benefits of a mixed diet, Oecologia 121 (1999) 107–112.
- [13] Gotwald W.H. Jr, Army Ants: the Biology of Social Predation, Cornell University Press, Ithaca and London, 1995.
- [14] Grassé P.P., Zoologie I., Invertébrés, Masson, 1961.
- [15] Gronenberg W., Hölldobler B., Alpert G.D., Jaws that snap: control of mandible movements in the ant *Myrmica*, J. Insect Physiol. 44 (1998) 241–253.
- [16] Hölldobler B., Wilson E.O., The Ants, The Belknap Press of Harvard University Press, Cambridge, Mass., 1990.
- [17] Lévieux J., Le rôle des fourmis dans les réseaux trophiques d'une savane préforestière de Côte d'Ivoire, Ann. Univ. Abidjan 5 (1972) 143–240.
- [18] Lévieux J., The soil fauna of tropical savannas, in: Bourlière F. (Ed.), Tropical Savannas, Elsevier, Amsterdam, the Netherlands, 1983, pp. 525–540.
- [19] Masuko K., Predation of centipedes by the primitive ant *Amblyopone silvestrii*, Bull. Assoc. Nat. Sci. Senshu Univ. 24 (1993) 34–43.
- [20] Moffett M.W., Mandibles that snap: notes on the ant *Myrmica camillae* Emery, Biotropica 18 (1986) 361–362.
- [21] Rice W.R., Analyzing tables of statistical tests, Evolution 43 (1989) 223–225.
- [22] Schatz B., Lachaud J.P., Beugnon G., Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*, Behav. Ecol. Sociobiol. 40 (1997) 337–349.
- [23] Suzzoni J.P., Schatz B., Dejean A., Essential and alternative prey in the ponerine ant *Plectroctena minor*, C. R. Acad. Sci. 323 (2000) 1003–1008.