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Hunting strategy of a generalist ant species proposed as a biological control agent against termites

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Abstract

We studied the hunting behaviour of *Myrmicaria opaciventris* (Hymenoptera: Formicidae) in order to evaluate if it can be used as a biological control agent against the termites that damage sugarcane plantations. Hunting workers foraged in groups and recruited nestmates at short-range when they encountered large termite soldiers or groups of small termite workers. Differences in prey capture concerned the: (1) means of detection (from a distance or by contact); (2) termite body part seized (small termites seized by the body; large termites by an appendage); (3) percentages of prey abandoned; and (4) use of venom. The sting of the workers is spatulated implying a topical application of the venom on the prey. Large termites were stretched by several workers whose adherence to the substrate is facilitated by well-developed arolia and claws on the legs while others spread venom on the body and carved it up. An adaptation to termite capture was noted with a distribution of tasks between the workers which subdued prey, and those which transported it. In the former case, the workers easily eliminated termite soldiers, successively attacked several termite workers and even captured new individuals while holding the first ones captured between their mandibles before retrieving them all at once. The remaining individuals were retrieved by the transporting workers. Given this particularly effective predatory strategy, we concluded that, under certain conditions, *M. opaciventris* can be used as a biological control agent against termites.

Introduction

During their 100 million years of coexistence, ants and termites have been engaged in a co-evolutionary arms race, with many ant species acting as predators while termites, the prey, have resisted (Hölldobler & Wilson, 1990). Termites have been noted as pests for numerous tropical cultivated plants, particularly in Central Africa with *Microtermes subhyalinus* (Isoptera: Termitidae) causing important damage to sugarcane (Mora et al., 1996). We studied the predatory behaviour of *Myrmicaria opaciventris* workers in order to investigate if they can be used as biological control agents against termites, as this species has very large, polydomous and polygynous colonies and is particularly frequent in zones of human habitation where it spreads out very quickly into newly-cleared areas. The nests are interconnected by trails, trenches and tunnels (up to 460 m long), permitting foraging workers easy access to food sources (vegetal and animal products in the field or in human refuse) far from the nests, so that their impact can be considerable (see Suzzoni et al., 1994; Kenne & Dejean, 1997, 1998, 1999a, b).

We hypothesised that this species has a strong behavioural flexibility owing to the fact that it has a wide range of prey (Kenne & Dejean, 1999b). The most important phenomenon usually noted in ants that hunt termites is the elimination of termite soldiers before attacking and capturing workers (Hölldobler & Wilson, 1990). These parameters are very important considering the energy costs related to subduing and retrieving prey, which determine the hunting strategy (solitary *versus* group attack; Schatz et al., 1997).

We therefore studied the predatory behaviour of *M. opaciventris* workers, using termites of different sizes and different levels of aggressiveness. Due to their importance in predatory behaviour, we also studied the morphology of the sting and pretarsi of the workers. In the latter case, adherence to the substrate enables groups of hunting workers to spread-eagle the prey (see Wojtusiak et al., 1995).

Materials and methods

To study the morphology of the sting and the pretarsi of *M. opaciventris*, we used a Leica Stereoscan 440 scanning electron microscope. Workers were killed by freezing, dehydrated in 95% ethanol, and cleaned in an ultrasonic wave bath, before metallisation with 80% gold and 20% palladium.

Field experiments were carried out in Yaoundé (Cameroon) on four colonies after the following methods were developed through preliminary experiments. We used 30 × 50 cm plywood plates as experimental territories, placed 3 m from the nests and 1 m from the tunnels. Observations were set up one week later once the plates were well integrated into the foraging territories of the ant colonies. Termites of different sizes were used as prey: (1) *Microtermes fuscotibialis* (3 to 4 mm in length) and *Macrotermes bellicosus* (Isoptera: Termitidae) (4 to 6 mm) workers; (2) small *Ma. bellicosus* (6 to 8 mm) soldiers; and (3) large *Ma. bellicosus* (12 mm) soldiers. We also studied the reaction of hunting *M. opaciventris* workers when confronted with groups of 15 *Mi. fuscotibialis* workers on a 3 × 3 cm surface.

Observations using the naked eye were set up during 4 months (2 to 3 observations per day, 2 to 5 days per week). The behavioural sequence was noted from the introduction of the prey (or the group of prey) on the plate of plywood until it was (they were) transported to the nest after being captured. At least 30 min. separated two trials. During preliminary experiments, we noted all behavioural sequences observed in order to establish data sheets that we used during experimentation to note each behavioural act performed, its duration and the part of the prey body seized (see also Dejean & Evreaerts, 1997).

For each kind of prey, a descriptive flow diagram was built from observed data. Throughout the text, values are given as means ± s.d. Percentages (transition frequency between behavioural acts) were calculated from the overall number of cases. Raw data were compared using Fisher's exact-test (StatXact 2.05 software). Appropriate probabilities were adjusted for the number of simultaneous tests, using the sequential Bonferroni procedure (Rice, 1989): at the significance level ($\alpha = 0.05$), statistical probabilities P were determined for k total number of pairwise tests and were ranked from smallest (P_1) to largest (P_k). For independent samples (our situation), the test corresponding to P_i indicated significance if $P_i \leq (1-[1-\alpha]^{1/(1+k-i)})$.

The size variation of prey detected from a distance was compared to that of prey detected by contact using the Mann–Whitney rank sum test, as the normality test failed (SigmaStat 2.03 software).

In order to illustrate the role of venom in short range recruitment, we conducted the following experiment using *Homorocoryphus* sp. grasshoppers approximately 3 cm long. For the control lot, the grasshoppers were artificially numbed; while for the experimental lot, they were first attacked and paralysed by *M. opaciventris* workers then removed with forceps. We used the foraging areas of two colonies; the experiment was repeated 12 times. Each time, we deposited one control and one experimental grasshopper 7 cm from each other. We noted the duration between the introduction of the grasshoppers and their discovery by a foraging worker (antennal contact), then the number of workers stretching these prey one minute after their introduction. Comparisons were made using the Wilcoxon signed rank test.

The duration of captures of the different prey were recorded as the time separating the detection-localisation of the prey to the phase of transport. For comparisons, we first used a Kruskal-Wallis one way ANOVA on Ranks (normality and equal variance tests failed), then pairwise multiple comparison procedures using Dunn's method for unequal samples.

Results

Worker morphology

The total length of the *M. opaciventris* workers varied from 5.1 to 7.9 mm (6.2 ± 0.8 mm; $n = 90$). We noted two important characteristics: (1) the extremity of the pretarsus of each leg has a well-developed arolium and curved claws, permitting the workers to adhere well to different substrates (Figure 1A); and (2) the proximal part of the sting is fluted and its extremity is spatulated

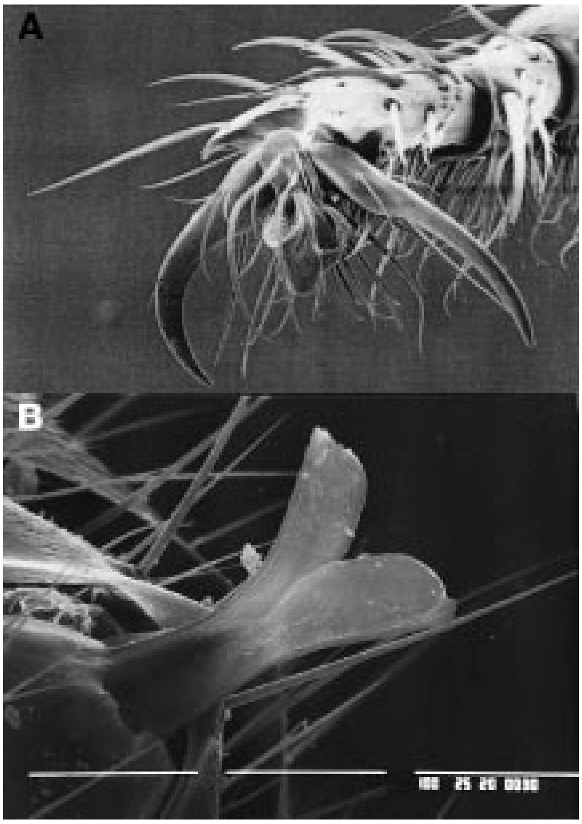


Figure 1. Scanning electron micrographs showing the well developed arolia on the tarsus (A) and the spatula shape of the sting (B) of an *M. opaciventris* worker.

with two lobes (Figure 1B), so that its function is to spread the venom on the prey.

Predatory behaviour (Figures 2–5)

Workers foraged in groups, each individual being permanently surrounded by four to 10 nestmates situated within a range of 20 cm, while moving in a sinuous path, antennae opened widely.

Detection. Isolated termite workers were detected by contact (*Mi. fuscotibialis*: P = 0.024; but a non-significant difference for *Ma. bellicosus*: P = 0.49) whereas soldiers were detected from a distance (*Ma. bellicosus* small soldiers: P = 0.006 and large soldiers: $P = 3.2 \times 10^{-5}$). Groups of *Mi. fuscotibialis* were always detected from a distance (significant differences with all other cases; Table 1). We also noted that prey detected from a distance were significantly larger than those detected by contact (median sizes: 12 mm; $n = 110$ versus 4.3 mm; $n = 59$; Mann–Whitney rank sum test: U = 980; P<0.001).

Table 1. Statistical comparisons between cases of detection from a distance as a function of the kind of prey (percentages of the compared raw data and number of cases: see Figures 4 and 5). 1 = *Microtermes* workers; 2 = *Macrotermes* workers; 3 = *Macrotermes* small soldiers; 4 = *Macrotermes* large soldiers; 5 = Groups of 15 *Microtermes*. α' = corrected significance level using the sequential Bonferroni procedure

Comparisons	α'	P values
1 vs. 2	0.025	0.465
1 vs. 3	0.013	0.012*
1 vs. 4	0.007	0.001*
1 vs. 5	0.005	7×10^{-10}*
2 vs. 3	0.017	0.056
2 vs. 4	0.010	0.007*
2 vs. 5	0.006	0.002*
3 vs. 4	0.025	0.057
3 vs. 5	0.006	2×10^{-4}*
4 vs. 5	0.009	0.003*

* = Significant differences: $P < \alpha'$.

Seizure. When prey was detected from a distance, approach and antennation rapidly followed (duration of approach from 1 to 3 s; mean: 2.3 ± 0.6 s; $n = 141$; antennation from 1 to 3 s; mean: 1.7 ± 0.8 s; $n = 141$). Variants reflecting the behavioural flexibility of the workers principally concerned the zone of the prey body seized. Comparisons of frequencies permitted us to note that small *Mi. fuscotibialis* workers and small *Ma. bellicosus* soldiers were seized at random (P = 0.176 and P = 0.167, respectively), while *Ma. bellicosus* workers were rather seized by the abdomen (P = 0.002), and large *Ma. bellicosus* soldiers by a leg (P = 0.022; Figure 2).

The use of venom. After seizure, large prey were pulled backward or lifted. These two postures permitted the worker to repeatedly flex its gaster with the sting protruded in order to spread venom on the prey's cuticle (these zones then shined). The percentages of cases of venom spreading increased with termite size (*Mi. fuscotibialis* vs. *Ma. bellicosus* workers: P = 0.049; *Ma. bellicosus* workers vs. small soldiers: P = 0.008; but a non-significant difference was noted

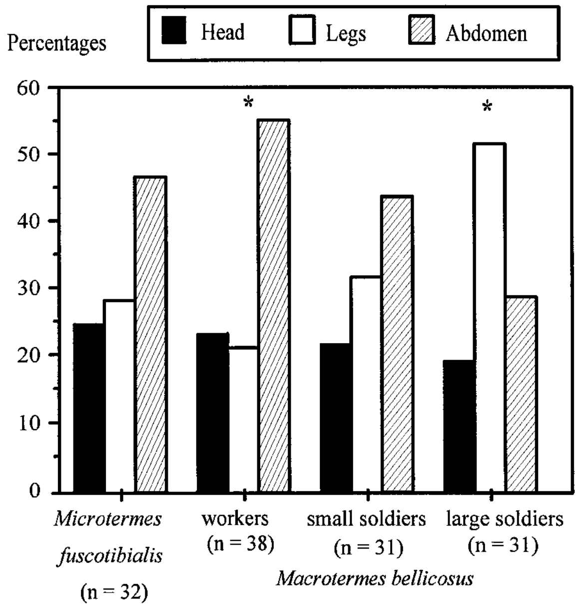


Figure 2. Part of the prey body seized by hunting ant workers. Statistical comparisons between the four classes of prey resulted in a non-significant difference (3x4 contingency table; Fisher exact test: P = 0.23). $*$: significant difference.

between small and large *Ma. bellicosus* soldiers: P = 0.49; Figures 3 and 4).

Short-range recruitment. When confronted with a large prey, the attacking worker momentarily left the prey and seemed excited as it ran in a looping pattern back to the prey. Then occurred a repeated behaviour consisting in seizing the prey again, pulling it backward, releasing it, and making another round trip. This behaviour attracted nestmates foraging within a distance of 10 to 15 cm. An autocatalytic effect was noted as the first recruited workers behaved similarly, resulting in the short-range recruitment of seven to 25 workers in a few seconds.

Venom alone also attracted nestmates, as in the experiment using pairs of grasshoppers, control individuals were discovered significantly later than those of the experimental lot (58.8 $\pm$ 6.5 s vs. 42.1 $\pm$ 2.3; W = $-$50.0 T+ = 8.0; T$-$ = $-$58; P = 0.024) and were stretched by fewer workers one minute after their introduction into the foraging areas (2.3 $\pm$ 07 workers vs. 4.7 $\pm$ 036; W = 57.0; T+ = 61.5; T$-$ = $-$4.5; P = 0.007).

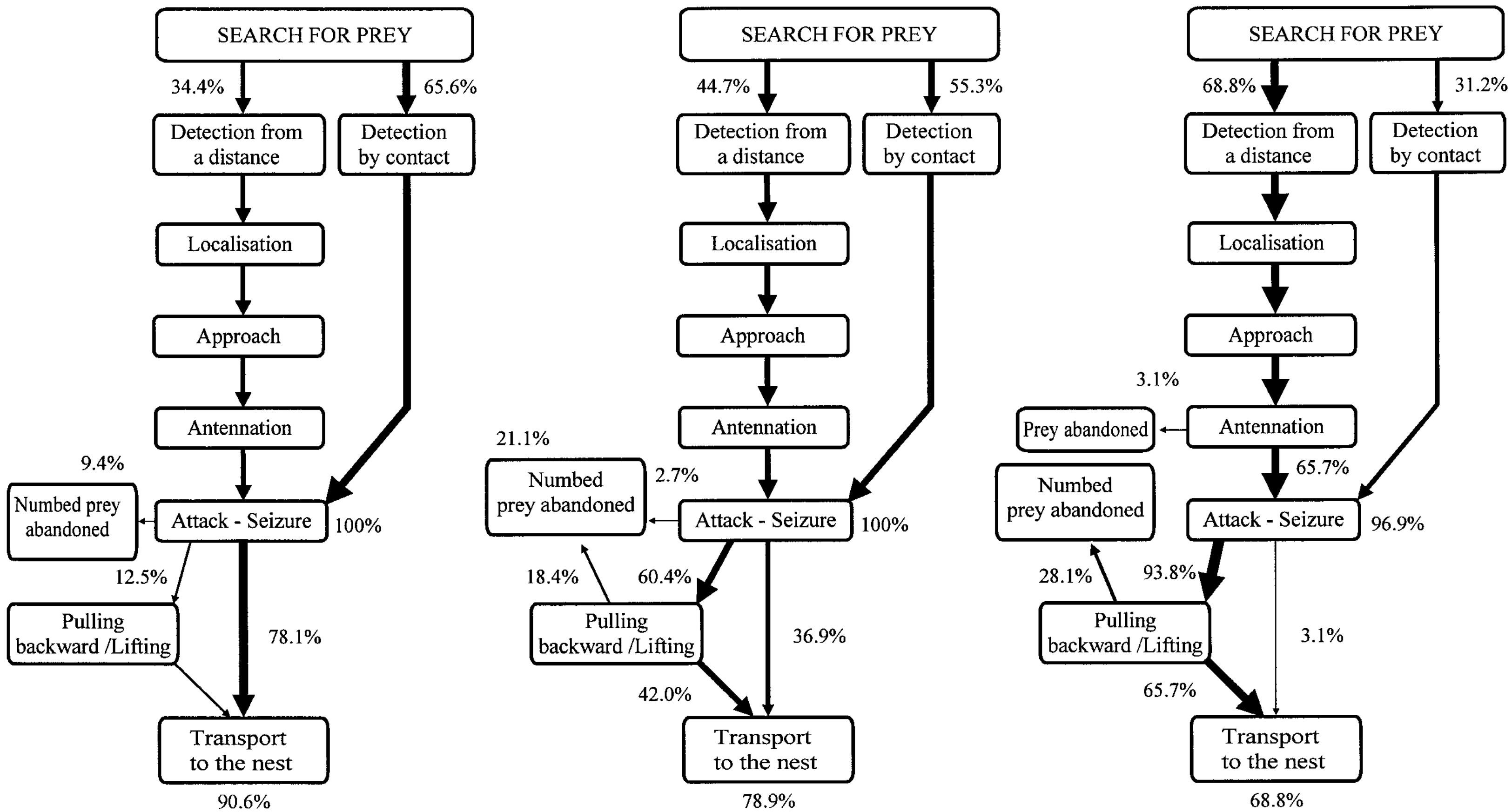
The mean number of recruited nestmates varied from 3 to 9 workers (5.6 $\pm$ 1.8; n = 13) when faced with large *Ma. bellicosus* soldiers (weak variation in the prey's size), in spite of the variability in the number of nestmates situated in the vicinity. However, the solitary capture of a prey concerned a relatively wide range, including very aggressive and agile small *Ma. bellicosus* soldiers.

When confronted with groups of small prey, the beginning of the sequence was similar to that observed with a single, large prey. After pulling backward or lifting the first prey encountered and spreading venom on its body, the ant generally released it (94.4% of the cases) in order to recruit nestmates in the vicinity. Then, the recruiting worker generally attacked another termite (88.9% of cases), so that, with this paralysed prey remaining between its mandibles, it captured a second (19.4%) and even a third (5.6%) before retrieving them all at once. The first recruited workers behaved in the same manner. However, in 75% of the cases the ant transported only its first prey to the nest.

Task distribution. Numerous termite workers, either isolated or in a group, were abandoned by the hunting workers that subdued them (Figures 3 and 5). These termites were then found and retrieved several seconds later by transporting workers foraging in the vicinity, recruited at short-range or encountering the subdued prey by chance.

Retrieval. The short-range recruitment for large prey stopped when a worker seized the prey by an appendage and pulled it backward, triggering the same behaviour by others, so that the spread-eagled prey was rapidly immobilised. The immobilised prey was then carved up on the spot or retrieved. Small pieces of large termite soldiers and entire termite workers were transported individually, while group retrieval was noted for large cut-up pieces of prey or entire large prey (*Ma. bellicosus* large soldiers: 2 to 6 workers; 4.4 $\pm$ 1.0; n = 22). Large *Ma. bellicosus* soldiers were viciously attacked, resulting in a greater percentage of capture from the first than for small soldiers (P = 0.022). Note that large *Ma. bellicosus* soldiers were abandoned in only 3.2% of the cases. For groups of small prey, contrary to the behaviour of the first recruited workers, later recruited individuals retrieved only a single prey as when they arrived only a few prey were available in the experimental situation, due to the effectiveness of the short-range recruitment. As a result, all the termites were quickly captured.

Duration of capture. Differences between the duration of capture of isolated workers and small termite soldiers were not significant (Table 2). On the



A: *Microtermes fuscotibialis* (3 to 4 mm; n = 32 cases)

B: workers of *Macrotermes bellicosus* (4 to 6 mm; n = 38 cases)

C: small soldiers of *Ma. bellicosus* (6 to 8 mm; n = 32 cases)

Figure 3. Flow diagrams of the capture of small termite prey.

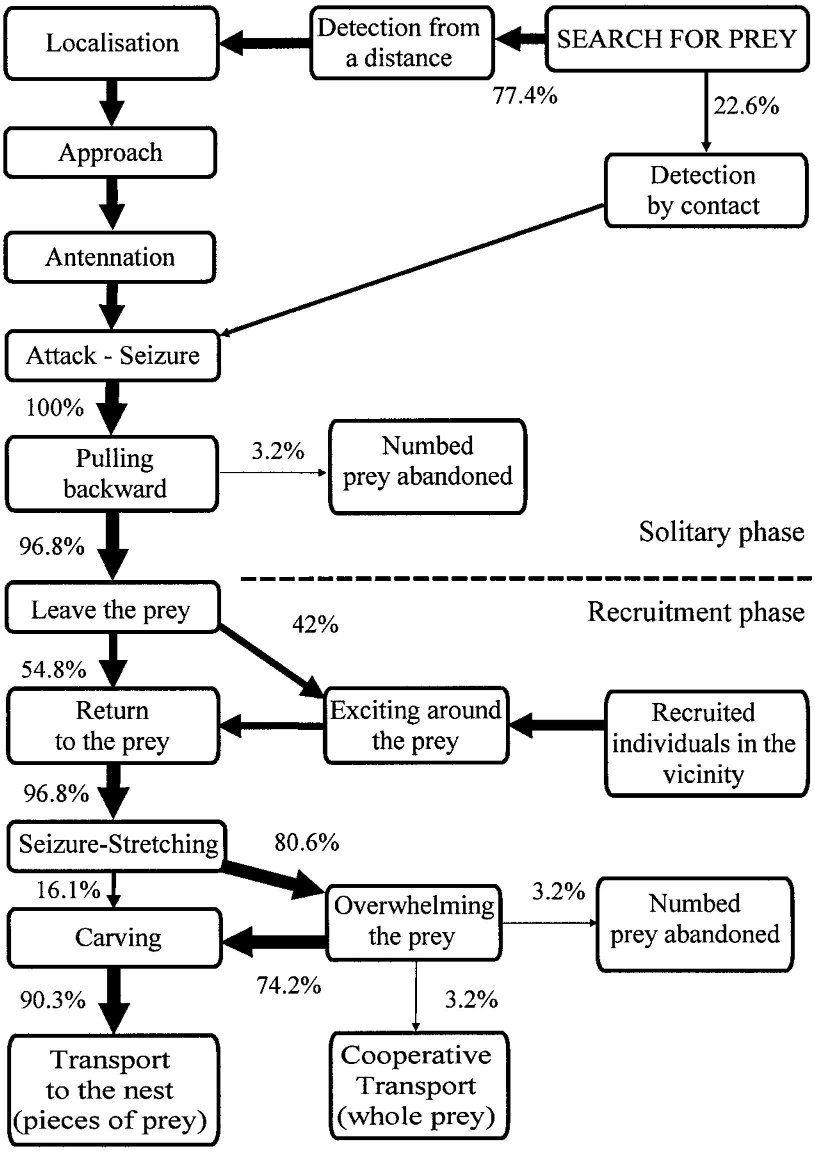


Figure 4. Flow diagrams of the capture of large termite prey.

contrary, the duration of capture of isolated large prey, significantly greater than for isolated small or medium-sized termites or for groups of 15 small *Mi. fuscotibialis* workers, shows that the spread-eagling of prey is long.

Discussion

Four aspects of the predatory behaviour of *M. opaciventris* have particular importance for the predation of termites: worker morphology, group hunting behaviour, short-range recruitment, and different kinds of behaviour previously noted for other ant species.

Worker morphology. Moderately spatulated stings have been described in several Myrmicinae, including *M. eumenoides* (Kugler, 1979, 1986; Kaib & Dittebrand, 1990). The particularity of *M. opaciventris* is that the spatula shape is well pronounced in comparison with all other cases, so that there is no doubt that the venom is deposited on the prey's cuticle during the wagging of the bent gaster. This venom contains

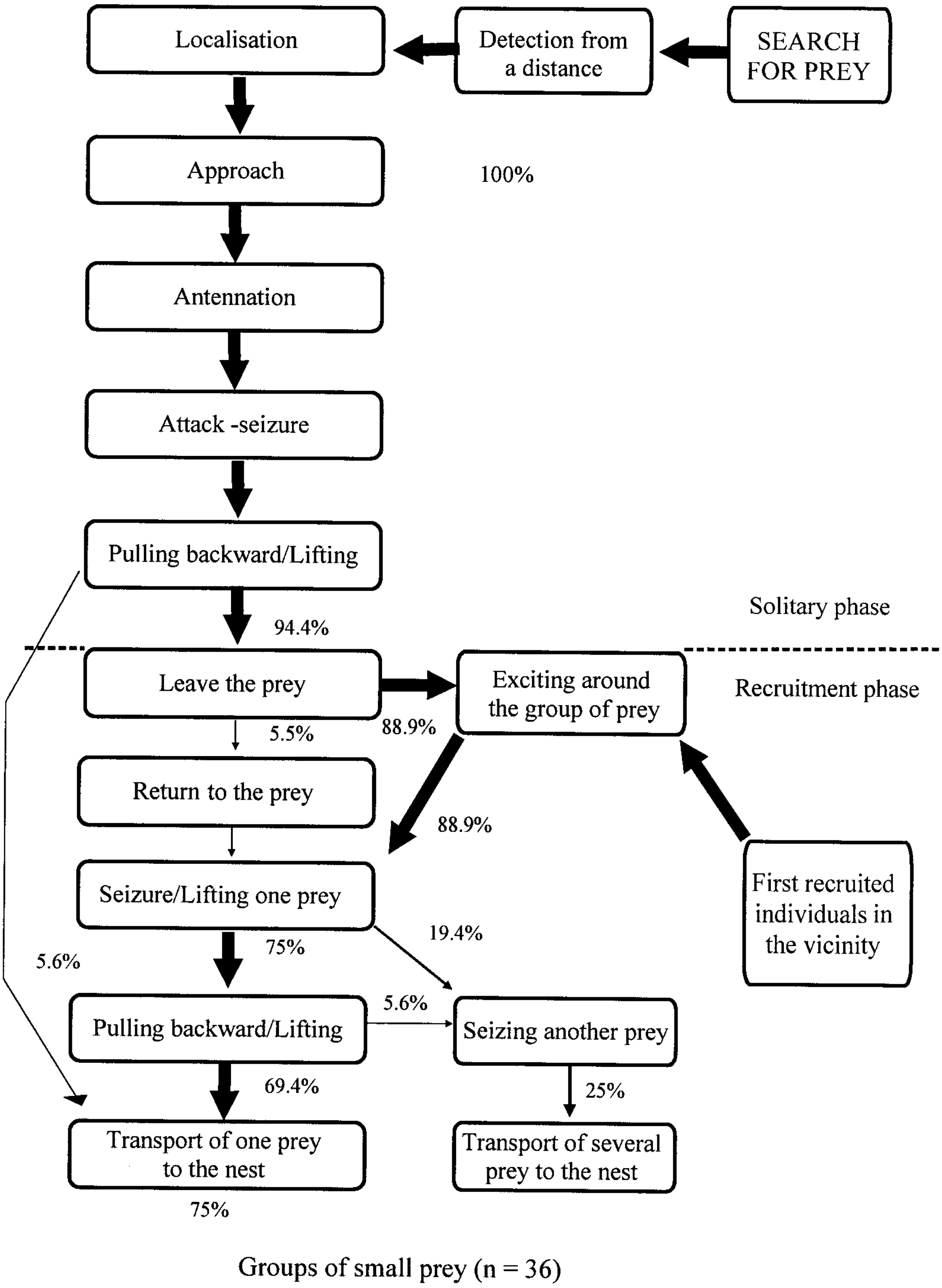


Figure 5. Flow diagram of the capture of groups of 15 small *Microtermes* workers.

Table 2. Comparisons of the duration of captures according to the kind of prey. *A posteriori* ordered tests resulted in significant differences in the median values among the five treatment groups (Kruskal–Wallis multiple test: H = 123.6; df = 4; P < 0.001). Pairwise comparison procedures following rank-based ANOVA using Dunn's method for unequal samples are given (number of cases: see Figures 4 and 5). D = difference of ranks

	Different kinds of prey	Mean ± s.d. (s)	Median duration (s)
1	*Microtermes* workers	37.0 ± 25.2	30.5
2	*Macrotermes* workers	35.9 ± 23.0	40.5
3	– small soldiers	15.6 ± 5.3	15.0
4	– large soldiers	576.8 ± 234.3	600.0
5	Groupes of 15 *Microtermes*	143.6 ± 85.1	125.0

Dunn's tests:

1 vs. 2: D = 2.159; Q = 0.184	2 vs. 4: D = 91.616; Q = 7.726∗
1 vs. 3: D = 28.641; Q = 2.341	2 vs. 5: D = 55.334; Q = 4.862∗
1 vs. 4: D = 89.457; Q = 7.255∗	3 vs. 4: D = 118.098; Q = 9.577∗
1 vs. 5: D = 53.175; Q = 4.473∗	3 vs. 5: D = 81.816; Q = 6.882∗
2 vs. 3: D = 26.482; Q = 2.256	4 vs. 5: D = 36.282; Q = 3.026∗

∗ = P < 0.05.

several monoterpene hydrocarbons, hexanoic nitriles, alkaloids and steroids (Schröder et al., 1996). These substances are known to be very toxic for insects even when topically applied on their cuticle, and we have noted here that this permits single workers to master very aggressive and agile *Ma. bellicosus* soldiers.

The well-developed arolia and claws, previously noted in *Oecophylla longinoda* (Wojtusiak et al., 1995; see also Freeland et al., 1982; and J. Orivel, M.-C. Malherbe & A. Dejean, unpublished, for comparisons of sizes) also play an important role during large prey spread-eagling and retrieval. The latter species spread-eagles even small prey and does not use venom during predation (Dejean, 1990; Hölldobler & Wilson, 1990), so that prey are killed only by stretching. In this study certain *M. opaciventris* workers used their venom and carved up prey on the spot.

Particularities of the group hunting behaviour. Group hunting is considered to be more evolved than solitary hunting because it implies co-operation between workers and enables the rapid exploitation of a greater range of prey sizes (Schatz et al., 1997). One of the most evolved cases corresponds to 'absolute territories' described for *Oecophylla*, dominant arboreal ants that exclude competitor colonies from their territories. Workers stalk the entire territory day and night, each always surrounded by nestmates able to perceive a pheromone used in short-range recruitment in order to then spread-eagle the prey (Hölldobler & Wilson, 1990). This behaviour permits very large prey to be overwhelmed (Wojtusiak et al., 1995). *Myrmicaria opaciventris*, that can also capture very large prey (Dejean et al., 1999), presents similarities with *Oecophylla*: large, polydomous colonies, workers never foraging far from a nest, trench or tunnel (can be compared to the territory of an arboreal ant), nor from their nestmates situated within reach of short-range recruitment (Kenne & Dejean, 1999a). Nevertheless, a major difference exists, as all kinds of prey, even large and aggressive, are first attacked by a single worker.

The collective retrieval of large prey, well known in army ants and in *Oecophylla*, permits the prey to be rapidly moved away from competitors. Like army ants, *M. opaciventris* workers carve up large prey at the site of combat, while *Oecophylla* retrieve entire prey, even when very large (Hölldobler & Wilson, 1990; Gotwald, 1995; Wojtusiak et al., 1995).

Short-range recruitment. Short-range recruitment depends on chemical, visual and acoustical cues, as noted for *M. brunea*, *M. eumenoides* and *Ectatomma ruidum* (Kaib & Dittebrand, 1990; Baumann & Kaib, 1994; Rastogi et al., 1997; Schatz et al., 1997). In *M. opaciventris*, short-range recruitment cannot be imputed to prey resistance as noted for certain other ants, because it is triggered by the perception of several small prey (Detrain & Deneubourg, 1997; Schatz et al., 1997). Recruited workers overwhelm the prey, a behaviour well described in army ants and *Oecophylla*

(Dejean, 1990; Hölldobler & Wilson, 1990; Gotwald, 1995). Such recruitment also provides a significant advantage in the course of interspecific competition (see de Biseau et al., 1997).

Short-range recruitment intervenes later in the behavioural sequence compared to other species' group hunting, for which it is noted from detection to prey seizure. This characteristic may be correlated to the very powerful venom of this species. Therefore, whatever their size, prey were spread with venom, limiting their mobility (easily found by recruited workers) and aggressiveness, so that we never noted prey escape.

Adaptations to hunting termites. Large termite soldiers, that defend gallery entrances, are a particular target of *M. opaciventris* workers. They are detected from a distance and subdued from the first at greater percentages than termite workers, permitting easier access to termite workers (Hölldobler & Wilson, 1990 and papers cited therein). Like army ants, *M. opaciventris* eliminates large soldiers by spread-eagling, while workers of termitophagous Ponerinae can singly kill them. *Myrmicaria opaciventris* workers are able to attack new termite workers with previously captured ones between their mandibles, then to retrieve them all at once (Hölldobler & Wilson, 1990; Dejean et al., 1993).

We recorded arguments suggesting that hunting workers are able to perceive a mortality risk associated with the type of prey before seizure. Hunting workers seize termite soldiers (large and aggressive prey) without being injured, as do other ants specialised in preying on termites or confronted with large prey (Dejean et al., 1990, 1993; Nonacs, 1990; Schatz et al., 1997).

In conclusion, *M. opaciventris* already noted as particularly efficient predators during field experiments (Kenne & Dejean, 1999b), captured and retrieved all of the termite individuals tested during the present study. Given such efficiency and flexibility, the use of this species as a biological control agent against termites can be proposed. However, its use should be accompanied by precautions because this species attends Hemipterans (Kenne & Dejean, 1999b), some of which could be vectors of plant diseases.

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