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Mandible strike: The lethal weapon of *Odontomachus opaciventris* against small prey

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Abstract

In order to study both the hunting efficiency and the flexibility of their predatory behavior, solitary hunters of the trap-jaw ant *Odontomachus opaciventris* were offered small prey (termites, fruit flies and tenebrionid larvae), presenting different morphological or defensive characteristics. The monomorphic hunters showed a moderately flexible predatory behavior characterized by short capture sequences and a noteworthy efficiency of their mandible strike (76.7–100% of prey retrievals), even when presented with *Nasutitermes* soldiers. Contrary to most poneromorph ants, antennal palpation of the prey before the attack was always missing, no particular targeted region of the prey's body was preferred, and no 'prudent' posture was ever exhibited. Moreover, stinging was regularly performed on bulky, fast moving fruit flies, very scarcely with sclerotized tenebrionid larvae, but never occurred with *Nasutitermes* workers or soldiers despite their noxious chemical defense. These results suggest that, whatever the risk linked to potentially dangerous prey, *O. opaciventris* predatory strategy optimizes venom use giving top priority to the swiftness and strength of the lethal trap-jaw system used by hunters as first strike weapon to subdue rapidly a variety of small prey, ranging from 0.3 to 2 times their own body size and from 0.1 to 2 times their weight. Such risk-prone predatory behavior is likely to be related to the large size of *O. opaciventris* colonies where the death of a forager might be of lesser vital outcome than in small colony-size species.
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1. Introduction

Many insect predators specialized in capturing leaf-litter arthropods – which may have evolved some type of defense or escape response as collembolans, flies, crickets, centipedes, millipedes, termites or ants – depend on speed to capture them. To enhance their predatory efficiency and reduce the time and energy necessary to overwhelm these prey, predators have evolved a large variety of morpho-physiological and mechanical adaptations ranging from mandible specialization (Manton and Harding, 1964; Prestwich, 1984) or raptorial grasping forelegs (Corrette, 1990; Gorb, 1995) to powerful stings and venoms (Schmidt et al., 1980; Blum, 1981; Schmidt, 1982; Piek, 1993).

In the ants, highly specialized mandibles with different structural properties are particularly frequent in poneromorph ants, and Wheeler (1936) listed 20 genera for this group alone in which such a mandible specialization occurred. Along with the slightly asymmetric, pitchforked mandibles of the genus *Thaumatomyrmex* (Brandão et al., 1991), the long, straight mandibles armed with numerous teeth of *Amblyopone* and *Mystrium* (Gotwald and Lévieux, 1972; Gronenberg et al., 1998) or the elongate, weakly curved mandibles crossing each other of *Plectroctena* (Dejean et al., 2001, 2002), the powerful mandibles and their associated snapping mechanisms found in the tribes Odontomachini, Dacetini and Myrmoteratini, are certainly among the most conspicuous of these structural specializations. All the species of these three ant tribes (belonging to three different subfamilies: Ponerinae, Myrmicinae and Formicinae, respectively), have evolved independently a 'trap-jaw' mechanism that allows them to close their mandibles almost instantaneously (Creighton, 1930; Brown and Wilson, 1959; Brown, 1976, 1978; Dejean, 1982; Moffett, 1986a). The com-

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parative study of this trap-jaw mechanism in different species (Barth, 1960; Gronenberg et al., 1993; Gronenberg, 1995a,b, 1996; Gronenberg and Ehmer, 1996) showed that the fast strike, at a speed much higher than that allowed by muscular contraction (about 0.13 ms in *O. bauri*, cf. Patek et al., 2006), ensues both from the storage of mechanical energy due to the preceding contraction of a slow mandible closer muscle, and from the sudden release of some structure (labrum or mandible protrusion, according to the species) functioning as a latch, that was locking the jaws in an opened position: 90° in most of the Dacetini (but up to 180° and more in *Strumigenys* and *Daceton*, Dejean, personal communication), 180° in *Odontomachus* and *Anochetus*, and up to 280° in *Myrmoteras*. Such a reflex catapult mechanism is monosynaptically controlled by giant motor neurons, so-called trigger muscles specialized for high-speed contraction and the stimulation of long trigger hairs located on the inner edge of the mandibles (Just and Gronenberg, 1999). The powerful resulting snap allows an increase in the efficiency of prey capture by hunting workers, especially for soft-bodied prey which are stunned and even killed by the strike strength (Fowler, 1980; Dejean and Bashingwa, 1985). However, one can wonder about the limits of such a technique in securing a successful attack of alternative prey with different characteristics, namely prey with hard cuticle protection or defensive mechanisms.

Though the genus *Odontomachus* is well represented in the tropics and neotropics, few studies have focused on its predatory behavior and even less on the degree of flexibility of this behavior depending on prey characteristics. Some dietary diversity has been reported in the genus: *O. bauri* exploits secretions from extrafloral nectaries (Schemske, 1982) and *O. troglodytes* tends Hemiptera for honeydew (Evans and Leston, 1971) and exhibits a specialized behavior related to sugary liquid collection (Lachaud and Dejean, 1991), whereas *O. laticeps*, *O. minutus* and *O. chelifer* commonly transport *Calathea* or *Clusia* seeds to their nest and feed on the lipid droplets contained in the arils which function as elaiosomes (Horvitz and Beattie, 1980; Passos and Oliveira, 2002). However, all the *Odontomachus* species are carnivorous and are generally considered as typical predatory ants mostly specialized on termites even if they can capture a large variety of small ground-dwelling arthropods relying essentially, as most other predatory ants, on their powerful sting (Wheeler, 1900; Ledoux, 1952; Brown, 1976; Briese and Macauley, 1981; Dejean, 1982; Ehmer and Hölldobler, 1995).

Given the likely limitation imposed both by the morphology of their specialized mandibles and the distinctive catapult-powered trap-jaw mechanism, the hunting behavior of *Odontomachus* foragers might depend on the characteristics of the prey encountered. Moreover, due to the larger size of the colonies of some *Odontomachus* species by comparison with other poneromorph species (Colombel, 1971a), and considering that the adaptive value of foraging strategies could vary according to colony size (Beckers et al., 1989; Thomas and Framenau, 2005; Detrain and Deneubourg, 2006), one can wonder if individual workers of such large colonies could be more prone to use risky strategies during hunting behavior. The present study was aimed at both evaluating the flexibility of the predatory behavior and studying the hunting efficiency of the foragers of an *Odontomachus* species, *O. opaciventris* Forel, faced with different types of small prey that present different morphological or defensive characteristics. We thus presented the ants with three types of small prey likely to be encountered in their natural diet or commonly used in experimental studies on ant predatory behavior and allowing comparison with other ant species yet studied, and we examined whether the predatory responses against small prey varied according to the presence or absence of chemical defenses (termites), rapid escape response (fruit flies), or sclerotized exoskeleton (tenebrionid larvae).

2. Materials and methods

Odontomachus opaciventris is a neotropical species with dark brown or black medium to large workers (10–13 mm) distributed in Mexico, Guatemala, Costa Rica, Panama and Colombia (Forel, 1899; Brandão, 1991; Longino, 1998; MacKay and MacKay, 2004). In the Soconusco region of Chiapas in Mexico, *O. opaciventris* is not infrequent in cocoa and coffee plantations (Lachaud and García Ballinas, 2001) where workers forage individually on the soil surface and within leaf-litter, mainly at dusk or at dawn but also during the day (De la Mora, unpublished data). The queenright monogynous colonies commonly nest in rotting tree trunks and in the soil beneath. Nest density is low but colony size commonly exceeds 1000 individuals and can reach up to 10,000 adults along with ca. 2000 larvae and cocoons (Lachaud, unpublished data), that is, much larger than the mean colony size of the majority of known poneromorph ant species (Beckers et al., 1989; Hölldobler and Wilson, 1990; Peeters, 1997). Feeding requirements necessary to secure the survival of colonies of such a size are likely to have an influence on the predatory strategy used by the workers, which makes this species an interesting model to study the flexibility of its predatory behavior.

The colony of *O. opaciventris* used in this study was collected on December 2005 at the community "2 de Mayo" located in Cacahoatan, Chiapas, where several colonies have been located previously. Adults (workers and sexuals), pupae, and larvae were separated in the laboratory. As some size variability has been previously noticed among *O. opaciventris* workers, during preliminary observations (De la Mora, unpublished data), head width between the eyes, thorax length and mandible length were measured on a sample of 150 workers to determine their morphometric variation range, and an additional set of 20 workers were weighed and measured for total length.

The original colony, consisting of one queen, 39 alate females, 14 males, 1468 workers, 696 pupae and 224 larvae, was subdivided and a reduced experimental fraction (one queen, 200 workers, 30 pupae and 30 larvae) was installed in an artificial nest. The nest was established in a plastic box (30 cm × 20 cm × 15 cm) with sides coated with Fluon® to prevent escape, provided with both pieces of rotting wood to facilitate nesting and water sources (glass vials, 2.2 cm in diameter × 15 cm in length, filled with water trapped by a cotton plug). It was connected with a flexible plastic tube (1.25 cm in diameter × 70 cm in length) to a second plastic box (50 cm × 50 cm × 14 cm) used as a foraging arena. The colony

was daily provided with larvae and sterile adults of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) and with honey and apple pulp as sugary sources, deposited in the foraging arena. As a common procedure in arthropod predatory studies (Dejean, 1982; Wigger et al., 2002; Dangles et al., 2006), food supply was suspended 2 days before every test to homogenize levels of hunger among individuals and to increase the motivation of the workers to forage outside the nest. The whole set-up was kept in a room at a temperature of 25 ± 2 °C, and a relative humidity of 80%.

Even if no precise data on the natural prey captured by *O. opaciventris* hunters are yet available, some termite items (workers and, less often, soldiers of *Nasutitermes* sp.) were occasionally seen to be retrieved to the nest during field observations (De la Mora and Lachaud, unpublished data) and, therefore, are likely to constitute a significant part of their natural diet, since most *Odontomachus* species are termite predators. Therefore, the basic predatory behavioral sequence of *O. opaciventris* hunters was determined using living workers of the termite *Nasutitermes* sp. (size: 4.4 ± 0.1 mm; weight: 4.6 ± 0.1 mg [mean ± S.E.M., $n = 20$]) which were collected in a cocoa plantation in the vicinity of the ants' collecting site. Subsequently, the possible existence of behavioral flexibility in the predatory sequences was studied analyzing the behavior of hunters faced with three other kinds of prey representative of the different types of protection likely to be used by small prey:

(1) Prey protected by a more sclerotized cuticle: tenebrionid beetle larvae of *Tenebrio molitor* L. from a laboratory culture (size: 15.3 ± 0.2 mm [range: 13.0–18.0 mm], weight: 34.8 ± 1.5 mg [range: 22.6–49.0 mg], $n = 30$). This kind of cylindrical-shaped prey has commonly been used in predatory behavior studies performed on various ant species (see Dejean and Bashingwa, 1985; Schatz et al., 1997; Dejean et al., 1999), which facilitates comparisons.
(2) Prey with soft cuticle comparable to that of *Nasutitermes* workers: sterile tephritid fruit flies, *Anastrepha obliqua* (Macquart), from the "Moscafruit mass-rearing facilities (SAGARPA-IICA)" located in Metapa de Dominguez, Chiapas, and different from that supplied in the laboratory diet. Although tephritid fruit flies have not actually been identified among the scarce observations of prey items collected by natural colonies, in the field fruit flies adults of both *C. capitata* and *A. obliqua* emerge from pupae buried beneath the soil and are likely to be found and captured by *O. opaciventris* workers under natural conditions. Preceding these tests, the wings of each fruit fly were cut after a 4-min chilling of the individuals, to prevent them from escaping out of the foraging arena. However, the dealated flies were still able to perform short jumps to attempt escaping the hunting ants. Because *A. obliqua* females have a large ovipositor that could obstruct their capture and transport by the ants, both males (size: 6.8 ± 0.1 mm, weight without wings: 12.2 ± 0.2 mg, $n = 20$) and females (size: 8.2 ± 0.1 mm, weight without wings: 12.4 ± 0.3 mg, $n = 20$) were tested.
(3) Prey displaying chemical defenses and representing an increased risk for the attacking ant. We used soldiers of the same previously tested *Nasutitermes* species (size: 3.8 ± 0.2 mm, weight: 2.5 ± 0.1 mg, $n = 20$). Soldiers of this termite genus project a sticky and noxious substance known to have a powerful repellent effect on ants (cf. Collins and Prestwich, 1983; Prestwich, 1984).

Preliminary observations (visual or video recorded) were performed to establish the list of the behavioral acts involved in a predatory sequence and allowed us to identify 13 distinct behavioral acts (see Section 3). For each kind of prey, 30 complete predatory sequences were video-recorded – starting with "prey search" and ending with "prey retrieval to the nest" or with "abandon" – with no time limitation with regard to the realization of the sequence. All tests were performed between 8:00 a.m. and 12:00 p.m., and prey were always individually deposited at the center of the foraging arena (25 cm from the nest connecting tube entrance). The behavioral sequences were recorded using a video camera (Sony DCR-TRV530) situated above the foraging arena; behavioral transcription and data analysis were realized with the software "The Observer" (version 5.0, Noldus). The handling time was recorded. It started at the moment the prey was detected and localized by an ant – characterized by reorientation toward the prey, slowing of movement, and extension of the antennae toward the prey in parallel position – and ended when the prey was lifted up by the hunter for transport to the nest. The prey's body part targeted during the ant attack was also recorded. In the case of sequences for which several hunters were involved, only the behavior of the first hunter was considered. For each type of prey, a flow diagram was devised from observational data. Transition frequencies between behavioral acts were calculated based on the overall number of transitions between each individual behavioral act (Schatz et al., 1997). Because data did not support normality, a non-parametric Kruskall–Wallis test was performed (Statistics 2003 software) for possible differences in the handling time duration among the different types of prey, and a Wilcoxon sum rank test for each pair comparison.

3. Results

3.1. Morphometric variation among workers

As for other species of the genus, *O. opaciventris* workers showed a small size and weight variation: mean size (±S.E.) = 11.6 ± 0.2 mm [range: 9.2–12.5 mm, $n = 20$]; mean weight = 23.6 ± 0.1 mg. A more detailed measurement of some variables on 150 workers gave similar results: head width between the eyes = 1.84 ± 0.01 mm [range: 1.49–2.18 mm]; thorax length = 3.73 ± 0.02 mm [range: 3.17–4.65 mm]; mandibles length = 1.75 ± 0.01 mm [range: 1.29–2.18 mm]. As an example, plotting thorax length against head width showed an isometric relation between both variables (Fig. 1); moreover, for both variables the distribution curves were clearly unimodal, which confirms the monomorphic status of this species.

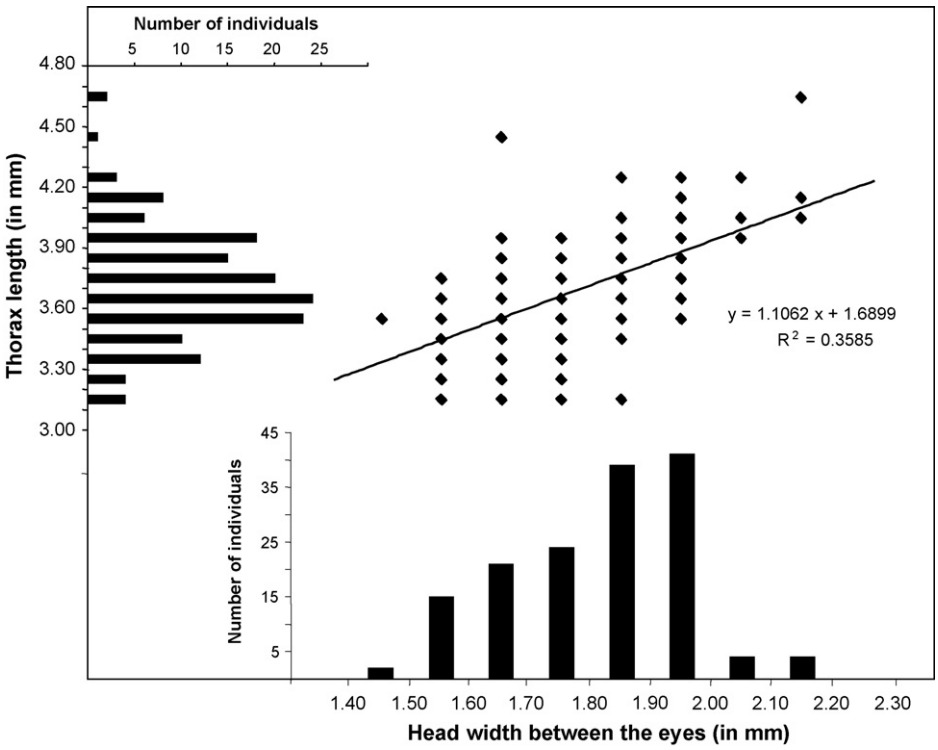

Fig. 1. Determination of the unimodal distribution of thorax length and head width (histograms) and of the isometric relation between both variables (scatter of points) for a sample of 150 *Odontomachus opaciventris* workers.

3.2. Predatory sequences

3.2.1. Predatory behavioral acts

A total of 13 different predatory behavioral acts could be distinguished during the hunting sequences performed by *O. opaciventris* workers. Not all of them were used in a same sequence but only a combination of some of them, according to the type of prey provided.

- Search for prey: the ant walked randomly at a moderate speed, jaws widely opened (180°), the antennal scape forming an obtuse angle with the lateral head margin and flagellae pointing ahead and nearly parallel.
- Detection: the ant repositioned the longitudinal axis of its body in direction to the prey and walked directly toward it, antennae outstretched ahead; jaws remained opened at 180°.
- Antennal contact: the ant did contact the prey with its antennae which eventually allowed an ultimate repositioning of its body with regard to the prey before the attack. This behavior was very brief (about 1 s), *O. opaciventris* workers extending and withdrawing their antennae in a very fast movement which could not be mistaken for "antennation", consisting in rapid shakes of the antennal funiculus as reported between workers of *O. affinis* (Brandão, 1983) and *O. simillimus* (van Walsum et al., 1998), or for "antennal palpation", a behavior allowing prey probing during various seconds as described in *O. troglodytes* (Dejean and Bashingwa, 1985) and *Anochetus traegaordhi* (Schatz et al., 1999).
- Skirting around: on having detected the prey, the hunting worker did not walk forward but changed its direction and slowly turned around the prey, avoiding any physical contact.
- Mandible strike: the sudden synchronized closing of the ant jaws upon the prey produced an audible snap used as the reference of the occurrence of the mandible strike; when such a click was not produced, the mandible closing was only considered as a simple seizure.
- Prey loss: when the ant did not provide a successful blow to knock out the prey on the spot, the prey could be propelled backward through the air for several centimeters and the ant lost its location.
- Intensive search: on having lost the prey, the hunting worker became very active and began a spiral shaped search characterized by a high sinuosity of the food searching path and a high speed at which the ant moved.
- Prey lifting: the ant picked up the stunned prey from the soil, lifting it up between its jaws; in some occasions, the ant stroke was so powerful that the partially crushed prey remained hung between its jaws and in this case the mandible strike was directly followed by the transport without any prey lifting.
- Stinging: the ant seized and maintained the prey between its jaws at the moment of the mandible strike, bent the tip of its abdomen and stung the prey through an intersegmental membrane. In some rare instances, stinging occurred after a previous lifting of the prey while it was hung between the ant jaws.

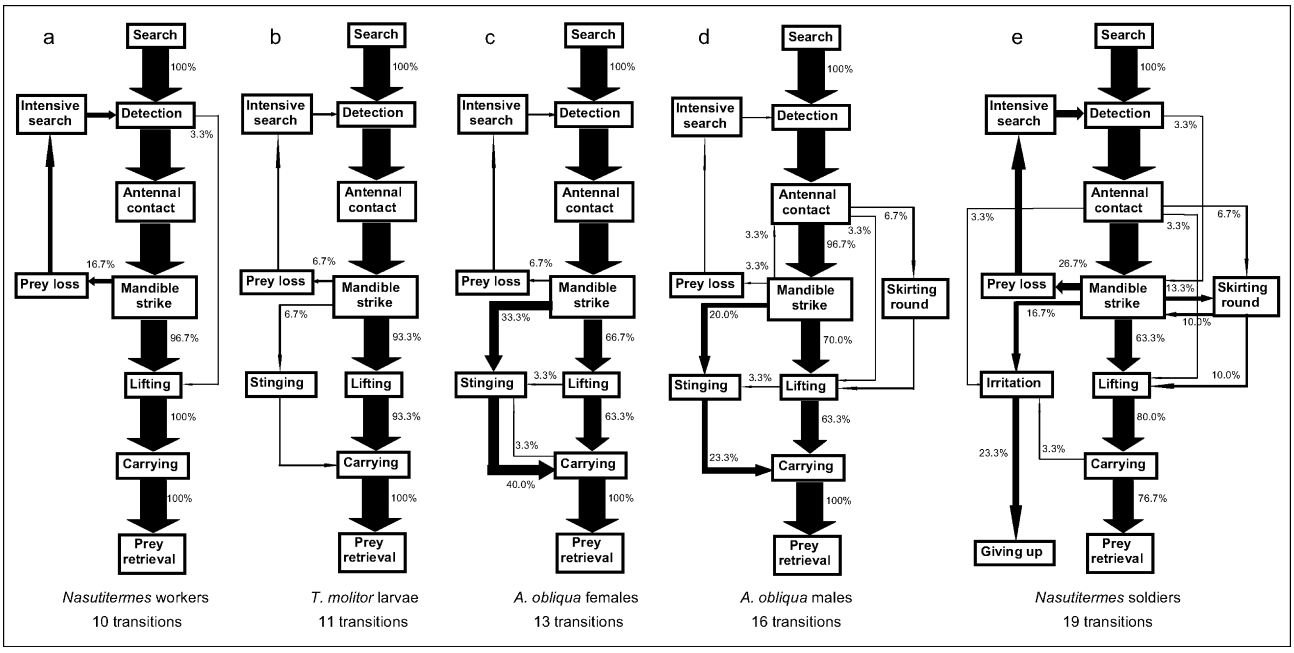

Fig. 2. Flow diagrams representing the specific predatory sequence exhibited by *Odontomachus opaciventris* hunters faced with: (a) *Nasutitermes* sp. workers (size: 4.4 ± 0.1 mm; weight: 4.6 ± 0.1 mg; $n = 30$); (b) *Tenebrio molitor* larvae (size: 15.3 ± 0.2 mm [range: 13.0–18.0 mm], weight: 34.8 ± 1.5 mg [range: 22.6–49.0 mg]; $n = 30$); (c) dealated *Anastrepha obliqua* females (size: 8.2 ± 0.1 mm, weight without wings: 12.4 ± 0.3 mg; $n = 20$); (d) dealated *A. obliqua* males (size: 6.8 ± 0.1 mm, weight without wings: 12.2 ± 0.2 mg; $n = 20$); (e) *Nasutitermes* sp. soldiers (size: 3.8 ± 0.2 mm, weight: 2.5 ± 0.1 mg; $n = 20$). For each kind of prey, 30 repetitions were completed and the percentage values were calculated based on the overall number of transitions between each individual behavioral act. The thickness of the arrows is proportional to the percentage values.

- Irritation: on some occasions, after a contact with the prey, the hunter rubbed its jaws against the soil and cleaned furiously its antennae with its forelegs.
- Carrying: the prey was carried in the ants' mandibles, always in a frontal position.
- Prey retrieval: the hunting worker, carrying the prey, got to the entrance of the exit tube and returned to the nest.
- Giving up: during the predatory sequence, the ant suddenly turned away from the prey and abandoned it.

3.2.2. Typical predatory sequence

When faced with a worker of *Nasutitermes* sp., *O. opaciventris* hunters exhibited a predatory sequence reduced to a minimum, that is, merely constituted of a nearly direct succession of the seven main behavioral acts: search for prey, detection, antennal contact, mandible strike, prey lifting, carrying and prey retrieval (Fig. 2a). The number of observed transitions between behavioral items was small (only 10). Detection and antennal contact occurred almost simultaneously. On five occasions, the ant mandibles struck the prey which was propelled backward for several centimeters. The hunting worker immediately undertook an intensive search, rapidly found again the prey and resumed the predatory sequence which always resulted in prey capture. In one instance, antennal contact and mandible strike were even unnecessary: the prey was easily picked up immediately on its detection. All *Nasutitermes* workers tested were retrieved to the nest.

3.2.3. Prey protected by a more sclerotized cuticle

Faced with *T. molitor* larvae, the predatory sequence of *O. opaciventris* was basically the same as that used against *Nasutitermes* workers (Fig. 2b) with only 11 observed transitions between behavioral acts. No particular protective posture (see Dejean and Bashingwa, 1985; Dejean et al., 1990; Schatz et al., 1997) was ever exhibited by the hunters despite the struggling movements of the prey which was stung only on two occasions without previous prey lifting. Prey loss occurred twice but the sequence was resumed and ended by prey capture in both cases. All tenebrionid larvae tested were retrieved to the nest.

3.2.4. Prey with soft cuticle comparable to that of termite workers

For both females and males of *A. obliqua* the predatory sequence of *O. opaciventris* (Fig. 2c and d) remained essentially the same as against the previous tested prey. However, the number of observed transitions between behavioral acts slightly increased (up to 13 and 16, respectively) due to some uncommon occurrences (like stinging after a previous prey lifting or after carrying) and the display, on two occasions with male flies, of a new behavior – skirting around the prey – that allowed the hunting worker to reposition itself before lifting the prey for transport. Stinging was more frequent against both female and male flies than against *T. molitor* larvae (33.3% and 20% of the cases, respectively, vs. 6.7%) but the difference between both sexes was not statistically significant ($\chi^2 = 2.04$, $p > 0.05$). All male and female flies tested as prey were retrieved to the nest.

3.2.5. Prey having chemical defenses

Despite the noteworthy lack of any stinging behavior, the predatory sequence exhibited against *Nasutitermes* soldiers was the most complex (Fig. 2e) with 12 different behavioral acts and 19 observed transitions between them. Skirting around the prey, occurring after mandible strike or even after antennal contact, was quite common (20% of the cases) and resulted in a repositioning of the hunter leading with the same probability to another mandible strike or to prey lifting. Prey loss and intensive search after mandible strike were frequent (26.7%) but direct prey picking up and transport without previous mandible strike was still seen on rare occasions. In various instances (23.3%), the hunter exhibited an irritation behavior after a direct physical contact with the termite soldier occurring during antennal contact, mandible strike or prey transport. All these cases led to a prey giving up, but up to 76.7% of all termite soldiers provided were still retrieved to the nest.

3.2.6. Comparisons between the different prey

Whatever the type of prey, mandible strike occurred indiscriminately ($\chi^2 = 0.97$, $p > 0.05$) whether on the head (or the first third part of the body in the case of *T. molitor* larvae) or on any other part of the body. Moreover, prey loss followed by intensive search did not appear to be linked to the prey's body part targeted during the attack ($\chi^2 = 0.13$, $p > 0.05$) and stinging (limited to the cases of fruit flies and *T. molitor* larvae) occurred also totally independently from the target of the attack ($\chi^2 = 0$, $p > 0.05$). However, in the case of termite soldiers, most of the frontal attacks (5 out of 9 cases) led to an irritation behavior and to a prey giving up, whereas such a behavior was rare after a non-frontal attack (1 occurrence out of 20 cases).

Handling time, that is, the time necessary for prey overwhelming (from detection to carrying), varied according to the type of prey (Kruskal–Wallis: $H_{(4, 145)} = 25.25$, $p < 0.001$; cf. Fig. 3). This variable was significantly higher for termite soldiers (14.6 ± 0.2 s) than for termite workers (4.9 ± 0.5 s; Wilcoxon rank sum test: $S = 4.39$, $p < 0.001$) or female (5.4 ± 0.4 s) and male (5.0 ± 0.5 s) flies (S = 3.46 and 4.27, respectively, $p < 0.001$ in both cases). Handling time for both fly sexes were similar, whereas the value obtained for *T. molitor* larvae was intermediate (7.3 ± 1.1 s) and did not differ significantly from that performed for termite soldiers ($S = 2.45$, $p > 0.05$) or the other prey.

4. Discussion

One of the most significant factors involved in the fitness of animals for escaping their predators is speed. Among the fastest movements reported for arthropods in the literature are the escape responses of various insects as fleas and locusts which present jump impulses lasting 50 ms and 25–30 ms, respectively (Bennet-Clark and Lucey, 1967; Brown, 1967; Bennet-Clark, 1975), of springtails which show a reflex latency between touch and escape jump ranging from 50 ms to 10 ms (Christian, 1979; Bauer, 1982), of flea-beetles which show take-off times varying from 7.7 ms to 1.1 ms (Brackenbury and Wang, 1995), of spittle bugs with take-off time averages of about 2 ms (Burrows, 2006; Burrows et al., 2007), or of the moss mites which can catapult themselves in a backward leap with a take-off time of about 0.5 ms (Wauthy et al., 1998). In response, numerous predators have evolved specific morphological tools and hunting strategies based on the use of very high speed attack movements, as fast run in the orthopteroïd hunter wasp *Liris niger* (Gnatzy and Kämper, 1990), or very quick strikes, as is the case for different collembolan specialized hunters like the carabid beetle *Loricera pilicornis* which can strike its prey with its specialized antennae in 12 ms (Bauer, 1982), and the staphylinid beetles of the genus *Stenus* which can protrude their sticky labium in 1–5 ms (Bauer and Pfeiffer, 1991; Betz, 1998), or for some specialized ants as the termite hunter *Odontomachus bauri* which can close its mandibles in about 0.13 ms to stun a prey (Gronenberg et al., 1993; Patek et al., 2006). Similar high speed attack mechanisms or tactics used to minimize time-to-capture of fast moving prey are widespread among vertebrates (fishes: Croy and Hughes, 1991; Waltzek and Wainwright, 2003; amphibians: Nishikawa and Gans, 1996; Deban et al., 2007; reptiles: Kardong and Bels, 1998; de Groot and van Leeuwen, 2004; birds: Rudebeck, 1950; Goslow, 1971; mammals: Langley, 1994; Anjum et al., 2006) and invertebrates (mollusks: Kier and van Leeuwen, 1997; crustaceans: Burrows, 1969; Patek and Caldwell, 2005; arachnids: Jackson et al., 1998; Barrantes and Weng, 2006; Dangles et al., 2006; insects: Tanaka and Hisada, 1980; Montgomery, 1983; Corrette, 1990; Gorb, 1995; Kral et al., 2000). Here we report how hunters of the ponerine ant *Odontomachus opaciventris* use such a high speed strategy, shortening their predatory sequences and relying on fast mandible strike rather than on venom use, when overwhelming prey that present different morphological and defensive characteristics.

In the genus *Odontomachus*, workers are considered as monomorphic (Ledoux, 1952; Colombel, 1971b; Brown, 1976) and the only report of size variation, in *O. troglodytes*, was related to food depletion during colony founding or after a starvation period (Colombel, 1971b). Workers of *O. opaciventris* also proved to be monomorphic and, consequently, a possible predatory specialization according to their size looks unlikely.

The behavioral strategy used by solitary hunters of *Odontomachus* for capturing small prey has been described in *O. assiniensis* (Ledoux, 1952), *O. bauri* (Jaffé and Marcuse, 1983; Ehmer and Gronenberg, 1997), *O. chelifer* (Fowler, 1980; Ehmer and Gronenberg, 1997) and *O. troglodytes* (Dejean, 1982; Dejean and Bashingwa, 1985; Dejean and Lachaud, 1991). Using a similar list of behavioral acts as that used in the present study the typical predatory sequence for these species consisted of: search for prey, prey detection and location, antennal palpation of the prey, antennae withdrawal just before the rapid closing of the jaws, prey lifting, stinging and transport of the prey. In *O. opaciventris*, the predatory sequence appeared basically similar but somewhat simpler and faster due to the combination of different behaviors in a single behavioral unit and to the non-display of some behavioral acts. In spite of a clear stereotypy in the behavioral sequences, some flexibility linked to prey characteristics was observed as far as the size of the behavioral repertoire and the number of transitions between behavioral acts are concerned.

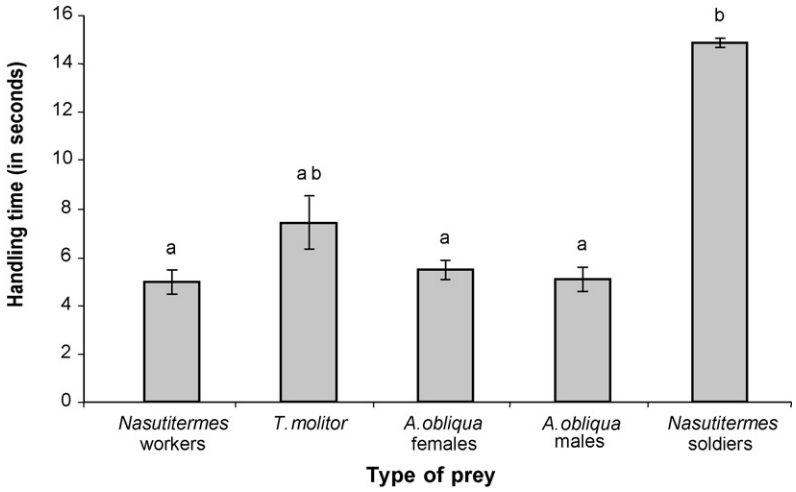

Fig. 3. Comparison of the handling time (from prey detection to carrying) performed by *Odontomachus opaciventris* hunters according to the type of prey. Means with different lowercase letters are significantly different (Wilcoxon sum rank test, $p < 0.05$).

By comparison with other predacious poneromorph ants, namely *Odontomachus* species, the hunting sequences of *O. opaciventris* faced with small prey were characterized by an extremely rapid succession of the behavioral acts: handling times barely rose above 5 s and it took only about 15 s to capture such difficult prey as *Nasutitermes* soldiers which are usually abandoned by other species. The antennal withdrawal reflex, found in some other species of the genus, was not observed in *O. opaciventris*. However, such a reflex is a very rapid movement (ca. 8 ms) that requires a high-speed video camera to be revealed (Ehmer and Gronenberg, 1997; Gronenberg, personal communication), and it might be that the temporal and spatial resolution of the video image we used did not allow resolving the swiftness of this movement. More obviously, the antennal palpation of the prey was always absent, this phase being limited to a simple flash contact, almost immediately followed by the attack, and stinging never occurred with termites – even after a failure at the first mandible strike attempt – and was rare with heavily sclerotized prey like tenebrionid larvae. In fact, it occurred only during encounters with male and female fruit flies, perhaps in relation with both the general shape of this bulky prey that made their lifting uneasy, and the numerous short jumps they performed to escape. A similar behavior occurs in the spider *Cupiennius salei* which normally uses the mechanical power of its strong chelicerae almost alone to kill rather soft insects which can be easily overwhelmed. However, this spider needs to inject an out of proportion dose of venom to kill blowflies (*Protophormia* sp.), a seemingly unproblematic prey type which behaves sluggishly when caught but produces high frequent vibrations with its flight muscles which likely gives a signal to the spider that there is a struggling item which might escape (Wigger et al., 2002).

Finally, in numerous occasions, the predatory sequence of *O. opaciventris* was also characterized by the fact that mandible strike and prey lifting almost merged into a single behavioral unit. As a global result, all the behavioral phases tended to maximize the running speed of the predatory sequence that was significantly shortened. As shown in some vertebrates, like the carnivorous grasshopper mice *Onychomys leucogaster* (Langley, 1994), a high level of aggressiveness and a faster attack can modulate the capture success of the predator allowing exploiting uncommon or difficult/dangerous prey. An analogous pattern has also been reported in different species of lizards. The highly specialized ant-eating iguanian lizard *Moloch horridus* displays an unusual predatory behavior characterized by the lack of a body lunge, a faster opening phase of the gape cycle, a faster tongue protrusion, and a reduced prey processing, which makes a single predatory event in *M. horridus* faster than that observed in any closely related dietary generalist species (Meyers and Herrel, 2005). Similarly, in the species *Eumeces okadae*, a lizard with high chemical prey discrimination ability, fast predatory attack immediately after prey detection, by omitting elaborate chemical confirmation and thus shortening of the predatory sequence, appears to be essential for successful capture of highly mobile prey (Hasegawa and Taniguchi, 1996).

The absence of stinging in the predatory repertoire of *O. opaciventris* against termites is noteworthy in comparison with most of the poneromorph ants which do sting them: *Anochetus kempfi* (Torres et al., 2000), *A. traegaordhi* (Schatz et al., 1999), *Centromyrmex bequaerti* (Dejean and Fénéron, 1999), *Cylindromyrmex striatus* (Overal and Bandeira, 1985), *Ectatomma ruidum* (Schatz et al., 1997), *E. tuberculatum* (Dejean and Lachaud, 1992), *Leptogenys chinensis* (Maschwitz and Schönegge, 1983), *O. assiniensis* (Ledoux, 1952), *Pachycondyla analis* (Corbara and Dejean, 2000), *P. berthoudi* (Peeters and Crewe, 1987), *P. commutata* (Wheeler, 1936; Mill, 1984), *P. goeldii* (Orivel et al., 2000), *P. hottentota* (Dean, 1989), *P. marginata* (Leal and Oliveira, 1995), *P. sennaarensis* (Lachaud and Dejean, 1994), *P. soror* (Dejean, 1991), *P. tarsata* (Dejean et al., 1993b), *P. villosa* (Dejean and Corbara, 1990), *Platythyrea modesta* (Djiéto-Lordon et al., 2001), *Plectroctena minor* (Schatz et al., 2001). However, this is not really surprising for an *Odontomachus* hunter faced with a very small prey (about 1/4 or 1/5) with respect to its own size. A similar absence of stinging behavior has been already reported for *O. troglodytes* (9–12 mm in length) faced with *Microtermes* work-

ers (2 mm in length) (Dejean, 1982; Dejean and Bashingwa, 1985) – whereas it was present in 19% of the cases ($n = 84$) involving *Allognathotermes* workers (5–6 mm in length) –, for *O. bauri* (9 mm in length) faced with *Nasutitermes* workers and soldiers (Ehmer and Hölldobler, 1995), for *O. ruginodis* (8–10 mm in length) faced with small *Nasutitermes* and *Reticulitermes* workers (Carlin and Gladstein, 1989), and for the large *O. chelifer* (12–15 mm in length) confronted to workers of *Procornitermes striatus*, *N. globiceps* or *Armitermes heterotypus* (Fowler, 1980). In the case of *O. opaciventris*, very small prey like male fruit flies and termites (soldiers included) are so easily subdued by the strength of the worker jaws that mandible strike is not always necessary, some of these prey being just picked up, killed by the pressure of the jaws and taken straight to the nest (see Fig. 2a, d and e). Such restrictive use of the sting or venom against small prey or prey easy to overwhelm has also been reported for arachnids. The African scorpions *Parabuthus liosoma* and *P. pallidus*, for example, do not sting non-resistant prey but crush them with their pedipalps, stinging only prey items that are difficult to handle (Rein, 1993), and the wandering spider, *Cupiennius salei*, delivered more venom into prey items that struggled more intensely (Boevé et al., 1995; Malli et al., 1999; Wigger et al., 2002). These studies, and others performed on snakes (Gennaro et al., 1961; Hayes, 1992; McCue, 2006) support the "venom optimization hypothesis" which infers that stinging (or biting) animals use their venom as economically as possible. Venom production may be costly from an energetics standpoint and injection of too much venom into smaller prey could be metabolically expensive and may deplete venom reserves, leaving the predator vulnerable to predation or unable to deal with subsequent prey (Nisani et al., 2007). In social insects like ants, stinging behavior and venom use may have three major functions: defense against predators or deterrence against a potential threat (painful effect), prey subduing and capture (paralytic and lethal effects), and social communication (alarm signaling effects) (Wilson, 1971; Orivel and Dejean, 2001). For stinging to be efficient, sufficient amounts of venom must be available to meet the colony's needs without undue sacrifice of any vital function (Haight and Tschinkel, 2003). In particular, individual workers of predatory ant species are likely to have evolved some capacity to modulate venom doses delivered for subduing prey in order to balance these needs and maintain a sustainable efficiency in colony defense. Restrictive use of sting by large *Odontomachus* species during predation, by relying on their powerful mandible strike, would tend both to shorten prey handling times and to limit the energetic cost of predation preserving the workers' ability to use their sting against difficult-to-handle prey or for colony defense.

Another factor of particular significance in the predatory sequence of *O. opaciventris*, is the lack of antennal palpation of the prey since this behavior is quite common in all other trap-jawed ants (Dacetini: Dejean, 1980, 1986; Gronenberg, 1996; Myrmoteratini: Moffett, 1986a; Odontomachini: Dejean and Bashingwa, 1985; Schatz et al., 1999), where it is supposed to provide the information allowing the repositioning of the ant with respect to the prey. According to Gronenberg (1995b), such positioning, along with the synchronization of the mandibles, is of critical importance for securing the success of the rapid mandible strike. In *O. opaciventris*, despite the absence of antennal palpation, a form of repositioning can occur through the skirting around behavior exhibited with termite soldiers and male fruit flies, but this behavior is infrequent and is not related to a better outcome of the predatory sequence. As a general rule, the efficiency of the mandible strike does not appear to be linked to the target of the attack on the prey's body or to a peculiar position of the hunting worker with respect to the prey. This is particularly true against *Nasutitermes* workers, but also applies for soldiers since, even if most of the giving up recorded occurred after a mandible strike, all of them only resulted from an irritation and not from a mandible strike failure, linked to a wrong positioning of the ant, and leading to prey loss (see Fig. 2e). For poneromorph ant species, the lack of an antennal palpation phase in *P. goeldii* and *Pla. modesta* has been considered to distinguish the predatory behavior of arboreal ants, allowing them to surprise and catch very fast moving arthropods before they fly, jump away or drop to the ground (Orivel et al., 2000; Djiéto-Lordon et al., 2001). However, this rule does not apply for all arboreal species since antennal palpation of the prey is always present in the predatory sequences exhibited by the ponerine *P. villosa* (Dejean and Corbara, 1990) and the ectatommine *E. tuberculatum* (Dejean and Lachaud, 1992) and even can vary according to prey species in *P. goeldii* (Orivel et al., 2000). The lack of antennal palpation in a ground-dwelling ant species such as *O. opaciventris*, even with slow moving insects – twice their size and weight – like tenebrionid larvae, suggests that it could be specific to small, mostly harmless prey. Alternatively, the swiftness and aggressiveness of the attack characterizing the predatory strategy of this species could be responsible for the absence of this behavioral phase, rather than its foraging habits. As a matter of fact, the key role of the swiftness and aggressiveness of the attack is likely to be supported by the recent results on another ground-dwelling ant species, the ectatommine *Gnamptogenys sulcata* (Daly-Schveitzer et al., 2007). Hunters of this species are characterized by a rapid execution of their attack: they never display antennal palpation of the prey but immediately rush toward all types of prey, even very large ones that can weigh up to 60 times their own weight.

Brown (1976) noted that most species of *Odontomachus* and *Anochetus* (like *O. brunneus*, *O. simillimus* and *A. inermis*) are usually cautious and hesitant in their attacks on potential prey. Numerous approaches consist merely in attempts and are not carried through in mandible strike attacks and, when the snap attack does occur, a characteristic sudden strike-and-recoil behavior is exhibited just after the antennal palpation of the prey, this rapid retreat helping the ant to avoid any possible defensive reaction of the prey. Furthermore, in normal, unstarved conditions, most *Odontomachus* and *Anochetus* species seem to attack preferentially prey that are smaller than their own size (Ledoux, 1952; Ehmer and Hölldobler, 1995; Dejean et al., 1999), to select a particular region of the prey's body for attacking (Dejean and Bashingwa, 1985; Schatz et al., 1999) and to avoid dangerous prey presenting chemical defenses (Dejean, 1988a; Ehmer and Hölldobler, 1995). By contrast, the hunting behavior exhibited by *O. opaciventris* workers is quite different. Workers subdue

rapidly a variety of prey ranging from 0.1 to 2 times their own weight and from 0.3 to 2 times their own size, that is, small prey but significantly larger than the prey captured by most species of *Odontomachus*. Moreover, they show no preference for any particular site of the prey's body during their attack which was never preceded by any strike-and-recoil behavior and no protective posture was observed when confronted with a dangerous prey like a *Nasutitermes* soldier or a struggling one like a *T. molitor* larva. During the capture of *Allognathotermes* soldiers, solitary *O. troglodytes* workers exhibit a 'prudent' posture, standing up on their median and hind legs and holding the prey in position with their forelegs before inserting their sting (Dejean, 1982; Dejean and Bashingwa, 1985). Similarly, *P. villosa* and *P. soror* hunters are able to distinguish between soldiers and workers of a Rhinotermitidae species and of *Cubitermes*, respectively (Dejean et al., 1990; Dejean, 1991). Confronted with soldiers, they exhibit a 'prudent' posture, antennae thrown back and both median and forelegs raised in order to avoid any contact of these appendages with the termite mandibles, whereas this 'prudent' posture is absent when faced with termite workers. By contrast, disregarding the potentially risky situation and whatever the target of the attack (frontal or not), no such postures are exhibited by *O. opaciventris* hunters which immediately strike *Nasutitermes* soldiers with their mandibles and never sting them, which makes needless any prey manipulation with the forelegs. Such prudent behavior was never observed for the range of prey used in this study, whereas it is typically exhibited in other ant species confronted with dangerous or difficult prey (Dejean and Bashingwa, 1985; Brandão et al., 1991; Dejean et al., 1993b, 1999; Lachaud and Dejean, 1994; Schatz et al., 1997). This absence of prey manipulation is of particular interest with prey equipped with chemical defense mechanisms since it reduces the probability of any physical contact inducing irritation and a subsequent giving up of the prey.

Finally, another particularly relevant feature of the predatory behavior of *O. opaciventris* appears to be the efficiency of the so-called 'reserve behavior' (Dejean, 1988c) performed after a failure in the first mandible strike attempt. As for other central-place-foraging insects exhibiting a solitary strategy (Orians and Pearson, 1979; Deneubourg et al., 1983; Detrain et al., 2000), food-searching paths of *O. opaciventris* hunters are erratic in comparison with the direct homing paths. Nevertheless, their foraging patterns change after a failure in capture attempt and lead to an intensive prey search. Such intensive food searching has been recorded for different poneromorph ant species specialized in termite predation (Longhurst et al., 1979; Dejean, 1991; Dejean et al., 1993a) and is known for other arthropod predators that prey on insects living in group (Banks, 1957; Bell, 1991; Benhamou, 1992; Dejean and Benhamou, 1993; Durou et al., 2001). After the failure of a first capture attempt, dacetine ants exhibit a stereotyped behavior: after resuming an intensive search they attack prey immediately after detection, trying to sting it before having secured a firm seizure. For different dacetine species, this behavior allows the recovery of 24–50% of the prey that had fled away (Dejean, 1980, 1985, 1988b). This strategy enhances the foraging efficiency of predators concentrating their hunting efforts on resource-rich areas. Unlike *Mystrium camillae* workers that ignored the small arthropods they have just struck even when they are momentarily stunned (Moffett, 1986b), the intensive search exhibited by *O. opaciventris* hunters after a mandible strike that only resulted in knocking the prey away, indicates an increase in their hunting motivation, even if stinging is not released. As a matter of fact, this intensive search following the loss of the prey after a failed mandible strike was always successful, resulting in 100% of prey retrieval when irritation behavior did not occur and thus, this 'reserve behavior' appears perfectly adapted to compensate the bouncing effect of the trap-jaw mechanism of *O. opaciventris* hunters (see Carlin and Gladstein, 1989; Patek et al., 2006).

All the behavioral characteristics exhibited by *O. opaciventris* appear to contribute to the shortening of the predatory sequence duration. Apart from allowing occasional escaping behavior by horizontally and vertically jumping as observed for *O. bauri* (Patek et al., 2006), the efficiency and swiftness of the trap-jaw mechanism of *O. opaciventris* may prevent the prey from projecting any defensive or repulsive substance in the case of *Nasutitermes* soldiers, or from struggling in the case of *T. molitor* larvae. Likely due to both the large size of *O. opaciventris* mandibles and the efficiency of their trap-jaw mechanism that allows a rapid prey overwhelming by knocking out or crushing, the hunting strategy of the solitary workers appears to give top priority to the swiftness and strength of their trap-jaw system that is used as first strike weapon to rapidly subdue a variety of small prey, potentially dangerous ones included. Despite the likely high-risk factor that characterizes such predatory strategy, its efficiency is amazing since 100% of all termite workers, fruit flies and tenebrionid larvae provided are successfully retrieved to the nest. This efficiency is even more obvious with *Nasutitermes* soldiers when compared with that performed by the few poneromorph ant species known to attack this kind of prey. Up to 76.7% of the soldiers are captured by *O. opaciventris* hunters, whereas *A. traegaordhi*, *Rhytidoponera metallica*, *P. villosa* and *P. tarsata* are successful in disabling and retrieving this kind of prey in only 19%, 18%, 17.8% and 7% of encounters, respectively (see Traniello, 1981; Dejean and Corbara, 1990; Schatz et al., 1999), and even *O. bauri*, regarded as the most efficient species tested at successfully attacking this prey item (Traniello, 1981; Ehmer and Hölldobler, 1995), does not succeed in more than 26% of the cases. On account of their regressed, non-functional mandibles, *Nasutitermes* species are known to rely solely on their chemical secretions for their defense and these secretions have been proved to be highly toxic and fast-acting on different ant species in topic applications (Mill, 1983; Prestwich, 1984). However, their effect on *O. opaciventris* seems to be limited to a low lasting irritation and no lethal issue was recorded even if it remains unclear whether this is due to a weaker toxicity of the secretion of the *Nasutitermes* species used in our experiments or to any eventual resistance capacity on the ant side, limiting its risk-taking effective level. Furthermore, considering the large size of the colonies of *O. opaciventris*, it is likely that the possible loss of one (or few) hunting ant(s) has a sharply lesser repercussion than for a species with small colony size, for which the small number of elite hunters makes every individ-

ual virtually indispensable (cf. Daly-Schveitzer et al., 2007). In such an event, a balance might exist between a potentially high-risk situation – real but that represents a limited cost at colony level –, and a maximization of the opportunities to exploit rich food sources, like termite nests or tunnels, that enhances the competitiveness of *O. opaciventris* against other invertebrate predators.

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