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**Sitemate Recognition: the Case of *Anochetus traegordhi*
(Hymenoptera; Formicidae) Preying on *Nasutitermes*
(Isoptera: Termitidae)**

by

B. Schatz¹, J. Orivel², J.P. Lachaud^{1,3}, G. Beugnon¹ & A. Dejean⁴

ABSTRACT

Workers of the ponerine ant *Anochetus traegordhi* are specialized in the capture of *Nasutitermes* sp. termites. Both species were found to live in the same logs fallen on the ground of the African tropical rain forest. *A. traegordhi* has a very marked preference for workers over termite soldiers. The purpose of the capture of soldiers, rather than true predation, was to allow the ants easier access to termite workers. During the predatory sequence, termite workers were approached from behind, then seized and stung on the gaster, while soldiers were attacked head on and stung on the thorax. When originating from a different nest-site log than their predator ant, termites were detected from a greater distance and even workers were attacked more cautiously. Only 33.3% of these termite workers were retrieved versus 75% of the attacked same-site termite workers. We have demonstrated that hunting workers can recognize the nature of the prey caste (workers versus termite soldiers) and the origin of the termite colony (i.e. sharing or not the log where the ants were nesting), supporting the hypothesis that hunting ants can learn the colony odor of their prey. This, in addition to the nest-site selection of *A. traegordhi* in logs occupied by *Nasutitermes* can be considered as a first step in termitolesty.

Key words: *Anochetus*, *Nasutitermes* prey recognition, predatory behavior.

INTRODUCTION

During their 100 million years of coexistence, ants and termites have been engaged in a coevolutionary arms race, with ants acting as the aggressor and employing many predatory strategies while termites are the prey presenting several defensive reactions (Hölldobler & Wil-

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son 1990). Even if a large percentage of ant species prey on termites when given the opportunity, the Ponerinae subfamily seems to be one of the most specialized, from both a behavioral and morphological standpoint, in their capture (Wheeler 1936; Hölldobler & Wilson 1990).

Ants from three subfamilies (the ponerine genera *Anochetus* and *Odontomachus*, the formicine genus *Myrmoteras* and the myrmicine tribe Dacetini with 24 genera) have each independently acquired a trap-jaw system that has emerged in response to the particular ecology of these ants (reviewed in Gronenberg & Ehmer 1996). *Anochetus* spp. are encountered all around the world in tropical zones covering North, Central and South America (Wheeler 1936; Mill 1982; Wilson 1987; Olson 1991; Jaffe & Lattke 1994; Longino & Hanson 1995; Dejean & Olmstead 1997), Australia (Wheeler 1936; Andersen & Clay 1996), Asia (Gronenberg & Ehmer 1996) and Africa (Lévieux 1972; Villet *et al.* 1991), where they have been generally recorded as specialized termite predators. Some species have been reported to be specialized on a few termite species (Wheeler 1936; Mill 1982).

We study here the predatory behavior of the African *A. traegordhi* specialized in the capture of *Nasutitermes* (Dejean *et al.* 1999). We compared the predatory sequences of foraging workers confronted with *Nasutitermes* workers and soldiers from colonies sharing or not the logs where we found the ant colonies.

MATERIALS AND METHODS

The ants and termites originated from the Democratic Republic of the Congo (Kikwit and Kinshasa) and from Cameroon (Abong Mbang, Bertoua, Ottotomo, Matomb, Nzi). Numerous rotten logs lying on the soil were examined to detect the simultaneous presence of colonies of *A. traegordhi* and of *Nasutitermes*.

Observations on predatory behavior were carried out according to a method developed during studies conducted on Dacetini (Dejean 1987; see also Dejean & Everaerts 1997). A preliminary study allowed us to determine the complete behavioral sequence used by hunting ants when confronted with termites. Index cards were compiled with the respective postures of the predators and the prey noted for each phase of the sequence. We compared the predatory behavior of *A. traegordhi* when confronted with *Nasutitermes* workers and soldiers nesting in the same log as the ant colony, or collected from a different log, using flow-diagrams illustrating the capture of these four types of prey. Percentages (transition frequency between behavioral acts) were calculated from the overall number of cases. We tested therefore the prey caste effect (workers *versus* termite soldiers) and the influence of the nest-site

Table 1: Coexistence of *Nasutitermes* termite colonies with *Anochetus traegordhi* and *Odontomachus troglodytes* colonies in logs.

Rotten logs with	Sites studied					Total	%
	Ottotomo	Bertoua	Abong Mbang	Matomb	Nzi		
<i>Nasutitermes</i> colonies	21	8	4	4	2	39	/
<i>Anochetus traegordhi</i>	17	6	3	4	1	31	79.5
<i>Odontomachus troglodytes</i>	2	1	1	0	1	5	12.8
Without ant colonies	2	1	0	0	0	3	7.7

origin of the prey (same *versus* different from the ants).

Comparisons were made using the Fisher's exact test (StatXact 2.05 software).

RESULTS

Nest site selection

Colonies of *Nasutitermes* termites were found in 39 logs, 92.3% of which were also inhabited by an Odontomachini subtribe ant colony

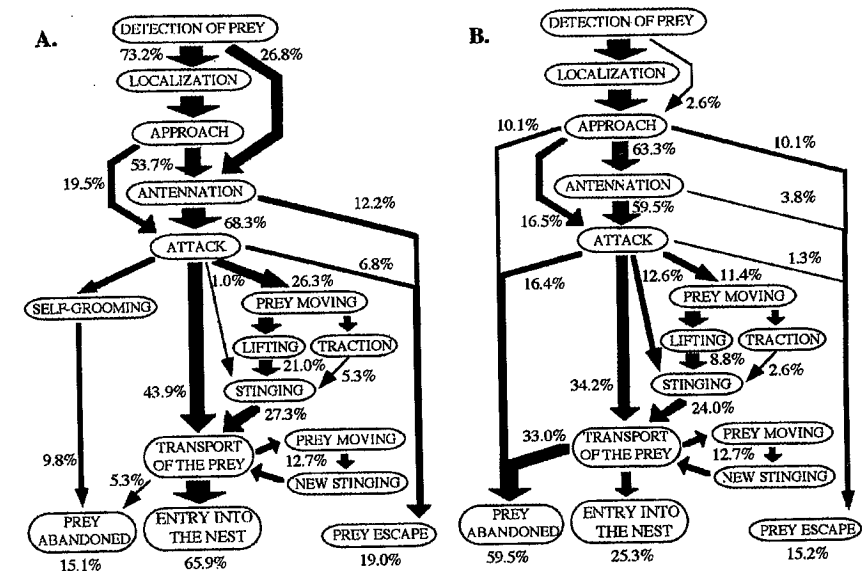


Fig. 1. Flow diagram of the *A. traegordhi* hunting workers when confronted with termite workers from the same log (A) (n = 205) or from a different nest site (B) (n = 79).

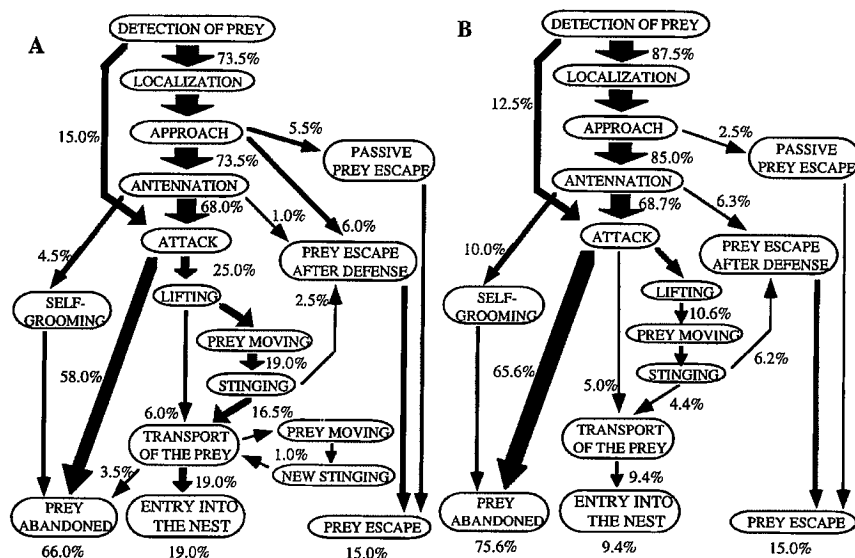


Fig. 2. Flow diagram of the *A. traerghordi* hunting workers when confronted with termite soldiers from the same log (A) ($n = 200$) or from a different nest site (B) ($n = 160$).

(Table 1). Four out of five logs (79.5%) were inhabited by *A. traerghordi* and one out of eight logs (12.8%) by *Odontomachus troglodytes*. No case of coexistence of both ant species in the same log was recorded.

Common traits of the predatory sequences for the four types of prey (Fig. 1 & 2)

During their search for prey, the *A. traerghordi* workers moved slowly and sinuously, antennae spread apart and mandibles opened to 180°. Prey were detected from a distance of 5 mm in at least 73% of the cases. This initiated the phase of localization followed by a very slow approach with the ant generally pointing its antennae towards the prey rather than keeping them bent. When prey were detected by contact, an attack rapidly followed after a short antennation. The attack consisted in the very rapid closure of the mandibles (the trap-jaw system). The prey was sometimes projected several centimeters away. In some cases, probably because the prey remained motionless, the mandibles were closed more slowly. Even if some attacked prey were directly transported to the nest, the hunting worker, in response to movements by the prey, could also lift or pull the termite in order to render it defenseless and generally stung it once. Prey could be abandoned at any point in the behavioral sequence, up to and including the start of the transport phase. Finally, prey retrieval was always performed by a single hunting

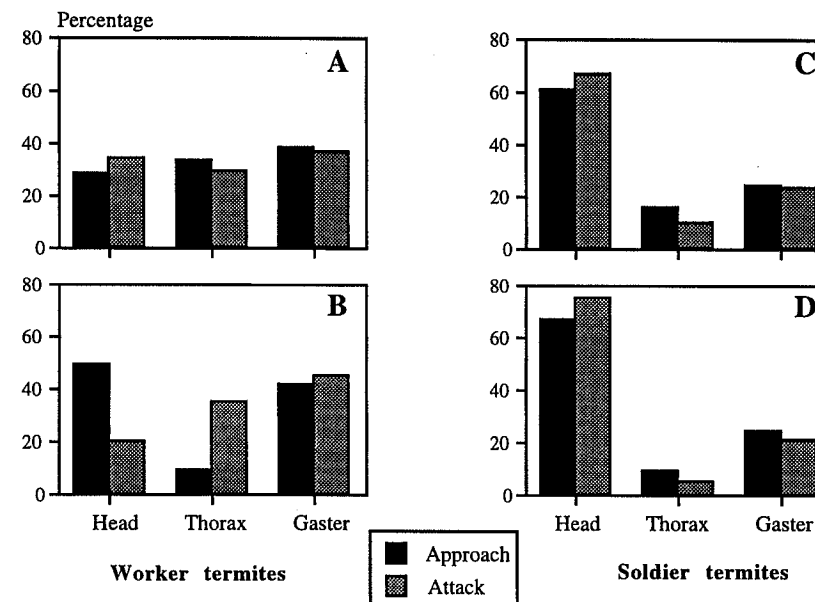


Fig. 3. Part of prey body used as a target during approach and seizure phases with termite workers living in the same log as their predator ants ($n = 180$) (A) and from a different nest site ($n = 60$) (B), and with termite soldiers from the same log ($n = 166$) (C) and from a different nest site ($n = 130$) (D).

worker. Whatever the type of prey, the hunting workers used the same general sequence of predatory behavior. Nevertheless, the duration of each predatory phase and some qualitative patterns varied according to prey caste and nest site.

Effect of prey caste

The effect of prey caste (workers versus termite soldiers) was observed for each phase of the sequence of predation, except for the position of the antennae and the speed of mandible closure. Even if generally both castes were approached very slowly, termite soldiers triggered a slow approach more often than workers. They also triggered shorter antennation only when they originated from the same logs as the hunting workers. The speed of mandible closure was fast whatever the prey caste. Whatever the origin of the nests, the target of hunting workers during approach and seizure was the gaster for termite workers and the head for soldiers. Among the few termites that were stung, soldiers were stung less often than workers when originating from a different nest site than the ant's, whereas no difference between the two castes existed when they shared the same log with the hunting worker.

Table 2: Comparison of the parameters characterizing each phase of the predation sequence of *Anochetus traegordhi*. The prey caste effect was analyzed at the population level with termites and ants living in the same log (SL) or in different nest sites (DNS). The nest-site effect was analyzed at the population level with predation conducted on termite workers (W) and on soldiers (S). The target of stinging was not recorded during the predation on termite soldiers from different nest sites. All significant results are in bold.

Predatory phases	Prey nature effect				Biotope effect				
	Compared parameters		Statistical comparisons		Compared parameters		Statistical comparisons		
	W	S	In total	According the nest site	SL	DNS	In total	According the termite type	
Detection from a distance	0-1 mm	60	61	5.0·10⁻¹⁶	SL: 0.15	96	35	5.3·10⁻¹⁹	W: 9.8·10⁻⁴
	2-3 mm	162	154		DNS: 1.5·10⁻¹⁶	217	99		S: 1.0·10⁻¹⁸
	4-5 mm	52	101			79	74		
	+ 5 mm	0	32			1	31		
Reaction distance	1-3 mm	177	187	4.2·10⁻⁶	SL: 0.55	242	122	2.4·10⁻⁷	W: 0.07
	+ 3 mm	36	100		DNS: 5.5·10⁻¹⁰	55	81		S: 6.2·10⁻¹¹
Position of the antennae	Pointed	166	241	0.15	SL: 1.6·10⁻⁴	150	257	2.0·10⁻³	W: 2.7·10⁻³
	Bent	45	46		DNS: 9.6·10⁻¹⁴	51	40		S: 4.9·10⁻¹⁷
Part of prey body approached	Head	73	182	4.0·10⁻⁹	SL: 6.7·10⁻⁸	131	124	9.6·10⁻⁶	W: 2.7·10⁻⁴
	Thorax	56	36		DNS: 4.3·10⁻²	73	19		S: 1.00
	Gaster	84	69			93	60		
Speed of the approach	Slow	132	259	4.3·10⁻¹⁴	SL: 6.2·10⁻⁵	213	178	1.5·10⁻⁵	W: 0.88
	Fast	81	28		DNS: 1.4·10⁻¹¹	84	25		S: 1.2·10⁻⁶
Type of the palpation	Short	178	262	1.1·10⁻¹¹	SL: 5.0·10⁻¹⁵	250	160	3.1·10⁻²	W: 4.5·10⁻³
	Long	74	20		DNS: 1.00	71	23		S: 7.5·10⁻⁴
Site of attack on the prey body	Head	68	215	7.3·10⁻²¹	SL: 2.0·10⁻⁹	174	109	0.24	W: 0.12
	Thorax	69	24		DNS: 1.8·10⁻¹³	66	27		S: 0.15
	Gaster	88	68			102	54		
Speed of the mandible closure	Slow	38	66	0.22	SL: 0.08	82	22	5.7·10⁻⁴	W: 0.84
	Fast	187	241		DNS: 0.33	260	168		S: 2.0·10⁻⁵
Stinging of the attacked prey	Sting	77	55	4.0·10⁻⁴	SL: 0.06	96	36	2.7·10⁻²	W: 1.00
	No sting	163	241		DNS: 4.7·10⁻³	250	154		S: 3.5·10⁻²
Site of stinging	Head	22	0	2.5·10⁻²	SL: 3.7·10⁻⁸	14	8	-	W: 0.30
	Thorax	24	34		DNS: -	52	6		S: -
	Gaster	29	4			28	5		

Termite workers were stung on their gaster, i.e. the same region of the body during approach and attack, while soldiers were stung on their thorax. However, 75.0% of the attacked termite workers were transported *versus* 22.9% of the attacked termite soldiers, when the predator ant and its termite prey originated from the same log. These values were 33.3% *versus* 11.5%, respectively, when their nest sites differed.

Effect of nest-site origin

The effect of nest-site origin (same log for the termite and the ant or not) was also observed for each phase of the predation sequence (Table 2), except for the duration of antennation, which was generally long regardless of the termite caste, and the part of the prey body seized. In general, this effect was more often greater with soldiers than with termite workers.

Both types of prey were detected from a greater distance when originating from different nest sites rather than from the same log (2-3mm *versus* 4-5mm). During localization, the hunting workers bent their antennae more often when encountering soldiers coming from a different nest site rather than from the same log. Termite workers were approached mostly from behind by hunting ants originating from the same log, and mostly head on by hunting ants living in a different log, while no effect was found for soldiers (see also Fig. 3). Hunting workers approached termite soldiers originating from a different nest site more rapidly than they approached soldiers originating from the same log. During seizure, the trap-jaw system was used more often on soldiers originating from a different nest site than on those originating from the same log. After seizure, soldiers from a different nest site were less frequently stung than those from the same log, while no difference was recorded for termite workers. It should be noted, however, that prey belonging to the same log as their predator ants were more often retrieved than those originating from a different site (termite workers: 75.0% of the cases *versus* 33.3%; termite soldiers: 22.9% *versus* 11.5%)

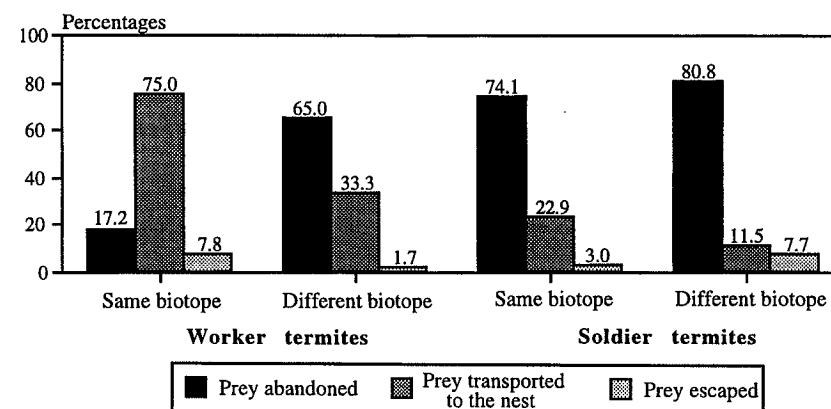


Fig. 4. Proportions of prey abandoned, transported to the nest or escaped from all prey attacked in the cases of the four prey types.

(Fig. 4). Thus, *A. traegordhi* hunting workers were clearly able to recognize termites from both nest-site origins and they strongly preferred those sharing the same nest site.

Prey defense

The behavior of the *Nasutitermes* prey generally changed when the predator started its antennation and continued until prey transport. The prey often stayed or became motionless even after an attack, as this behavior can trigger the hunting worker to abandon the prey. Interestingly, some termite soldiers transported inside the ant nest were subsequently observed outside it. Thus, they were not killed by the *A. traegordhi* attack nor were they eaten. We never observed such prey escape behavior by termite workers. *Nasutitermes* can also actively defend themselves by struggling and by stridulating or, in the case of soldiers, by projecting their glue and by trying to hit the head of the predator with their rostrum. They can also try to escape by changing their direction and moving away quickly. All these defensive behaviors permitted *Nasutitermes* termites to escape in 15 to 19% of the observed cases.

DISCUSSION

Ants of the *Anochetus* genus are known to nest in sites such as cavities in roots and logs (Hölldobler & Wilson 1990). We noted a strong nest-site selection in *A. traegordhi*, as colonies were recorded in 79.5% of the logs occupied by *Nasutitermes*. Interestingly, a similar association was found in Mexico between *A. emarginatus* and *Nasutitermes* colonies nesting in the same ramets of a bromeliad (Dejean & Olmstead 1997). Both in Africa and Mexico, other ants do not share their nest site with *Nasutitermes* spp., as the latter have developed very efficacious anti-ant defenses (Mill 1982; Grassé 1984; Hölldobler & Wilson, 1990).

As an illustration of the development of the termite-ant arms race, the hunting workers of *A. traegordhi* displayed several specialized behaviors during the capture of *Nasutitermes*. Several similarities with *Odontomachus troglodytes* were noted, such as foraging with the mandibles opened to 180° and the antennae widely spread apart. The stealthy approach characteristic of trap-jaw system bearers is particularly marked in the case of *A. traegordhi* (see Brown 1976; Dejean & Bashingwa 1985; Schatz *et al.* 1999).

In the genus *Anochetus*, although mandible closure is very powerful and rapid, the prey are not killed by the strike. They can be stunned or may continue to move, thus triggering stinging. Because of their smaller mandibles, *A. traegordhi* hunting workers stung more fre-

quently than *Odontomachus* whose larger mandibles permit strikes sufficient to subdue their prey (Brown 1976; Dejean & Bashingwa 1985; Gronenberg *et al.* 1993; Gronenberg & Ehmer 1996).

In spite of their relatively small size, *A. traegordhi* workers efficiently captured *Nasutitermes* termites although this genus is considered as having one of the most efficient defensive systems among termites (Mill 1982; Grassé 1984; Hölldobler & Wilson 1990).

After being attacked and transported to the ant nests, some termite soldiers were seen leaving these nests. This suggests that ants attack termite soldiers to allow easier access to termite workers. In other termitophagous ant species, termite soldiers are also captured to facilitate access to termite workers, but they are consumed. This is the case for *Myrmecaria opaciventris* preying on *Macrotermes bellicosus* (Kenne *et al.* submitted). This can explain the marked preference of *A. traegordhi* for termite workers over termite soldiers in all our experimental situations.

No recruitment or collective prey transport were observed in the present study. Nesting in the same log with their prey, *A. traegordhi* hunting workers individually and regularly captured termites one by one rather than simultaneously preying on several termites as was observed in larger termitophagous ant species such as *Pachycondyla foetens* or *P. tarsata* (Hölldobler & Wilson 1990; Dejean *et al.* 1993).

Thanks to the analysis of each step of prey capture and retrieval, we have also been able to demonstrate that *A. traegordhi* hunting workers can distinguish termites originating from two different sites and strongly prefer those with which they share the same log. Termite prey from a different nest-site origin were detected and localized by hunting workers from a greater distance, suggesting that olfaction is important during the first phases of the predatory sequence (Dejean 1991; Schatz *et al.* 1997) and is surely based on identifying volatile substances. From the end of the approach phase and the start of antennation, the strong preference for termites sharing the same log as the ants can be associated with the recognition of prey cuticular substances (Dejean, 1988a). Such cases of recognition of prey cuticular substances are also involved in predation by other ponerine ants: *Centromyrmex bequaerti* on *Cubitermes* and *Cephalotermes* termites, and *Pachycondyla foetens* on *Periplaneta* and *Macrotermes* (Dejean *et al.* 1999). It is already known that several ant species are able to adjust their predatory behavior according to different prey characteristics such as weight, size, density and the potential mortality risk due to prey defense (Dejean 1987; Dejean *et al.* 1990; Schatz *et al.* 1997, 1999b). We have demonstrated here that ants can also recognize the nature of the prey caste (workers

versus termite soldiers) and the origin of the termite colony (i.e. sharing or not the log where the ants were nesting), supporting the hypothesis that hunting ants are able to build a representation of their prey also including the learning of the colony odor of their prey (Schatz *et al.* 1999). These prey characteristics are likely to explain the avoidance of some dangerous prey (Dejean 1988b), the adjustment of the predatory strategy according to the nature of the prey (Dejean *et al.* 1993; Schatz *et al.* 1997) and feeding preferences in different ant species based on prey odors (Dejean *et al.* 1999).

In conclusion, the nest-site selection of *A. traegordhi* in logs occupied by *Nasutitermes*, combined with the fact that hunting workers strongly prefer the *Nasutitermes* prey with which they share the same log rather than those originating from another nest site, can be considered as a first step in termitolesty (Wheeler 1936).

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