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Territorial aggressiveness and predation: two possible origins of snapping in the ant *Plectroctena minor*

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Abstract – *Plectroctena minor* workers have long mandibles that can snap and deliver a sharp blow to intruders or prey, stunning or killing them. Encounters between homocolonial *P. minor* workers separated for 24 h or 15 days never resulted in snapping, while this behaviour was always noted during encounters between heterocolonial workers on neutral arenas or on the territory of a colony. In the latter case, only the aliens, that generally tried to escape, were snapped at. Snapping also occurred during encounters with workers belonging to sympatric ponerine species. During predation, the percentages of snapping varied according to prey nature, suggesting prey discrimination. Termite soldiers were always snapped at, while other prey were more often snapped close to rather than far from the nest entrances, indicating an intermingling of territorial aggressiveness and predatory behaviour. We discuss the adaptive value of snapping for hunting in galleries. ***To cite this article: A. Dejean et al., C. R. Biologies 325 (2002) 819–825.***

Hymenoptera / ants / *Plectroctena minor* / mandible / snapping behaviour / aggressiveness / nestmate recognition / prey discrimination

Résumé – Territorialité et prédation : deux origines équiprobables de mandibules pouvant se croiser brutalement chez la fourmi *Plectroctena minor*. Les ouvrières de *Plectroctena minor* sont pourvues de mandibules hypertrophiées pouvant se croiser brutalement (*snapping*), infligeant un choc puissant aux ennemis et aux proies, qui sont assommés ou tués. Les rencontres entre ouvrières homocoloniales, préalablement séparées les unes des autres, n'aboutissent jamais au *snapping*, alors que ce comportement est systématiquement utilisé lors des rencontres entre ouvrières hétérocoloniales, tout comme vis-à-vis des ouvrières d'espèces sympatriques. Durant la prédation, la fréquence du *snapping* varie selon la nature de la proie, suggérant une discrimination de ces dernières. Les soldats de termites font systématiquement l'objet de *snapping*, alors que ce comportement, facultatif pour les autres proies, est plus fréquent à proximité de l'entrée du nid qu'à une distance éloignée. Il y aurait donc un effet de la territorialité sur le comportement prédateur. Enfin, nous discutons la valeur adaptative du *snapping* pour la chasse dans les galeries ainsi que l'origine de ce comportement. ***Pour citer cet article : A. Dejean et al., C. R. Biologies 325 (2002) 819–825.***

Hymenoptera / fourmis / *Plectroctena minor* / comportement de *snapping* / territorialité / reconnaissance des congénères / discrimination des proies

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Version abrégée

Chez les insectes sociaux, la territorialité est souvent définie comme correspondant à l'ensemble des comportements liés à la défense d'une aire située autour du nid. Chez les fourmis terricoles, l'aire défendue peut être limitée aux zones situées près du nid ou autour des sources de nourriture, et aux pistes qui y conduisent. Chez certaines espèces arboricoles, elle peut être étendue à un territoire entier. La zone défendue peut l'être contre des colonies de même espèce ou d'espèces différentes, généralement compétitrices, mais aussi contre d'autres animaux. Dans ce dernier cas, il est difficile de faire la distinction entre prédation et territorialité. Nous avons expérimenté sur *Plectroctena minor*, une fourmi Ponerinae terricole spécialisée dans la capture des iules, mais qui chasse aussi des proies alternatives. Les ouvrières ont des mandibules hypertrophiées pouvant se croiser brutalement en infligeant un choc puissant contre tout ennemi ou proie lorsque, fortement appuyées l'une contre l'autre par contraction des muscles adducteurs, elles se croisent soudainement produisant un claquement bien audible (*snapping*). Ce comportement, qui ici peut étourdir ou tuer l'adversaire, est utilisé pour la défense des colonies par les soldats de termites *Capritermes* et *Pericapritermes* et les ouvrières de fourmis des genres *Orectognathus* et *Mystrium*. Nous avons vérifié que ce *snapping* est bien impliqué dans la défense territoriale chez *P. minor* lors de tests de confrontation entre ouvrières. En effet, après séparation de 24 h ou de 15 j, les ouvrières provenant d'une même colonie n'effectuent jamais de *snapping*, alors que ce comportement est toujours utilisé lors des rencontres entre ouvrières de colonies différentes, que ce soit sur une aire neutre ou sur le territoire d'une colonie. Dans ce dernier cas, seules les étrangères, qui essaient généralement de s'échapper, font l'objet de *snapping*. Ce comportement, qui se retrouve lors de confrontations avec d'autres Ponerinae sympatriques, a donc aussi une valeur interspécifique. Sur les aires de chasse des colonies, le comportement des ouvrières varie en fonction de la nature de la proie et du point de rencontre avec les proies. Le *snapping* est peu fréquent vis-à-vis des iules de petite taille et des isopodes, intermédiaire pour les ouvriers de termite *Cubitermes*, fréquent pour les larves de grillons et de *Tenebrionidae* et systématique vis-à-vis des grands soldats du termite *Macrotermes bellicosus*. En dehors de ces derniers, les proies testées font plus souvent l'objet de *snapping* quand elles sont rencontrées sur la zone de l'aire de chasse située à moins de 5 cm de l'entrée du nid que sur des zones plus éloignées (plus de 20 cm de l'entrée du nid). Il y a donc une sorte de mixité entre les comportements prédateur et territorial. Dans la prédation, le *snapping* a une forte valeur adaptative pour la chasse dans les galeries, car il permet aux ouvrières de se déplacer puis d'attaquer des proies tout en gardant les mandibules fermées. Ces ouvrières peuvent donc utiliser des galeries d'un diamètre à peine supérieur à celui de leur corps. Ce n'est pas le cas chez les autres fourmis qui ne pratiquent pas le *snapping*, en particulier les *Odontomachus* et les *Anochetus*, qui chassent avec leurs mandibules hypertrophiées ouvertes à 180°.

1. Introduction

In social insects, 'territoriality' is generally defined as all the defensive behaviours used against all kinds of intruders in an area centred around the nest entrance. In most ants, territoriality contributes to the defence of spatiotemporally stable food resources and to the trails towards these sources. The range of the area defended can also vary from a restricted zone around the nest entrance [1–3] to the entire territory (nests and food sources). The first example corresponds to most predatory ant species with individual foraging strategies when faced with unpredictable distributions of prey; the second example is related to absolute territories of arboreal dominant ant species [4].

The expression of territorial defence also varies according to the behavioural repertoire of the species considered, with intraspecific aggressiveness, often resulting in full attacks that can end with the destruction of one colony by another in *Formica* spp. Nevertheless, ritualised behaviours in which the participants are not killed also exist both at the intra- and interspecific levels [5–8].

In predatory ants, it is often difficult to distinguish aggressiveness from predation, as the same behaviours can occur in both cases. Spread-eagling offers a good example of this. Indeed, it is very frequent in ants for several recruited workers to spread-eagle an intruder. If the intruder is overwhelmed, it is very often taken back to the nest to be eaten. In ecologically dominant arboreal species known for their territoriality, spread-eagling is used both against other ants, including conspecifics, and in prey capture, with only very small prey being captured by single workers [3, 9–11].

It was with the aim of distinguishing territorial aggressiveness from predatory behaviour that we decided to conduct a study on *Plectroctena minor*, a

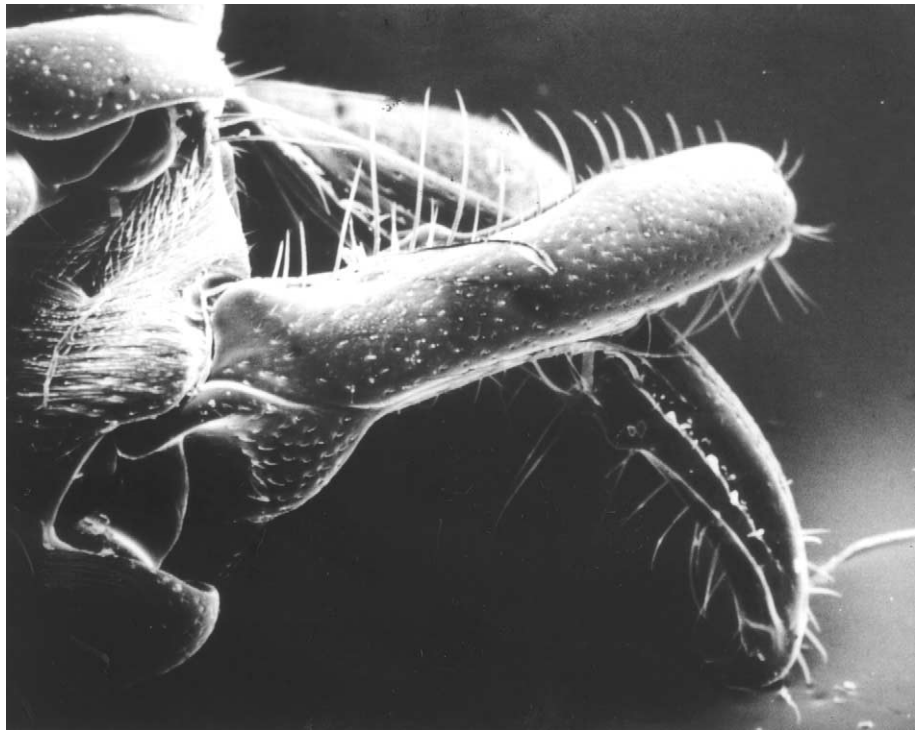

Fig. 1. Scanning electron photograph of the mandibles of a *Plectroctena minor* worker after snapping (mandible length: 3 mm).

ponerine ant species equipped with hypertrophied mandibles that can snap [12] (Fig. 1). The snapping of mandibles results in a sharp blow to intruders, stunning or killing them. Snapping, also noted in soldiers of several termite genera and in the ant genera *Mystrium* (Ponerinae) and *Orectognathus* (Myrmicinae), is considered to be firstly used for nest defence [13–16]. Nevertheless, we noted that *P. minor* workers, rather specialised in millipede capture, sometimes use this behaviour during the predation of alternative prey or large millipedes [17–19]. We therefore compared snapping occurrences when *P. minor* foraging workers encountered nestmates or alien conspecific workers, workers of sympatric competing ponerine ant species, and different kinds of preys.

2. Materials and methods

We carried out this study in Yaoundé (Cameroon) on five queenright *P. minor* colonies containing 70 to 100 workers and abundant brood. In the laboratory, the colonies were bred in test tubes (22×2.5 cm) supplied with a watering place and opening into hunting arenas ($45 \times 35 \times 5$ cm) covered with a plate of glass. These arenas were plastic, without sand or leaf litter, to fully expose the tested items and to standardise the test conditions. Ants marked the nest entrance and the hunting arena with anal spots as their natural foraging area.

In order to study the territorial behaviour of *P. minor* workers at the intraspecific level, we conducted two series of confrontation tests. In the first series, encounters between *P. minor* foraging workers occurred in neutral arenas (15 cm in diameter), where two individuals were introduced. In the second series, a worker was introduced into the hunting arena of a colony, and the encounters occurred more than 20 cm away from the nest entrances. Each time, we used homocolonial (the workers were separated for 24 h or during 15 days), then heterocolonial workers.

A study on the reactions of *P. minor* workers vis-à-vis sympatric, competing ponerine species was conducted by individually introducing workers of these species into the hunting arenas of *P. minor* colonies. We noted each time if the *P. minor* workers snapped at the alien or not. In the first series of experiments, we tested *Plectroctena gabonensis* workers in order to obtain information on the reactions of *P. minor* workers at the intrageneric level. In the second series of experiments, we tested workers of *Leptogenys* sp., *Pachycondyla analis*, *Pa. tarsata*, *Pa. soror*, and *Pa. pachyderma* (all Ponerinae; results pooled). This time, we compared encounters between *P. minor* workers and test workers taking place in the hunting arenas less than 5 cm vs more than 20 cm from the nest entrances.

We used the same protocol with insects previously known as potential prey of *P. minor* workers [18]:

5–7 mm long *Cubitermes* sp. workers, 10–12 mm long oniscoid isopods, 20–25 mm long Grillidae larvae, 25–35 mm long Tenebrionidae larvae, and 30–35 mm long millipedes. We also experimented with large *Macrotermes bellicosus* soldiers (20–25 mm long) whose role consists in defending termitary chambers by preventing enemies from penetrating into galleries.

For statistical comparisons, we used Fisher's exact-tests (StatXact-3 software). Appropriate probabilities were adjusted for the number of simultaneous tests, using the sequential Bonferroni procedure [20].

3. Results

Antennal contact always occurred during encounters, but, depending on the cases, it was followed by a brief antennal palpation (most of the cases) or by the folding back of the antennae when confronted with millipedes and termite soldiers. Snapping never occurred during encounters between homocolonial workers, or in neutral arenas, or when an individual was introduced into the foraging arena of its colony after 24 h or even 15 days of separation (Table 1). On the contrary, snapping was always noted during encounters between heterocolonial individuals. Territorial marks probably play a role in the workers' behaviour as, in the latter case, it was always the aliens that were snapped at, and they tried to escape before being snapped at in 22 cases out of 35. The strong blow received during snapping sometimes led to the death of the alien worker.

A very similar behaviour was noted when *P. minor* workers snapped at *P. gabonensis* workers in 22 cases out of 23, independently of the zone of the hunting arenas where they encountered them (Table 1). Otherwise, they snapped at *Pachycondyla* spp. and *Leptogenys* workers more frequently when encountered less than 5 cm from the nest entrances than at a distance greater than 20 cm (Fisher's exact-test: $P = 0.0011$; Table 1). Note that during these interspecific encounters reciprocal avoidance, and mostly avoidance by alien individuals, was frequent. Nevertheless, fighting was noted in nine cases out of 78 (11.5%) and even resulted once in the death of a *P. minor* worker.

Except for large *Macrotermes* soldiers that were snapped at in all cases (Figs. 2 and 3, Table 2), *P. minor* hunting workers also significantly snapped at their prey more frequently when encountered near the nest entrances than at a distance greater than 20 cm in the hunting arenas (Fig. 3). Otherwise, we noted a gradation in the occurrence of snapping according to prey nature when we compared the reactions of the hunting workers during encounters more than 20 cm from the nest entrances (Fig. 3, Table 2). In all cases, the workers folded their antennae backward when approaching *Macrotermes* soldiers in order to snap at them. The same behaviour was noted in certain cases for Grillidae.

4. Discussion

In *P. minor* intraspecific aggressiveness was illustrated by the systematic occurrence of snapping at alien conspecific workers. This behaviour can be compared to 'full attacks' noted in different ant species in the same situation. In these cases, the differences in colony odour (cuticular substances) trigger the aggressive behaviour in the workers, with olfaction being the basis for alien and nestmate recognition [5, 7]. The same was true at the interspecific, intrageneric level when *P. minor* workers encountered *P. gabonensis* individuals that were snapped at independently of the zone of encounter in the hunting arenas. On the contrary, other tested ponerine species were snapped at when encountered around the nest entrances rather than elsewhere in the hunting arenas. There are therefore differences in the responses to encounters with alien ants, with greater aggressiveness toward conspecific or congeneric aliens than toward workers of other sympatric ponerine species. These differences might be related to the semi-specialisation of *P. minor* and other *Plectroctena* species in the capture of millipedes. The latter, not being the most frequent litter-dwelling arthropods, are essential in the diet of *P. minor* colonies for worker and queen production [17]. As a result, congeneric individuals are more important competitors than other predatory ant species. Snapping seems then to be indirectly dependent on two principal parameters: the

Table 1. Snapping frequency during encounters between *Plectroctena minor* workers and others ant species according to the zone of confrontation.

	Neutral arena	Foraging arena	
Homocolonial *P. minor* workers	0% ($N = 30$)	0% ($N = 30$)	
Heterocolonial *P. minor* workers	100% ($N = 20$)	100% ($N = 35$)	
P. gabonensis workers	N.D.	95.6% ($N = 23$)	
		< 5cm from nest entrance	> 20 cm from nest entrance
Sympatric Ponerinae	N.D.	75% ($N = 24$)	33.3% ($N = 54$)

Fig. 2. A *Plectroctena minor* worker preparing to snap at the head of a *Macrotermes bellicosus* soldier under laboratory conditions (**A**). The worker prepares to retrieve the soldier stunned by the snapping (**B**). Worker length is 17 mm.

type of encountered individuals and the site of the encounter. The combination of these two factors directly influences the aggressiveness of *P. minor* workers, and thus snapping.

The initial hypothesis was that snapping is related to territorial aggressiveness. Our results highlight that this behaviour also concerns predation, for which the above-cited assertion remains true. Large *Macrotermes* soldiers were always snapped at, while prey selected during cafeteria experiments, namely small millipedes, isopods and *Cubitermes* workers [17, 18], were the least frequently snapped at. Also, the size of the prey intervenes as large millipedes were snapped at in certain cases, while smaller individuals were not [19]. Snapping frequencies recorded for Grillidae and Tenebrionidae larvae still remain difficult to interpret. As

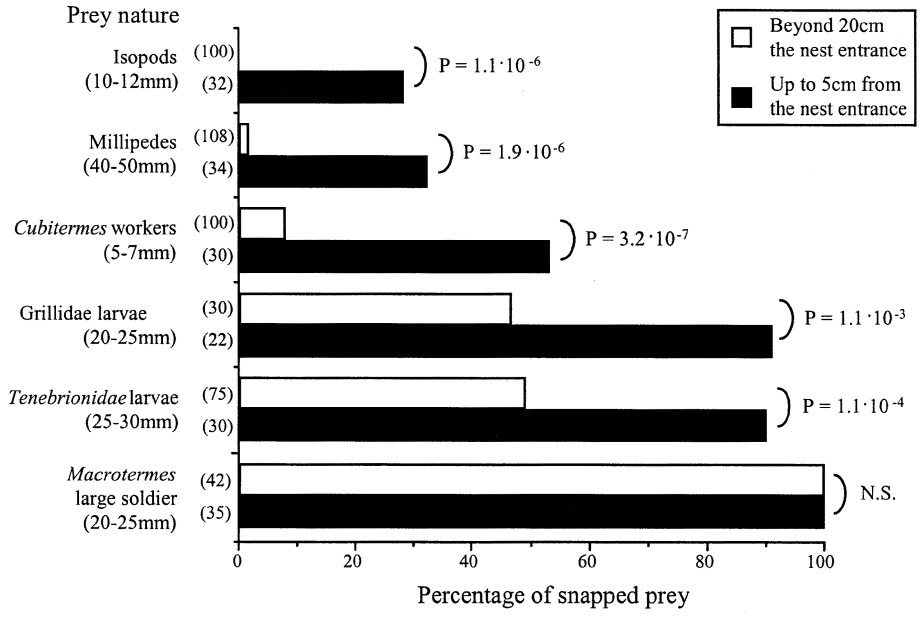

Fig. 3. Comparison of percentages of prey snapped at according to their nature and their distance from the nest entrance (number of prey tested in brackets). Statistical comparisons of the number of prey snapped at from a distance up to 5 cm and beyond 20 cm from the nest (Fisher's exact-test).

Table 2. Statistical comparisons of snapping between prey during encounters occurring at more than 20 cm from the nest entrances (Fisher's exact-test and sequential Bonferroni procedure).

Prey nature	Millipedes	*Cubitermes* workers	Grillidae larvae	Tenebrionidae larvae	*Macrotermes* large soldiers
Isopods	NS	$P < 0.05$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Millipedes		NS	$P < 0.001$	$P < 0.001$	$P < 0.001$
Cubitermes workers			$P < 0.001$	$P < 0.001$	$P < 0.001$
Grillidae larvae				NS	$P < 0.001$
Tenebrionidae larvae					$P < 0.001$

antennal contact always occurred and was followed by palpation or, for dangerous prey, by the folding back of the antennae when confronted with dangerous prey, behaviour previously reported in ponerine ants, we deduced that workers discriminated encountered insects during this contact. One can hypothesise that the nature and the perception of the cuticular substances of these insects trigger aggressiveness and snapping in the ants. As all prey other than termite soldiers were significantly more frequently snapped at when encountered close rather than far from the nest entrances, we can assert that territorial aggressiveness intermingles with predatory behaviour. Although less salient, a similar result was also illustrated by *Ectatomma tuberculatum* (Ponerinae) hunting workers that stung more frequently small or stunned prey during encounters close rather than far from the nest entrances [21].

Plectroctena minor workers snapped at all large *Macrotermes* soldiers, even those encountered far from the nest entrances (this study), while this behaviour decreased to 80% for small soldiers and only 17% for workers [18]. These differences highlight the fact that *P. minor* workers can discriminate dangerous prey from others of the same species. Termite soldiers are extremely aggressive and can cut a worker into two pieces thanks to their very powerful mandibles. They assume the role of colony defence, plugging galleries, so that termite predators need to eliminate them in order to have access to the rest of the termitary. For this purpose, other ponerine ants bend their gaster in order to direct their devaginated sting toward the termite soldiers, killing them with venom [22, 23]. Snapping seems to be a well-adapted behaviour for stunning or killing termite soldiers, as it does not require the workers to bend their gaster, a behaviour necessitating wider galleries. We found again that ants fold their antennae backward when detecting termite soldiers, this 'prudence' behaviour being general in ponerine ants preying on termites ([22, 23] and references cited therein).

According to our results, snapping is then related both to territorial aggressiveness and to prey capture. *Plectroctena* spp. workers forage under the litter, beneath the bark of rotting logs, or in underground galleries ([12, 24]; Dejean, pers. obs.). In this case, the snap-jaw design of the mandibles is advantageous when compared to species equipped with 'normal' mandibles that cannot be used to stun prey. The trap-jaws mandibles of *Odontomachus* and *Anochetus* permit them to stun prey, but when open are wider than the worker's body and so poorly adapted to narrow galleries. In conclusion, contrarily to termites for which snapping was selected for nest defence, the evolutionary process that conducted ants to the same adaptation may be different. Indeed, this behaviour could result from an adaptation for preying in galleries, which was secondarily selected for territorial aggressiveness.

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