

## Nesting and foraging habits in the arboreal ant *Atopomyrmex mocquerysi* ANDRÉ, 1889 (Hymenoptera: Formicidae: Myrmicinae)

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### Abstract

*Atopomyrmex mocquerysi* ANDRÉ, 1889 is a West-Central African wood-excavating myrmicine species whose colonies construct galleries in the main live branches of their host trees, causing the distal parts of these branches to dry out. In southeastern Cameroon, this species was mainly found in woody savannahs that are burned annually. It was also present in the canopy of a secondary forest, but was relatively rare on trees growing along forest edges and entirely absent from the canopy of an old-growth forest. It was absent from oil palm and coffee tree plantations, rare on cocoa trees, present on 0.2% to 5.3% of the avocado, guava, mango and *Citrus* spp. trees monitored, and frequent on safoo trees (12.4%). A fire in a mango plantation seems to have favored its presence. The colonies generally exploit Aleyrodidae, Aphididae, Coccidae, and Stictococcidae. Workers forage for prey diurnally, mostly on the ground. Their predatory behavior is characterized by detection through contact. Workers recruit nestmates at short-range (within range of an alarm pheromone), rarely at long-range, after which they spread-eagle the prey and immediately cut it up on the spot. Individual workers retrieve the prey pieces. Unlike other territorially-dominant arboreal ants, *A. mocquerysi* is a threat to host trees because, in addition to being a wood-excavating species, its workers only slightly protect the foliage of their host tree from herbivorous insects since they mostly hunt on the ground.

**Key words:** Cameroon, wood-excavating ant, nest site selection, pest ant, predatory behavior, rhythm of activity, life history.

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### Introduction

Arboreal-nesting ants represent a major component of the fauna in the canopies of rainforests and tree crop plantations; among them, territorially-dominant arboreal species have very populous (several thousands of individuals) and polydomous colonies, and are very aggressive toward other dominant ants at both the intra- and interspecific level (DEJEAN & al. 2007a). As a consequence, competition for space results in a mosaic distribution pattern of their territories, creating what has become known as an "arboreal ant mosaic" (LESTON 1973, BLÜTHGEN & STORK 2007, DEJEAN & al. 2007a).

Until now, the foraging behavior of territorially-dominant, African arboreal ants has been well-documented only for *Oecophylla longinoda* (LATREILLE, 1802) (see DEJEAN 1990, HÖLLDOBLER & WILSON 1990, WOJTUSIAK & al. 1995), *Tetramorium aculeatum* (MAYR, 1866) (see DJIÉTO-LORDON & al. 2001) and *Crematogaster* sp. (RICHARD & al. 2001). All of these species feed principally on hemipteran honeydew, extrafloral nectar when available, and prey. Since they consume different arthropod taxa, they have frequently been used as biological control agents (DEJEAN & al. 2007a).

Amongst myrmicine ants, the genus *Atopomyrmex* (Formicoxenini tribe) is widely distributed in woody savannahs and forested areas of the Afrotropical region (TAYLOR 2006). Three species have been described: *A. calpocalycola* SNELLING, 1992 has only been reported in Cameroon, whereas the two others, *A. cryptoceroides* EMERY, 1892 and *A. mocquerysi* ANDRÉ, 1889, have been widely noted in Central and West Africa (TAYLOR 2006). These wood-excavating ants are typically present in tree crop plantations and forests, where they damage the main live branches and trunks (BUYCKX 1962, LÉVIEUX 1976, KENNE & al. 2003). Their nests are composed of a network of parallel galleries that causes the distal parts of the occupied branches to dry out. Consequently, the presence of *Atopomyrmex* colonies is harmful to their host trees so that species of this genus are considered to be pest ants, especially for coffee and cocoa trees on which the infestation spreads to all of the branches and may lead to the death of the infested individuals (BUYCKX 1962).

The scattered information available on the biology of *A. mocquerysi* shows that it is a dominant arboreal species (LESTON 1973). A 7-year old nest contains more than 60,000 adults and 25,000 larvae (LÉVIEUX 1976). Workers forage in columns on adjacent trees, including shrubs, and on the ground to collect food such as prey, hemipteran honeydew or extrafloral nectar, sap, plant resins, seeds and leaf fragments (LÉVIEUX 1976, 1977).

In this study, we: (1) verified if *A. mocquerysi* nests in only a limited number of cultivated trees, or if it is a generalist, (2) examined what kinds of hemipterans workers attend, (3) studied the workers' daily activity cycle, and (4) investigated their predatory behavior to compare it to that of other dominant African ants.

## Materials and methods

**Study sites:** These studies were carried out between 1995 and 2006 in forested zones of Cameroon on host trees situated on the campus of Yaoundé University (3° 53' N, 11° 30' E), in Minkoméyos (3° 59' N, 11° 28' E), Matomb-Brousse (3° 53' N, 11° 4' E), Ebodjié (2° 38' N, 9° 53' E), Kala (3° 50' N, 11° 21' E), around Buéa (4° 15' N, 9° 22' E), Muéa (4° 35' N, 9° 36' E) and Batchenga-Nzi (3° 51' N, 11° 42' E). The region is characterized by a "tropical monsoon" climate (Köppens's standard climatic classification) with a roughly constant annual temperature (averaging from 26.1°C in February to 22.8°C in August) and continuously high levels of atmospheric humidity (varying from 71% in January to 82% in July and August); variations in monthly precipitation range from 5.6 mm in January to 383.3 mm in October.

Field research on *A. mocquerysi* colonies was conducted in the region of Yaoundé along forest edges (to a depth of 15 m; a total of 9 km monitored), in the crowns of 41 trees in a 60-year old secondary forest (0.78 ha; Matomb-Brousse), on 167 large trees (40 - 45 m tall) in an old-growth forest (Ebodjié) using the canopy raft and the canopy sledge (see DEJEAN & al. 2007a), and over 5 ha of a woody savannah (Batchenga-Nzi). The same kind of research was conducted in tree crop plantations not treated with insecticides situated around Buéa, Muéa and Yaoundé. We monitored in total: 615 oil palm trees *Elaeis guineensis* JACA. (Arecaceae), 400 coffee trees *Coffea robusta* L. (Rubiaceae), 15,133 cocoa trees *Theobroma cacao* L. (Sterculiaceae),

659 mandarin *Citrus deliciosa* TEN. and orange trees *C. sinensis* L. (Rutaceae), 412 safoo trees *Dacryodes edulis* (G. DON) LAM. (Burceraceae), 591 guava trees *Psidium guajava* L. (Myrtaceae), 560 mango trees *Mangifera indica* L. (Anacardiaceae) and 49 avocado trees *Persea americana* MILL. (Lauraceae).

For the tree crop plantations managed by the Institut de Recherche Agricole pour le Développement (IRAD) situated in Minkoméyos, sunlight reaches the ground all around the mango trees so that the grasses growing between them are cut regularly. Nevertheless, a fire from the neighboring area spread to the mango tree plantation, burning these grasses. We then verified whether the fire triggered a response in the associated ant species of these trees by comparing data before and 1 year after the fire (n = 204 trees).

**Host plants and honeydew collection:** An inventory was conducted during both the dry and rainy season at different sites around Yaoundé, including the urban zone, plantations and an old, secondary forest. This enabled us to catalogue the hemipterans this species exploited; voucher specimens were deposited in the Museum National d'Histoire Naturelle, Paris. Voucher specimens of ants were deposited in the Museum of Natural History, London.

**Daily activity cycle:** This study was carried out on three colonies found on the University campus. Their daily rhythm of activity was recorded over two 24-hour periods using the method developed by LÉVIEUX (1976): we drew a mark on the main foraging trails (situated on the trunks of host trees) used by the workers to reach the ground or neighboring trees where they forage for food, and counted the number of workers entering and leaving the nest. Each observation lasted 3 minutes and was repeated every hour. Two series of measurements were conducted during the rainy season, and two others during the dry season. To evaluate the relationship between ant activity and environmental conditions, the air temperature and relative humidity were measured each hour using a thermohygrometer placed one meter above the ground.

**Hunting strategies:** We studied the predatory behavior of the workers from five mature nests (they produce winged sexuals) located on the University campus. A plywood board (30 × 40 cm) placed on the ground at the base of each tree served as an experimental hunting arena. Experiments began one week after we judged the board to be well integrated into the foraging territory of the ant colony. Small (3 - 5 mm long; n = 60; a size similar to that of a worker) and large (15 - 20 mm long; n = 60) live grasshoppers (Tettigoniidae) were used as prey. The tibia of their hind legs were cut off to prevent them from jumping away and escaping, since it was not our purpose here to study their anti-predator strategy.

For each test (repeated 60 times), we used a protocol perfected during our prior research on the predatory behavior of other territorially-dominant arboreal ants (RICHARD & al. 2001, DEJEAN & al. 2008b). The sequence of behavioral acts was recorded from the introduction of the prey into the centre of each hunting arena until their capture and retrieval to the nest (three to five trials per day, two to five days per week). At least 30 minutes separated two trials. Data sheets containing the full repertoire of the behavioral sequences were first established during preliminary experiments. We recorded the behavioral acts performed by the hunting workers when faced with the prey: detection, anten-

Tab. 1: List of hemipterans attended by *A. mocquerysi* workers and their host plants. Workers frequently attend hemipterans on plants surrounding their host trees, especially the invasive vine, eupatoire. <sup>1</sup> = economically important plant species; <sup>2</sup> = imported, invasive species.

Hemiptera		Host plant	
Family	Species	Species (Family)	Vegetal organs
Aleyrodidae	undetermined	<i>Citrus</i> spp. <sup>1</sup> (Rutaceae)	Leaves
Aphididae	<i>Aphis spiraeicola</i> PATCH, 1914	Eupatorium: <i>Chromolaena odorata</i> L., 1759 (Asteraceae) <sup>2</sup>	Leaves; twigs and buds
Coccidae	<i>Inglisia conchiformis</i> MASKELL, 1879	Soursop: <i>Annona muricata</i> L., 1753 (Annonaceae) <sup>1</sup>	Fruits; leaves; branches
Stictococcidae	<i>Stictococcus</i> sp.	Bitter leaves: <i>Vernonia amygdalina</i> DEL., 1826 (Asteraceae) <sup>1</sup>	Leaves; twigs and buds

nal palpation, attack, seizure, stinging, immobilization, nest-mate recruitment, spread-eagling, cutting up, and transporting the prey. The part of the prey body seized by the ants discovering the prey was noted. The data recorded permitted us to build flow diagrams with transition frequencies between behavioral acts. Percentages (corresponding to these transition frequencies) were calculated from the overall number of cases.

**Morphological analysis:** Whole, dead *A. mocquerysi* workers were mounted on aluminum stubs and coated with a mixture of 80% gold and 20% palladium to be examined with a scanning electron microscope (Leica Stereoscan 440; Solms, Germany). The structure of the pretarsus and the sting apparatus was studied in order to compare it with those of other arboreal ant species.

**Statistical analysis:** As normality and equal variance tests passed in all of the comparisons, mean values ( $\pm$  SE) were compared using Student's *t*-test and correlations between parameters were determined using Pearson's correlation coefficients (SigmaStat 2.03 software). Percentages were compared from the core results using Fisher's Exact-test (StatXact-3 software).

## Results

**Distribution of the *A. mocquerysi* colonies:** We did not record any *A. mocquerysi* colonies in the canopy of old-growth forest at Ebodjié, although we had direct access to the canopy (167 tree crowns monitored). At Matombrousse, the colonies were extremely dispersed along the forest edges (nine colonies noted for 9 km of forest edge; about 1% of the trees;  $n \approx 900$  trees), whereas we noted three colonies in a study of 41 trees in a 60 year-old secondary forest (7.3% of the trees). Their density was comparatively high in the woody savannah at Batchenga-Nzi, where we noted 58 colonies for five hectares monitored (about 11.6% of the trees;  $n \approx 500$  trees).

In tree crop plantations, *A. mocquerysi* was absent from oil palm trees ( $n = 615$  trees) and coffee trees ( $n = 400$  trees), rarely noted on cocoa trees (0.7% of 15,133 trees), avocado trees (2.0% of 49 trees), guava trees (3.0% of 591 trees), mango trees (3.2% of 560 trees) and mandarin or orange trees (5.3% of 659 trees), but had a greater presence on safoo trees (12.4% of 412 trees).

The fire in the mango plantation in Minkoméyos seems to have favored the presence of *A. mocquerysi* (6 trees before *versus* 31 trees 1 year after the fire;  $n = 204$  trees;

Fisher's Exact-test:  $P < 0.001$ ), while we did not note any variation in the parts of the plantation that were not burned during this period (M. Kenne, unpubl.).

Workers attended hemipterans belonging to four species from the Sternorrhyncha suborder on both host and adjacent trees (Tab. 1). These hemipterans proliferated on only four out of 56 closely-monitored trees, and consisted of Aleyrodidae on orange trees, Aphididae on Eupatorium, Coccidae on soursop trees, and Stictococcidae on bitter leaves.

**Daily activity cycle:** *Atopomyrmex mocquerysi* workers foraged during the day, but some residual activity was recorded in two nests at night during the dry season (Fig. 1). The correlation between the number of ants entering and exiting the nest each hour was significant during both the dry season (Pearson's correlation coefficient:  $r = +0.864$ ,  $P < 0.0001$ ,  $n = 72$ ) and the rainy season ( $r = +0.559$ ,  $P < 0.0001$ ,  $n = 72$ ), illustrating a regular flux. The flow of workers was positively correlated with air temperature and negatively correlated with air humidity (Tab. 2). In terms of the number of ants leaving the nests, the colony's investment in foraging varied seasonally, with more workers observed on the main foraging trail during the dry season (mean  $\pm$  S.E.:  $30.2 \pm 4.6$  workers per 3-minute series and per day,  $n = 72$ ) than during the rainy season ( $19.4 \pm 2.6$  workers,  $n = 72$ ; Student's *t*-test,  $t = 2.03$ ,  $df = 142$ ,  $P = 0.044$ ).

**Hunting behavior:** During their period of activity, regardless of the season, *A. mocquerysi* workers foraged for prey on the ground, and only infrequently on the tree foliage. In the savannah, scout workers discovering ripe figs recruited nestmates to capture all of the agaonid pollinators taking shelter inside of the figs, and then cut the figs themselves into small pieces that they then retrieved.

Workers patrolling the hunting arena that we installed at the base of the trees moved in a sinuous path with their antennae wide open and pointed toward the ground. The following sequence was observed (Fig. 2). Whatever their size, prey were mostly detected by contact, and only rarely from a distance (1 to 6 mm;  $3.0 \pm 0.3$  mm;  $n = 27$ ). After brief contact, the ants seized the prey; after detection from a distance, they antennated it (Fig. 2). All prey were seized by an appendage (a leg or an antenna), but antennated prey were sometimes seized and then released, so that some of them were lost. When a prey escaped after antennal contact, the workers searched for it by noticeably increasing their

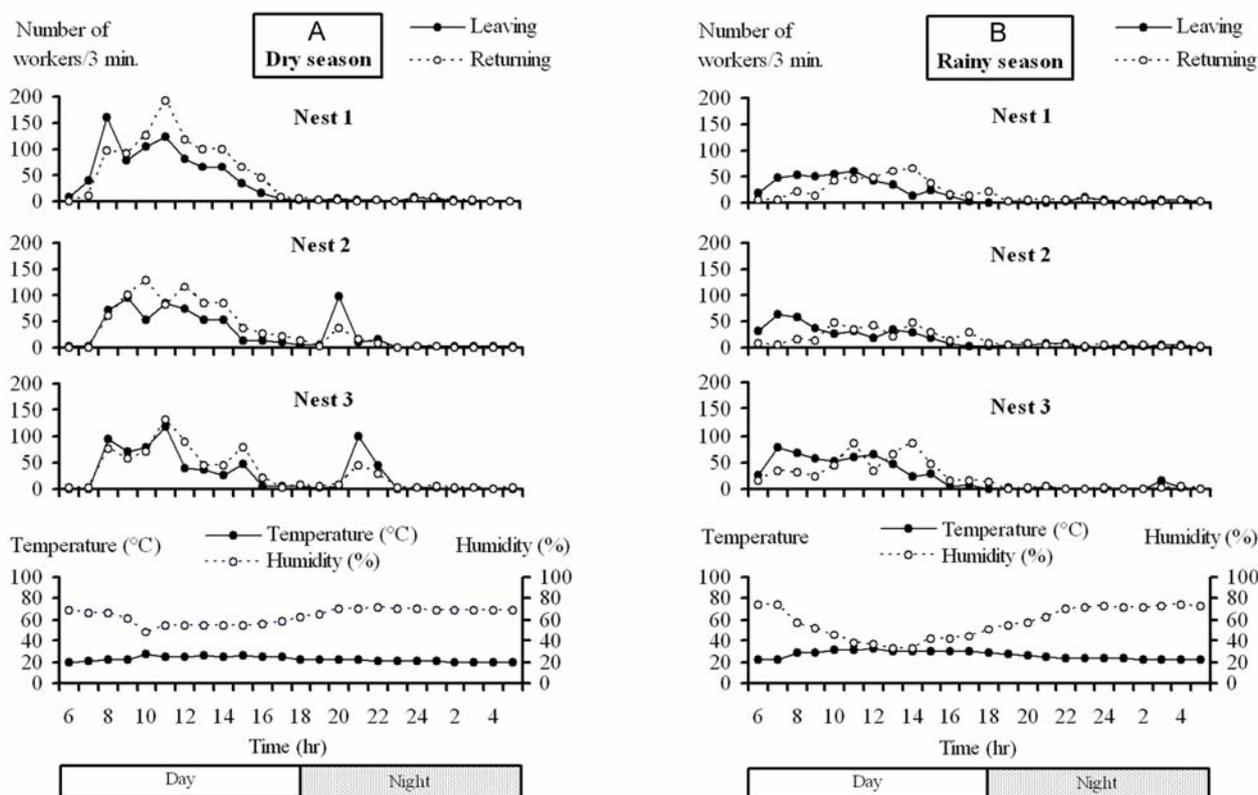


Fig. 1: Daily rhythm of foraging activity for *Atopomyrmex mocquerysi* workers during both the dry and the rainy seasons. Workers leaving or returning to their nest were counted during 3 consecutive minutes each hour. Microclimatic parameters (i.e., air temperature and relative humidity) were also recorded.

Tab. 2: Pearson's correlation coefficient between the flow rate of *A. mocquerysi* workers on the main trail and values for microclimatic conditions during the daily rhythm of activity during both the dry and the rainy seasons. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

	Dry season (n = 24)		Rainy season (n = 24)	
	Temperature (°C)	Relative humidity (%)	Temperature (°C)	Relative humidity (%)
<b>Nest 1:</b> Leaving	0.633 ***	-0.536 **	0.509 *	-0.599 **
Returning	0.791 ***	-0.743 ***	0.814 ***	-0.849 ***
Global traffic	0.739 ***	-0.667 ***	0.753 ***	-0.826 ***
<b>Nest 2:</b> Leaving	0.634 ***	-0.576 **	0.245 ns	-0.334 ns
Returning	0.819 ***	-0.752 ***	0.876 ***	-0.894 ***
Global traffic	0.772 ***	-0.706 ***	0.653 ***	-0.723 ***
<b>Nest 3:</b> Leaving	0.521 **	-0.420 *	0.439 *	-0.540 **
Returning	0.735 ***	-0.663 ***	0.709 ***	-0.776 ***
Global traffic	0.649 ***	-0.559 **	0.630 ***	-0.723 ***
<b>All nests pooled (n = 72):</b> Global traffic	0.710 ***	-0.636 **	0.650 ***	-0.728 ***

speed and the sinuosity of their path, so that they recovered the prey in a few seconds.

After this solitary phase, a collective phase occurred with the arrival of several nestmates recruited at short- (the discovering worker did not leave the prey) or long-range. During short-range recruitment, workers foraging in the vic-

inity of the nestmate that discovered and seized a grasshopper changed the sinuosity of their paths so as to head toward the discovering worker, probably because that worker released an alarm pheromone. Indeed, in all cases these individuals firstly antennated the discovering worker's abdomen before helping to capture the prey. In the absence of



mosaics are dynamic, changing as the trees age: the trees are first occupied by "ground-nesting, arboreal-foraging" species, and then by arboreal nesting *Oecophylla longinoda*, *Tetramorium aculeatum* and *A. mocquerysi*, followed by *Crematogaster* sp. (KENNE & al. 2003, DEJEAN & al. 2008a). Like *O. longinoda* and *T. aculeatum*, *A. mocquerysi* was absent from an old-growth forest and present in a secondary forest, but was rare along forest edges (DEJEAN & al. 2007a, this study). The fact that savannahs are burned annually, and that a fire in a mango tree seems to have favored the presence of *A. mocquerysi* over that of *O. longinoda* and *T. aculeatum* (whose colonies were destroyed by the flames), suggests that this species is able to withstand fire due to its nesting habit. Indeed, we observed *A. mocquerysi* foraging on the ground several times one or a few days after savannahs were burned; we even saw columns forming between the host trees to large arthropods and earth worms killed by the fire, illustrating that this ant also has a scavenging behavior.

The nests of wood-excavating ants usually cause the distal parts of the occupied branches to dry out. Consequently, their presence is harmful to host trees. In our study, host tree selection was noted in plantations, and, like other live-wood-nesting ants (see MONY & al. 2007), *A. mocquerysi* can be an agricultural pest on tree species of economical importance, mostly safoo trees, but also on sour-sop, guava, mandarin, mango, and orange trees.

Differences in climatic conditions can explain why we noted a typically diurnal, unimodal pattern of foraging activity for *A. mocquerysi* workers which differed from the bimodal rhythm described in the Ivory Coast (LÉVIEUX 1976). Indeed, cues from the physical environment are known to override the specific circadian rhythm affecting foraging activity rhythms (HÖLLDOBLER & WILSON 1990, ORR & CHARLES 1994).

All of the dominant arboreal ant species studied so far attend large numbers of honeydew-producing hemipterans (MAJER 1993, BLÜTHGEN & STORK 2007, DEJEAN & al. 2007a). In Central and West Africa, they typically forage in the canopy where they mostly attend Stictococcidae (TAYLOR 2006), whereas *A. mocquerysi*, adapted to the savannah, mainly hunts on the ground and surrounding vegetation, and mostly exploits Aleyrodidae, Aphididae and Coccidae – all known vectors of plant diseases (MAJER 1993). Because ants consume a proportion of these hemipterans, under natural conditions the latter do not proliferate and the amount of sap the host plant loses is generally counterbalanced by the protection the ants provide it from defoliating insects (STYRSKY & EUBANKS 2007). Nevertheless, in plantations a vicious cycle can lead to the proliferation of hemipterans that directly affects the host trees or indirectly affects them through the transmission of diseases (MAJER 1993).

Although *A. mocquerysi* workers can forage on the trees (see also LÉVIEUX 1976), here we show that they usually hunt on the ground, while other territorially-dominant arboreal ant species mostly hunt in tree crowns. Host tree protection is therefore reduced to the sole territoriality of the workers (see also DEJEAN & al. 2008a), so mostly in the area immediately around the nest and along the trails to the ground.

As with other typically territorially-dominant arboreal ants, *A. mocquerysi* workers mostly detect prey by contact

(DEJEAN & al. 1994, ORIVEL & al. 2000, DJIÉTO-LORDON & al. 2001, RICHARD & al. 2001, DEJEAN & al. 2008b). By contrast, *Oecophylla* workers group ambush prey, something facilitated by the detection of prey by sight, and hence operate at greater distances (DEJEAN 1990). The reaction of *A. mocquerysi* workers towards escaping prey (i.e., increasing their speed and the sinuosity of their path) seems to be a general pattern in predatory ants and enhances the chances of finding the prey again, particularly on the ground. In tree foliage prey can escape by flying away or letting themselves fall (KENNE & al. 2000, ORIVEL & al. 2000, KENNE & al. 2005).

The *A. mocquerysi* workers' predatory behavior is based on spread-eagling prey following short-range recruitment. This seems to be general in dominant, arboreal ants whose hunting workers are always surrounded by several nestmates situated within the range of a recruitment pheromone. Long-range recruitment is used only in certain situations (DEJEAN 1990, HÖLLDOBLER & WILSON 1990). The ability of the workers to spread-eagle prey is facilitated by well-developed adhesive pad arolia, and horn-shaped claws on their pretarsus (WOJTUSIAK & al. 1995, DJIÉTO-LORDON & al. 2001, ORIVEL & al. 2001, RICHARD & al. 2001, this study).

Like *O. longinoda*, *A. mocquerysi* workers never use venom (DEJEAN 1990); here this behavior is associated with a short spatula-shaped sting which is used to lay recruitment trails, like in the genus *Pheidole* (DEJEAN & al. 2007b). By contrast, both *T. aculeatum* and *Crematogaster* sp. (both Myrmicinae) generally sting their prey several times. Only *O. longinoda* workers retrieve prey as whole individuals, whereas others, including *A. mocquerysi*, cut them up, with individual ants retrieving the small pieces (WOJTUSIAK & al. 1995, DJIÉTO-LORDON & al. 2001, RICHARD & al. 2001).

In conclusion, *A. mocquerysi* is a diurnal species that nests in certain tree species of economic importance. Workers attend hemipterans belonging to taxa known to be vectors of plant diseases. Furthermore, unlike other dominant arboreal ant species that hunt mostly on tree crowns, *A. mocquerysi* workers hunt mainly on the ground, reducing host tree protection and reinforcing its status of pest-ant due to its nesting habits.

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### Zusammenfassung

*Atopomyrmex mocquerysi* ANDRÉ, 1889 ist eine westzentralafrikanische, Holz aushöhlende Ameisenart der Myrmicinae. Ihre Kolonien bauen Galerien in den lebenden Hauptästen ihrer Nestbäume und verursachen so das Absterben der distalen Teile dieser Äste. Wir haben diese Art im südöstlichen Kamerun vor allem in Savannen mit Baumbestand, der jährlich abgebrannt wird, gefunden. Ebenfalls wurde die Art im Kronenbereich eines Sekundärwaldes gefunden, war aber vergleichsweise selten auf Bäumen des Waldrandes und fehlte völlig im Kronenbereich eines Altbestandes. Die Ameise wurde in Ölpalmen- und Kaffee-

plantagen nicht gefunden, war selten auf Kakaobäumen, wurde auf 0,2 bis 5,3 % der untersuchten Avocado-, Guave-, Mango- und Zitrusbäume gefunden, und war häufig (12,4 %) auf der Baumart *Dacryodes edulis*. Ein Feuer in einer Mangopflanzung scheint der Ameise zuträglich gewesen zu sein. Kolonien von *A. mocquerysi* pflegen trophobiotische Beziehungen zu Aleyrodidae, Aphididae, Coccidae und Stictococcidae. Die Art ist auch räuberisch. Arbeiterinnen fouragieren tagsüber nach Beute, vor allem am Boden. Das räuberische Verhalten ist durch Erkennen von Beute durch Kontakt gekennzeichnet. Arbeiterinnen rekrutieren Nestgenossinnen auf kurze Distanz (innerhalb des Wirkungsradius von Alarmpheromonen) und nur selten auf weite Distanz. Rekrutierte Arbeiterinnenteams immobilisieren die Beutetiere indem sie deren Extremitäten auseinanderziehen. Sie zerteilen sie sofort, und die Teile werden dann von einzelnen Arbeiterinnen werden. Im Gegensatz zu anderen territorial-dominanten, Bäume bewohnenden Ameisen stellt *A. mocquerysi* durch das Aushöhlen des Holzes eine Bedrohung für die bewohnten Nestbäume dar, die wegen des Beutejagens am Boden durch den nur geringen Schutz des Laubes nicht ausgeglichen wird.

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