



Nesting System and Foraging Behaviour of *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 (Hymenoptera: Formicidae: Myrmicinae) in Douala (Littoral-Cameroon)

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Abstract: Nesting system, diet behaviour, activity rhythm and predatory behaviour of *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 were studied in the field situation in suburbs of Douala (Littoral-Cameroon). Polycalic and polydomous nesting system were recorded. Large independent nests were positioned on the bark surface of trunks (50.8%) or the underside bark of the fork of large branches (49.2%) of cultivated or wild trees (45.8% and 54.2% respectively). Workers collected nectar from 18 plants from eight families: Asteraceae, Costaceae, Ehretiaceae, Euphorbiaceae, Mimosaceae, Phyllanthaceae, Poaceae and Rutaceae. They collected honeydew from Aleyrodidae and four Hemipteran families from Sternorrhyncha suborder: Aphididae, Coccidae, Pseudococcidae and Stictococcidae. These Hemipterans proliferated on 11 plant families: Anacardiaceae, Annonaceae, Apocynaceae, Asteraceae, Costaceae, Euphorbiaceae, Myrtaceae, Poaceae, Rutaceae, Solanaceae and Urticaceae. Solid particles brought back to the nest were mostly from plants (72.5%) and weakly preys (27.5%). Sugary liquids were preferred over fats, carbohydrate sources, and even preys. Products were collected continuously (day and night) in the foliage of the host plant and neighbouring plants, shrubs and grasses. Workers occasionally brought back to the nest dead or dying larvae of grasshoppers and small particles of other arthropods (ants, flies, caterpillars). The sequence of behavioural acts recorded during the capture of larvae of *Ruspolia differens* (Orthoptera: Tettigoniidae) and adults of *Zonocerus variegatus* (Orthoptera: Pyrgomorphidae) (3 to 5 mm and 15 to 20 mm long respectively) were compared. The main sequence presented succession of seven acts: (1) detection by contact; (2) antennation; (3) attack-seizure; (4) short-range recruitment of nestmates in the vicinity; (5) spread-eagling of preys; (6) cutting up the prey on the spot; and (7) transport of pieces or whole prey to the nest. The stinging phase was not recorded. The duration of the capture of small prey (66 min. to 1 hr. 25 sec.; mean \pm se: 1 hr. 57 min. 25 sec. \pm 12 min. 2 sec.; 10 essays) was lower than that of large preys (2 hrs. 33 sec. to 4

hrs. 16 sec.; 2 hrs. 58 min. 32 sec. \pm 17 min. 15 sec.; 10 essays; Mann-Withney test: $T = 72.00$; $p = 0.014$). The long duration of captures suggested that spread-eagling and cutting up preys on the spot lasted a long time. *Cr. stadelmanni* is a poor predator indirectly harmful for wild or cultivated trees since their predatory aptitude is low compared to aggressive dominant arboreal-nesting ants and is counterbalanced by the propensity to honeydew.

Keywords: Dominant Arboreal Ants, *Crematogaster (Nematocrema) stadelmanni*, Diet Behaviour, Predatory Behaviour, Cameroon

1. Introduction

Arboreal-nesting ants are major components of the entomofauna in the canopies of rainforests and tree crop plantations; among them, territorially-dominant arboreal species present large populous colonies (several thousands of individuals), highly polygynous (several reproductive queens) and these colonies are composed of several interconnected nests (polydomy). Workers are very aggressive toward other dominant ants at both the intra- and inter-species level [1]. As a consequence, competition for space results in a mosaic distribution pattern of their territories, creating the "arboreal ant mosaic" [1, 2]. Ants of the genus *Crematogaster* Lund, 1831 are very diverse in species, dominant in the canopies of the tropical African forests and plantations. The subgenus *Nematocrema* Santschi, 1918 is represented in Africa by 3 species: *Crematogaster breviventris* Santschi, 1920 frequently found in Cameroon, *Cr. magitae* Forel, 1910 in West African forests and *Cr. (Nematocrema) stadelmanni* Mayr, 1895 found in both West Africa and the Congo basin forest zones [3]. The rare information available on *Cr. (Nematocrema) stadelmanni* relates to the morphology and wing venation [4], the taxonomic history and distribution in Africa [5], the morphology of three larval stages recalling the description in another African arboreal myrmicine *Cr. (Sphaerocrema) striatula* Emery 1892 [6, 7], the revision of its systematic position within the ant genus *Crematogaster* [8], and the composition of the alarm pheromone [9]. Until now, the foraging behaviour of African territorially dominant, arboreal-nesting ants was documented only for *Atopomyrmex mocquersyi* Andre, 1889 [10], *Crematogaster* sp., *Cr. clariventris* Mayr, 1895 and *Cr. striatula* Emery, 1892 [11-13], *Oecophylla longinoda* (Latreille, 1802) [13] and *Tetramorium (Macromischoides) aculeatum* (Mayr, 1866) [13, 14]. All of these species feed principally on Hemipterans honeydew, extrafloral nectaries when available, and prey. Since they consume different arthropod taxa, they have frequently been proposed as biological control agents against pest insects [1]. For example this is the case of *O. longinoda* successfully used in Benin against fruit flies (Diptera: Tephritidae) which damage mango crops [15-18]. The scattered reports available have shown that among the dominant arboreal nesting *Crematogaster*, *Cr. (Nematocrema) stadelmanni* has the ability to form cardboard material from masticated wood fibres and use it to various extents in nest construction or to shelter trophobionts [19]. Large independent populous nests are constructed and positioned on the trunk or the underside of large branches of large host trees. Nevertheless, the diversity of

the host trees, the distribution and the biology of 'carton' making ants are poorly understood and require further investigation. It is known that in the tropical forest zone of Africa, in orchards and food crop plantations, arboreal-nesting ants of the genus *Crematogaster* are numerically dominant just like *At. mocquersyi*, *O. longinoda*, and *Tetramorium (Macromischoides) aculeatum* Mayr and they are typically present in tree crop plantations and along the forest edges [1, 20, 21]. They are characterized by very populous, polydomous colonies, a strong aggressiveness toward nearly all intruders, and a highly developed intra- as well as inter-species aggressiveness resulting in a mosaic distribution pattern of their territories on the canopy of the rain forest [20, 21]. Their workers forage on adjacent trees including shrubs and on the surface of the earth [3, 21]. The aggressiveness of their workers and their painful venom pose problems in agricultural milieu, although the non-occupied branches of the sheltering trees and the visited adjacent trees are protected against herbivores [1, 3, 8, 15-18, 20, 21]. The biology and ecology of *Cr. (Nematocrema) stadelmanni* has remained little known. To fill the gap of knowledge about this ant we decided to conduct a study of the nesting system, diet, foraging activity and the predatory behaviour of workers in the suburbs of Douala (Cameroon) where it is frequently found on trees. The aim of this work was to compare its foraging and predatory behaviour with that of other dominant arboreal-nesting ant species, in order to verify whether common characteristics exist. For example, in *At. mocquersyi*, *Crematogaster* sp. *O. longinoda* and *T. aculeatum*, although different in terms of prey detection (the first species detect prey by sight at long range while it is the contrary in the two latter species where prey are detected by contact) and prey are always spread-eagled after a first worker had seized it by an appendage and recruited nestmates at a short range. Two differences can be noted in *O. longinoda* workers that never use venom and retrieve entire prey, while *Crematogaster* sp. and *T. aculeatum* workers use their venom and cut up prey on the spot in order to retrieve them in small pieces [11, 14]. We therefore asked the following questions: (1) what are the nesting system, the range of products collected in the environment and the daily rhythm of foraging that allow the success of the colonies? (2) is the predatory behaviour of *Cr. (Nematocrema) stadelmanni* workers based on spread-eagling the prey after a short range recruitment as reported in dominant arboreal-nesting ants? (3) as widely reported in dominant arboreal nesting ants, do workers of *Cr. (Nematocrema) stadelmanni* use their venom during predation and are the prey retrieved entirely or in small pieces?

2. Materials and Methods

2.1. Study Sites

Studies were carried out from 2018 to 2021 in seven suburbs of Douala (Littoral-Cameroon) situated 12 to 27 km from the centre of the city: Japoma (4°02'1780"N, 9°48'4.51"E, 27 m a.s.l.), four localities in Ngoma (4°06'51.00"N, 9°47'17.00"E, 17 to 53 m a.s.l.) [PK20 (4°06'36.81"N, 9°48'39.97"E, 18 m a.s.l.), PK21 (4°07'19.41"N, 9°49'31.25"E, 17 m a.s.l.), PK25 (4°08'41.28"N, 9°49'34.50"E, 53 m a.s.l.), PK27 (4°09'57.65"N, 9°50'25.06"E, 51 m a.s.l.)] and Yassa (3°58'20.15"N, 9°49'22.92"E, 27 m a.s.l.) (Figure 1). The climate in Douala is tropical [22], characterized by rainfall most months, with a short dry season (mid-November to mid-March of the following year) and a long rainy season (mid-

March to mid-November). The average annual rainfall is 3174 mm in October and the hottest month is February is (26.9°C). The range of monthly rainfall variation is high (5.6 mm in January to 383.3 mm in October) and the average annual precipitation reaches 3,702 mm. A roughly constant annual temperature (average: 25.7°C) and a high level of air humidity (71% in January to 82% in July and August) are reported. A variation of 2.5°C is recorded, the average being 24.4°C in August (coldest month of the year) [24]. December is the driest month (39 mm of rains). Precipitation reaches the peak in August (average: 681 mm) [23]. Between the driest and the wettest of the months, the amplitude of precipitation is 295 mm. October is the month with the highest relative humidity (89.6%) while January presents the lowest relative humidity (84.2%).

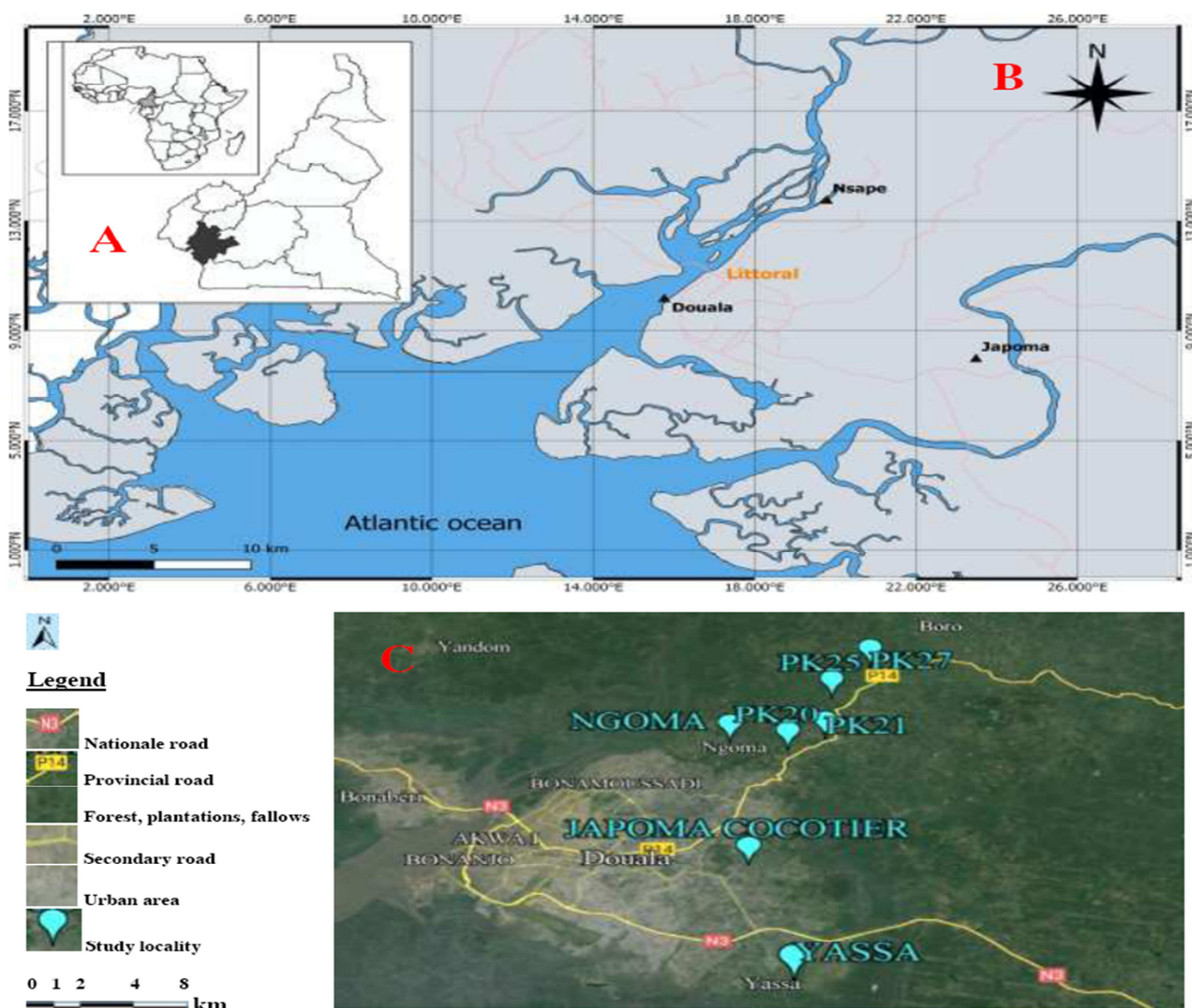


Figure 1. Location of the study localities in suburban areas of Douala (Littoral-Cameroon). A = location of the Littoral region in Cameroon; B = map of the littoral region of Cameroon; C = Location of the study sites in suburbs of the Douala city.

2.2. Host Plants and Attended Hemipterans

Field investigations on the nesting system of *Cr.*

(*Nematocrema*) *stadelmanni* was conducted in the eight study sites. At the edge of a 10-year old secondary forest as well as in 3-years old fallow lands located in Ngoma locality, we

explored in each site two transects of 15x500 m. Four plantations were selected. Four plots of 2 to 4 ha each (plantations of oil palms, cocoa trees, and food crops) were selected after advice from the owners. In each transect or plantation plot, we identified and counted the plants that supported at least one nest of *Cr. (Nematocrema) stadelmanni*. For unknown plant species, specimens of plant organs (leaves, bark fragment, available fruits and flowers) were collected and labelled for identification. The same kind of research was conducted in Yassa locality in tree crop plantations not treated with insecticides and occasional additional investigations were carried out in food crop plots at Missolè II and Bonépoupa located not far from Edéa town. For each host plant found, we measured the diameter of the trunk at the breast height (DBH) and for each nest found we measure the distance from the ground surface to the location on the plant, the largest and smallest diameters and the position on the host plant (trunk, branch or fork). The nest structure was determined (Figure 2A, 2B, 2C).

An inventory of attended Hemipterans was conducted during both the dry and rainy season at Ngoma locality, at the urban zone of Japoma and Yassa, in plantations and old fallows at Missolè II and Bonépoupa. Thus for each host plant found, we inspected around within a radius of 5 m, the foliage of the plants, possibly epiphytes and grasses. The Hemipterans exploited by the ant workers were collected and stored in labelled tubes containing 70° alcohol. The point of attachment of epiphytes suckers was opened in order to collect the Hemipterans in the hollow. This enabled us to catalogue the Hemipterans this ant species attended.

2.3. Daily Activity Rhythm

This study was carried out on four nests situated in Ngoma. The daily activity rhythm of workers from each nest was recorded over four 24-hour periods using the method implemented on the arboreal nesting ant *Atopomyrmex mocquersyi* Andre [10]: we drew a mark on the main foraging trail (situated on the trunk of the host trees) used by the workers to reach the ground or neighbouring trees, where they forage for food, and counted workers entering and leaving the nest. Each observation lasted five minutes and was repeated every hour. The food supply being more intense during the rainy season than the dry season, we carried out investigations during the unfavourable period of the year (dry season). Four series of measurements were conducted during the dry season. To evaluate the relationship between ant activity and environmental conditions, air temperature and relative humidity were recorded each hour using a thermohygrometer suspended one meter above the ground surface.

2.4. Collected Solid Particles

The composition of the diet of *Cr. (Nematocrema) stadelmanni* was determined by sampling solid particles brought back to the nest by workers from four large nests located in Ngoma and Yassa, using the procedure described

by Kenne and collaborators [10]: during two days per week (4 hrs. each day: from 8 a.m. to 12 p.m. and 2 p.m. to 6 p.m.) during six weeks, the workers carrying a solid particle were captured, particles were collected and workers were released and these particles were stored in labelled tubes containing 70° alcohol for further identification using a stereomicroscope.

We carried out a study of the food source preference by testing four different sources [droplets of palm oil as fat, honey as sweet liquid, breadcrumbs as carbohydrate source and live amputated hind legs larvae of grasshopper *Ruspolia differens* (Serville, 1838) (Orthoptera: Tettigoniidae) as prey]. On a 20x50 cm plywood positioned on the floor surface (25 cm from a trail and 0.5 m from the trunk of the host tree), we simultaneously placed food sources (10 cm gap between 2 neighbouring sources) and counting every 2 minutes during 60 min., workers on each food source. For each nest, two trials were conducted a day (one in the morning and another in the afternoon), repeated two days per week during three weeks ago. Records were conducted on three nests situated in three localities.

2.5. Hunting Strategy of Workers

The hunting strategy used by the workers was studied in field condition at Japoma on a 3-year old mature nest positioned on the trunk of a mango tree *Mangifera indica* L., 17531 (Sapindales: Anacardiaceae). A plywood plank (30x40 cm) was used as experimental hunting arena. The plywood was placed horizontally (one meter from the soil surface) against the host tree and near a foraging trail of *Cr. (Nematocrema) stadelmanni* workers. Experiments began one week later once the plate was well-integrated to the foraging territory of the ant colony. Living larvae of the grasshoppers *R. differens* (Orthoptera: Tettigoniidae) and adults of *Zonocerus variegatus* (Linné 1758) (Orthoptera: Pyrgomorphidae) (3 to 5 mm and 15 to 20 mm long respectively) used as prey were introduced one by one into the hunting arena. The predatory behaviour of the workers was recorded when confronted with small sized grasshoppers (30 trials) and large sized ones (30 trials). The tibia of their hind legs were first cut off to prevent them from jumping and escaping out of the arena since their anti-predatory strategy was not the aim of our study, rather the behaviour of the workers when confronted with a prey. The entire sequence of predatory behaviour was recorded by direct observation using the naked eye and the procedure described by Djiéto-Lordon, Richard, Kenne and collaborators [10, 11, 14]: from the introduction of prey into the centre of the plywood plank until their capture and retrieval to the nest (three to five observational sessions per day and two to five days per week). At least 30 min. separated two trials. Data sheets containing the full repertoire of behavioural sequences were established during preliminary experiments. Referring to the complete list of the sheets, we recorded each behavioural act performed *vis-à-vis* the prey (the detection behaviour, antennal palpation, attack, seizure, immobilization, nestmates recruitment, spread-eagling the prey, cutting up, and

transporting the prey). The portion of the prey body seized by the ant was noted. The duration of each behavioural act was noted and the total duration of the capture of each tested prey was recorded as the time separating the detection of the prey to its retrieval. Recorded data permitted us to built flow diagrams with transition frequencies between behavioural acts. For each size range of prey, percentages (i.e. transition frequencies between behavioural acts) were calculated from the overall number of cases (30 trials).

2.6. Identifications and Statistical Analysis

Plant specimens were identified using keys and illustrated catalogs of Fabaceae [24], Mimosaceae [25, 26], Apocynaceae [27], Lauraceae [28], Annonaceae [29], Euphorbiaceae [30], Phyllanthaceae [31], Combretaceae [32], Myrtaceae [33], Moraceae [34], Urticaceae [35-37]. The other host trees, shrubs and grasses on which workers collected nectaries and/or sap or Hemipterans honeydew, were identified by botanist colleagues. Grasshoppers were identified by reference to the illustrated checklists [38, 39]. Epiphytes were identified by reference to the available descriptions [40-42]. The ant species was identified by reference to Taylor's catalog [3]. Hemipterans were identified by comparing collections with the identifications done by Danièle Matile-Ferrero and Barry Bolton as reported in our previous publications [10, 43].

Data are given in term of percentage of occurrence for plants, insects, nests and behavioural praxems, or in term of mean \pm standard error (se) for quantitative series. Two percentages were compared using Fisher's exact-tests (StatXact-3 software) while two mean values (\pm se) were compared using Student t-test when normality and equal variance tests passed, and Mann-Whitney rang sum test (for independent series) or Wilcoxon rang sum test (for dependent series). Several rates were simultaneously compared using Fisher-Freeman-Halton test. Several mean values were simultaneously compared using Kruskal-Wallis rang sum test (normality and equal variance tests failed) and post-hoc analysis was done using Dunn's pairwise procedure (SigmaStat software).

2.7. Abbreviations

Ac. cordifolia: *Alchornea cordifolia*, *Al. adianthifolia*: *Albizia adianthifolia*, *Al. zygia*: *Albizia zygia*, a.m.: ante meridiem: before noon, *An. muricata*: *Annona muricata*, *An. senegalensis*: *Annona senegalensis*, *At. mocquerysi*: *Atopomyrmex mocquerysi*, a.s.l: above sea level, *Br. micranta*: *Bridelia micranta*, °C: degree Celsius, cm: centimetre, *Ch. odorata*: *Chromolaena odorata*, *Ci. ×limon*: *Citrus ×limon*, *Ci. sinensis*: *Citrus sinensis*, *Co afer*: *Costus afer*, *Cr. clariventris*: *Crematogaster clariventris*, *Cr. magitae*: *Crematogaster magitae*, *Cr. (Nematocrema) stadelmanni*: *Crematogaster (Nematocrema) stadelmanni*, *Cr. (Sphaerocrema) striatula*: *Crematogaster (Sphaerocrema) striatula*, *D. edulis*: *Dacryodes edulis*, DBH: diameter at the breast height, df: degree of freedom, *F. saussureana*: *Ficus*

saussureana; *F. sur*; *Ficus sur*, *F. sycomorus*: *Ficus sycomorus*, *F. valliscloudae*: *Ficus valliscloudae*, H: Kruskal-Wallis test statistic, ha: hectare, hr. hour, hrs: hours, km: kilometer, m: meter, mm: millimeter, min.: minute, *Ma. indica*: *Mangifera indica*, Max. T: Maximum temperature (°C); RH: Relative air humidity (%); Min. T: Minimum temperature (°C), *Mu. cecropioides*: *Musanga cecropioides*, *My. arboreus*: *Myrianthus arboreus*, ns: not significant ($p \geq 0.05$), *O. longinoda*: *Oecophylla longinoda*, p: statistic p-value, *Pe. americana*: *Persea americana*, p.m.: post meridiem: after noon, *Ph. nigriflora*: *Phragmanthera nigriflora*, *Ps. guajava*: *Psidium guajava*, Q: Dun's statistic for the post-hoc pairwise comparison, r: Pearson correlation coefficient, *R. differens*: *Ruspolia differens*, sec: second, se: standard error, T: Mann-Whitney statistic, *Sa. officinarum*: *Saccharum officinarum*, t: Student test statistic, *T. aculeatum*: *Tetramorium (Macromischoides) aculeatum*, *T. africanum*: *Tetramorium africanum*, *T. ogowensis*: *Tapinanthus preusii*, *V. amygdalina*: *Vernonia amygdalina*, *Z. mays*: *Zea mays*, *Z. variegatus*: *Zonocerus variegatus*, %: percent, *: significant ($0.01 < p < 0.05$), **: very significant ($0.001 < p \leq 0.01$), ***: highly significant ($p < 0.001$).

3. Results

3.1. Nesting System and Hemipterans

Ecological surveys conducted in the forest zones and plantations located in eight localities of the suburbs of Douala permitted us to identify and list plant species supporting nests of *Cr. (Nematocrema) stadelmanni* Mayr, 1895. The DBH of the host plants varied from 0.1 to 1.95 m (mean \pm se: 0.56 ± 0.03 m, 191 trees). The nests were positioned on the bark surface of the trunk of the trees (50.8%, 191 trees) or on the underside bark of the fork of large branches (49.2%; Figure 2A) and the difference between the two positions was not significant (Fisher's exact test: $p = 0.838$). Most nests were elongated (67.5%; Figure 2B) rather than conical (32.5%) (Fisher's exact test: $p = 9.0 \times 10^{-12}$). Nests were made of cardboard material from plant fibers mixed and hardened using the secretions of ant workers (Figure 2A and 2B). The surface of the nest was impermeable to rainwater and several ground-facing entrances did not allow rainwater infiltration (Figure 2A and 2B). The porous interior showed a dense network of interconnected chambers (Figure 2C) allowing aeration, movement of workers, storage and brood care. The main nests were positioned 0.5 to 11.5 m (mean \pm se: 2.8 ± 0.1 m, 191 nests) from the ground surface and their length varied from 0.11 to 1.60 m (0.53 ± 0.02 m, 191 nests). The larger diameter of the main nest varied from 0.08 to 0.95 m (0.36 ± 0.01 m, 191 nests) and the smaller diameter varied from 0.04 to 0.80 m (0.205 ± 0.009 m, 191 nests). The nesting system of *Cr. (Nematocrema) stadelmanni* showed a larger main nest and several smaller secondary nests on the same host tree. The secondary nests were small in size compared to the main nests and were positioned at the base of small twigs or even

at the hollow structures of the sucker of epiphytes. Six epiphytes were identified [*Viscum album* L. 1753 (Santalales: Santalaceae), five Lauranthaceae (Santalales) [*Globimetula dinklagei* (Engl.) Van Tiegh, *Tapinanthus preusii* (Engl.) Tiegh. *T. ogowensis* (Engl.) Danser, *Phragmanthera capitata* (Spreng.) and *Ph. nigriflora* (Hook f. ex. Benth.) Balle].

The number of secondary nests on a host tree varied from one to five (3 ± 0 nests, 76 trees) and were connected to the main nest by trails on the surface of the trunk and branches.

In the secondary nests, Hemipterans Coccidae were protected for honeydew. The permanent activity of the workers leads to the production of sooty mold on the trunk and the branches along the trails as well as the grasses located at the foot of the host tree. A total of 961 host plants were recorded belonging to eight orders, 13 families, 19 genera and 24 species among which 11 species (45.8%) were cultivated for food (nine species, 37.5%) or ornamental plants (two species, 8.3%) and 13 species (54.2%) were wild plants (Table 1).



Figure 2. Illustration of the morphology and structure of the cardboard nest of *Crematogaster* (*Nematocrema*) *stadelmanni* Mayr, 1895. A: a small nest built on the underside of the fork of a branch of *Dacryodes edulis* (G. Don) H. J. Lam, 1932 (Gentianales: Apocynaceae); B: A large elongated nest on tree's trunk of *Albizia adianthifolia* (Schumach.) W. Wight, 1909 (Fabales: Mimosaceae); C: porous interior of a large open-sided nest.

The nine plants (37.5%) cultivated for food were soursop *Annona muricata* L., 1753 (Annonaceae), wild soursop *An. senegalensis* Pers., 1806 (Annonaceae), Safoo *Dacryodes edulis* (G. Don) H. J. Lam, 1932 (Apocynaceae), mango *Mangifera indica* L., 1753 (Anacardiaceae), avocado *Persea americana* Mill., 1768 (Lauraceae), wild mango *Pseudospondia microcarpa* (A. Rich.) Engl., 1883 (Anacardiaceae), guava tree *Psidium guajava* L., 1753 (Myrtales: Myrtaceae) and cassimango *Spondias dulcis* Foster (Anacardiaceae)]. In addition the Myrtaceae (Myrtales) wild species *Syzygium guineense* (Willd.) DC., 1828 is in the process of domestication. The ornamental plants were pink shower tree *Cassia javanica* L., 1753 (Fabaceae) and frangipani *Plumeria alba* L. 1753 (Apocynaceae). The 13 wild species (54.2%) were two Mimosaceae [*Albizia adianthifolia* (Schumach.) W. Wight, 1909 and *Al. zygia* (DC.) J. F. Macbr., 1919], two Euphorbiaceae (Malpighiales) [*Alchornea cordifolia* (Schumach. & Thonn.) Müll. Arg., 1865 and *Macaranga albescens* L. M. Perry, 1953], *Bridelia micranta* (Hochst.) Baill. 1862 (Phyllanthaceae), four Moraceae [*Ficus saussureana* De Candolle 1841, *F. vallisclouade* Delile, *F. sur* Forssk. 1775 and *F. sycomorus* L., 1753], two Urticaceae [umbrella tree *Musanga cecropioides* R. Br. ex Tedlie, 18191 and monkey fruit tree *Myrianthus arboreus* P. Beauv., 1805] and *Terminalia glaucescens* Planch. ex Benth., 1849 (Combretaceae). The difference between percentages of cultivated and wild species was not significant (Fisher's exact test: $p = 0.773$). According to the relative abundance of host plants, *D. edulis* (Apocynaceae) was the most recorded

(14.6%) followed by *Ma. indica* (Anacardiaceae) (13.3%) and *Pe. americana* (Lauraceae) (12.2%). Highly represented wild plants were *Br. micranta* (Phyllanthaceae) and *Mu. cecropioides* (Urticaceae) (8.3% respectively) and percentages of other host plants were below 5.0% respectively (Table 1).

3.2. Sweet Liquids and Solid Particles

Around host plants, *Cr. (Nematocrema) stadelmanni* collected nectar from 18 plants: two Mimosaceae [*Albizia adianthifolia* and *Al. zygia*], two Euphorbiaceae [*Ac. cordifolia* and *Ma. albescens*], *Br. micranta* (Phyllanthaceae), *Cordia africana* Lam., 1792 (Ehretiaceae), *Citrus sinensis* (L.) Osbeck, 17651 (Rutaceae), *Ci. ×limon* (Rutaceae), *Chromolaena odorata* (L.) R. M. King & H. Rob., 1970 (Asteraceae), *Costus afer* Ker Gawl., 1823 (Costaceae), *D. edulis* (Apocynaceae), *F. saussureana* (Rosales), *F. sur* (Rosales), *F. sycomorus* (Rosales), *F. vallisclouade* (Rosales), *Ps. guajava* (Myrtaceae), *Vernonia amygdalina* Delile, 1826 (Asteraceae) and *Zea mays* L., 1753 (Poaceae). Workers attacked seeds of *Z. mays* (Poaceae), young twigs of *Ch. odorata* (Asteraceae), *V. amygdalina* (Asteraceae) and young stems of sugarcane *Saccharum officinarum* L., 17531 (Poaceae). Within a 5 m space radius around the host trees, workers attended Hemipterans on host and adjacent trees and shrubs and grasses. Seven Hemipterans from the Sternorrhyncha suborder were recorded including unidentified Aleyrodidae. These Hemipterans proliferated on 11 (19.6%) out of 56 monitored plants. Aleyrodidae proliferated on six plants [*Capsicum frutescens* L., 1753

(Solanaceae), orange *Citrus sinensis* (L.) Osbeck, 17651 *D. edulis* (Apocynaceae), *Ps. guajava* (Myrtaceae) and *V.* (Rutaceae), lemon *Ci. ×limon* (L.) Burm. f., 1768 (Rutaceae), *amygdalina* (Asteraceae)].

Table 1. Absolute abundance, percentages and list of 21 plant species hosting a nest of *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895.

ORDER/family	Host plant species	Abundance (%)
FABALES (8.5%)		
Fabaceae	<i>Cassia javanica</i> L., 1753 #	15 (1.6)
Mimosaceae	<i>Albizia adianthifolia</i> (Schumach.) W. Wight, 1909 §	41 (4.3)
	<i>Al. zygia</i> (DC.) J. F. Macbr., 1919 §	25 (2.6)
GENTIANALES (0.9%)		
Apocynaceae	<i>Plumeria alba</i> L. 1753 #	9 (0.9)
LAURALES (12.1%)		
Lauraceae	<i>Persea americana</i> Mill., 1768 *	116 (12.1)
MAGNOLIALES (1.9%)		
Annonaceae	<i>Annona muricata</i> L., 1753 *	8 (0.8)
	<i>An. senegalensis</i> Pers., 1806 *	10 (1.1)
MALPIGHIALES (15.7%)		
Euphorbiaceae	<i>Alchornea cordifolia</i> (Schumach. & Thonn.) Müll. Arg., 1865 §	53 (5.5)
	<i>Macaranga</i> sp. Thouars 1806 §	18 (1.9)
Phyllanthaceae	<i>Bridelia micranta</i> (Hochst.) Baill. 1862 §	80 (8.3)
MYRTALES (3.9%)		
Combretaceae	<i>Terminalia glaucescens</i> Planch. ex Benth., 1849 §	20 (2.1)
Myrtaceae	<i>Psidium guajava</i> L., 1753 *	1 (0.1)
	<i>Syzygium guineense</i> (Willd.) DC., 1828 * §	16 (1.7)
ROSALES (23.0%)		
Moraceae	<i>Ficus saussureana</i> De Candolle 1841 §	40 (4.2)
	<i>F. vallisclaudae</i> Delile §	31 (3.2)
	<i>F. sur</i> Forssk. 1775 §	14 (1.5)
	<i>F. sycomorus</i> L., 1753 §	22 (2.3)
Urticaceae	<i>Cecropia peltata</i> Linnaeus, 1759 §	6 (0.6)
	<i>Musanga cecropioides</i> R. Br. ex Tedlie, 18191 §	80 (8.3)
	<i>Myrianthus arboreus</i> P. Beauv., 1805 §	28 (2.9)
SAPINDALES (34.1%)		
Anacardiaceae	<i>Mangifera indica</i> L., 17531 *	128 (13.3)
	<i>Pseudospondia microcarpa</i> (A. Rich.) Engl., 1883 *	46 (4.8)
	<i>Spondias dulcis</i> Foster *	14 (1.5)
Burseraceae	<i>Dacryodes edulis</i> (G. Don) H. J. Lam, 1932 *	140 (14.6)
	TOTAL	961 (100.0)

*: cultivated plant species, #: ornamental plant species, §: wild plant species.

Aphis spiraecola Patch, 1914 (Aphididae) was recorded on leaves of the eupatorium *Ch. odorata* (Asteraceae). Three Coccidae (*Ceroplastes* sp. Gray, 1828, *Coccus celatus* De Lotto, 1960 and *Inglisia conchiformis* Newstead) were recorded on twig's base and buds of four plants [*Ac. cordifolia* (Euphorbiaceae), *An. muricata* (Annonaceae), *My. arboreus* (Urticaceae) and *Ps. guajava* (Myrtaceae)].

Melanaphis sacchari (Zehntner, 1897) (Aphididae) and *Stictococcus formicarius* Newstead (Stictococcidae) were attended on the underside and on the base of leaves of nine plants [*Ac. cordifolia* (Euphorbiaceae), *Ch. odorata* (Asteraceae), *Ci. sinensis* (Rutaceae), *Ci. ×limon* (Rutaceae), *Co. afer* (Costaceae), *D. edulis* (Apocynaceae), *Ma. indica* (Anacardiaceae), *Ps. guajava* (Myrtaceae) and *V. amygdalina* (Asteraceae)]. *Saccharicoccus saccharis* (Cockerell, 1895) (Pseudococcidae) proliferated at the base of young shoots of sugarcane *Sa. officinarum* (Poaceae).

The solid particles brought back to the nest were of different origins but the particles coming from the plants were the most frequent. Indeed, the solid particles collected along the trails of three large nests (5 sessions in the morning, 5 other sessions in the afternoon during 5 days of

repetition for each nest, during the dry and the rainy season respectively) made it possible to collect a total of 4,683 particles (26 to 153 particles, mean \pm se: 78 ± 4 particles, 60 sessions). The overall collection consisted of 3,397 (72.5%) particles from plants (21 to 103 particles per session, 57 ± 3 particles, 60 sessions) and 1,286 (27.5%) fragments of Arthropods including grasshoppers, or whole individuals of Arthropods (ants, Orthoptera larvae, caterpillars) (4 to 66 fragments per session, 21 ± 2 fragments, 60 sessions). Different coloured, unidentified pasty substances were recorded. The solid particles were more numerous during the rainy season (3,196 particles i.e. 68.2%, 68 to 153 particles, 107 ± 4 particles, 30 sessions) than during the dry season (1,487 particles i.e. 31.8%, 30 to 26 particles, 72 ± 2 particles, 30 sessions) (Fisher's exact test: $p = 2.9 \times 10^{-279}$). The difference between vegetal particles and prey collected during the dry and the rainy season was highly significant (vegetal fragments: 24.6% versus 47.9% for dry and rainy season respectively, Fisher's exact test: $p = 1.9 \times 10^{-7}$). This result was also valid for prey particles (7.2% versus 20.3% for dry and rainy season respectively, Fisher's exact test: $p = 1.9 \times 10^{-7}$). During each season, the solid particles from plants

were more numerous than the prey brought back to the nest [dry season: 1,152 vegetal particles i.e. 24.6% versus 335 prey i.e. 7.2%, Fisher's exact test: $p = 6.1 \times 10^{-208}$; rainy season: 2245 vegetal particles i.e. 47.9% versus 951 prey i.e. 20.3%, Fisher's exact test: $p = 3.7 \times 10^{-236}$].

During the exploitation of food sources, the number of recruited workers increased according to the type of resource (Figure 3). Sugary liquids seemed to interest workers more than fats, carbohydrate sources and prey. Indeed, an experiment relating to the choice of the preferred type of food source has shown that for a total of 23,570 recruited workers (null to 1,549 workers, 760 ± 94 workers; 31 essays), honey droplets were more attractive than palm oil droplets, carbohydrate sources and even prey (droplets of palm oil: 1,735 workers i.e. 7.4% workers, null to 120 workers, 56 ± 7 workers; honey: 18,081 workers i.e. 76.7%,

null to 1,190 workers, 583 ± 75 workers, breadcrumbs: 996 workers i.e. 4.2%, null to 55 workers, 32 ± 2 workers; and prey: 2,758 workers i.e. 11.7%, null to 184 workers, 89 ± 11 workers) (Kruskall-Wallis rang sum test: $H = 45.14$; $df = 3$; $p < 0.001$). Pairwise comparisons showed that honey was the most preferred over palm oil droplets ($Q = 4.86$, $p < 0.001$), breadcrumbs ($Q = 6.42$, $p < 0.001$) and prey ($Q = 3.37$, $p < 0.001$). Prey were preferred over breadcrumbs ($Q = 3.05$, $p < 0.001$). Exploitation of palm oil did not differ from that of breadcrumbs ($Q = 1.56$, $p > 0.001$) or prey ($Q = 1.49$, $p > 0.001$). For each food source, the number of recruited workers increased with time (Figure 3), as indicated by positive Pearson correlation coefficient (palm oil: $r = 0.972$, $p = 7.6 \times 10^{-20}$; honey: $r = 0.992$, $p = 2.8 \times 10^{-27}$; breadcrumbs: $r = 0.630$, $p = 1.5 \times 10^{-4}$; prey: $r = 0.978$, $p = 2.0 \times 10^{-21}$; and overall data: $r = 0.993$, $p = 3.5 \times 10^{-28}$).

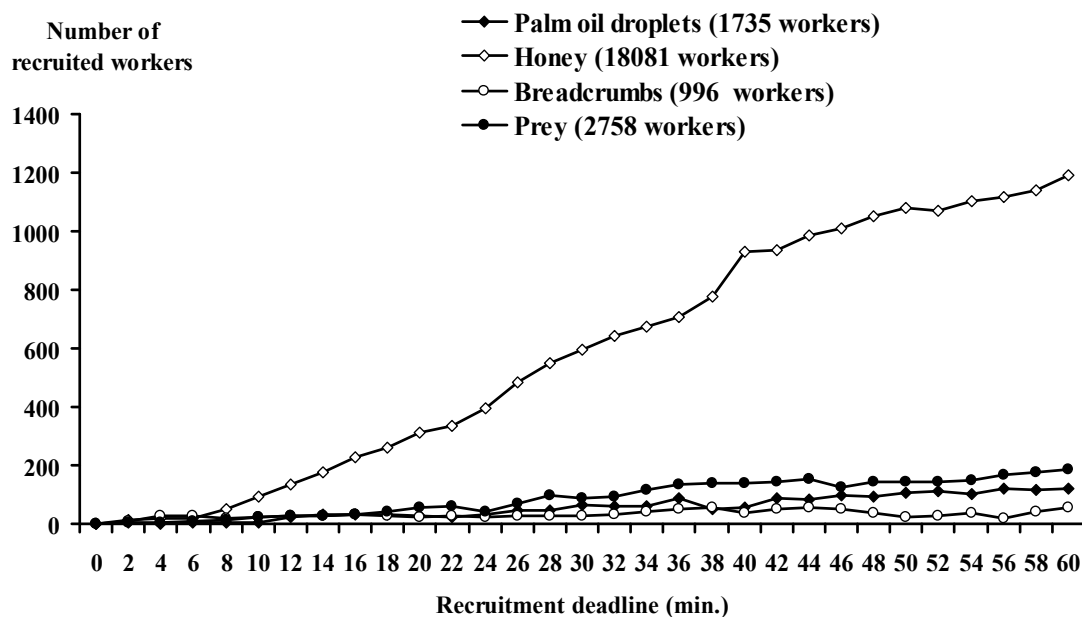


Figure 3. Preference of a food source by *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 (Formicidae: Myrmicinae) workers of evolution over time of the recruited workers for the exploitation of a permanent food source.

3.3. Daily Rhythm of Activity

During the dry season studies conducted in Ngoma II locality enabled us to note that *Cr. (Nematocrema) stadelmanni* workers foraged day and night (Figure 4). A total of 16 nycthemeral cycles from four nests of different sizes (four cycles for each nest) made it possible to count 81,326 workers (11 to 570 workers, mean \pm se: 239 ± 7 workers, 340 five minutes counting sessions/hour) crossing a marker placed 10 cm from a trail leading to the main nest. The marker was positioned on the trunk of the host tree 1 m above the ground. Overall data showed that the number of workers leaving the nest (five to 275 workers, 110 ± 3 workers, 340 sessions) was lower than that of workers returning to the nest (five to 333 workers, 129 ± 4 workers, 340 sessions) (Student test: $t = 3.710$, $df = 678$, $p < 0.001$) (Figure 4E).

This observation was valid for nest 2 (Leaving: 9,028 workers, 37 to 190 workers, 106 ± 4 workers, 85 sessions;

Returning: 11,783 workers, 52 to 276 workers, 139 ± 4 workers, 85 sessions; $t = 5.217$, $df = 168$, $p < 0.001$) (Figure 4B) and for nest 3 (Leaving: 11,933 workers, 61 to 237 workers, 140 ± 5 workers, 85 sessions; Returning: 14,310 workers, 76 to 252 workers, 168 ± 5 workers, 85 sessions; $t = 4.204$, $df = 168$, $p < 0.001$) (Figure 4C). The difference was not significant for nest 1 (Leaving: 12,099 workers, five to 275 workers, 142 ± 7 workers, 85 sessions; Returning: 12,765 workers, six to 333 workers, 150 ± 8 workers, 85 sessions; $t = 0.727$, $df = 168$, $p = 0.468$) (Figure 4A) and nest 4 (Leaving: 4,471 workers, 7 to 220 workers, 53 ± 5 workers, 85 sessions; Returning: 4,937 workers, five to 240 workers, 58 ± 5 workers, 85 sessions; $t = 0.765$, $df = 168$, $p = 0.445$) (Figure 4D). The correlation between the number of ants entering and leaving the nests each hour was significant in the case of overall data (Pearson's correlation coefficient: $r = +0.857$, $p = 3.4 \times 10^{-99}$, 340 sessions; Table 2E), illustrating a regular flux.

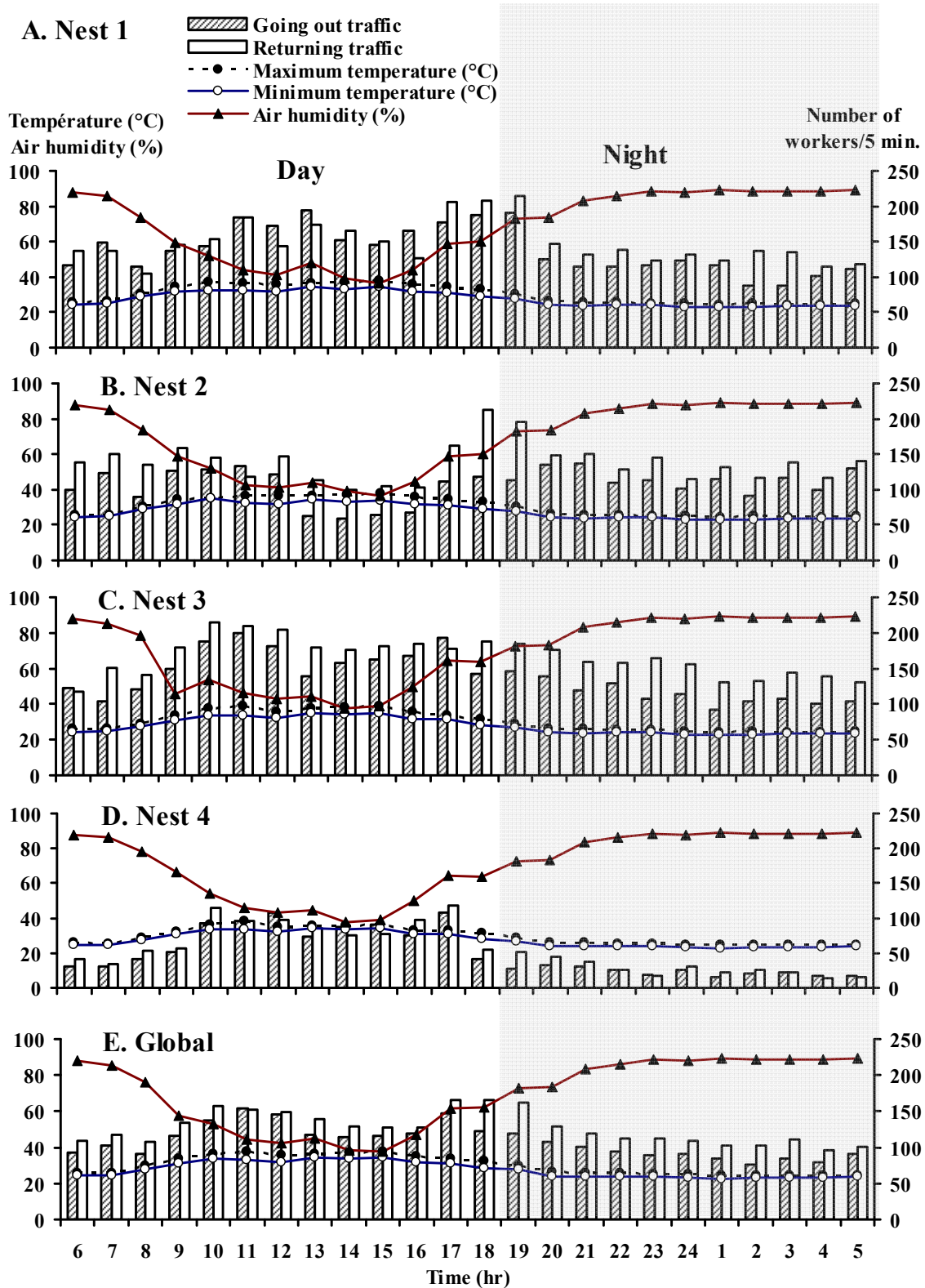


Figure 4. Daily activity rhythm of *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 (Formicidae: Myrmicinae) workers recorded during the dry season along the tracks joining four large nests and the surface of the ground. Workers who moved away from the main nests or who returned to it and who crossed the marker placed 1 m above the ground and 10 cm from the track, were counted during five minutes every hour throughout the duration of the nycthemeral cycle.

The same conclusion was valid for each of the four nests (nest 1: $r = +0.845$, $p = 3.0 \times 10^{-24}$, 85 sessions; Table 2A; nest 2: $r = +0.482$, $p = 3.0 \times 10^{-6}$, 85 sessions, Table 2B; nest 3: $r = +0.787$, $p = 4.0 \times 10^{-19}$, 85 sessions, Table 2C; and nest 4: $r =$

+0.930, $p = 9.3 \times 10^{-38}$, 85 sessions; Table 2D). The flow of workers was positively correlated with the minimum air temperature (Leaving: $r = +0.285$, $p = 8.6 \times 10^{-8}$, $n = 340$ sessions; Table 2E; Returning: $r = +0.219$, $p = 4.8 \times 10^{-5}$, 340 sessions; 85 count session, Table 2E), the maximum air

temperature (Leaving: $r = +0.313$, $p = 3.7 \times 10^{-9}$, 340 sessions; Table 2E; Returning: $r = +0.253$, $p = 2.2 \times 10^{-6}$, 340 sessions; Table 2E) and negatively correlated with air humidity (Leaving: $r = -0.248$, $p = 3.9 \times 10^{-6}$, 340 sessions; Table 2E; Returning: $r = -0.193$, $p = 3.6 \times 10^{-4}$, 340 sessions; Table 2E).

Table 2. Pearson's correlation coefficient "r" between the flow rate of *Crematogaster (Nematoctrema) stadelmanni* Mayr, 1895 (Formicidae: Myrmicinae) workers on the main trail and values for microclimatic conditions during the dry season's daily rhythm of activity. Records were done at Ngoma locality in January and February 2018.

Traffic	Day (n = 13)			Night (n = 11)			Global (n = 24)		
	Min. T	Max. T	RH	Min. T	Max. T	RH	Min. T	Max. T	RH
A. Nest 1									
Leaving	0.475 ns	0.489 ns	-0.526 ns	0.894 ***	0.917 ***	-0.740 **	0.744 ***	0.746 ***	-0.732 ***
Returning	0.313 ns	0.265 ns	-0.295 ns	0.929 ***	0.903 ***	-0.774 **	0.505 *	0.489 *	-0.479 *
Global	0.413 ns	0.372 ns	-0.427 ns	0.949 ***	0.947 ***	-0.787 **	0.665 ***	0.658 ***	-0.644 ***
B. Nest 2									
Leaving	-0.305 ns	-0.222 ns	0.335 ns	0.188 ns	0.218 ns	-0.454 ns	-0.376 ns	-0.334 ns	0.372 ns
Returning	-0.393 ns	-0.390 ns	0.441 ns	0.838 ***	0.918 ***	-0.746 **	-0.101 ns	-0.089 ns	0.160 ns
Global	1.000 ***	0.939 ***	-0.986 ***	1.000 ***	0.957 ***	-0.804 **	1.000 ***	0.980 ***	-0.982 ***
C. Nest 3									
Leaving	0.782 **	0.676 *	-0.636 *	0.870 ***	0.753 **	-0.894 ***	0.879 ***	0.830 ***	-0.822 ***
Returning	0.791 ***	0.738 **	-0.751 **	0.780 **	0.716 *	-0.826 **	0.791 ***	0.758 ***	-0.795 ***
Global	0.829 ***	0.743 **	-0.728 **	0.849 ***	0.760 **	-0.884 ***	0.870 ***	0.826 ***	-0.840 ***
D. Nest 4									
Leaving	0.833 ***	0.812 ***	-0.787 ***	0.573 ns	0.355 ns	-0.746 **	0.924 ***	0.914 ***	-0.897 ***
Returning	0.764 ***	0.701 **	-0.650 *	0.815 **	0.656 *	-0.905 ***	0.906 ***	0.879 ***	-0.851 ***
Global	0.876 ***	0.775 **	-0.736 **	0.765 **	0.581 ns	-0.889 ***	0.925 ***	0.907 ***	-0.885 ***
E. Overall nests									
Leaving	0.661 ***	0.588 *	-0.579 *	0.873 ***	0.836 ***	-0.908 ***	0.836 ***	0.809 ***	-0.800 ***
Returning	0.515 ns	0.462 ns	-0.423 ns	0.941 ***	0.914 ***	-0.885 ***	0.719 ***	0.702 ***	-0.671 ***
Global	0.615 *	0.550 ns	-0.525 ns	0.932 ***	0.902 ***	-0.915 ***	0.800 ***	0.778 ***	-0.757 ***

Min. T: Minimum temperature (°C); Max. T: Maximum temperature (°C); RH: Relative air humidity (%); ns: not significant correlation ($p \geq 0.05$); *: significant correlation ($0.05 < p < 0.01$); **: very significant correlation ($0.01 < p < 0.001$); ***: highly significant correlation ($p \leq 0.001$). Significant correlations are in bold.

The non-significant correlations for nests 1, 2 and 4 would be due to their small size (major diameter: 15, 20, 150 and 35 cm for nests 1 to 4 respectively). At each nycthemeral period, whatever the nest, a large number of workers was deployed in the environment, to collect solid particles (plant debris and prey) and sweet liquids (Hemipterans honeydew, nectaries, sap and plant gum) for the colony feeding and/or to build the nest. Exits from the nest were permanent and the returns to the nest were progressive during the nycthemeral cycle (Figure 4). A slight peak was noted in the late morning (10 a.m. to 12 p.m.) and a second slight peak was noted from the late afternoon (5 p.m.) to dusk (7 p.m.). The traffic of workers was more intense during the day than at night (Figure 4).

3.4. Predatory Behaviour

During the period of activity, *Cr. stadelmanni* workers foraged for prey on the ground, and on the leaves shrubs and grasses situated in the immediate vicinity of the host tree of the main nest. Larvae and dying insects were captured and retrieved. The hunting arena was permanently squared by several ant workers (47 to 77 workers; mean \pm se: 60 ± 7 workers; 4 counting sessions). The hunting workers moved slowly in a sinuous path with their antennae wide open and antennae apices pointed forwards and towards the ground, the

mandibles closed. At each contact, foraging worker placed its antennae apices on the obstacle before resuming its movement. As soon as it found the prey, it raised the gaster and attacked the intruder. Workers exhibited specific behavioural praxems that we recorded in order to establish its behavioural repertoire. Data allowed us to determine the behavioural sequences. The succession of behavioural acts was noted when workers were confronted with prey (Figure 5).

Detection-Palpaton. Prey were detected either at a short distance (4 to 5 mm from the prey, mean \pm se = 3.0 ± 1.3 mm; 27 cases) or on contact. During the detection at a distance, the hunting worker made an abrupt stop at a distance, directed the antennae apices towards the prey (localization), moved towards the prey (approach), placed the antennae apices on a prey body part (appendage, abdomen or head) (antennation), attacked and seized it or very excited, ran around the prey with widely-opened mandibles and thereafter resized it at an appendage. Cases of detection at a distance were rare: 13.3% for larvae of *Ruspolia differens* (Serville, 1838) (Orthoptera: Tettigoniidae) (Figure 5A) and 20.0% for larvae of *Zonocerus variegatus* (Linné 1758) (Orthoptera: Pyrgomorphidae) (Figure 5B). As for contact detection, the hunting worker collided with the prey before realizing its presence. It laid the antennae apices on the prey and seized it.

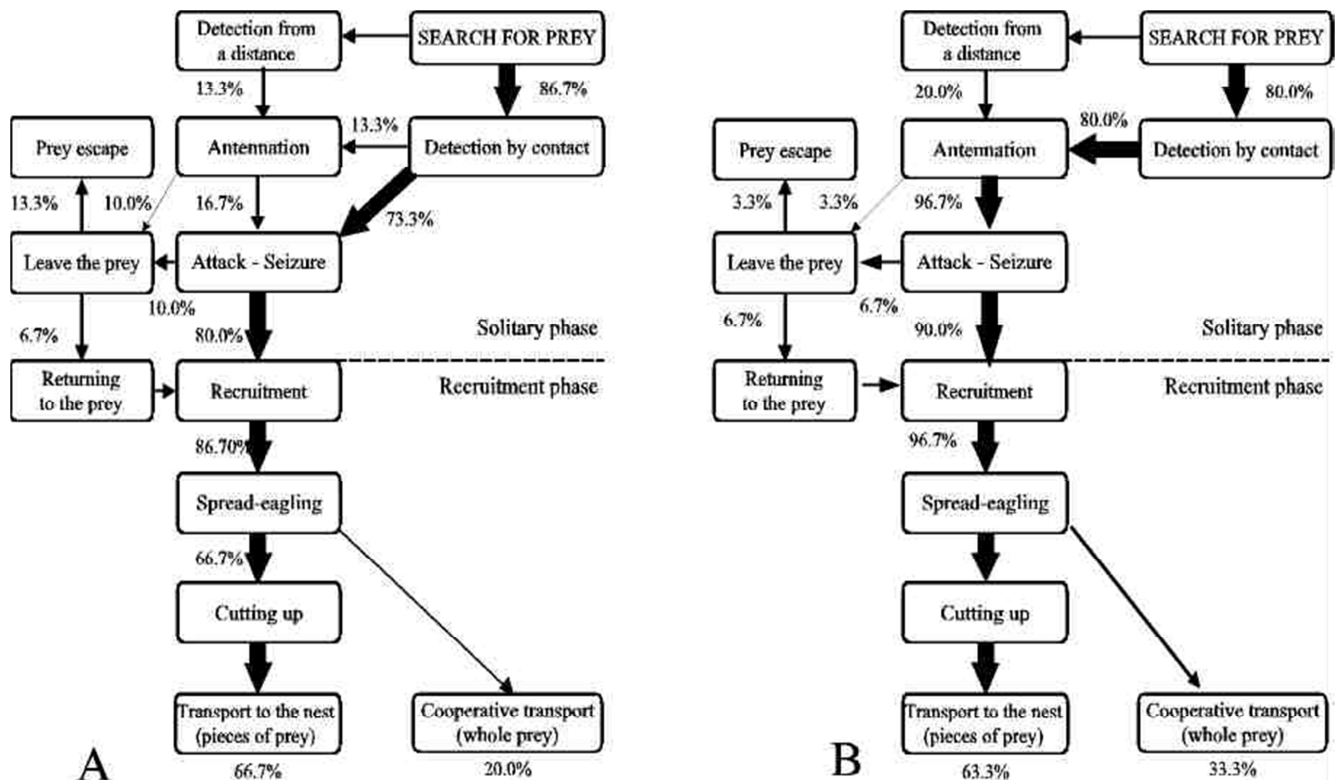


Figure 5. Flow diagrams of the behavioural events observed when *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 (Formicidae: Myrmicinae) workers attempted to capture grasshoppers of two size ranges. A: capture of 3 to 5 mm long larvae of *Ruspolia differens* (Serville, 1838) (Orthoptera: Tettigoniidae) (30 cases); B: capture of 15 to 25 mm long larvae of *Zonocerus variegatus* (Linné 1758) (Orthoptera: Pyrgomorphidae) (30 cases).

Small sized grasshoppers were either seized without antennal palpation in most of the cases (73.3%; Figure 5A) or rarely antennated before seizure (13.3%) while large sized grasshoppers were all antennated during contact detection (80.0%) (Figure 5B). Antennal palpation (during a few seconds) occurred mostly during capture of large sized grasshoppers (13.3% and 80.0% for small and large sized grasshoppers respectively; Fisher's exact test: $p = 3.3 \times 10^{-7}$; Figure 5). The overall comparison of detection rates (at a short distance or on contact) between the types and sizes of prey, showed a significant variation (Fisher-Freeman-Halton test: $df = 3$; $p = 1.3 \times 10^{-12}$). Whatever the type of prey, cases of contact detection were the most frequent (Fisher's exact test: $p = 1.3 \times 10^{-8}$ and $p = 6.3 \times 10^{-6}$ for small and large sized grasshoppers respectively), suggesting that vision played a minor role (Figure 5A and 5B). Between the two types of prey, the difference in percentage of detection was not significant (Fisher's exact test: $p = 0.731$ for contact and distance detection respectively). Duration of the antennal palpation varied from 1 to 10 sec. and between the two sizes of prey, the variation in the mean values was not significant (6.0 ± 2.4 sec.; 27 sessions and 5.3 ± 3.0 sec.; 40 sessions for small and large prey respectively; Student t-test: $t = 0.968$; $df = 65$; $p = 0.337$) (Figure 5A and 5B).

Attack-Seizure. Antennated prey were in the most cases seized immediately (16.7% and 96.7% for small and large sized prey respectively) or rarely escaped (13.3% and 3.3% for small and large sized prey respectively). Antennated prey

was sometimes abandoned and then released, so that some of them were lost. Seized prey were temporarily left in some occasion after a first attack (10.0% for small sized prey *versus* 6.7% for large sized prey; Fisher's exact test: $p = 1.00$). Few cases of prey escape were noted and workers moved rapidly on the hunting site, increasing the sinuosity of their moving path, so that they recovered the prey in a few seconds. Stinging behaviour was not observed. The attack-seizure phase occurred indifferently during capture of the two types of grasshoppers (90.0% for small sized prey *versus* 96.7% for large sized prey; Fisher's exact test $p = 0.612$). The difference in occurrence rate of abandoned prey was not significant between small and large sized grasshoppers (13.3% and 3.3% respectively; Fisher's exact test: $p = 0.353$; see Figures 5A and 5B).

Recruitment Phase. The retrieval of a large sized prey by one worker was not noted. Prey seizure usually set off a short-range recruitment. After the first attempt at seizure, the workers that discovered the prey seized and immobilized it until the arrival of recruited workers and even after the arrival of recruited workers. The hunting worker probably released an alarm pheromone as in all cases recruited nestmates foraging nearby approached, very excited, antennated the recruiter's abdomen before cooperating in prey capture. An autocatalytic effect was noted as first recruited workers behaved similarly, resulting in a short-range recruitment of several workers in a few seconds. In few cases where nestmates were not present nearby, the

discovering workers released the prey and went back to the trail, laying a scent trail which was progressively reinforced by recruited individuals. Less mobile or dying grasshoppers were always rediscovered and reattacked on the site. The use of both recruitment systems (short-range and long-range recruitment) permitted a high number of workers on the hunting site, sufficient to immobilize by stretching and to kill the prey by spread-eagling.

Spread-Eagling and Cutting Up the Prey on the Spot. Each recruited worker seized a part of the prey and pulled it backward, resulting in the spread-eagling of the prey. Hunting workers did not use their venom. Certain workers continued to immobilize the prey by stretching while others were cutting it up on the spot in order to retrieve it in small pieces to the nest. Only a few small preys were transported entirely (20.0% of small sized prey).

As the overall studies of the predatory behaviour, *Cr. (Nematocrema) stadelmanni* workers showed alternative hunting strategies as a function of prey size: (1) a solitary hunting phase where workers attacked and seized preys unaided, immobilizing them until the arrival of recruited nestmates; and (2) a group hunting phase during which prey were captured, spread-eagled, cut up on the spot and pieces were transported either by one worker or by a small group of hunting workers. Thus, *Cr. (Nematocrema) stadelmanni* workers ensured a high rate of successful grasshoppers capture: (86.7% of the small ones and 96.7% of the large ones) and retrieval to the nest, the difference being not significant ($p = 0.353$). The other preys escaped or were abandoned in the hunting arena.

Prey Retrieval and Capture Duration. The prey was either taken whole to the nest (case of small insects and small larvae) or cut into small pieces (case of large sized grasshoppers) and then individually or collectively retrieved. Small whole preys were mainly transported individually to the nest while large pieces of preys and sometimes large whole preys were cooperatively pulled by groups of two to eight workers (mean \pm se: 4 ± 0 workers; 40 cases) towards the trail leading to the main nest. The duration of the capture of small sized grasshoppers (3,960 to 3,625 sec. i.e. 66 min. to 1 hr 25 sec.; mean \pm se: $7,045 \pm 722$ sec. i.e. 1 hr 57 min. 25 sec. \pm 12 min. 2 sec.; 10 essays) was significantly lower than that of large sized captured prey (7,233 to 14,416 sec. i.e. 2 hr 33 sec. to 4 hr 16 sec.; $10,712 \pm 1,035$ sec. i.e. 2 hr 58 min. 32 sec. \pm 17 min. 15 sec.; 10 essays; Mann-Whitney test: $T = 72.00$; $p = 0.014$). The very long capture times regardless of prey size suggested that phases of spread-eagling and cutting up prey on the spot lasted a long time.

4. Discussion

4.1. Nesting System and Hemipterans

Crematogaster (Nematocrema) stadelmanni is one of the dominant arboreal-nesting ant able to form 'carton' from masticated wood fibres and use it to various extents in nest construction or to shelter trophobionts. These independent

carton nests are constructed around the fork of branches or on tree trunks. The distribution and biology of carton making *Crematogaster* species is poorly understood. Our study is the first attempt to catalog the host plant species of this ant. We did not record any large nests along small sized branches or at the ends of branches as is the case in several *Crematogaster* species [8], suggesting that workers of *Cr. (Nematocrema) stadelmanni* are able to select solid parts of the plant (50.8% on trunks and 49.2% on the branch fork), avoiding weak parts which could break under the weight of their large nest [67.5% elongated and 49.2% conical; larger diameter: 0.08-0.95 m (mean \pm se: 0.36 ± 0.01 m); smaller diameter: 0.04-0.80 m (0.205 ± 0.009 m)]. Small sized nest located on the base of twigs and the base of epiphytes, were only to protect attended Hemipterans.

Cr. (Nematocrema) stadelmanni is able to nest in several plants found in secondary forests and fallow lands. Tree crop plantations can also offer this species a good nesting opportunity as it is the case in the woody dweller *At. mocquerysi* [10]. In secondary forests and crop plantations, the fact that this species nests equally on wild or cultivated plants (54.2% and 45.8% respectively; Fisher's exact test: $p = 0.773$) suggest that colonies may compete for space with typical territorially-dominant arboreal ants as already reported in *At. mocquerysi*, *O. longinoda*, *T. aculeatum*, *T. africanum* and other *Crematogaster* species. This competition is obvious because ant mosaics are dynamic and changes as the trees age. Indeed, it has been shown that the trees are first occupied by "ground-nesting, arboreal-foraging" ant species, then by dominant arboreal nesting ants *At. mocquerysi*, *O. longinoda* and *T. aculeatum* and lastly by *Crematogaster* sp. [10, 21, 43]. The nesting system of *Cr. (Nematocrema) stadelmanni* is both polydomous and polycalic in the sense of Debout and collaborators and Robinson [44, 45] because individuals (workers and brood) of its constituent nests function as a social and cooperative units and are regularly interchanged among nests (polydomous system). However, small cardboard structures containing no brood were usually built at the base of twigs of host plants just to cover and protect Hemipterans (polycalic system). Hemipterans were also attended in hollowed suckers of epiphytes. Consequently, the presence of *Cr. (Nematocrema) stadelmanni* is indirectly harmful to host trees since this ant is a good Hemipterans-attending species. The honeydew excreted by sap-feeding Homopterans is a critical source for many ant species including arboreal-nesting dominant and subdominant ants [10, 21, 43, 46]. As *Cr. (Nematocrema) stadelmanni* continuously gathers sweet liquids (sap and honeydew), the host plant may be permanently occupied, permitting it to be defended against defoliating insects. But this protective role is counterbalanced by the affinity to pest Homopterans. Several authors have noted the wide range of Hemipterans, most of them considered as agricultural pests as vectors of plant diseases of fungal, viral or bacterial origin [43, 46-53]. On the contrary, dominant arboreal ants have been considered as good biological control agents because they are good predators and

especially when they do not protect Hemipterans harmful to cultivated plants. For example, *O. longinoda* has effectively protected orchard plantations in West Africa [54, 55], although exceptions exist like the case of *Crematogaster* spp. whose workers tend Pseudococcidae vectors of cocoa diseases [46]. Our observations on *Cr. (Nematocrema) stadelmanni* therefore illustrate once more this exception on economical important plants. In our study, host trees were mostly recorded in plantations, and for this reason, *Cr. (Nematocrema) stadelmanni* could be an indirect agricultural pest on economical importance trees, mostly safoo (14.6%), mango (13.3%), avocado (12.2%), also soursop (0.8%), guava (0.1%), orange and lemon trees. Similar observations have been reported in the living wood-nesting arboreal myrmicine *At. mocquerysi* [10] but unlike the latter species, *Cr. (Nematocrema) stadelmanni* seems to prefer sweet liquids over prey.

4.2. Collected Solid Particles

Cr. (Nematocrema) stadelmanni is remarkable by its very opportunistic ability to forage all kinds of products, including plant particles (72.5% i.e. 24.6% and 47.9% during the dry and rainy season respectively) and dead or live arthropod larvae (27.5% i.e. 7.2% and 20.3% during the dry and rainy season respectively). Solid particles and pasty substances from plants were probably collected for the construction of the cardboard nest. This generalist diet, especially nectarivorous (propensity for sugary liquids) has probably contributed to the success of this ant species in crop plantations. Workers are weak predators because of the very long duration of capturing a prey. In addition, because of their propensity for Hemipterans honeydew, most of attended Hemipterans being harmful on cultivated plants, we cannot recommend this ant species as a biological control agent against phytophagous insects. This is contrary to reports for other dominant arboreal-nesting ants such as *At. mocquerysi* [10, 43], *O. longinoda* [21, 54-58], *O. smaragdina* [58, 59], *T. aculeatum* [14] and other *Crematogaster* species [11].

4.3. Daily Rhythm of Activity

The circadian rhythm of activity displayed by ant species is of ecological importance because it permits the study of the spatio-temporal distribution of sympatric species and the possible adaptability of their workers behaviour to any vagaries of the environment [10]. During the dry season, workers of *Cr. (Nematocrema) stadelmanni* are continuously deployed day and night in the immediate environment of the host tree, a slight drop in activity being noted during the afternoon and late at night. The influence of climatic conditions (positive for temperature and negative for air humidity) is significant. The activity rhythm of *Cr. (Nematocrema) stadelmanni* is very close to the continuous rhythm described in *O. longinoda* in which the diurnal activity is greater than the nocturnal activity and the species is characterized by a strong sense of territoriality and the workers occupy: central territories, trees and immediate

surroundings occupied by the society; secondary territories, used for hunting purposes, in natural conditions located on the ground; and intermittent territories in the forest zone (diurnal), scarcely used for hunting, but mainly in relation to the tending of Homopterans [57]. However, activity rhythm of *Cr. (Nematocrema) stadelmanni* is different from the diurnal rhythm of *At. mocquerysi* with residual activities during the night, the flow of workers being positively correlated with air temperature and negatively correlated with air humidity [10].

4.4. Predatory Behaviour

In this study, *Cr. (Nematocrema) stadelmanni* workers mostly detected prey by contact, resulting in an important proportion of prey escape after antennal palpation (13.3% and 3.3% for small sized and large sized grasshoppers respectively). The low percentage of large prey that escaped would be due to the combined action of groups of hunting worker that were in the immediate vicinity of the attack site. Detection of the prey by contact has been noted in the diurnal *Polyrhachis laboriosa* Smith, 1858 (Hymenoptera: Formicinae) and the nocturnal ponerine *Pachycondyla goeldii* (Forel, 1912) (Hymenoptera: Ponerinae) (both species being known as non-dominant; [60, 61]), and in three dominant arboreal myrmicine ants (*At. mocquerysi*, *Crematogaster* sp. and *T. aculeatum*; [10, 11, 14]. Prey detection recorded in these arboreal ants is different from the situation described in the arboreal dominant ant *O. longinoda* whose workers detect prey by sight at long range even when small, and approach them rapidly and directly with their mandibles wide open. The reaction of *Cr. (Nematocrema) stadelmanni* workers to escaping prey by increasing their moving speed and the sinuosity of their path, seems general in predatory ants (see [10, 11, 14, 60, 62]. In predatory ants, it is known that when prey escaped, the moving pattern of workers around the hunting site combined with greater speed and the increase in their aggressiveness usually enhanced the chances of finding them again and successfully attacking them, particularly when workers are able to use their venom. Like *At. mocquerysi* and *O. longinoda* [10], workers of *Cr. (Nematocrema) stadelmanni* never use their venom even during capture of large sized prey. In arboreal dominant ants hunting workers usually seize large and aggressive prey by an appendage or to a lesser degree by the head or the abdomen, as reported in *Crematogaster* sp., *O. longinoda* and *T. aculeatum* [11, 14]. Whatever the size of prey *Cr. (Nematocrema) stadelmanni* workers always seized them by an appendage. This behaviour can suggest an argument that although preys are mostly detected by contact, workers behave carefully without undue risk. It suggests that hunting workers of *Cr. (Nematocrema) stadelmanni* were able to assess a mortality risk associated with the prey capture before seizure. Preys were always retrieved using a group-hunting strategy with a short-range recruitment system. This predatory strategy seems general in arboreal dominant ants whose hunting workers are always surrounded by several nestmates situated within the range of short-range

recruitment, making the recruitment system efficient [10]. Moreover it is reported that arboreal ants present well-developed arolia in the form of adhesive pads and horn-shaped claws on the pretarsa. These structures may allow them to keep hold of prey until the arrival of recruited nestmates situated within the range of a recruiting pheromone [10, 11, 14]. These morphological structures may exist in *Cr. (Nematocrema) stadelmanni* workers since they were able to immobilize preys until the arrival of recruited nestmates for a joint attack and for the spread-eagling activity.

5. Conclusion

Cr. (Nematocrema) stadelmanni exhibits both a polydomous and polycalic nesting system, with large independent nests constructed using cardboard material and positioned on the surface of the bark of the trunk or fork of large branches of cultivated plants and/or wild ones. The diet composition is generalist type with the dominance of sweet liquids (preys are brought back to the nest only occasionally). The activity rate of the workers is continuous during the nycthemeral cycle, with a slight decrease at the end of the morning and another slight decrease late at night. Thus, large numbers of workers are deployed day and night in the environment to collect in each season of the year, a sufficient quantity of provision (solid particles, food sources, sweet liquids) to maintain and extend the nest, and to feed the large population (adults and brood) of the society.

It is well known that a group-hunting strategy with short-range recruitment system is more evolved than a solitary hunting strategy since it implies cooperation between workers and enables the retrieval of a greater range of prey sizes. *Cr. (Nematocrema) stadelmanni* captures very large prey items, as do other arboreal dominant ants (see [10, 11, 14]). The principal difference occurs after the prey is killed: *O. longinoda* kills the preys only by stretching them without using the venom and transport them entire to the nest; *Crematogaster* sp. and *T. aculeatum* workers use the venom and cut the prey on the spot; while *At. mocquerysi* kills the preys by stretching, cut them up down on the spot and transport them to the nest in small pieces.

Then *Cr. (Nematocrema) stadelmanni* is an indirect agricultural pest especially on economical importance trees, through the protected Hemipterans (propensity to honeydew collection) and workers exhibit a poor predatory aptitude due to the very long lasting capture duration, compared to that of other highly aggressive dominant arboreal-nesting ants known as good predators.

Farmers should avoid the presence in the fields of the ant species *Crematogaster (Nematocrema) stadelmanni* Mayr, 1895 (Hymenoptera: Formicidae: Myrmicinae), and it must be fought in the same way as known harmful insects. We cannot recommend it as a biological control agent because of its propensity for honeydew produced by Hemipterans, which include several vectors of plant diseases of viral, fungal and bacterial origin.

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