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RESEARCH ARTICLE

Seasonal pattern in food gathering of the weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) in mango orchards in Benin

Jean-François Vayssières[a,b]*, Issa Ouagoussounon[c], Appolinaire Adandonon[d], Antonio Sinzogan[c], Sam Korie[e], Raymond Todjihoundé[b], Seidou Alassane[b], Rosine Wargui[c], Florence Anato[c] and Georg Goergen[b]

[a]*CIRAD Persyst, UPR HortSys, Montpellier, France;* [b]*IITA, Biological Control Centre for Africa, Cotonou, Republic of Benin;* [c]*Faculté des Sciences Agronomiques, Université d'Abomey Calavi, Cotonou, Republic of Benin;* [d]*ENSTA – Kétou, Université d'Agriculture de Kétou, Kétou, Republic of Benin;* [e]*IITA, Ibadan, Nigeria*

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Prey capture and food scavenging activities of *Oecophylla longinoda* were monitored through regular weekly samplings during two consecutive years (2009–2010) in a large mango orchard of the Borgou Department of Benin, West Africa, a main mango production area located in the Sudan agro-ecological zone. In both years, interspecific competition with other ants occurred mainly during the dry season (January to March) resulting in increased captures of Formicinae, Myrmicinae and Ponerinae. More prey was caught during the rainy season (end April to end October) than during the rest of the year, with Diptera and Coleoptera prey peaking in May and June, respectively, along with the mango season. As insect prey quickly decreased during November to December weaver ants increasingly collected seeds and plant debris. A total of 241 species of insects were captured including 61 species (25.3%) associated with mango and a few with cashew, among which 48 mango pest species (78.7% of species associated with mango tree). Only five species (2.1%) of beneficial insects were captured. It is concluded that the presence of *O. longinoda* colonies is beneficial to perennial tree cropping systems such as mango and cashew.

Keywords: biological control; *Oecophylla longinoda*; *Mangifera indica*; seasonality of captures; nest contents

Introduction

The bio-ecology of the weaver ant *Oecophylla longinoda* Latreille (Hymenoptera Formicidae) has been well documented in East Africa (Vanderplank, 1960; Way, 1954), but there is little information available from West Africa especially concerning food gathering in mango orchards during the seasons. Like many ant species, weaver ants collect two types of food, carbohydrates as honeydew from different Hemipteran species (Way, 1963) and proteins from various arthropods captured by workers (Dejean, 1986). On young stems, petioles and sometimes fruits, weaver ants protect coccids to collect their honeydew, while proteins are provided by predation on many kinds of arthropods, mainly insects. Due to their high territoriality, permanent alert, sophisticated communication (Bradshaw, Baker, & Howse, 1975) and very effective

*Corresponding author. Email: j.vayssieres@cgiar.org

recruitment (Dejean, 1991), weaver ants quickly respond to prey numbers (Hölldobler & Wilson, 1977; Wilson, 1959). The highly organised predatory behaviour explains their success in capturing, killing (Hölldobler, 1979; Way, 1954) or driving away (Offenberg, Nielsen, Mc Intosh, Havanon, & Aksornkoae, 2004) many insects and crop pests of citrus, cashew, mango, cocoa, coconut trees and clove plantations.

The Asian weaver ant species, *Oecophylla smaragdina* (Fab.) is one of the most ancient biocontrol agents as it has already been managed against citrus pests in orchards in South-East Asia beginning around 304 AD (Groff & Howard, 1924). In the Mekong Delta of Vietnam, growers have a long tradition of ant husbandry using *O. smaragdina* (Barzman, Mills, & Cuc, 1996; Van Mele & Cuc, 2000). In Australia, *O. smaragdina* is used in biocontrol programmes against cashew (Peng, Christian, & Gibb 1995) and mango pests (Peng & Christian, 2005a). In Africa, *O. longinoda* is reported to significantly reduce damage by *Distantiella theobroma* (Dist.) (Hemiptera Miridae) on cocoa trees (Majer, 1972; Room, 1971), *Pseudotheraptus wayi* Brown (Hemiptera Coreidae) in coconut plantations (Simmonds, 1924; Vanderplank, 1960; Way, 1951, 1953), *Ceratitis cosyra* (Walker) and *Bactrocera dorsalis* (Hendel) (Diptera Tephritidae) in mango plantations (Van Mele, Vayssières, Van Tellingen, & Vrolijks, 2007). In West Africa, the impact of *O. longinoda* in fruit plantations remains largely unknown (Van Mele & Vayssières, 2007a). This is primarily attributable to the aggressive behaviour of weaver ants. In fact, West African farmers usually destroy weaver ants and their nests when they are found in their orchards. In Benin, for instance, about 50% of mango pickers considered weaver ants a nuisance (Sinzogan, Van Mele, & Vayssières, 2008). In West Africa, farmers' have many questions about the benefits that can be obtained from the use of weaver ants.

In order to respond to growers' questions, experiments providing evidence for the advantages of weaver ants in mango orchards were executed. The objectives of this study were to characterise: (1) the abundance of different groups of preyed-gathered insect species in relation to different mango fruit stages; (2) the abundance of different captures, 'seeds and plant debris' in relation to abiotic factors [temperature and relative humidity (RH)], and (3) the composition of ant castes and developmental stages during the collection of 'seeds and plant debris' to show eventual specialisation between ant castes.

Material and methods

Climate and field site

The Sudan zone, the most favourable area for growing mango, is characterised by a unimodal rainfall pattern with a yearly total of 1000–1300 mm. The rainy season usually starts at the end of April and lasts for six months until the end of October. In the South Sudan zone, where about 75% of the mango orchards of Benin grow (Vayssières, Korie, Coulibaly, Temple, & Boueyi, 2008), we selected one of the largest mango orchards of the region. The GPS references of this large mango orchard (~40 ha) situated at Korobourou (near Parakou) are 9° 37′ 01 N, 2° 57′ 10″ E. Mean temperatures and mean RH were recorded by means of two Tinytag devices [Tintag Plus 2 – Gemini Data Loggers (UK) Ltd] that were set up in two different shaded locations in the targeted mango orchard. Precipitations were recorded daily with a rain gauge set up in an open area in the middle of the orchard. A cashew orchard was adjoining this large mango orchard.

In this mango orchard, weaver ants were protected because they were introduced by the owner himself about 10 years ago. According to the owner (M. W. Zoumarou), one of the objectives of this ant introduction was to decrease mango losses due to theft and fruit bats.

Assessing the diet of weaver ants

During two consecutive years (2009–2010), prey and seeds collected by *O. longinoda* were sampled at weekly intervals in a 40 ha mango orchard with about 4000 mango trees. At every sampling event, we observed weaver ants on the trunks (0–2 m height) of 10 marked mango trees, hosting each about a dozen *Oecophylla*-nests. Forty mango trees were selected and divided into 4 groups (A, B, C, D) of 10 trees each. Once a week, all 10 mango trees from one group were monitored for a full day. Groups were rotated at weekly intervals. Thus, each group was examined once per month thereby minimising the anthropic influence on weaver ants. On rainy day observations were postponed to the following day. The number of prey items captured by *O. longinoda* was monitored on each tree during 6-min every hour within the daily foraging period from 7 am until 7 pm. At each hourly observation, a labelled vial received the pooled prey and seeds from all 10 mango trees. Each individual arthropod, including fruit fly larvae, carried by weaver ants, either entire or fragmentary, was counted as one item. All prey, seeds and plant debris collected by *O. longinoda* were seized on the tree trunks with tweezers and stored in alcohol. Food gathering was recorded on the ground and not in the canopy.

Sorting the nest contents of weaver ants

Preliminary observations (2006–2008) had revealed that in mango orchards *O. longinoda* collected seeds and plant debris mainly towards the end of the year. During November and December 2009, at the beginning of the dry season, we therefore assessed the food content of ant nests. We carried out a randomised stratified sampling of 3 nests per tree on each of the 10 sample trees, i.e., 30 nests per week. During the sampling process, we avoided picking up the small nests, with most ant trails, hosting the colony's queen (Peng, Christian, & Gibb, 1998) so as to save the colonies for the next season. Location and height in the tree of each selected nest to be observed for seeds and plant debris were recorded. Ten mango trees each bearing more than 15 nests were located and labelled. Thirty nests per week were cut off from their branch and put individually into a bag for overnight storage and inspection in the laboratory. One data sheet was used per nest to record main parameters of the nest (length, width and height), the brood and the number of coalescing mango leaves. On a large blank paper, each nest was then separately opened and its contents sorted, counted and recorded distinguishing the following categories: (1) weaver ant adults, (2) larvae and pupae, (3) prey and (4) seeds and plant debris. Furthermore the colony was described by the following criteria: (1) major workers, (2) minor workers, (3) larvae and pupae and (4) winged adults if present. By this method we recorded data from 30 *Oecophylla*-nests per week during eight weeks totalling 240 nests. Three types of nests per tree were differentiated: nest

(++) with many (>7) seeds and plant debris; nest (+) with few (1–7) seeds and plant debris; and nest (–) without (0) seeds and plant debris.

Taxonomic identification

A comprehensive characterisation of afrotropical insects is difficult and time-consuming due to the lack of appropriate or the fragmentary state of identification keys available for this geographic area. In many cases and depending on the focal taxonomic group, complete identifications can only be conducted, if at all, by specialists as being the case for West African Formicidae that were examined in this study by B. Taylor University of Nottingham, UK. All remaining taxa were determined by Georg Goergen and Jean-François Vayssières using primarily the arthropod reference collection at the IITA Biodiversity Center, Cotonou, Benin which has an extended coverage of West African insects and pertinent literature (Delvare & Aberlenc, 1989; Medler, 1980). Voucher specimens were deposited at the IITA-Benin collection in Cotonou.

Data analysis

Linear correlations were examined between different groups of insect species and also between insect species and abiotic factors (temperature and RH) in relation to different mango tree stages. Analysis of variance (ANOVA) was performed on counts of each group of insect species, seeds and plant debris, total nest contents, temperature (Temp) and RH. Furthermore, Principal Components (with bi-plot) Analysis was done with all nest-contained components to examine the pattern of their relationships with fruit stages over the two-year period. All count data were log10(x +1) transformed before analysis to stabilise the variance and normalise the data. All analyses were performed using the SAS statistical software (SAS, 2007). The significance level for the correlation coefficient and the significance level for separation of means in the ANOVA were set at the conventional 0.05 and mean separation was done by pair-wise t test under the general linear model ANOVA. ANOVA was performed on nest compositions major workers, minor workers and larvae and nymphs, as well as on seeds and plant debris, to examine the significance or otherwise of the effects of Weeks and presence or absence of seeds and plant debris.

Results

Diet of weaver ants in their trails

Workers of *O. longinoda* gathered a total of 241 species of arthropods representing 14 orders of insects (with 84 families) and 2 orders of millipedes (with 3 families) during these 2 years of weekly observations (Appendix 1). Of these, 61 species (25.3%%) are associated with mango tree whereby 48 are known to be mango pest species namely fruit flies (Tephritidae), leaf and stem pests (Cicadellidae, Coreidae, Lygaeidae, Pentatomidae, Geometridae), stemborers (Bostrichidae, Buprestidae, Cerambycidae) and some damaging saproxylophagous pests (Termitidae). The most abundant species captured were *Pheidole aberlii* Forel, *Pheidole welgelegenensis* Forel, *Crematogaster painei* Donisthorpe, *Pachycondyla tarsata* (Fabricius) (Formicidae), *Apion* sp. (Apionidae), *Rhadinocerus albus* Hustache (Curculionidae), *Phenolia* sp. (Nitidulidae), *Callosobruchus maculatus* Fab. (Bruchidae), *Pseudaspis* sp. (Apidae), *Lasioglossum* spp. (Halictidae), *Drosophila* sp. (Drosophilidae) and *Mesomorphus pauper* Ferrer (Tenebrionidae).

Results of the principal component analysis showed that, in both 2009 and 2010, the pattern of fruit stages with concomitant nest compositions was globally similar (Figure 1). Hymenopteran insects (other than Formicidae Formicinae, Myrmicinae and Ponerinae) were collected in higher numbers during the periods of fruit growing and prematurity which corresponded to higher temperatures; Coleoptera, Diptera, Hemiptera and Isoptera were more abundantly recorded during the period of fruit maturity (Table 1) which coincided with higher RH; other insects were found more frequently during the vegetative period; and seeds and plant debris were collected with increasing frequency by weaver ants towards the end of the year. These results are consistent for both 2009 and 2010 surveys (Figure 1). The combined ANOVA showed similar pattern and association between fruit stages, insect groups and plant debris recovered in nests (Table 1). Weekly observations of 2009 (Figure 2) and 2010 (Figure 3) revealed the same trend. The quantity of prey collected was greater in the wet season than in the dry one, reflecting a seasonal difference in the abundance of prey.

Formicidae were mainly captured from January to March during the second half of the dry season (Figures 2 and 3). Prior to the rainy season, many species of ants (Formicinae, Myrmicinae and Ponerinae) were regularly captured by *O. longinoda* among which the most abundant were *C. painei*, *P. aberlii*, *P. welgelegenensis*, *Pheidole megacephala* (Fab.) of the sub-family Myrmicinae, *Camponotus maculatus* (Fab.) of the sub-family Formicinae and *P. tarsata* of the sub-family Ponerinae (Table 2). During the rainy season, *O. longinoda* also captured, under mango trees, large species such as 'African stink ant' *P. tarsata* and the 'driver ant' *Dorylus nigricans* Illiger (Dorylinae), a primary ground forager. Two species of antagonist ants dominated over *O. longinoda* in this mango orchard, namely *Lepisiota cacozela* (Stitz) and *Lepisiota oculata* (Santschi). According to our observations these little 'black ants' were able to occupy alone a mango tree, nesting in hollow branches and to defend themselves effectively against weaver ants. The nature of the diet all the year-round is important for the metabolism of these ants and plays an important role in their phenotypical occurrence. According to our field observations, the bright orange colour of weaver ant adults is due to a more proteic diet whereas a yellow colour signals a more glucidic one. These field observations were confirmed later on by lab experiments (Vayssières, 2012).

Coleoptera were captured by weaver ants from April to September with a peak in June (Figures 2 and 3) at the end of the mango season. Coleoptera include the following families: Anthribidae, Apionidae, Bostrichidae, Bruchidae, Buprestidae, Carabidae, Cerambycidae, Cetoniidae, Chrysomelidae, Coccinellidae, Curculionidae, Elateridae, Histeridae, Nitidulidae, Scarabaeidae, and Tenebrionidae. Bostrichidae (*Sinoxylon* spp.), Buprestidae (*Belionota prasina* Th.) and Cerambycidae (*Ceroplesis* sp.) are xylophagous beetles boring into the branches of the mango tree (Appendix 1). Cetoniidae as *Chondrorrhina abbreviata* (Fab.) feed on the inflorescence during the dry season and *Pachnoda marginata* Drury pierce ripe mangoes to

Table 1. Correlation between different groups of insects and seeds and plant debris collected by *O. longinoda* in relation to different mango tree stages sampled at weekly intervals in a 40 ha mango orchard in Benin during two consecutive years (2009–2010).

		Hymeno.	Hemiptera	Isoptera	Coleoptera	Diptera	Other insects	Seeds and plant debris	Total contents	Temperature	RH
Fruit stage	*N*	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Flowering	11	36.3 ± 7.0 b	0.3 ± 0.2 c	0.0 ± 0.0 c	0.2 ± 0.2 d	0.6 ± 0.2 c	25.6 ± 8.2 cd	39.0 ± 10.0 a	102.0 ± 10.5 bc	28.4 ± 0.5 b	26.0 ± 2.7 d
Fruit growing	18	78.1 ± 5.3 a	0.9 ± 0.4 b	0.0 ± 0.0 c	1.8 ± 0.5 c	0.6 ± 0.2 c	16.9 ± 4.0 d	6.0 ± 1.2 b	104.4 ± 7.3 bc	31.3 ± 0.5 a	40.0 ± 2.9 c
Prematurity	6	27.7 ± 8.2 b	6.7 ± 1.6 a	3.0 ± 2.6 ab	4.0 ± 1.5 bc	4.2 ± 1.4 b	34.5 ± 11.4 bc	0.8 ± 0.4 c	80.8 ± 15.9 c	31.2 ± 1.2 a	54.8 ± 6.4 bc
Maturity	27	15.4 ± 2.6 c	4.7 ± 1.1 a	6.7 ± 2.0 a	26.2 ± 4.4 a	28.6 ± 3.5 a	71.4 ± 9.0 a	0.1 ± 0.1 c	153.0 ± 9.9 a	28.2 ± 0.4 b	71.7 ± 1.7 a
Without fruit	42	13.2 ± 2.3 c	2.1 ± 0.4 b	2.9 ± 0.9 b	4.6 ± 0.9 b	2.0 ± 0.4 b	58.6 ± 7.0 ab	52.1 ± 8.4 a	135.5 ± 7.7 ab	27.6 ± 0.2 b	60.0 ± 2.8 b
F value (4, 53)		26, 07	6, 33	4, 85	21, 05	56, 37	18, 59	11, 03	5, 00	11, 48	18, 05
P value		<0.0001	0.0003	0.0021	<0.0001	<0.0001	<0.0001	<0.0001	0.0017	<0.0001	<0.0001

Note: Means with the same letter(s) are not different at 5% level of significance.

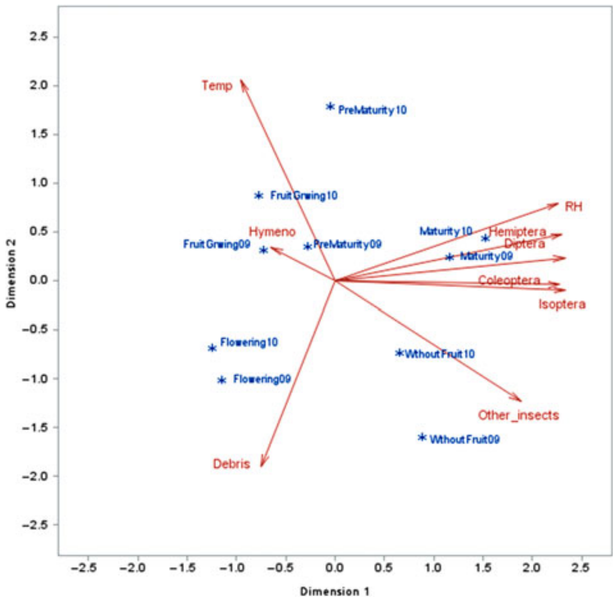

Figure 1. (Colour online) Principal Components Analysis (with bi-plot) with all nest-contained components to examine the pattern of their relationships with fruit stages over the two consecutive years (2009–2010).

suck them. Surprisingly, an important number of species of Tenebrionidae was collected.

Diptera were mainly captured by weaver ants during the rainy season (Figures 2 and 3). Diptera included the following families: Calliphoridae, Drosophilidae, Muscidae, Platystomatidae, Phoridae, Stratiomyidae, Syrphidae, Tabanidae, Tephritidae and Therevidae. Syrphidae were captured during flowering time (January to

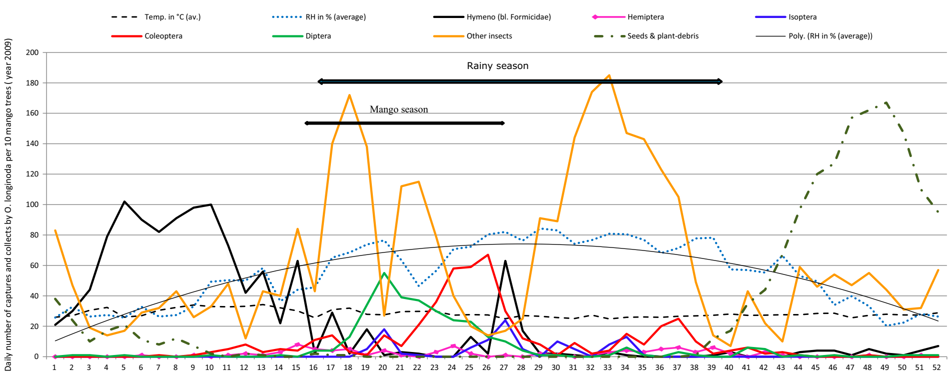

Figure 2. (Colour online) Yearly overview of captures of different kind of insects and collects of seeds and plant debris in Benin (central part) by *O. longinoda* in a mango orchard during 52 weeks (2009).

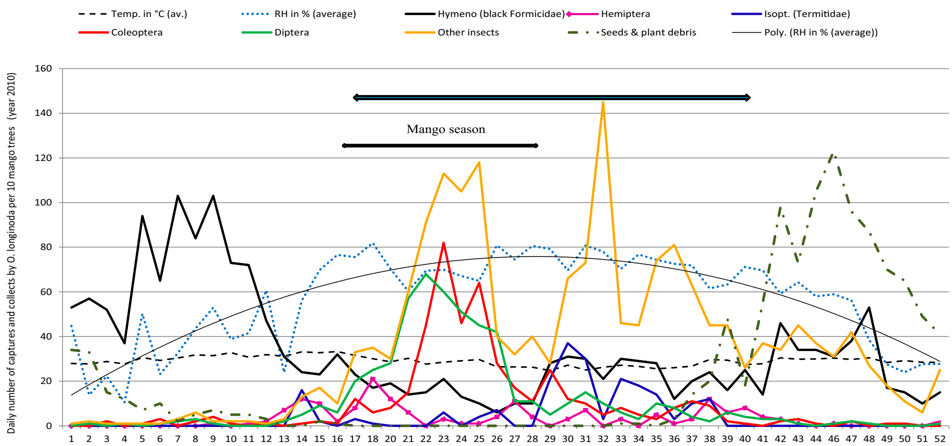

Figure 3. (Colour online) Yearly overview of captures of different kind of insects and collects of seeds and plant debris in Benin (central part) by *O. longinoda* in a mango orchard during 52 weeks (2010).

February) in very low numbers. Captures of fruit fly peaked during the second half of the mango season (May to June) when a large amount of rotten fruits, which contained tephritid larvae, were available (Appendix 1). The amount of fruit fly larvae captured by major ant workers on infested mangoes lying on the ground under mango trees was impressive. Some scarce adults of Tephritidae were also captured. By chance, we even observed worker ants capturing live adults of *B. dorsalis* and *C. cosyra* (Appendix 1) that were sucking juice from ripe mangoes though most flies took off after catching sight of weaver ants.

Hemiptera were frequently captured by weaver ants from March to October with a peak in May mainly in 2010 (Figure 2) during the mango season. Some captures also took place at the end of the rainy season. Hemiptera included the following families: Alydidae, Aphrophoridae, Cicadellidae, Coccidae, Coreidae, Cydnidae, Lygaeidae, Membracidae, Miridae, Nabidae, Pentatomidae, Plataspidae, Pseudococcidae, Reduviidae, Scutelleridae and Tettigometridae. The Homopteran species were driven from one plant or tree to another plant or tree by weaver ants for sugar collection and were more abundant during the dry season. On mango trees, the main carbohydrate source of weaver ants comes from farming Coccidae, especially *Udinia catori* (Green) (Appendix 1). This species was localised on young stems, petioles and fruits in this orchard. During the dry season, the number of prey collected was generally low and carbohydrates dominated.

Many Isoptera adults, especially different species of Termitidae, were captured by weaver ants at dawn and twilight from June to September with a peak in July (Figures 2 and 3). These peaks corresponded with the swarming of the different species. The most frequently collected species were *Macrotermes bellicosus* Smeathmann and *Pseudacanthotermes militaris* (Hagen) in May to June (Appendix 1).

Other insects [OI; Blattodea, Dermaptera, Hymenoptera (other than ants) Lepidoptera, Odonata, Orthoptera, Mantodea and Neuroptera], were also picked

Table 2. Ant species (Hymenoptera: Formicidae) captured by *O. longinoda* assessed at weekly intervals in a 40 ha mango orchard in Benin during two consecutive years (2009–2010).

Order	Family	Sub-family	Genus	Species	Incidence	Main periods of capture
Hymenoptera	Formicidae	Formicinae	*Camponotus*	*haereticus* (Santschi)	+	February, March and April
Hymenoptera	Formicidae	Formicinae	*Camponotus*	*flavomarginatus* (Mayr)	+	January, February and March
Hymenoptera	Formicidae	Formicinae	*Camponotus*	*schoutedeni* (Forel)	+	December and January
Hymenoptera	Formicidae	Formicinae	*Camponotus*	*maculatus* (Fabricius)	++	January, February, March and April
Hymenoptera	Formicidae	Formicinae	*Lepisiota*	*cacozela* (Stitz)	+	November, December and January
Hymenoptera	Formicidae	Formicinae	*Lepisiota*	*oculata* (Santschi)	+	January, February and March
Hymenoptera	Formicidae	Formicinae	*Oecophylla*	*longinoda* (Latreille) (males)	++	February and March beginning
Hymenoptera	Formicidae	Dorylinae	*Dorylus*	*gribodoi* (Emery)	+	March, April and June
Hymenoptera	Formicidae	Dorylinae	*Dorylus*	*nigricans* (Illiger)	++	May, June, July, August and September
Hymenoptera	Formicidae	Myrmicinae	*Crematogaster*	*chlorotica* (Emery)	+	November, December and January
Hymenoptera	Formicidae	Myrmicinae	*Crematogaster*	*painei* (Donisthorpe)	+++	January, February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Crematogaster*	*senegalensis* (Roger)	+	January, February and March
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*aberlii* (Forel)	+++	January, February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*andrieui* (Santschi)	+	February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*aurivilli* (Mayr)	++	February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*buchholzi* (Mayr)	++	February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*impressifrons* (Wasmann)	+	March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*megacephala* (Fabricius)	+++	February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*mentita* (Santschi)	+	March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*saxicola* (Wheeler)	+	March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*senilifrons* (Wheeler)	++	February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Pheidole*	*welgelegenensis* (Forel)	+++	January, February, March and April
Hymenoptera	Formicidae	Myrmicinae	*Tetramorium*	*sericeiventre* (Emery)	+	February and March
Hymenoptera	Formicidae	Ponerinae	*Odontomachus*	*troglodytes* (Santschi)	+	January, February, March and April
Hymenoptera	Formicidae	Ponerinae	*Pachycondyla*	*caffraria* (F. Smith)	+	January, February, March and April
Hymenoptera	Formicidae	Ponerinae	*Pachycondyla*	*tarsata* (Fabricius)	+++	January, February, March and April

up by weaver ants (Appendix 1) from April to September with a peak in August (Figures 2 and 3). Lepidoptera, Mantodea, Neuroptera and Odonata concerned dead insects that were scavenged. Live Blattodea and Dermaptera were captured within the thick layer of fallen mango leaves. *O. longinoda* also captured specimens of Apidae (bees), Ichneumonidae, Pompilidae (spider-hunter), Scoliidae (beetle-hunter), Sphecidae and even Vespidae (wasps). Adults of bees (*Apis mellifera andersonii* Lat.) and other adult Hymenoptera (Appendix 1) were captured on ripe mangoes and over-ripe ones under mango trees.

In 2009, the OI category represented 32.5% of the total captures whereas seeds and plant debris accounted for 21.7%, Hymenoptera (Myrmicinae, Formicinae, Ponerinae, Dorylinae) 22.7%, Coleoptera 8.9%, Diptera 6.6%, Hemiptera Homoptera 1.3%, Heteroptera 5.3% and millipedes 1% (Figure 2 and Table 3). In 2010, OI accounted for 26% of the total captures, Hymenoptera (Myrmicinae, Formicinae, Ponerinae, Dorylinae) 26.2%, seeds and plant debris 19.4%, Diptera 10%, Coleoptera 10.5%, Hemiptera Homoptera 2.8%, Heteroptera 3.9% and millipedes 1.2% (Figure 3 and Table 3).

Half a dozen moth species were also captured by weaver ants; but due to their bad state no identification was possible. Spiders were presently not identified but preserved for further study. Among millipedes (Diplopoda) two species of Polydesmida and one species of Spirostreptida were also captured by *O. longinoda* (Appendix 1). We observed that dead adults of *Archispirostreptus* sp. (Spirostreptidae) were cut by weaver ants into several pieces before being taken back to their arboreal nests.

Some cashew pests occasionally present in the mango orchard were also captured by weaver ants, namely *Apate terebrans* (Pallas) (Col.: Bostrichidae), *Mirperus*

Table 3. Percentage of different arthropod orders with seeds and plant debris captured by *O. longinoda* at weekly intervals in a 40 ha mango orchard in Benin during two consecutive years (2009–2010).

Arthropods/seeds and plant debris	Orders		Different orders (%) 2009	2010
Insects	Blattodea (other than Isoptera)		0.8	0.1
	Coleoptera		8.9	10.5
	Diptera		6.6	10
	Hemiptera	Homoptera	1.3	2.8
		Heteroptera	5.3	3.9
	Hymenoptera	Formicid	22.7	26.2
		Other	5.3	7.4
	Isoptera		1.9	3.3
	Lepidoptera		5.8	4.3
	Neuroptera		1.2	0.5
	Orthoptera		17.5	10.4
Millipeds			1	1.2
Seeds and plant debris			21.7	19.4
Total			100.00	100.00

jaculus Thunberg (Hem.: Alydidae), *Tupalus fasciatus* (Dallas) (Hem.: Alydidae), *Anoplocnemis curvipes* Fab. (Hem.: Coreidae), *Pseudotheraptus devastans* (Distant) (Hem.: Coreidae) and *Dysdercus voelkeri* Schmidt (Hem.: Pyrrhocoridae). Furthermore, pests of other crops were collected by weaver ants i.e. soybean bugs (*Clavigralla tomentosicollis* Stål, *M. jaculus*) or cotton bugs (*Aspilocoryphus fasciativentris* Stål) (Appendix 1). The cumulated number of pests from all crops (including mango pests) collected by weaver ants sums up to a total of 89 species, i.e. 36.9% of all species captured.

Beneficial insects were only caught in small numbers. The Appendix 1 shows the ratio between pest and beneficial insects: 89 species for all pests (including mango pests) vs. 5 beneficial species (total of 241 species gathered).

The following pest species were more frequently caught during the three critical phases in the development of mango fruits.

(1) Flowering: *Callosobruchus maculatus*, *Apion* sp., *R. albus*, *Eristalinus tabanoides*, *Eristalinus* sp., *C. tomentosicollis*, *Nysius* sp., *Dysdercus fasciatus*, *A. mellifera andersonii*, *C. painei*, *P. aberlii*, *P. megacephala*, *P. welgelegenensis*, *P. tarsata*, *Ropalidia* sp., *Polistes tenellus*.
(2) Flushing: *Sinoxylon transvalense*, *B. prasina*, *Myla microphtalma*, *M. bellicosus*, *Trinervitermes trinervius*, *Trinervitermes* sp., *P. militaris*, *Microcerotermes* sp., *Odondototermes* sp., *Gastrimargus* sp., *Oecanthus* sp.
(3) Fruiting: *Carpophilus dimidiatus*, *Chrysomya regalis*, *Drosophila* sp., *B. dorsalis*, *C. cosyra*, *Ceratitis quinaria*, *Ceratitis silvestrii*, *U. catori*, *Agonoscelis haroldi*, *D. voelkeri*, *Meliponula togoensis*, *C. painei*, *P. aberlii*, *P. megacephala*, *P. welgelegenensis*, *P. tarsata*, *M. bellicosus*, *T. trinervius*, *Trinervitermes* sp., *P. militaris.*

An interesting observation on weaver ants concerns the gathering of seeds and various plant debris during the dry season peaking at the end of November and beginning of December (Figures 2 and 3). From October onwards, ants collected a large number of seeds and plant debris of Poaceae mainly *Chasmopodium caudatum* (Hack.) Stapf, *Panicum maximum* Jacq., *Hyparrhenia* sp. and *Andropogon* sp. Within this category, seeds constituted the most important fraction (from November to December) together with plant debris of Poaceae and, to a lesser extent, some mango inflorescences (from December to January). This is probably the first record of seeds and different plant debris harvesting by *O. longinoda* in West Africa and perhaps for all of sub-Saharan Africa.

Examination of weaver ant nest content

From a total of 240 sampled nests, the mean number of major workers averaged 636 ± 544, minor workers 580 ± 608 and larvae pupae 180 ± 325 per nest. The nest composition, calculated from all pooled data, showed an average ratio of major workers, minor workers and larvae and pupae of 43.5%:39.7%:16.8%.

ANOVA of nest composition

The proportion of major workers and minor workers increased significantly (Table 4) with increasing levels of seeds and plant debris ($F_{(2,230)}$ = 16.97, P < 0.001 and

Table 4. Means ± SE of nest compositions major workers, minor workers, larvae and pupae, as well as seeds and plant debris and ANOVA in 2009 (n = 240).

		Major workers	Minor workers	Larvae and pupae	Seeds and plant debris	Number of prey
Types of nests	*N*	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
(–)	106	530.20 ± 36.75 c	525.10 ± 53.22 c	167.05 ± 29.35 a	0.00 ± 0.0 c	7.31 ± 1.23 c
(+)	104	673.25 ± 72.77 b	592.59 ± 52.54 b	198.61 ± 35.46 a	3.21 ± 0.18 b	8.07 ± 1.27 b
(++)	30	877.00 ± 62.49 a	731.33 ± 172.86 a	162.17 ± 50.17 a	13.85 ± 1.11 a	18.13 ± 3.22 a
F (2, 230)		16, 97	8, 25	0, 55	551, 29	19, 99
P value		<0.0001	0.0003	0.5787	<0.0001	<0.0001

Note: Means with the same letter(s) are not different at 5% level of significance.
(–) without (0) seeds and plant debris; (+) with few (1–7) seeds and plant debris; (++) with many (>7) seeds and plant debris.

Table 5. Eigenvectors of the first four principal components axes (PCA1–PCA4) of nest composition in 2009.

Covariates	PCA1	PCA2	PCA3	PCA4
Major workers	0.47	–	–	–
Minor workers	0.47	0.37	–	–
Larvae and pupae	0.33	0.53	–	−0.31
Seeds and plant debris	–	−0.53	–	–
Volume (cm^3)	0.38	–	0.37	–
Height of the nest in the tree	–	0.35	–	0.86
Number of coalescent leaves	0.36	−0.30	0.51	–
Number of prey	0.32	–	−0.65	0.32
Proportion of variance accounted for by PCA	0.35	0.18	0.13	0.12
Cumulative proportion of variance accounted for by PCA	0.35	0.53	0.66	0.78

Note: Only eigenvectors with values equal to or higher than 0.30 are shown.

$F_{(2,230)} = 8.25$, $P < 0.001$, respectively). Also, number of prey increased significantly with increasing levels of seeds and plant debris ($F_{(2,230)} = 19.99$, $P < 0.001$). There was a significant positive association, as measured by the linear correlation (r), between number of prey and seeds and plant debris in the combined data ($r = 0.272$, $N = 240$, $P < 0.001$).

Principal Components Analysis of the covariates

The first principal component axis (PCA1) measures a weighted average or approximately a weighted importance of the covariates with the exclusion of seeds and plant debris and height of the nest. These covariates were about equally weighted, between 0.32 and 0.47, on that axis, and the proportion of the total variance accounted for was about 35%. PCA2 accounted for about 18% and it was a contrast or comparison of minor workers, larvae and pupae and height of the nest with seeds and plant debris and number of coalescent leaves. The more minor workers and larvae and pupae and also the taller the tree the less of seeds and plant debris and number of coalescent leaves were found in the nest. PCA3 contrasted nest volume and number of coalescent leaves with number of prey. Similarly, PCA4 contrasted height of the nest and number of prey with larvae and pupae (Table 5).

Discussion

Food gathering, competition mechanisms and defence strategies of organisms are among the most discussed topics in ecology, behaviour and evolution (Thompson, 1997). These relationships determine fluctuations in populations of prey species in a first step and, finally, the survival or not of these species within their communities. In East Africa, *O. longinoda* is well adapted to foraging and hunting activities on a large array of insect species (Way, 1954) and even on other arthropods. In mango orchard, *O. longinoda* acts as a top predator capturing, as documented in this study, 241 species of arthropods including Diplopoda. Among this large array of prey *O. longinoda*'s competiveness is underlined by the capture of 26 ant species including

Anomma ants (Dejean, 1991; Gotwald, 1972) and other competitive ant species (*Camponotus* spp.) which also protect associated trophobionts on mango trees. Capture is a general word integrating individual fights, fights with several workers, and also collection of dead ants. Two species of antagonist ants, namely *L. cacozela* and *L. oculata*, can occupy alone a mango tree, nesting in hollow branches and defending themselves effectively against weaver ants (Vayssières, personal observation). These antagonistic black Formicinae should be managed in order to strengthen biological control of mango pests with weaver ants.

Predation by weaver ants was observed to take place on many kinds of shrubs and trees called primary territories but also on the ground called secondary territories under and around trees (Dejean, 1991). This study presents results on arthropods collected on the ground and on weeds growing under the mango trees. So, these results are restricted to secondary territories of weaver ants. Inventory of prey collected on primary territories should be carried out to complement the present fieldwork. In these secondary territories, *O. longinoda* is able to capture a great deal of prey types and functions as a generalist predator.

During weekly monitoring, this competitive ant species captured 61 species of insects associated with mango tree including 48 mango pest species i.e. 78.7% of all species associated with mango tree. Little quantitative information is actually available on the impact of African weaver ants on mango pests. In many life table studies, predators and unknown losses are important parameters, yet direct predation is not often quantified (Bernays & Graham, 1988). Furthermore, we actually know this arthropod predation by weaver ants is also strengthened by the production of chemical cues that repel mango fruit flies (Adandonon, Vayssières, Sinzogan, & Van Mele, 2009; van Mele, Vayssières, Adandonon, & Sinzogan, 2009). This can give us some reasons to explain and support the effectiveness of African weaver ants in managing mango fruit flies (Van Mele et al., 2007).

Predation is an important, but underexplored, aspect in the evolution of arthropod specialisation that affects phytophagous insects and the monitoring of their population fluctuations (Zalucki, Clarke, & Malcom, 2002). *Oecophylla longinoda* workers steadily captured prey during the rainy season though a significant decrease was observed during November to December. During the dry season most workers were collecting honeydew from coccids on flush and young fruits and captures of arthropods were relatively rare during the first three months of every year. The farming of Coccidae, especially *U. catori* assembled on flushes and fruits, is common in Benin, Burkina Faso (centre and south), Côte d'Ivoire, Ghana, Guinea, Mali (centre and south), Niger (south), Nigeria, Senegal (centre and south) and Togo. Many field observations throughout West Africa emphasise the key importance of *U. catori* for *O. longinoda* in the food-web structure of mango agroecosystems (Vayssières, 2012).

Captures of arthropods by weaver ants are dependent on the period when these become available along the yearly sequence of phenological stages of the tree. For instance, in 2005 and 2006 we noticed that fruit fly larvae (mainly third larval instar) were commonly captured during the second half of the mango season, in central Benin, during the months of May and June (Vayssières, Lokossou, Ayegnon, & Akponon, 2006). It is the same kind of sequence that Peng and Christian (2005b) observed in Australia with the green ant, *O. smaragdina*, in mango orchards. Fruit sampling and observations in a mango orchard of the same district of Parakou during two days, in May 2007 in one hectare of mango trees (cultivar Eldon, 30 years old), showed that *O. longinoda* workers were able to gather from the ground a total of 8059 fruit fly larvae (third larval instar 95%, L2 second larval instar 5%; Vayssières et al., unpublished data). Ants are also important biological control agents of fruit flies in other countries. In Brazil, the ants *Pheidole* spp. (Myrmicinae) were considered to be important regulators of *Anastrepha* populations through larval predation (Fernandes, Sant'Ana, Raizer, & Lange, 2012). In south Morocco, *Monomorium subopacum* Mayr (Hymenoptera: Formicidae) was by far the most efficient predator of larvae of *Ceratitis capitata* Wiedemann under argan trees (*Argania spinosa* (L.) Skeels) (El Keroumia et al., 2010). The beneficial role of ants in fruit tree protection is also shown by *Wasmania auropunctata* Roger on cocoa trees (Bruneau De Miré, 1969) in Cameroon or *Dolichoderus thoracicus* (Smith) on *Manilkara sapota* (L.) in Vietnam (Van Mele & Cuc, 2001), though the overall impact of *W. auropunctata* is now being challenged (Foucaud et al., 2009; Tindo et al., 2012; Walker, 2006).

Beside bites which are not particularly hurting because the pain disappears within seconds (according to Hölldobler & Wilson, 2000), weaver ants can be the source of other nuisances. In the present study, few specimens of beneficial insects such as carabid beetles (Carabidae) and pollinators like bees (Apidae) and hoverflies (Syrphidae) were captured by weaver ants. However, because of the small numbers of captured beneficial insects the overall impact on this group remains negligible. A more important issue is the potential predation and disturbing of fruit fly parasitoids (Hym.: Braconidae) by *O. longinoda*. This key question was discussed several times by colleagues involved in fruit fly biological control using parasitoids. During all our field activities (2005–2012) in all agro-ecological zones of Benin, we never saw any predation of parasitoids (*Fopius* spp.; *Psyttalia* spp.; *Diachasmimorpha* spp.) by *O. longinoda* (Vayssières et al., unpublished data). Adults of these braconids were often observed pacing up and down mangoes with ant workers on the same fruit without causing any trouble to the micro-wasps. In confined conditions, however, the results were different. Biotic interference has been observed between *O. longinoda* and *Fopius arisanus* (Sonan) (Appiah, Ekesi, Afreh-Nuamah, Obeng-Ofori, & Mohamed, 2014). According to Aluja and Birke (2003), valid conclusions should be deduced from experiments carried out under natural conditions (vs. confined conditions). Similarly, Peng and Christian (2013) showed that weaver ants, in the field, either benefit or have no impact on the natural enemy diversity and abundance.

Major workers, and to a lesser extent minor workers, captured prey all year-round and more copiously during the rainy season. By contrast seeds and plant debris were only collected at the beginning of the dry season when seeds became available and prey started to decrease together with a scarcity of water and honeydew. So far, the gathering of plant material has never been reported for weaver ants. For the moment, we do not know the reason for the accumulation of seeds inside the nest. Is it a kind of diversification of their diet? The collected seeds may possess elaiosomes, containing lipids, proteins, carbohydrate and essential sterols and thus would be welcome as supplements during food scarcity. Olfactory cues emitted by seeds may play a role for the observed myrmecochory (Youngsteadt, Nojima, Häberlein, Schulz, & Schal, 2008). Further studies are necessary to elucidate the strange behaviour of these predatory ants.

Colony growth depends heavily on prey availability (Kay, Rostampour, & Sterner, 2006). Dietary variation has been implicated in the evolution of castes (Smith & Suarez, 2010). When nest samplings were carried out in November to December 2009 we did not observe any sexual forms within the nests. The covariates of Group 2 (Table 5) suggest that major workers foraged, killed and brought many kinds of insects back to their nests. The covariates of Group 3 (Table 5) showed an interesting association of seeds and plant debris with higher nest volume and larger number of coalescent leaves. Congruent to observations made by Ledoux (1950) and Way (1954), the present data show a predominance of major workers (43.5%), followed by minor workers (39.7%) and larvae pupae (16.8%).

Together with our field observations these preliminary results suggest that *O. longinoda* may play an important role in mango fruit protection (Van Mele et al., 2007) similar to reports on *O. smaragdina* in Asia (Offenberg, Cuc, & Wiwatwitaya, 2013; Peng & Christian, 2005b). In Benin, as in other West African countries, the presence of *O. longinoda* colonies in mango orchards do offer the following comparative advantages to orchards without these ants: (1) a large range of pests and other prey being captured, (2) a quick response to any increased availability in prey numbers on and under mango trees, (3) a persisting ant population able to overcome temporal fluctuations in food supply by feeding on food reserves stored in nests, (4) the presence of foraging weaver ants shying off large sized pests, (5) control of low density pests through constant foraging. It is interesting to note that some cashew pests such as the cashew borer (Bostrichidae) and five species of cashew bugs (Alydidae, Coreidae, Pyrrhocoridae) of economic significance, incidentally occurring in the mango orchard, were also captured by weaver ants as recorded in Ghana (Dwomoh, Afun, Ackonor, & Agene, 2009). These are key elements for an Integrated Pest Management using *O. longinoda* (Van Mele & Vayssières, 2007a) in West African mango and also cashew orchards.

Due to their regional distribution in sub-Saharan Africa, abundance and dominance in forest savanna eco-systems, *O. longinoda* exerts a substantial ecological impact on the fluctuation of populations and the evolution of other sympatric species (Hölldobler & Wilson, 2000). A better understanding of the seasonality of prey captures and their nest-containing diet would provide key elements to enhance the efficiency of *O. longinoda* in mango and cashew orchards through biological control of pests. Increased market demand for organically and sustainably managed crop and forest products has to be met by holistic approaches such as conservation biological control (Van Mele & Vayssières, 2007b). The current study provides African farmers with an idea about the rich diversity of pests weekly captured by *O. longinoda* in their orchards and the role of weaver ants in mango orchard sanitation. In this way, the general preservation of weaver ant colonies in West African orchards is recommended as a primary principle followed, as a second step, by their adequate dissemination according to stringent rules. Furthermore, *Oecophylla* ant farming (Offenberg, Cuc, & Wiwatwitaya, 2010) can generate an agricultural system where weaver ants convert harmful pest biomass into edible ant brood.

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Appendix 1. Arthropod species (except spiders) captured by weaver ants at weekly intervals in a 40 ha mango orchard in Benin during two consecutive years (2009–2010).

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
Blattodea	Blatellidae	Undet. spp.	+	?		?			1
	Termitidae	*Macrotermes bellicosus* Smeathmann	++	Yes	Yes	Fruiting–flushing		Yes	2
		Trinervitermes trinervius (Rambur)	+	Yes	Yes	Fruiting–flushing		Yes	3
		Trinervitermes sp.	+	Yes	Yes	Fruiting–flushing		Yes	4
		Pseudacanthotermes militaris (Hagen)	++	Yes	Yes	Fruiting–flushing		Yes	5
		Microcerotermes sp.	+	Yes	Yes	Fruiting–flushing		Yes	6
		Odondototermes sp.	+	Yes	Yes	Fruiting–flushing		Yes	7
Coleoptera	Anthribidae	*Araecerus fasciculatus* (De Geer)	+	Yes		Fruiting			8
	Apionidae	*Apion* sp. 1	+	?		Fruiting			9
		Apion sp. 2	+	?		Flowering			10
		Cylas puncticollis Boheman	+	No		Fruiting		Yes	11
		Piezotrachelus sp.	+	?		?			12
	Bostrichidae	*Apate terebrans* (Pallas)	+	No		Flushing		Yes	13
		Sinoxylon transvalense Lesne	+	Yes	Yes	?		Yes	14
		Xylion senegambianus Lesne	+	Yes	Yes	?		Yes	15
		Xylloperthella picea (Olivier)	+	Yes	Yes	?		Yes	16
		Xylloperthella scutula (Lesne)	+	Yes	Yes	?		Yes	17
	Buprestidae	*Belionota prasina* Thunb.	+	Yes	Yes	Flushing		Yes	18
		Chrysobothris dorsata Fabricius	+	Yes	Yes	Flushing		Yes	19
		Agrilus sp.	+	?		Flushing			20
	Bruchidae	*Bruchidius dilaticornis* (Pic)	+	?		Flowering			21
		Bruchidius sp.	+	?		Flowering			22
		Callosobruchus maculatus Fabricius	++	?		Flowering			23
	Carabidae	*Agonum patroboides* Murray	+	No		Fruiting	Yes		24
		Aulacoryssus luteoapicalis Burgeon	+	No		Flushing	Yes		25
		Chlaenius bipustulatus Boheman	+	No		Flushing	Yes		26
	Cerambycidae	*Ceroplesis* sp.	+	Yes	Yes	Flushing		Yes	27
		Coptops aedificator (Fabricius)	+	Yes	Yes	Flushing		Yes	28

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
	Cetoniidae	*Chondrorrhina abbreviata* (Fabricius)	+	Yes	Yes	Flowering			29
		Gametis sanguineolenta (Olivier)	+	Yes	Yes	Flowering		Yes	30
		Oxythyrea petit (Gory & Percheron)	+	?		Flowering			31
		Pachnoda marginata (Drury)	++	Yes	Yes	Fruiting		Yes	32
		Pachnoda cordata (Drury)	+	Yes	Yes	Fruiting		Yes	33
		Rhabdotis sobrina Gory & Percheron	+	Yes	Yes	Flowering		Yes	34
	Coccinellidae	*Cheilomenes vicina* (Mulsant)	+	No		?			35
	Chrysomelidae	*Afrocrania* sp.	+	No		?			36
		Aspidimorpha sp.	++	No		?			37
		Cryptocephalus sp.	+	?		?			38
		Monolepta goldingi Bryant	+	No		Flowering		Yes	39
		Ootheca mutabilis (Sahlberg)	+	No		Flushing		Yes	40
		Podagrixena sp.	+	No		?			41
	Curculionidae	*Rhadinocerus albus* Hustache	+++	No		Flowering		Yes	42
		Isaniris decorsei Marshall	+	No		Fruiting		Yes	43
		Lixus sp.	++	?		?			44
		Lobotrachelus sp.	+	?		?			45
		Undet. sp.	+	?		?			46
	Elateridae	Undet. sp.	+			Flowering			47
	Histeridae	*Epitoxus circulifrons* (Marseul)	+	No		?			48
	Nitidulidae	*Carpophilus dimidiatus* (Fabricius)	+++	Yes	Yes	Flowering–fruiting		Yes	49
		Lasiodactylus sp.	++	?		Fruiting			50
		Phenolia (*Lasiodites*) sp.	++	?		Fruiting			51
	Scarabaeidae	*Aphodius* sp. 1	+	No		?			52
		Aphodius sp. 2	+	No		?			53
		Ontophagus sp. 1	+	No		?			54
		Ontophagus sp. 2	+	No		?			55

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
	Tenebrionidae	*Cheirodes villiersi* (Ardoin)	+	?		Fruiting			56
		Endustomus senegalensis (Laporte)	+	?		Fruiting			57
		Gonocephalum simplex Fabricius	+	?		Fruiting			58
		Gonocephalum yelamosi Espanol	+	?		Fruiting			59
		Mesomorphus pauper Ferrer	++	?		Flowering			60
		Oncosma gemmatum (Fabricius)	++	?		Flushing			61
		Oplocheirus striatus (Guérin-Méneville)	+	?		Fruiting			62
		Pogonobasis rugosula Guérin-Méneville	+	?		Flushing			63
		Polycoelogastridium decellei Ardoin	+	?		Flushing			64
Dermaptera	Forficulidae	*Diaperasticus* sp.	+	?		?			65
Diptera	Bombyliidae	*Bombylius nigrilobus* Bezzi	+	No		Flowering			66
		Undet. sp.	+	?		Flowering			67
	Calliphoridae	*Chrysomya regalis* Robineau-Desvoidy	+	Yes	Yes	Flowering		Yes	68
		Chrysomya sp.	+	?		Flowering			69
		Rhinia sp.	++	?		Fruiting			70
	Drosophilidae	*Drosophila* sp.	+++	Yes	Yes	Fruiting			71
	Muscidae	*Musca* sp.	+	?		Flowering–fruiting			72
	Platystomatidae	*Plagiostenopterina westermanni* Hendel	+	?		Fruiting			73
		Rivellia sp.	+	?		Flowering			74
	Stratiomyidae	*Hermetia* sp.	+	?		Fruiting			75
		Sternobrithes sp.	+	?		Fruiting			76
		Undet. sp.	+	?		Fruiting			77
	Syrphidae	*Allobacha* sp.	+	?		Flowering			78
		Eristalinus tabanoides (Jaennicke)	+	Yes	No	Flowering			79
		Eristalinus sp.	+	?		Flowering			80
		Ischiodon aegyptius (Wiedemann)	+	Yes	No	Flowering	Yes		81
		Paragus serratus (Fabricius)	+	Yes	No	Flowering			82

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
		Paragus sp.	+	?		Flowering			83
		Syritta flaviventris Macquart	+	?		Flowering			84
	Tabanidae	*Chrysops turiebris* Austen	+	No		Flushing			85
		Haematopota sp.	+	?		Flushing			86
		Tabanus sp.	+	?		Flushing			87
	Tephritidae	*Bactrocera dorsalis* (Hendel)	++	Yes	Yes	Fruiting		Yes	88
		Ceratitis cosyra (Walker)	++	Yes	Yes	Fruiting		Yes	89
		Ceratitis quinaria (Bezzi)	++	Yes	Yes	Fruiting		Yes	90
		Ceratitis silvestrii Bezzi	++	Yes	Yes	Fruiting		Yes	91
		Dacus vertebratus Bezzi	+	Yes	Yes	Fruiting		Yes	92
		Gymnaciura sp.	+	No		Flushing			93
		Sphaeniscus sexmaculatus Macquart	+	No		Flushing			94
	Therevidae	*Poecilagenia* sp.	+	?		?			95
Hemiptera	Alydidae	*Stenocoris southwoodi* Ahmad	+	?		Fruiting		Yes	96
		Mirperus jaculus Thunberg	++	Yes	Yes			Yes	97
		Riptortus dentipes Fabricius	+	No		Flowering		Yes	98
		Tupalus fasciatus (Dallas)	+	No		Flowering		Yes	99
	Aphrophoridae	*Poophilus* sp.	+	?		?			100
	Cicadellidae	*Cicadella nigrifrons* Distant	+	Yes	Yes	Flowering		Yes	101
		Undet. sp.	+	?		Flushing			102
	Coccidae	*Ceroplastes uapacae* (Hall)	+	Yes	No	Flowering–fruiting		Yes	103
		Parassaisetia nigra (Nietner)	+	Yes	Yes	Flowering–fruiting		Yes	104
		Saissegnia privigna (De Lotto)	+	Yes	No	Flowering–fruiting		Yes	105
		Udinia catori (Green)	+++	Yes	Yes	Flowering–fruiting		Yes	106
	Coreidae	*Acanthocoris* sp.	++	No		Flushing			107
		Anoplocnemis curvipes Fabricius	+	No		Flowering–fruiting		Yes	108

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
		Clavigralla shadabi Dolling	+	No		Flowering–fruiting		Yes	109
		Clavigralla tomentosicollis Stål	++	No		Flowering–fruiting		Yes	110
		Cletus ochraceus Herrich-Schäffer	+	No		Flowering–fruiting		Yes	111
		Myla microphtalma Linnavuori	+	No		Flushing		Yes	112
	Cydnidae	*Cydnus* sp.	++	?		Flowering			113
		Undet. sp.	+	?		?			114
	Lygaeidae	*Aspilocoryphus fasciativentris* Stål	+	No		Fruiting		Yes	115
		Graptostethus servus Fabricius	+	No		Flushing		Yes	116
		Nysius sp.	+	Yes	Yes	Flowering		Yes	117
		Oxycarenus sp.	+	?		Flowering		Yes	118
		Paromius paraclypeatus Scudder	+	No		Flushing		Yes	119
		Pseudopachybrachius reductus (Walker)	+	No		Flushing		Yes	120
		Spilosthetus elegans (Wolffenstein)	++	No		Fruiting		Yes	121
		Undet. sp. 1	+	?		?			122
		Undet. sp. 2	+	?		?			123
	Membracidae	Undet. sp.	+			?			124
	Miridae	*Campylomma plantarum* Lindberg	+	Yes	Yes	Flushing		Yes	125
		Eurystylus oldi Poppius	+	?		Flushing			126
		Stenotus sp.	+	?		?			127
		Taylorilygus (cf *vosseleri* Poppius)	+	?		Flushing			128
	Nabidae	*Phorticus flavus* Stein	+	?		Flushing		Yes	129
		Prostemma amyoti Reuter	+	?		Flushing		Yes	130
	Pentatomidae	*Agonoscelis haroldi* Bergroth	+	Yes	Yes	Flowering–fruiting		Yes	131
		Aspavia armigera (Fabricius)	+	No		Flushing		Yes	132
		Aspavia hastator (Fabricius)	+	Yes	Yes	Flushing		Yes	133
		Carbula marginella (Thunberg)	+	No		Flushing		Yes	134
		Diploxys arkheana Linnavuori	+	No		Flushing		Yes	135

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
		Nezara viridula (L.)	+	?		Flowering		Yes	136
		Piezodorus pallescens (Germar)	+	No		Flushing		Yes	137
	Plataspidae	*Coptosoma* sp.	+	?		Flushing			138
	Pseudococcidae	*Ferrisia virgata* (Cockerell)	+	Yes	Yes	Flowering–fruiting		Yes	139
		Paracoccus interceptus (Lit)	+	Yes	Yes	Flowering–fruiting		Yes	140
	Pyrrhocoridae	*Dysdercus fasciatus* Signoret	+	?		Flushing		Yes	141
		Dysdercus melanoderes Karsch	+	?		Flushing		Yes	142
		Dysdercus voelkeri Schmidt	++	Yes	Yes	Flushing		Yes	143
	Reduviidae	*Cleptria corallina* Villiers	+	No		Flushing		Yes	144
		Endochus africanus Bergroth	+	No		Flushing		Yes	145
		Sphedanolestes picturellus Schouteden	+	No		Flushing		Yes	146
		Tribelocephala sp.	+	?		?			147
		Undet. sp.	+	?		?			148
	Scutelleridae	*Sphaerocoris testudogrisea* (De Geer)	+	No		Flushing		Yes	149
	Tettigometridae	*Hilda* sp.	+	?		Flowering–fruiting			150
Hymenoptera	Apidae	*Apis mellifera andersonii* Latreille	+	Yes	No	Flowering–fruiting	Yes		151
		Ceratina viridis (Guérin-Méneville)	+	Yes	No	Flowering			152
		Ceratina sp.	+	?		Flowering			153
		Hypotrigona squamuligera (Benoit)	+	Yes		Flowering			154
		Meliponula togoensis (Stadelmann)	++	Yes	No	Flowering–fruiting			155
		Pseudapis sp.	+	?		?			156
		Stictonomia schubotzi (Strand)	+	?		?			157
	Bethylidae	Undet. sp.	+	?		Flushing			158
	Braconidae	*Apanteles* sp.	+	?		Flushing			159
		Bracon sp.	+	?		Flushing			160

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
		Chelonus curvimaculatus Fabricius	+	No		Flushing			161
		Coccygidium sp.	+	?		?			162
	Chalcididae	*Brachymeria* sp.	+	Yes		Flushing			163
		Hockeria sp. 1	+	?		Flushing			164
		Hockeria sp. 2	+	?		Flushing			165
	Chrysididae	*Stilbum* sp.	+	No		Flowering–fruiting			166
	Crabronidae	*Cerceris* sp.	+	?		Flushing			167
		Oxybelus sp.	+	?		Flushing			168
	Eumenidae	*Eumenes* sp.	+	No		Flushing			169
	Evaniidae	Undet. sp.	+	?		?			170
	Formicidae	*Camponotus haereticus* Santschi	+	No		Flowering–fruiting			171
		Camponotus flavomarginatus (Mayr)	+	Yes	Yes	Flowering–fruiting		Yes	172
		Camponotus schoutedeni Forel	+	Yes	Yes	Flowering–fruiting		Yes	173
		Camponotus maculatus (Fabricius)	++	Yes	Yes	Flowering–fruiting		Yes	174
		Lepisiota cacozela (Stitz)	+	Yes	Yes	Flowering–fruiting		Yes	175
		Lepisiota oculata (Santschi)	+	Yes	Yes	Flowering–fruiting		Yes	176
		Oecophylla longinoda (Latreille)	++	Yes	No	All the year			177
		Dorylus gribodoi Emery	+	No		Fruiting-flushing			178
		Dorylus nigricans Illiger	++	No		fruiting-flushing			179
		Crematogaster chlorotica Emery	+	Yes	Yes	Flowering–fruiting		Yes	180

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
		Crematogaster painei Donisthorpe	+++	Yes	Yes	Flowering–fruiting		Yes	181
		Crematogaster senegalensis Roger	+	Yes	Yes	Flowering–fruiting		Yes	182
		Pheidole aberlii Forel	+++	?		Flowering–fruiting			183
		Pheidole andrieui Santschi	+	?		Flowering–fruiting			184
		Pheidole aurivilli Mayr	++	?		Flowering–fruiting			185
		Pheidole buchholzi Mayr	++	?		Flowering–fruiting			186
		Pheidole impressifrons Wasmann	+	?		Flowering–fruiting			187
		Pheidole megacephala (Fabricius)	+++	?		Flowering–fruiting			188
		Pheidole mentita Santschi	+	?		Flowering–fruiting			189
		Pheidole saxicola Wheeler	+	?		Flowering–fruiting			190
		Pheidole senilifrons Wheeler	++	?		Flowering–fruiting			191
		Pheidole welgelegenensis Forel	+++	?		Flowering–fruiting			192
		Tetramorium sericeiventre Emery	+	?		Flowering–fruiting			193
		Odontomachus troglodytes Santschi	+	?		Flowering–fruiting			194
		Pachycondyla caffraria (F. Smith)	+	?		Fruiting-flushing			195
		Pachycondyla tarsata (Fabricius)	+++	?		Fruiting-flushing			196

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
	Halictidae	*Lasioglossum* sp. 1	+	?		Flowering–fruiting			197
		Lasioglossum sp. 2	+	?		Flowering–fruiting			198
		Seladonia sp.	+	?		?			199
	Ichneumonidae	*Goryphus* sp.	+	?		Flushing			200
	Leucospidae	*Leucospis* sp.	+	?		Flowering			201
	Mutillidae	Apterous females	++	No		Flowering–fruiting			202
	Nyssonidae	*Bembix* sp.	+	No		Flowering–fruiting			203
	Philanthidae	*Philanthus* sp.	+	No		Flushing			204
	Pompilidae	*Pepsis* sp.	+	No		Flowering–fruiting			205
	Sphecidae	*Tachysphex* spp.	+	No		Flushing			206
		Trypoxylon sp.	+	No		Flushing			207
		Undet. sp.	+	No		?			208
	Tiphiidae	Undet. sp.	+	No		?			209
	Vespidae	*Belonogaster* sp.	+	?		?			210
		Ropalidia sp.	+	?		Flowering			211
		Polistes fastidiosus (Saussure)	+	Yes	Yes	All the year		Yes	212
		Polistes tenellus (du Buysson)	+	Yes	Yes	Flowering		Yes	213
		Polistes sp.	+	?		?			214
Lepidoptera	Acraeidae	*Acraea nebule* Doubleday	++	No		Flowering–fruiting			215
	Geometridae	Undet. sp. 1	+	?		Flushing		Yes	216
		Undet. sp. 2	+	?		Flushing		Yes	217
	Noctuidae	Undet. sp. 1	+	?		Flushing		Yes	218
		Undet. sp. 2	+	?		Flushing		Yes	219
		Undet. sp. 3	+	?		Flushing		Yes	220
	Pyralidae	Undet. sp. 1	+	?		?		Yes	221
Mantodea	Hymenopodidae	*Sibylla* sp.	+	No		?			222
	Mantidae	*Sphodromantis* sp.	+	No		?			223

Appendix 1 (*Continued*)

Order	Family	Species	Incidence	Arthropods associated with mango tree	Mango pests	Mango phenology	Beneficial	Pests of mango or other crops	Nb
	Sybillidae	*Sibylla* sp.	+	No		?			224
Neuroptera	Chrysopidae	*Brinckochrysa* sp.	+	?		Flowering–fruiting			225
	Mantispidae	*Afromantispa* sp.	+	?		Flowering–fruiting			226
Odonata	Coenagrionidae	*Ceriagrion* sp.	+	No		?			227
	Libellulidae	*Palpopleura* sp.	+	No		?			228
		Trithemis sp.	+	No		?			229
Orthoptera	Acrididae	*Gastrimargus* sp.	+	No		Flushing			230
	Gryllidae	*Oecanthus* sp.	++	No		Flushing			231
		Scapsipedus sp.	++	?		All the year			232
	Tetrigidae	*Trachyttetix scaberrimus* Stål	+	No		?			233
		Xerophyllum platycoris (Westwood)	++	No		?			234
	Tettigoniidae	*Phaneroptera* sp.	+	?		Flushing			235
		Zabalius sp.	+	?		Flushing			236
Phasmida	Phasmatidae	*Gratidia* sp. 1	+	No		?			237
		Gratidia sp. 2	+	No		?			238
Polydesmida	Ammodesmidae	*Ammodesmus* sp.	+	?		All the year			239
	Gomphodesmidae	*Tymbodesmus* sp.	++	?		All the year			240
Spirostreptida	Spirostreptidae	*Archispirostreptus* sp.	+	?		All the year			241