



# Recruitment Rate of Nestmate in Six Tropical Arboreal Ants (Hymenoptera: Formicidae)

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**Abstract** We examined the recruitment rate of nestmates during prey capture in six arboreal ant species: *Myrmecaria opaciventris*, *Platythyrea conradti*, *Crematogaster* sp., *Crematogaster clariventris*, *Tetramorium aculeatum*, and *Oecophylla longinoda*. Termites and grasshoppers were used as prey. Prey were grouped by size: for termites, we presented ants with either workers or soldiers and for grasshoppers, we used small nymphs, mature nymphs and adults. After prey detection by a foraging ant, the total recruits present were counted every 30 s over the course of 15 min, and the mean numbers of workers counted at each time interval was computed and plotted for each prey type. We tested the effect of prey type, prey size and termite caste for each ant species on the number of nestmates recruited using ANOVA (GLM proc). Prey size, prey type and termite caste significantly influenced the mean number of nestmates following initial prey detection. We found that the observed recruitments were well explained by linear models for less arboreal (*M. opaciventris*) and primitive arboreal species (*P. conradti*), reflecting stochastic movement by individuals or stochastic collective recruitment. For specialized arboreal ant species, recruitment was well

explained by exponential models, reflecting within-group recruitment, either with limited or with unlimited group sizes. Overall, *T. aculeatum* had the highest level of nestmate recruitment. Surprisingly, *O. longinoda*, known to be one of the most specialized arboreal ant species, fit a recruitment model more like that of either ground ants with some arboreal foraging habits or primitive arboreal species.

**Keywords** Arboreal ant · Prey capture · Nestmate · Recruitment

## Introduction

Predatory behavior is widespread in ants. Typically observed behaviors include detection, attack, seizure, immobilization of prey, nestmate recruitment, and transportation of prey (Dejean 1988; Dejean 1990; Dejean et al. 2007; Dejean 2011; Djiéto-Lordon et al. 2001a; Djiéto-Lordon et al. 2001b; Djiéto-Lordon et al. 2001c; Richard et al. 2001).

Although some ant species forage individually, ant foraging behavior is a complex process, involving large numbers of individuals collecting food from many sources (Sumpter and Pratt 2003). When an important food source is discovered, ant species will use various mechanisms to alert their nestmates, a process known as recruitment (Deneubourg et al. 1987). Recruitment is a collective name for the system which enables ants to effectively indicate to their

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nestmates the location of a resource (Deneubourg et al. 1987; Bonabeau et al. 1998).

In many ants, various methods are used to recruit nestmates for food gathering, nest construction, colony defense, and colony relocation (Hölldobler 1990; Planque et al. 2010). The recruitment process can be divided into two steps: (1) the “invitation” of nestmates, i.e., the actual recruitment itself, which takes place mostly inside the nest and (2) the “orientation” process, i.e., the transmission of directional information (Liefke et al. 2001). Recruitment strategies can be described as (1) stochastic individual strategies, (2) stochastic collective (tandem) strategies, (3) group recruitment strategies with limited or (4) unlimited group sizes (Lachaud et al. 1984; Deneubourg et al. 1987; Liefke et al. 2001; Sumpter and Pratt 2003), and (5) leader-independent trail communication (Liefke et al. 2001). Nevertheless, recruitment numbers depend on colony size in each of these recruitment methods (Planque et al. 2010).

Despite the importance of recruitment in social insects, little is known about the temporal dynamics of worker abundance during prey capture in tropical arboreal ants, apart from the work of Rousson (2002) on neo-tropical arboreal *Azteca* ants. Ants that are ground-dwelling species with arboreal habits, primitive and specialized arboreal ant species found in tree canopies of tropical agroforestry systems have not been well studied (Tadu et al. 2014 a). Ground ant species with arboreal habits are species that nest in the soil and forage in trees to collect floral and extrafloral nectars (Kenne et al. 2000). Primitive arboreal ants nest opportunistically in a pre-existing cavity on the host plant; they have simple social organization, which involves morphological similarities with wasps; their queens are similar in size with the workers and there is absence of trophallactic feeding among workers due to the lack of a social crop (Orivel 2000). Specialized arboreal ants nest either independently or do so partially from their host trees; their colonies are polymorphic and the division of labor known as polyethism has been observed in the colony organization (Hölldobler 1990).

To understand the evolutionary forces influencing predatory behavior in arboreal ant species, we hypothesized that adaptation to arboreal habitat would affect the recruitment rate of nestmates during prey capture and that this could be reflected in modeling of such behaviors. The main objective of this study was to examine variation in the nestmate recruitment rate in tropical ants

with various degrees of specialization for arboreal foraging, in relation to prey type and size.

## Materials and Methods

### Study Sites

The study was conducted in the Minkoa Meyos orchard (02°31', 10°55') near Yaoundé, Cameroon (West Africa) and in a laboratory at the University of Yaoundé 1, in Cameroon. Minkoa Meyos orchard is an experimental station for fruit trees of “Institut de Recherche Agronomique pour le Développement (IRAD)”. The orchard is comprised of *Mangifera indica*, *Dacryodes edulis*, *Psidium goyava*, *Carica papaya*, *Elaeis guineensis*, *Citrus sinensis*, *Citrus limon*, *Citrus medica*, planted in a regular spatial pattern. Plots of *Zea mays*, *Manihot esculenta*, *Xanthosoma* sp. *Musa sapienta* and *Musa paradisiaca* were intermingled within the orchard.

### Study Species

This study focused on responses of six ant species belonging to five genera with varying levels of adaptation to foraging in the tree canopy. These species were (1) *Myrmicaria opaciventris*, a ground-dwelling ant species with arboreal habits (Kenne et al. 2000); (2) *Platythyrea conradtia* primitive arboreal ant species (Dejean 2011) and (3–6) four specialized arboreal ant species found in greatest abundance and frequency on the trees in cocoa agroforestry systems in southern Cameroon: *Tetramorium aculeatum*, *Oecophylla longinoda*, *Crematogaster clariventris*, and *Crematogaster* sp. (Tadu et al. 2014 b), also named *Crematogaster* “tsapi” by Richard et al. (2001).

### Experimental Apparatus

For each species, hunting arenas where prey were deposited were established; there was also a control arena that was identical to that of the test arena, but without prey. In the experimental treatment, the number of workers was not a limiting factor for recruitment. The experimental apparatus used in the study is illustrated in Fig. 1.

## Ground-Dwelling Ant Species with Arboreal Habit

Experiments were conducted on 10 colonies of *M. opaciventris* inside the Minkoa Meyos orchard. We used a modified version of the protocol of Kenne et al. (2001), in which two rectangular plywood sheets (40 × 40 cm) were placed on the soil three meters from the principal tunnel. One piece of plywood served as the hunting arena while the second one served as the control. The plywood pieces were spaced 50 cm apart.

## Primitive Arboreal Ant Species

Due to their scarcity, just five colonies of *P. conradti* were collected from traditional cocoa farms at Ngomedzap (03°16'N, 11°13'E) around the Mbalmayo forest reserve and Djazeng village (02°31' N, 10°55' E) in the Ntem valley and reared in the laboratory inside a "Chauvin" -type Nest. All the collected colonies lived inside *Platynerium* epiphytes (Dejean 2011), sometimes with other ant species like *Pheidole* sp. Foraging activity by *P. conradti* workers including prey capture, occurs between 5:00 and 8:00, and sugary substances exploited between 5:00 and 17:00 (Dejean 2011). For data collection, we used the modified protocol of Djiéto-Lordon et al. (2001b) as applied to *Platythyrea modesta*. Three parallel piped boxes (each 25 × 25 × 5 cm) covered by glass (30 × 30 cm) were used. The central box serves as nesting box while the two others serve foraging and control arenas (Fig. 1 a & b).

## Specialized Arboreal Ant Species

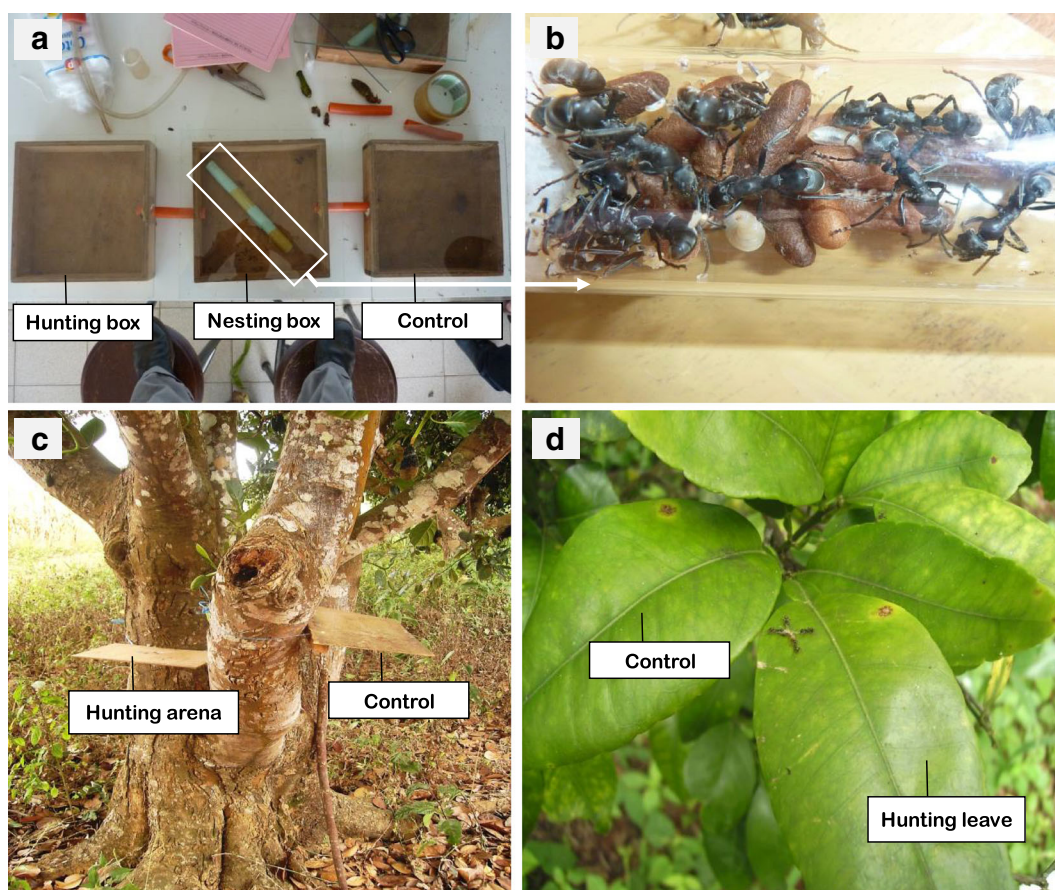
For *T. aculeatum* and *O. longinoda*, leave surfaces of the host plant were used as experimental arenas. We adopted the protocol of Rousson (2002), in which one leaf served as a foraging arena and a second situated just beside or below served as the control. During observations, we noted that *C. clariventris* and *Crematogaster* sp. forage mostly on the trunk compared to the leaves. Because of this, a modified protocol of Djiéto-Lordon et al. (2001c) was used to study *T. aculeatum* foraging behavior, in which plywood sheets (40 × 51 cm) were attached to tree trunks 1 m above the ground. One of the plywood pieces served as a foraging arena while the other served as the control (Fig. 1 c, & d).

## Data Collection

During one week, honey and small prey were deposited alternatively on the foraging arena and on the control to stimulate chemical marking of the territory in breeding condition in the Chauvin nest type at the laboratory by workers of *P. conradti*. The same process was applied in the farm on the plywood for *Crematogaster* sp. and *M. opaciventris*. For *T. aculeatum* and *O. longinoda*, the preys were deposited directly on the leave without any chemical marking process. Termites (*Macrotermes bellicosus*) and green grasshoppers (Tettigonidae) were used as prey. For termites, we used (1) workers ranging from 2 to 3 mm, or (2) 5–7 mm, or (3) soldiers (5–8 mm). For grasshoppers, we used (1) small nymphs (4–7 mm), (2) large nymphs (10–15 mm), or (3) adults (≥17 mm). We removed the hind tibia from the grasshoppers to prevent them from jumping away. For all prey, size correspond to the total body length, which takes in account the oviscape in female grasshoppers. Prey were placed on the foraging arena and after detection, the total recruits present at each time point the foraging arena were counted every 30 s for 15 min (Rousson 2002). Thirty cases were observed for each prey size, for a total of 90 observations for each prey species per ant species.

## Data Analysis

The mean numbers of workers counted after each time interval were computed for each ant species for each prey size and flux diagrams were plotted. We tested the main effect of prey type and prey size on the variation of mean number of workers present on the foraging arena at each time interval for each ant species and between ant species. For termites, the main effects of termite castes were also tested on the variation of the mean number of workers during the first 15 min after prey detection, for each ant species tested and for all ant species combined. For grasshoppers, the effect of grasshopper size on the number of workers present was tested for each of the six ant species during prey capture. Statistical analyses were done using ANOVA (GLM proc). Tukey's HSD, corrected with sequential Bonferroni procedure, was used for pairwise comparison when it was necessary. Over dispersion was corrected by quasi-Poisson error for the count data. R software (version 3.2.2.) was used for analysis and significance was attributed at the 5% level.



**Fig. 1** experimental apparatus uses to study recruitment rate behavior. Experimental apparatus use for recruitment rate behavior study during prey capture (a) and colony breeding (b) in

*Platythyrea conradti*, (c) *Crematogaster* sp. and *Crematogaster clariventris* and (d) for *Oecophylla longinoda* and *Tetramorium aculeatum*

## Results

### Time Elapsed until Maximum Recruitment

Best fit models of nestmate recruitment were linear (Fig. 2a, b, f; 3a, b; 4a, b; 5a, b; 6a, b, 7a & b), Gaussian (Fig. 3d, e, f; 5d, e & 6f), or exponential (Figs. 4e; 6c, d, e, 7c, d, e & f), depending on the prey size and the ant species.

Time elapsed to reach maximum number of recruits varied with prey size and ant species. With small prey (termites), recruitment occurred during the first 5 min after prey detection, but for larger prey (grasshoppers), recruitment required a longer period which extended over the first 5 min or more.

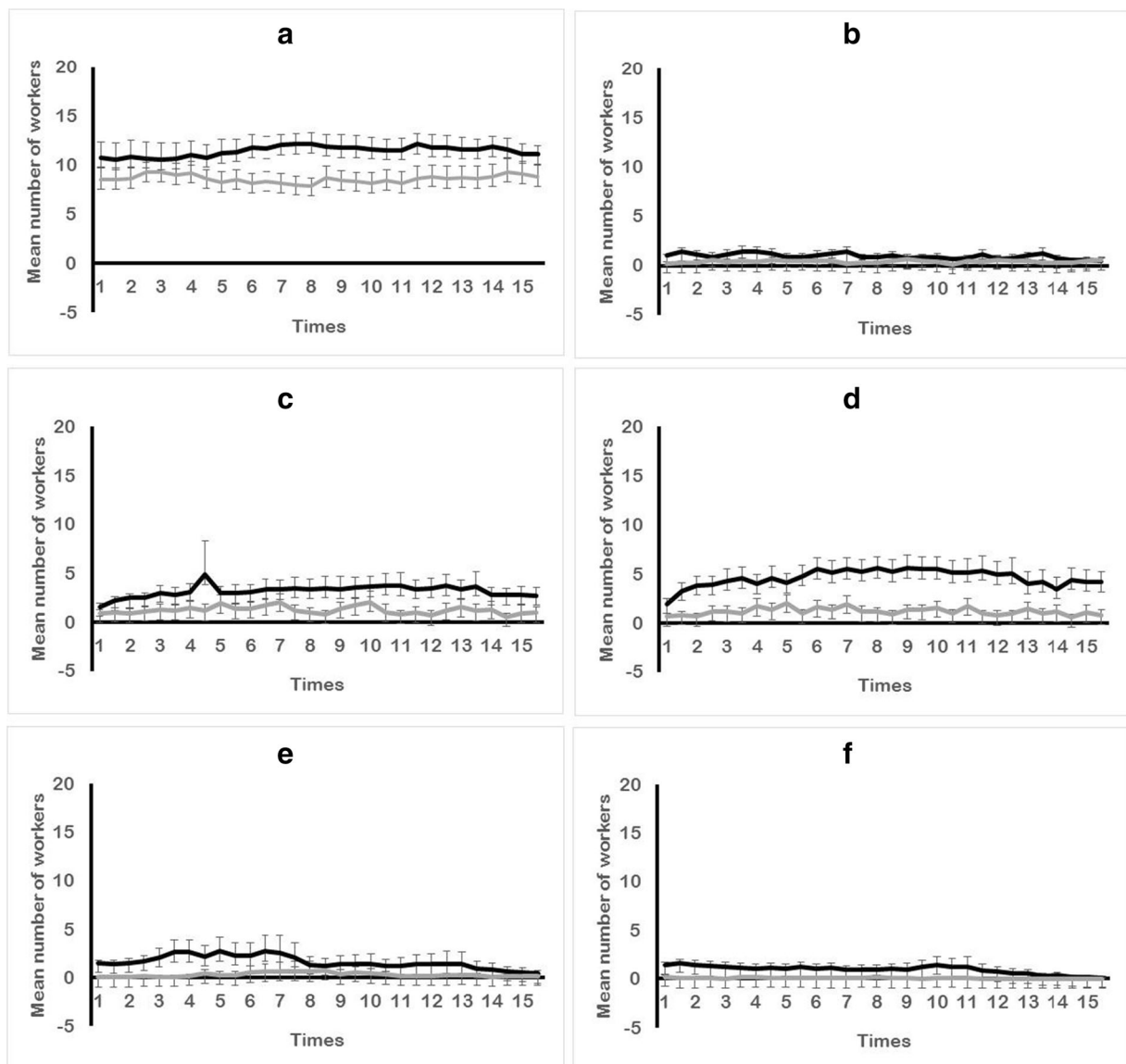
For ground-dwelling ant species with arboreal habit (*M. opaciventris*) and primitive arboreal ant (*P. conradti*) there was a small difference between the

hunting and the control arenas during nestmate recruitment over time (Figs. 2a & b).

The specialized arboreal ant, *O. longinoda* showed a similar distribution curve to *M. opaciventris* and *P. conradti* for termites of 2–3 mm size (Fig. 2f). For other specialized arboreal ants, recruitment periods varied with prey size. After encountering termites (size = 2–3 mm), the maximum number of recruits is reached between 3 and 4 min for *T. aculeatum* and 5–6 min for *C. clariventris*. For larger termite prey (5–7 mm) (Fig. 3d), time intervals ranged from 4 to 5 min for *Crematogaster* sp. to 8–9 min for *T. aculeatum*. In the presence of termite soldiers (5–8 mm), recruitment times ranged from 3 to 4 min for *Crematogaster* sp. and *C. clariventris*, respectively, to more than 15 min for *T. aculeatum* (Fig. 4e).

In presence of grasshoppers (4–7 mm size), the maximum mean number of workers were recruited between





**Fig. 2** Recruitment rate of nestmate of six arboreal ant species in the presence of termites of 2–3 mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of mean number

of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmicaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

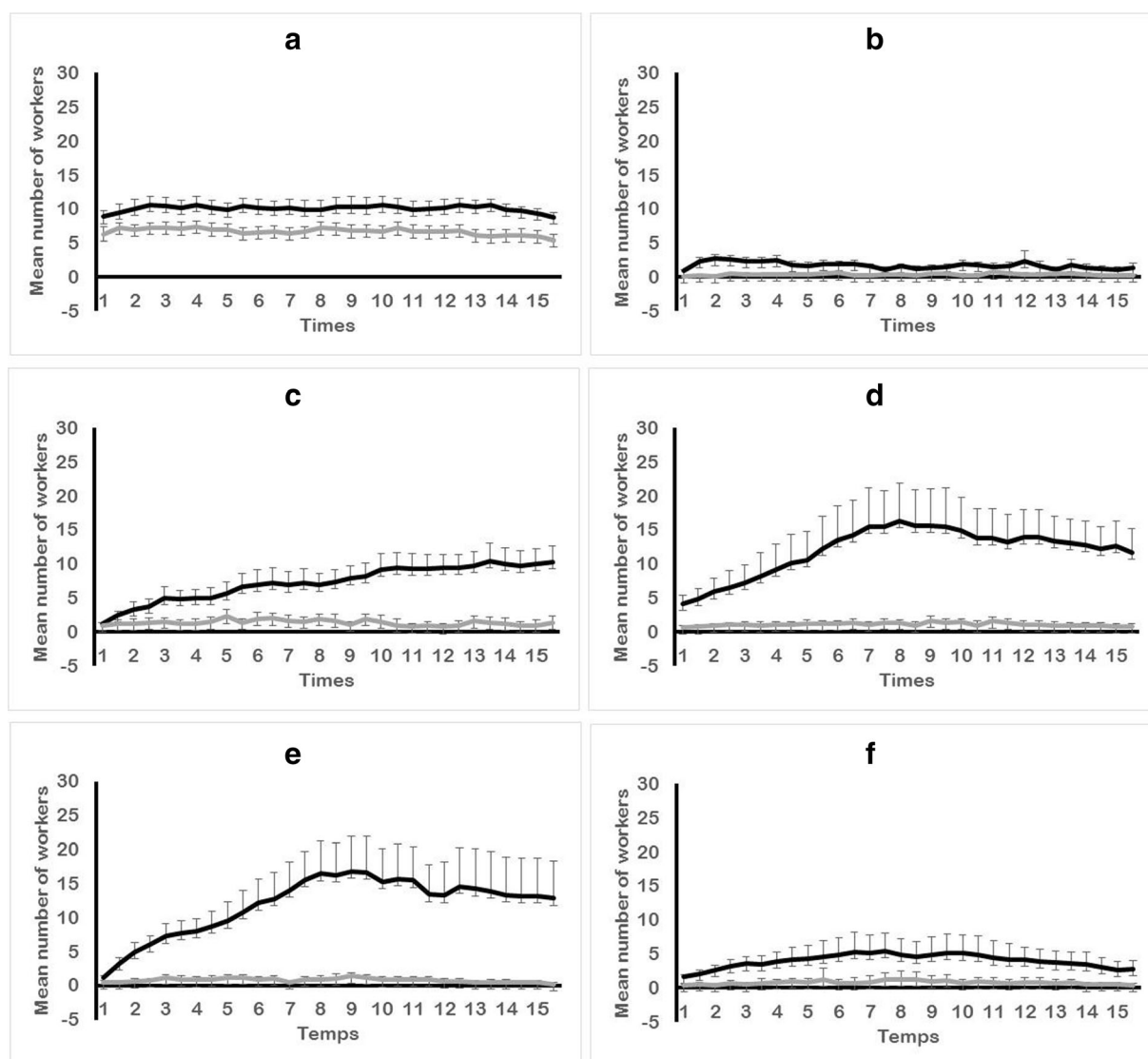
10 to 11 min after initial encounter for *C. clariventris* to more than 15 min for *Crematogaster* sp. (Figs. 5c & d). For *O. longinoda*, when presented with grasshoppers as prey (10–15 mm) (Fig. 6f) the maximum in mean numbers of recruited nestmates was observed at 7–8 min after first encounter with the prey and at more than 15 min when they faced larger grasshoppers ( $\geq 17$  mm) (Fig. 7f). *Crematogaster clariventris*, *Crematogaster* sp., and *T. aculeatum* all took more than 15 min for the maximal number to be recruited when confronted

of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmicaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

with grasshoppers or either 10–15 mm (Fig. 5) or  $\geq 17$  mm size (Fig. 7c, d & f).

#### Influence of Prey Type on Worker Recruitment

In ground-dwelling ant species with arboreal habit (*M. opaciventris*), the mean number of recruits was significantly higher ( $F = 35.62$ ;  $df = 1$ ;  $P < 0.0001$ ) in the presence of grasshoppers ( $2.47 \pm 0.13$ ) compared to termites ( $1.33 \pm 0.04$ ). The same tendency



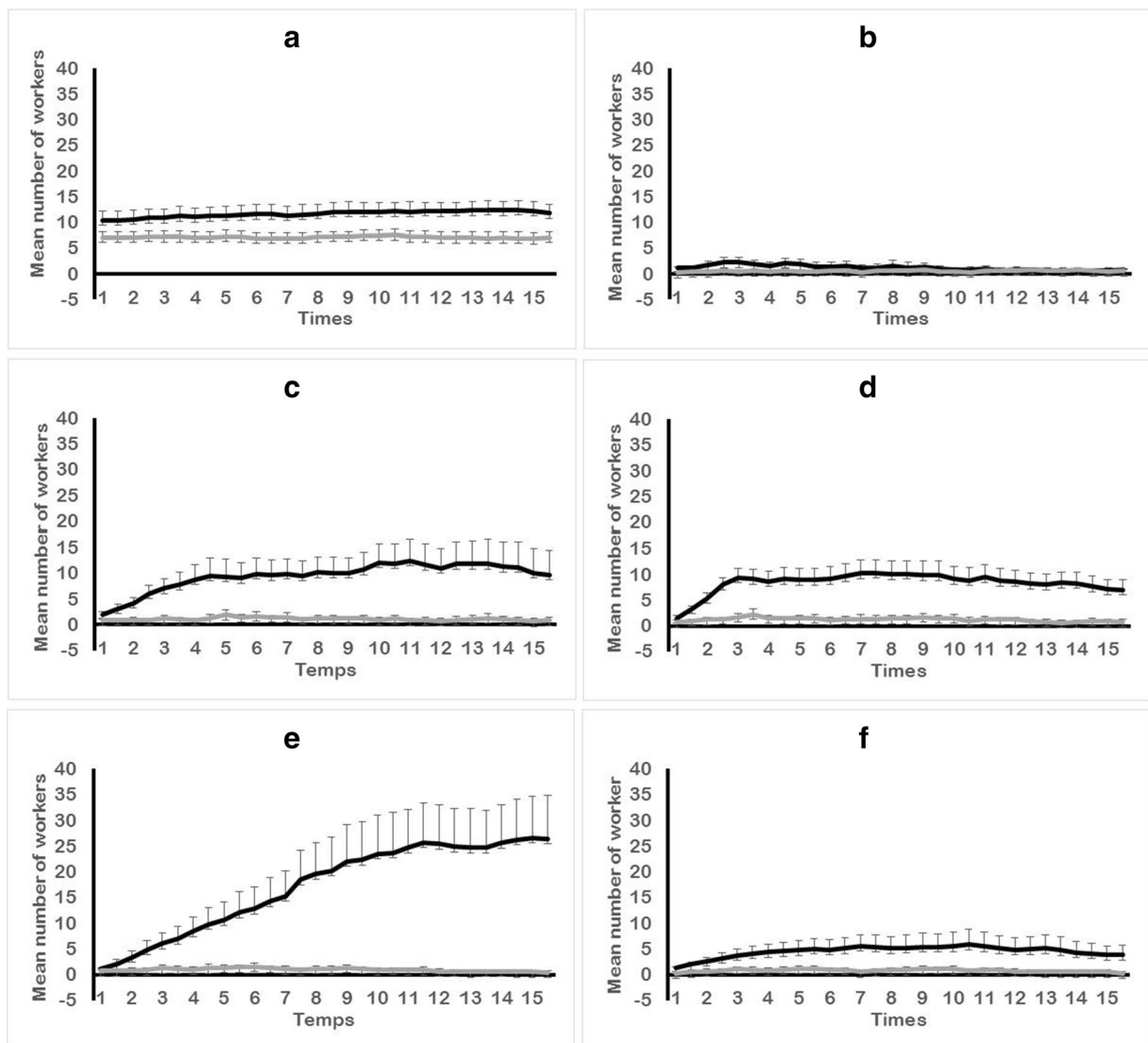
**Fig. 3** Recruitment rate of nestmate of six arboreal ant species in the presence of termites of 5–7 mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of mean number

of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmicaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

was observed for *P. conradti*, a primitive arboreal ant which recruits more in the presence of termites with  $11.05 \pm 0.07$  recruits against  $7.14 \pm 0.13$  in presence of grasshoppers ( $F = 70.03$ ;  $df = 1$ ;  $P < 0.0001$ ) (Table 1).

In specialized arboreal ant species: *Crematogaster* sp. ( $F = 4.80$ ;  $df = 1$ ;  $P < 0.0001$ ), *C. clariventris* ( $F = 75.17$ ;  $df = 1$ ;  $P < 0.0001$ ), *T. aculeatum* ( $F = 25.69$ ;  $df = 1$ ;  $P < 0.0001$ ) and *O. longinoda* ( $F = 80.88$ ;  $df = 1$ ;  $P < 0.0001$ ) we also found significant variation in total mean number of recruits between termites and

grasshopper prey. In the presence of termites, mean number of recruits for *C. clariventris* sp. was  $8.32 \pm 0.28$  versus  $25.24 \pm 1.35$  in the presence of grasshoppers, whereas for *Crematogaster* sp. the mean number of recruits was close to that of *C. clariventris*. *Tetramorium aculeatum* also recruit more in the presence of grasshoppers ( $30.88 \pm 1.50$ ) than termites ( $10.19 \pm 0.63$ ). The same trend was observed for *O. longinoda* with, respectively,  $9.26 \pm 0.84$  and  $3.13 \pm 0.13$  mean recruits in presence of grasshoppers and termites (Table 1).



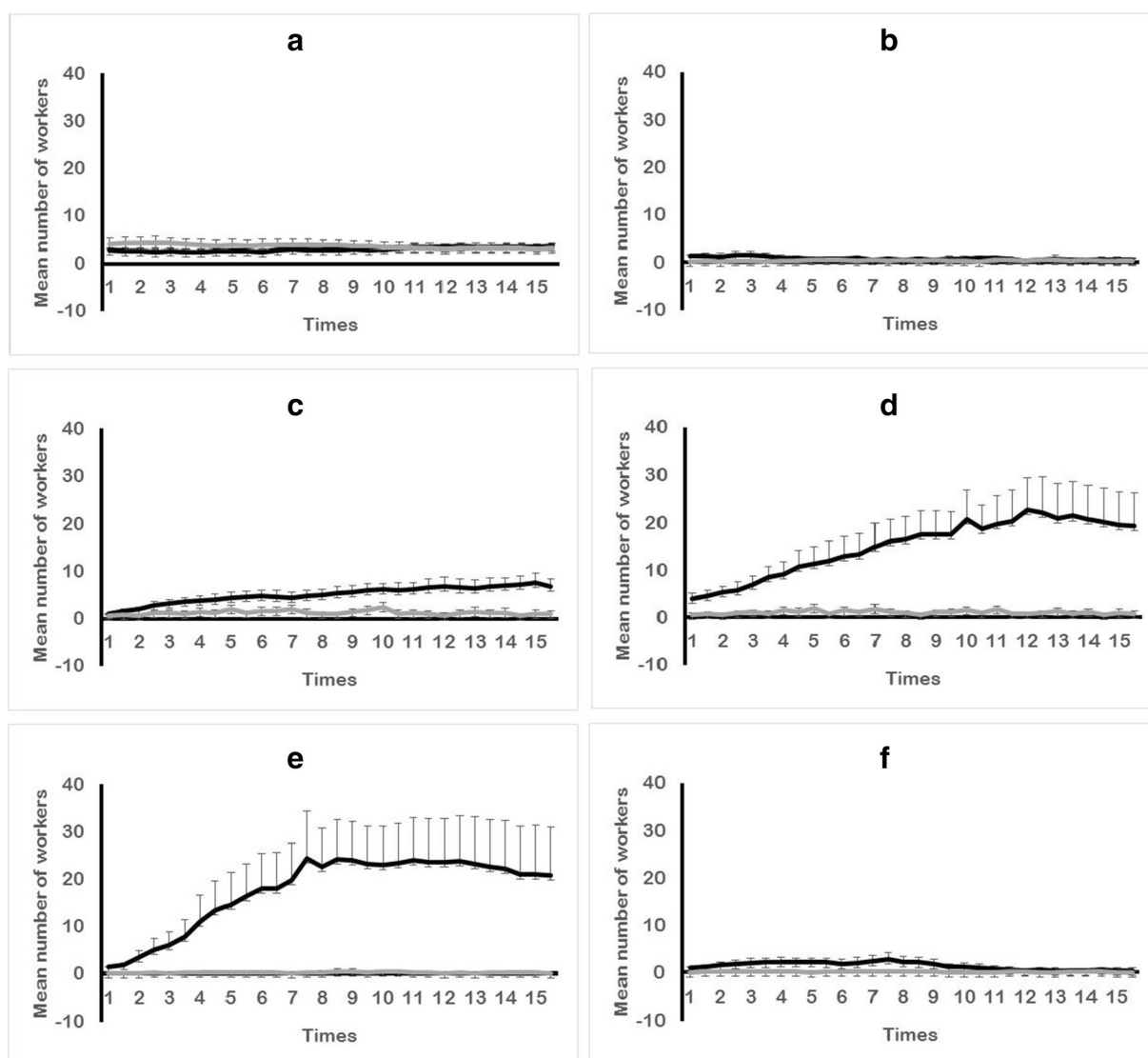
**Fig. 4** Recruitment rate of nestmate of six arboreal ant species in the presence of termites of 5–8 mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of mean number

of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmecaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

Recruitment rate of nestmates was significantly influenced by prey type and ant species ( $F = 66.84$ ;  $df = 11$ ;  $P < 0.0001$ ). As a whole, in the presence of termites and grasshoppers, the total mean number of recruits by *T. aculeatum* was higher than that of *C. clariventris*, *Crematogaster* sp., *O. longinoda*, *M. opaciventris* and *P. conradti*. Pairwise comparison showed that, *C. clariventris*, *Crematogaster* sp., *O. longinoda*, and *T. aculeatum* recruited more nestmates in the presence of grasshoppers than termites ( $P < 0.05$ ), compared to *M. opaciventris* and *P. conradti* who did not ( $P > 0.05$ ).

#### Influence of Termite Caste on Nestmate Recruitment

In ground-dwelling ant species (*M. opaciventris*) the total mean number of recruits was approximately the same ( $F = 0.26$ ;  $df = 1$ ;  $P = 0.43$ ) in the presence of worker termites ( $1.36 \pm 0.57$ ) and soldiers ( $1.27 \pm 0.09$ ) (Table 1), whereas *P. conradti*, a primitive arboreal ant, showed a high total mean number of recruits in the presence of termite soldiers ( $11.65 \pm 0.11$ ) compared to termite workers ( $10.76 \pm 0.84$ ) ( $F = 26.56$ ;  $df = 1$ ;  $P < 0.0001$ ) (Table 1).



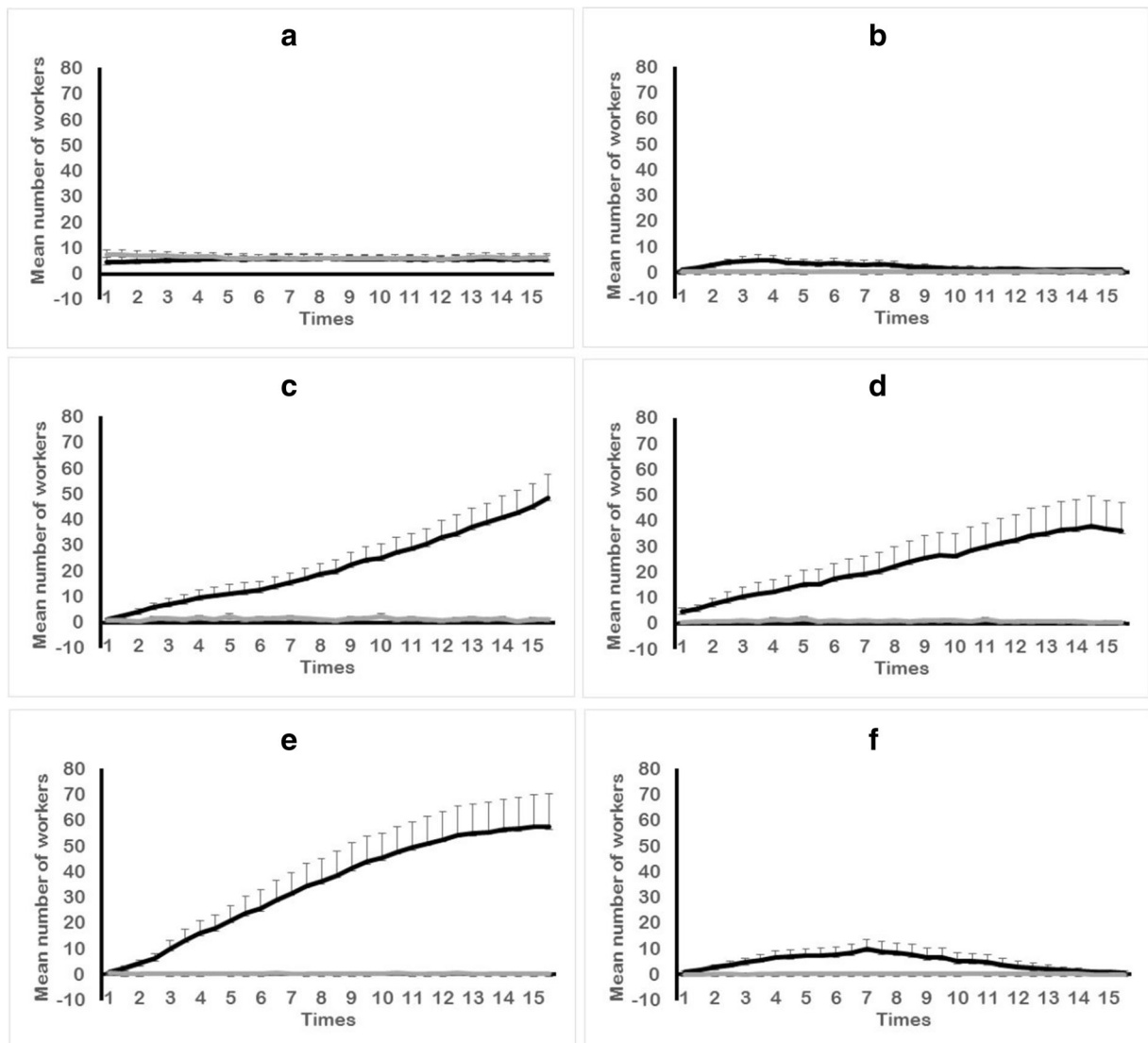
**Fig. 5** Recruitment rate of nestmate of six arboreal ant species in the presence of grasshoppers of 4–7 mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of mean

number of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmicaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

In specialized arboreal ants, the comparison of total mean number of recruits between worker and soldier termites showed that, except for *C. clariventris* ( $F = 0.01$ ;  $df = 1$ ;  $P = 0.92$ ), all the other species recruit more in the presence of soldiers than workers ( $P < 0.05$ ) (Table 1). In fact, in the presence of termite workers, the total mean number of recruits is about  $2.46 \pm 0.22$  for *O. longinoda* to  $8.29 \pm 0.58$  for *C. clariventris*, whereas in the presence of soldiers this number ranges between  $4.48 \pm 0.20$  for *O. longinoda* to  $17.09 \pm 1.57$  for *T. aculeatum* (Table 1).

The total mean number of workers recruited varied significantly with termite caste and among ant species ( $F = 69.58$ ;  $df = 11$ ;  $P < 0.0001$ ). Globally, in the presence of termite workers *C. clariventris* recruited more than *T. aculeatum*, *Crematogaster* sp., *O. longinoda*, *M. opaciventris* and *P. conradti*. In contrast, in the presence of termite soldiers, *T. aculeatum* recruited more than *Crematogaster* sp., *C. clariventris*, *O. longinoda*, *M. opaciventris* and *P. conradti* (Table 1). Pairwise comparisons showed that the total mean number of workers recruited for soldier termites varied





**Fig. 6** Recruitment rate of nestmate of six arboreal ant species in the presence of grasshoppers of 10–15 mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of

mean number of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythreya conradti*; **b:** *Myrmicaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

significantly ( $P < 0.05$ ) only for *Crematogaster* sp. For the other ant species, no significant differences were found ( $P > 0.05$ ).

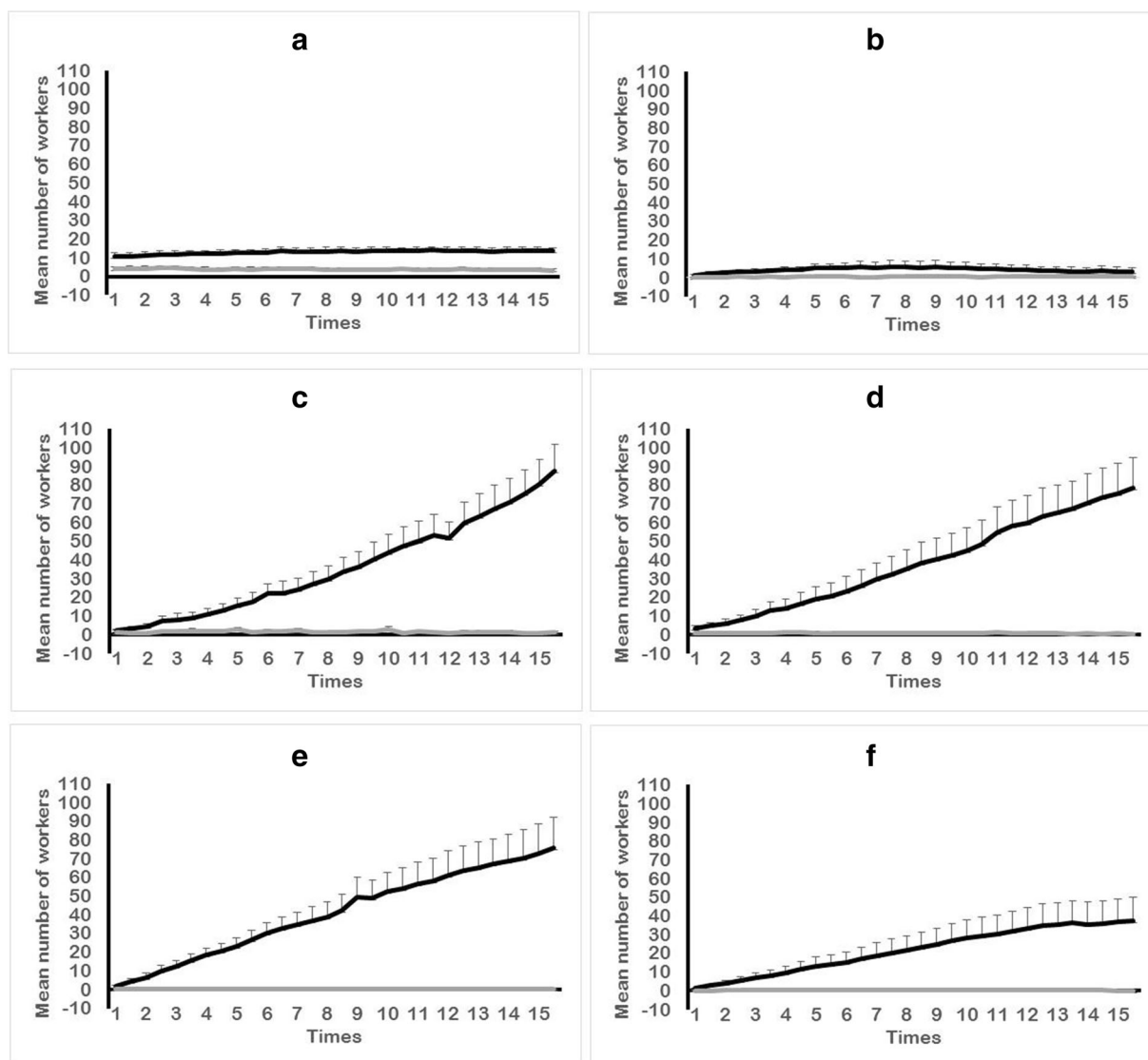
#### Influence of Prey Size on Total Mean Number of Workers Recruited

##### Ant Species and Termite

In the presence of termites, *Myrmicaria opaciventris* was recruited more by the 5–7 mm prey size ( $1.77 \pm$

$0.09$ ) than the 5–8 mm ( $1.27 \pm 0.09$ ) and 2–3 mm ( $0.96 \pm 0.05$ ) prey sizes ( $F = 26.37$ ;  $df = 2$ ;  $P < 0.0001$ ) (Table 2). In *P. conradti*, the total mean number of workers on the hunting box during the first 15 min was similar, but varied significantly ( $F = 69.44$ ;  $df = 2$ ;  $P < 0.0001$ ) with termite sizes. In fact, total mean number of workers of *P. conradti* ranged between  $10.06 \pm 0.08$  (5–7 mm) and  $11.65 \pm 0.11$  (5–8 mm) (Table 2).

In specialized arboreal ants, the total mean number of recruits increased with prey size for *Crematogaster* sp. ( $F = 67.21$ ;  $df = 2$ ;  $P < 0.0001$ ), *C. clariventris* ( $F =$



**Fig. 7** Recruitment rate of nestmate of six arboreal ant species in the presence of grasshoppers of  $\geq 17$  mm sizes. The black continuous line represents variation of mean number of workers during prey capture on the hunting area and grey line variation of mean

number of workers on the control. Error bars indicate 95% confidence interval. **a:** *Platythyrea conradti*; **b:** *Myrmecaria opaciventris*; **c:** *Crematogaster* sp.; **d:** *Crematogaster clariventris*; **e:** *Tetramorium aculeatum*; **f:** *Oecophylla longinoda*

74.50;  $df=2$ ;  $P<0.0001$ ), *T. aculeatum* ( $F=139.95$ ;  $df=2$ ;  $P<0.0001$ ) and *O. longinoda* ( $F=60.69$ ;  $df=2$ ;  $P<0.0001$ ) (Table 2). *Crematogaster* sp. were recruited more by 5–8 mm termites with  $9.48 \pm 0.48$  recruits compared to  $7.26 \pm 0.46$  and  $3.17 \pm 0.10$  for 5–7 mm and 2–3 mm termite sizes respectively; whereas *C. clariventris* recruit more in the presence of 5–7 mm ( $11.99 \pm 0.63$ ) compared to the 5–8 mm ( $8.38 \pm 0.36$ ) and 2–3 mm ( $4.60 \pm 0.15$ ) termite sizes. *Tetramorium aculeatum* and *O. longinoda* recruits more in the

presence of 5–8 mm termites size respectively with a mean  $17.09 \pm 1.57$  and  $4.48 \pm 0.20$  recruits (Table 2).

The total mean number of ants recruited at each time interval was significantly influenced by the interaction between ant species and termite size ( $F=102.58$ ;  $df=17$ ;  $P<0.0001$ ). A significant difference was observed among ant species in the presence of small termites (2–3 mm) ( $F=14.58$ ;  $df=5$ ;  $P<0.0001$ ), medium termites (5–7 mm) ( $F=86.84$ ;  $df=5$ ;  $P<0.0001$ ), or soldiers (5–8 mm) ( $F=63.70$ ;  $df=5$ ;  $P<0.0001$ ). As a whole,

**Table 1** Variation of mean number of workers recruited during prey capture in relation with prey type and termites caste

Ant species	Prey type		F-test (GLM Proc)	Termites caste		F-test (GLM Proc)
	Termites vs	Grasshoppers		Workers vs	Soldiers	
<i>Myrmicaria opaciventris</i>	1.33 ± 0.04	2.47 ± 0.13	F = 35.62; <i>P</i> < 0.0001	1.36 ± 0.57	1.27 ± 0.09	F = 0.26; <i>P</i> = 0.43 NS
<i>Platythyrea conradti</i>	11.05 ± 0.07	7.14 ± 0.32	F = 70.03; <i>P</i> < 0.0001	10.76 ± 0.84	11.65 ± 0.11	F = 26.56; <i>P</i> < 0.0001
<i>Crematogaster</i> sp.	6.64 ± 0.25	20.86 ± 1.55	F = 40.80; <i>P</i> < 0.0001	5.21 ± 0.36	9.48 ± 0.48	F = 49.39; <i>P</i> < 0.0001
<i>Crematogaster clariventris</i>	8.32 ± 0.28	25.24 ± 1.35	F = 75.17; <i>P</i> < 0.0001	8.29 ± 0.58	8.38 ± 0.36	F = 0.01; <i>P</i> = 0.92 NS
<i>Tetramorium aculeatum</i>	10.19 ± 0.63	30.88 ± 1.50	F = 25.69; <i>P</i> < 0.0001	6.74 ± 0.77	17.09 ± 1.57	F = 35.49; <i>P</i> < 0.0001
<i>Oecophylla longinoda</i>	3.13 ± 0.13	9.26 ± 0.84	F = 80.88; <i>P</i> < 0.0001	2.46 ± 0.22	4.48 ± 0.20	F = 44.50; <i>P</i> < 0.0001

For each ant species, *N* = 90 for termites and grasshoppers respectively; *N* = 60 for workers and *N* = 30 for soldiers. NS: Non Significant result at 5% confidence intervals; *df* = 1

in the presence of 2–3 mm sized termites *C. clariventris* followed by *Crematogaster* sp. recruited more than *T. aculeatum* *O. longinoda* and *M. opaciventris*. With 5–7 mm prey size, *C. clariventris* and *T. aculeatum* recruited approximately the same mean number of nestmates. In the presence of 5–8 mm termite sizes, *T. aculeatum* recruit more than *Crematogaster* sp., *C. clariventris*, *O. longinoda*, *M. opaciventris* and *P. conradti*.

Pairwise comparison showed significant differences among all ant species to the 2–3 mm termite size (*P* < 0.05) except between *O. longinoda* and *M. opaciventris* (*P* = 1.0). For medium-sized termite workers (5–7 mm), *C. clariventris* and *T. aculeatum*

showed no significant differences (*P* = 1.0); the same result was found between *O. longinoda* and *P. conradti* (*P* = 1.0). For other pairs of ant species, significant differences were found (*P* < 0.05). In presence of soldiers (5–8 mm) significant differences were found between all species (*P* < 0.05) except for *O. longinoda* and *P. conradti*, which were statistically not different (*P* = 0.16).

#### Ant Species and Green Grasshoppers

In ground-dwelling ant species (*M. opaciventris*) we found significant (*F* = 83.44; *df* = 2; *P* < 0.0001) variation on total mean number of workers recruited after

**Table 2** Variation of mean number of workers recruited during termites capture by various ant species after each time interval

Ant species	Termite sizes						F-test (GLM Proc)
	2-3 mm		5-7 mm		5-8 mm		
	A	B	A	B	A	B	
<i>Myrmicaria opaciventris</i>	0.96 ± 0.05 <sup>a</sup>	0.40 ± 0.02	1.77 ± 0.09 <sup>bc</sup>	0.40 ± 0.03	1.27 ± 0.09 <sup>bd</sup>	0.59 ± 0.03	F = 26.37; <i>P</i> < 0.0001
<i>Platythyrea conradti</i>	11.44 ± 0.09 <sup>a</sup>	8.61 ± 0.07	10.06 ± 0.08 <sup>bc</sup>	6.69 ± 0.09	11.65 ± 0.11 <sup>ad</sup>	7.13 ± 0.03	F = 69.44; <i>P</i> < 0.0001
<i>Crematogaster</i> sp.	3.17 ± 0.10 <sup>a</sup>	1.22 ± 0.07	7.26 ± 0.46 <sup>bc</sup>	1.37 ± 0.07	9.48 ± 0.48 <sup>bd</sup>	1.12 ± 0.05	F = 67.21; <i>P</i> < 0.0001
<i>Crematogaster clariventris</i>	4.60 ± 0.15 <sup>a</sup>	1.17 ± 0.07	11.99 ± 0.63 <sup>bc</sup>	1.11 ± 0.05	8.38 ± 0.36 <sup>bd</sup>	1.24 ± 0.06	F = 74.50; <i>P</i> < 0.0001
<i>Tetramorium aculeatum</i>	1.61 ± 0.12 <sup>a</sup>	0.29 ± 0.04	11.86 ± 0.77 <sup>bc</sup>	0.78 ± 0.05	17.09 ± 1.57 <sup>bc</sup>	0.92 ± 0.06	F = 139.95; <i>P</i> < 0.0001
<i>Oecophylla longinoda</i>	0.96 ± 0.07 <sup>a</sup>	0.07 ± 0.01	3.96 ± 0.18 <sup>bc</sup>	0.75 ± 0.05	4.48 ± 0.20 <sup>bd</sup>	0.76 ± 0.05	F = 60.69; <i>P</i> < 0.0001

A is hunting arena and B is control, *N* = 30 for each prey size, *df* = 2, different letters indicate significant differences between species pair found with pairwise comparisons

15 min observations. In fact, in the presence of 4–7 mm grasshoppers,  $0.86 \pm 0.06$  nestmates were recruited while in the presence of 10–15 mm and  $\geq 17$  mm grasshoppers,  $2.29 \pm 0.23$  and  $4.25 \pm 0.22$  nestmates were recruited respectively. Nevertheless, *P. conradti* showed a great total mean number of recruits which varied significantly ( $F = 2018.44$ ;  $df = 2$ ;  $P < 0.0001$ ) with prey size between  $2.95 \pm 0.07$  to  $13.02 \pm 0.18$  respectively for 4–7 mm and  $\geq 17$  mm grasshopper (Table 3).

For specialized arboreal ants, recruitment rates of each ant species increased significantly ( $P < 0.05$ ) with prey size in presence of grasshoppers. For *O. longinoda*, mean number of recruits varied between  $1.38 \pm 0.13$  (4–7 mm) to  $21.64 \pm 2.17$  ( $\geq 17$  mm), whereas for *T. aculeatum* the mean number of recruits varied between  $17.54 \pm 1.39$  to  $40.61 \pm 4.19$  for the same prey size respectively (Table 3). For *Crematogaster* species, *C. clariventris* and *Crematogaster* sp. recruited more nestmates ( $38.09 \pm 4.37$  and  $35.96 \pm 4.64$ ) in the presence of 17-mm grasshoppers than in presence of 10–15 mm and 4–7 mm grasshoppers (Table 3).

The variation of mean number of workers during the 15 min observations was influenced by the interaction between prey size and ant species ( $F = 38.78$ ;  $df = 17$ ;  $P < 0.0001$ ). The mean number of workers recruited every 30 s during 15 min varied significantly ( $F = 98.82$ ;  $df = 5$ ;  $P < 0.0001$ ) in the presence of 4–7 mm grasshoppers. In response to grasshoppers with sizes of 10–15 mm, all studied species showed significantly ( $F = 44.81$ ;  $df = 5$ ;  $P < 0.0001$ ) different recruitment potential. Similar results were observed with adult grasshoppers (more than 17 mm) between ant species ( $F = 21.30$ ;  $df = 5$ ;  $P < 0.0001$ ). Globally, in the presence of 4–7 mm, 10–15 mm and more than 17 mm grasshoppers, *T. aculeatum* recruited more than *C. clariventris*, *Crematogaster* sp., *M. opaciventris* and *P. conradti*. In each study case, *O. longinoda* recruited less than other specialized arboreal ant species.

Pairwise comparisons showed no significant difference ( $P > 0.05$ ) in the recruitment rate between *T. aculeatum* and *C. clariventris*, and between *O. longinoda* and *M. opaciventris*, whereas the other species pairs showed significant differences ( $P < 0.05$ ) for the prey size 4–7 mm. With 10–15 mm prey size, similar recruitment rates ( $P > 0.05$ ) were observed between *C. clariventris* and *Crematogaster* sp., between *P. conradti* and *O. longinoda*, between *T. aculeatum* and *C. clariventris*, and between *T. aculeatum* and *Crematogaster* sp. For the other species, significant

differences ( $P > 0.05$ ) were found in recruitment rate between species pairs. In the presence of  $\geq 17$  mm grasshoppers, the following species pairs showed no significant difference ( $P > 0.05$ ): *C. clariventris* and *Crematogaster* sp.; *C. clariventris* and *O. longinoda*; *Crematogaster* sp. and *O. longinoda*; *C. clariventris* and *T. aculeatum*; *Crematogaster* sp. and *T. aculeatum*. The other species pairs were significantly different ( $P < 0.05$ ).

## Discussion

Linear models gave a good fit to recruitment data for *M. opaciventris*, *P. conradti*, and in some cases *O. longinoda*. This may be explained by their solitary foraging behavior that is largely focused on small prey. Solitary foraging behavior and a typically individual foraging strategy (Pie 2004) has been described in many Ponerinae species (Lachaud and Dejean 1994; Orivel 2000; Schatz et al. 2001) and in *M. opaciventris* (Kenne et al. 2000). For ants that forage for medium sized termites as prey, a Gaussian model was found, for *C. clariventris* and *T. aculeatum*, suggesting a predictable aspect of the recruitment rate for these species over time. As prey size increased further, the recruitment rate followed an exponential model, as documented with *T. aculeatum*, *C. clariventris* and *Crematogaster* sp. during the first 15 min of observation, suggesting the existence of alerting and trail marking mechanisms that recruit new nestmates to prey after encounter. Communication in ant species occurs mainly through the emission of tactile and chemical signals (Hölldobler 1990; Viana 1996; Passera and Aron 2005) and such signals play an important role in nestmate recruitment (Hölldobler and Wilson 1976). For all ant species, when solitary foraging becomes frequent (as occurred for the 2–3 mm termite size), recruitment of nestmates is reduced. For *T. aculeatum*, the maximum number of workers recruited appeared later or was apparent for some prey sizes, compared to other ant species. We suggest that, the recruitment mechanism in this species is faster and gradual, but persists more through time compared to other species perhaps in compensation of the small worker size of this species. In fact, *T. aculeatum* workers split their prey in smaller pieces (Djiéto-Lordon et al. 2001c) compared to *Crematogaster* species and *O. longinoda* before returning to the nest.



**Table 3** Variation of mean number of workers recruited during grasshopper capture by various ant species after each time interval

Ant species	Grasshopper sizes						F-test (GLM Proc)
	4–7 mm		10-15 mm		≥ 17 mm		
	A	B	A	B	A	B	
<i>Myrmecaria opaciventris</i>	0.86 ± 0.06 <sup>a</sup>	0.45 ± 0.03	2.29 ± 0.23 <sup>bc</sup>	0.45 ± 0.03	4.25 ± 0.22 <sup>bd</sup>	0.45 ± 0.03	F = 83.44; <i>P</i> < 0.0001
<i>Platythyrea conradti</i>	2.95 ± 0.07 <sup>a</sup>	<b>4.58 ± 0.23</b>	5.43 ± 0.07 <sup>bc</sup>	<b>6.25 ± 0.08</b>	13.02 ± 0.18 <sup>bd</sup>	4.59 ± 0.22	F = 218.3; <i>P</i> < 0.0001
<i>Crematogaster</i> sp.	5.05 ± 0.32 <sup>a</sup>	1.33 ± 0.09	21.57 ± 2.52 <sup>bc</sup>	1.33 ± 0.09	35.96 ± 4.64 <sup>bd</sup>	1.33 ± 0.09	F = 25.64; <i>P</i> < 0.0001
<i>Crematogaster clariventris</i>	15.03 ± 1.07 <sup>a</sup>	0.95 ± 0.06	22.60 ± 1.94 <sup>ac</sup>	0.95 ± 0.06	38.09 ± 4.37 <sup>bd</sup>	0.95 ± 0.06	F = 17.26; <i>P</i> < 0.0001
<i>Tetramorium aculeatum</i>	17.54 ± 1.39 <sup>a</sup>	0.22 ± 0.02	34.50 ± 3.47 <sup>ac</sup>	0.22 ± 0.02	40.61 ± 4.19 <sup>bd</sup>	0.22 ± 0.02	F = 71.03; <i>P</i> < 0.0001
<i>Oecophylla longinoda</i>	1.38 ± 0.13 <sup>a</sup>	0.20 ± 0.02	4.75 ± 0.50 <sup>bc</sup>	0.20 ± 0.02	21.64 ± 2.17 <sup>bc</sup>	0.20 ± 0.02	F = 13.59; <i>P</i> < 0.0001

A is hunting arena and B is control, N = 30 for each prey size, df = 2, different letters indicate significant differences between species pair found with pairwise comparison, while values in bold represent the mean number of workers on the control after inversion

The number of workers recruited at each time interval increased with increasing prey size. This observation confirms previous observations that more workers participate in the capture of larger prey and that such enhanced recruitment increases prey capture rates as stated by Djîéto-Lordon et al. (2001b, 2001c) in *P. modesta* and *T. aculeatum*.

*Crematogaster clariventris* showed a similar pattern (and model) of recruitment as *T. aculeatum*, suggesting a similar ability to recruit nestmates under some circumstances. Nevertheless, we observed that, in regard to the polymorphism in this species, an increase in prey size and the ability of prey to defend itself favored the arrival of the major caste, which sped up prey capture and prey dismemberment. Furthermore, the limited arrivals of the minor caste to the foraging arena ceased more rapidly than in *T. aculeatum* which does not have major workers.

#### Recruitment Rate Models

Understanding the recruitment behavior of social insects is crucial in understanding the origin of their ecological success. Our study reveals the collective aspect of prey capture in Afro-tropical ant species and documents some variability in their recruitment behaviors. We identified the following patterns and their correlation with different levels of adaptation for arboreal foraging: (1)

individuals move stochastically (randomly), (2) collectively recruitment may be stochastic, (3) group recruitment strategies may be constrained by the number of available recruits, or (4) group recruitment strategies may be constrained due to a very large potential number of recruits, (Lachaud et al. 1984; Deneubourg et al. 1987; Sumpter and Pratt 2003).

We found that *M. opaciventris* workers adopted a fundamentally stochastic individual strategy when confronted with small prey size and stochastic collective (tandem) recruitment when confronted with large prey. The evidence of these behaviors is well illustrated by their recruitment rate models, which tend to follow a linear trend based on a theoretical model (Sumpter and Pratt 2003), with nestmates attracted at short range, exhibiting low coordination during prey retrieval. In this study, very little recruitment of workers has been found for *P. conradti* regardless of prey size. During a field survey in a cocoa agroforestry system, *P. conradti* workers were observed foraging alone and were generally found on only a few trees (Tadu 2016). These observations confirm the influence of the experimental apparatus on the recruitment behavior of this species, due to the settling of workers on the foraging arena and the proximity of the foraging arena to the nest. In fact, after reversing the control and foraging arenas, the number of workers in the new foraging arena was less than the number in the old foraging arena, suggesting that

workers can search a location regardless of a presence or absence of prey. This idea has been supported by a study of the ant *Cataglyphis florica*, widely thought to have lost its recruitment capacity, but which, when confronted with a large prey near its nest, was able to solicit the help of nestmates to carry it cooperatively (Amor et al. 2010). Based on this example, we confirm that nestmate recruitment in *P. conradti* is doubtful, a conclusion that is further supported by the solitary foraging behavior of this species (Levieux 1976; Dejean 2011), where single workers retrieve prey independently regardless of their size (Dejean 2011). The food recruitment behaviors for most ponerine ants have not been established with the exception of *Platythyrea modesta* (Djiéto-Lordon et al. 2001a). For several ponerine species, including *Neoponera villosa*, *N. apicalis* and *Ectatoma ruidum*, stochastic and “tandem-running” recruitment was observed during colony migration but alimentary recruitment was not observed (Lachaud et al. 1984).

In this study, we observed a group recruitment strategy, with a small group of workers being recruited when confronted with a small prey and unlimited group size recruited when confronted with a large prey, as was shown in *T. aculeatum*, *O. longinoda*, *Crematogaster* sp. and *C. clariventris*, these findings agree with theoretical models (Sumpter and Pratt 2003). When a scout discovers a food source, the ant returns to the nest, generally laying a chemical trail (Deneubourg et al. 1987), a process that has been observed for *T. aculeatum*, *O. longinoda*, *Crematogaster* sp. and *C. clariventris* species. For instance, *O. longinoda* will deposit a pheromone trail secreted by rectal and sternal glands (Hölldobler and Wilson 1976). Workers recruit nestmates for short- and long-range recruitment with tactile and chemical signals (Hölldobler and Wilson 1976; Hölldobler 1990; Lachaud and Dejean 1994; Viana 1996). The same strategies have also been observed in *T. aculeatum* (Djiéto-Lordon et al. 2001c) and *Crematogaster* sp. (Richard et al. 2001).

For *Crematogaster* sp. and *C. clariventris*, foragers that have found prey raise their gasters and secrete a white-colored alerting pheromone while returning to the nest. Along this trail, we observed antennal palpation with other nestmates and the number of workers at the prey's location subsequently increased rapidly.

In the experiments using leaves as arenas, we observed the solitary foragers of *T. aculeatum*, and *O. longinoda* vibrating leaves upon detecting and

seizing prey. This leaf vibration signaled to nestmates on the tree, who searched actively for the origin of this signal, and then used pheromone trails after the forager had been located. Thus, the orientation of workers became more precise over time and the number of workers increased rapidly.

The recruitment model that best fit the recruitment behavior of *O. longinoda*, one of the most highly specialized arboreal ants (Hölldobler 1990), was surprising. *Oecophylla longinoda* workers have individual strategy when encountering small prey, a strategy also observed in *Ectatoma ruidum* by Lachaud et al. (1984). Such a limited group size has also been found in some specialized arboreal ant species when workers were confronted with a large prey.

In summary, ant species have adopted different recruitment strategies linked to their degree of arboreal adaptation. Ground-dwelling species with arboreal habits and primitive arboreal ants have similar strategies, which include stochastic individual and stochastic collective strategies. *Tetramorium aculeatum*, *Crematogaster* sp., and *C. clariventris*, meanwhile, display a group strategy recruitment with unlimited group size and a limited group size for *O. longinoda*. Of the six studied species *T. aculeatum* had the highest potential recruitment during prey capture, a trait that might be confused with their territorial behavior. In fact, intrusion of other dominant ant species in a territory controlled by *T. aculeatum*, induces a recruitment response similar to the presence of prey. It seems that, in dominant arboreal ant, recruitment behavior is the first stage in territorial defense. *Oecophylla longinoda*, known as a well-adapted arboreal ant species, has developed a recruitment behavior intermediate between that of primitive arboreal ants and specialized arboreal ants.

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## References

- Amor F, Ortega P, Cerda X et al (2010) Cooperative prey-retrieving in the ant *Cataglyphis florica*: an unusual short-distance recruitment. *Ins Soc* 57:91–94
- Bonabeau E, Theraulaz G, Deneubourg JL (1998) Group and mass recruitment in ant colonies the influence of contact rates. *J Theo Biol* 195:157–166

- Dejean A (1988) Prey capture by *Camponotus maculatus* (Formicidae-Formicinae). Biol Behav 13:97–115
- Dejean A (1990) Prey capture strategy of the african weaver ant. Westview Press Boulder, Colorado
- Dejean A, Moreau CS, Uzac P et al (2007) The predatory behavior of *Pheidole megacephala*. C R Biol 330:701–709
- Dejean A (2011) Prey capture behavior in an arboreal African ponerine ant. PLoS One 6:1–7
- Deneubourg JL, Aron S, Goss S et al (1987) Error, communication and learning in ant societies. E J Opera Res 30:168–172
- Djiéto-Lordon C, Orivel J, Dejean A (2001a) Consuming large prey on the spot: the case of the arboreal foraging ponerine ant *Platythyrea modesta* (Hymenoptera, Formicidae). Ins Soc 48:324–326
- Djiéto-Lordon C, Orivel J, Dejean A (2001b) Predatory behavior of the African ponerine ant *Platythyrea modesta* (Hymenoptera: Formicidae). Sociobiology 38:1–13
- Djiéto-Lordon C, Richard FJ, Owona C et al (2001c) The predatory behavior of the dominant arboreal ant species *Tetramorium aculeatum* (Hymenoptera: Formicidae). Sociobiology 38:1–11
- Hölldobler B, Wilson ED (1976) Weaver ants: social establishment and maintenance of territory. Science 195: 900–902
- Hölldobler B, Wilson ED (1990) The ants. The Belknap of Harvard University Press Cambridge, Massachusetts
- Kenne M, Schatz B, Durand JL et al (2000) Hunting strategy of a generalist ant species proposed as biological control agent against termites. Ent Exp Appl 94:31–40
- Kenne M, Schatz B, Fénéron R et al (2001) Hunting efficacy of workers from incipient colonies in the myrmicine ant *Myrmicaria opaciventris* (Formicidae, Myrmicinae). Sociobiology 37:121–134
- Lachaud JP, Dejean A (1994) Predatory behaviour of seed-eating ant: *Brachyponera senaarensis*. Ent Exp Appl 72:145–155
- Lachaud JP, Fresneau D, García-Pérez J (1984) Etudes des stratégies d'approvisionnement chez 3 espèces de fourmis Ponerines (Hymenoptera, Formicidae). Folia Ent Mexicana 61:159–177
- Levieux J (1976) La nutrition des fourmis tropicales. IV cycle d'activité et regime alimentaire de *Platythyrea conradti* Emery (Hymenoptera Formicidae, Ponerinae). Annales de l'Université d'Abidjan 5:353–365
- Liefke C, Hölldobler B, Maschwitz U (2001) Recruitment behavior in the ant genus *polyrhachis* (Hymenoptera, Formicidae). J Ins Behav 14:637–657
- Orivel J (2000) L'adaptation a la vie arboricole de la fourmi *Pachycondyla goeldii* (Hymenoptera : Ponerinae). Université de Paris XIII, Thèse de Doctorat
- Passera L, Aron S (2005) Les fourmis: comportement, organisation sociale et évolution. Les presses scientifiques du CNRS, Ottawa, Canada
- Pie MR (2004) Foraging ecology and behaviour of the ponerine ant *Ectatomma opaciventre* Roger in a Brazilian savannah. J Nat Hist 38:717–729
- Planque R, van den Berg JB, Franks NR (2010) Recruitment strategies and colony size in ants. PLoS One 5(8):1–8
- Richard FJ, Fabre A, Dejean A (2001) Predatory behaviour in dominant arboreal ant species: the case of *Crematogaster* sp. (Hymenoptera: Formicidae). J Ins Behav 14:271–282
- Rousson L (2002) Etude et modélisation du comportement prédateur de cinq espèces de fourmis arboricoles néotropicales du genre *Azteca* (Fam. Dolichoderinae). Mémoire de D.E.A, Université Paul Sabatier, Toulouse III
- Schatz B, Suzzoni JP, Corbara B et al (2001) Selection and capture of prey in the African ponerine *Plectroctena minor* (Hymenoptera: Formicidae). Acta Oecol 22:55–60
- Sumpter DJT, Pratt SC (2003) A modelling framework for understanding social insect foraging. Behav Ecol Sociobiology 53: 131–144
- Tadu Z (2016) Organisation spatiale des communautés de fourmis arboricoles tropicales: rôle structurant et importance du comportement prédateur. Thèse de Doctorat, Université de Yaounde I, Cameroun
- Tadu, Z., C. Djiéto-Lordon, Yede et al. (2014a) Ant mosaics in cocoa agroforestry systems of southern Cameroon: influence of shade on occurrence and spatial distribution of dominant ants. Agroforestry System :1067–1079
- Tadu Z, Djiéto-Lordon C, Yede et al (2014b) Ant diversity in different cocoa agroforest habitats in the Centre region of Cameroon. Afri Entomol 22:388–404
- Viana AM (1996) La reconnaissance coloniale du couvain et du champignon chez la fourmi champignoniste (*Acromyrmex subteraneus subteraneus*). Université Paris XIII, Thèse Doctorat

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