Foraging activity and diet of the ant, *Anoplolepis tenella* Santschi (Hymenoptera: Formicidae), in southern Cameroon

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Anoplolepis tenella is a ground-nesting ant of the tropical forest zone of Central Africa, commonly associated with African root and tuber scale, *Stictococcus vayssierei* Richard, an emerging cassava pest. Understanding the ant's foraging activity and diet breadth is an important step towards developing control measures against *S. vayssierei.* The present study was carried out in cassava fields in Awae II and Mengomo, southern Cameroon, during the short wet and dry seasons of 2006. Foraging activity of *A. tenella* was continuous during the circadian cycle and showed four peaks of activity; two during the day and two at night at both localities and in both seasons. Activity was greater at night than during the day, and greater in the wet than in the dry season. During the day, activity was significantly positively correlated with relative humidity, and negatively correlated with air temperature. During the night, it was positively correlated with relative humidity but not with air temperature at both localities. The diet of *A. tenella* consisted of solid items, mainly live prey (63.3 %) but also dead prey (36.7 %) and sugary secretions collected from various hemipterans. *Stictococcus vayssierei* was the most commonly tended hemipteran (98.5 %). Continuous foraging activity, omnivory and especially association with hemipterans are factors that favour the numerical dominance of *A. tenella* in cassava fields.

Key words: *Stictococcus vayssierei,* Stictococcidae, Hemiptera, Hymenoptera, Formicidae trophobiosis.

INTRODUCTION

Foraging activity of ants can be affected by many environmental factors including predation, interspecific competition, density and renewal rate of food, availability of foragers, moisture and temperature (Torres 1984; Hölldobler & Wilson 1990; Cerdá *et al.* 1998; Holway 1998; Kaspari & Weiser 2000; Hahn & Wheeler 2002; Menke & Holway 2006). Ants consume very diverse solid or liquid food items including animal and plant material. Some ant species are active hunters of mobile prey or feed directly on plant parts, including fruits, leaves and seeds, while others are opportunistic scavengers of dead animals and wastes, or feed indirectly on plant sap by harvesting exudates from extra-floral nectaries and their hemipteran counterparts (Carroll & Janzen 1973; Buckley 1987; Sudd 1987; Delabie 2001). Ant–hemipteran mutualism may be beneficial to the host plant in cases where ants attack other herbivores (Way & Khoo 1992; Vandermeer *et al.* 2002; Van Mele *et al.* 2004; Peng & Christian 2006) but in most cases it is harmful because it always leads to the proliferation of mutualistic partners. For instance, the presence of invasive ants is frequently associated with local increase in hemipteran abundance (Helm & Vinson 2002; Holway *et al.* 2002; Abbott *et al.* 2007).

The genus *Anoplolepis* Santschi is most diversified in Africa, which is most likely its native range (Bolton 1995). It is principally known through the pantropical species *A. gracilipes* (Smith), which has been widely introduced across the subtropics and tropics (Haines & Haines 1978; Hill *et al.* 2003; O'Dowd *et al.* 2003), and *A. custodiens* (Smith), which is a major predator of indigenous insects in South Africa (Steyn 1954; Löhr 1992), and can be highly invasive in citrus and guava orchards and vineyards (Addison & Samways 2000; Addison & Samways 2006). *Anoplolepis tenella* (Santschi) is a ground-nesting species of the tropical forest zone of Central Africa commonly associated with African root and tuber scale, *Stictococcus vayssierei* Richard (Dejean & Matile-Ferrero 1996; Hanna *et al.*, unpubl. data). *Stictococcus vayssierei* is the only

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known underground species of the Afrotropical scale insect family Stictococcidae. Recent research has highlighted its increased pest status on several root and tuber crops – especially on cassava – in the Congo Basin (Dejean & Matile-Ferrero 1996; Ambe *et al.* 1999; Ngeve 2003; Hanna *et al.*, unpubl. data). Current research efforts focus on understanding factors responsible for this increased pest status. While *A. tenella* is considered one of these factors (Dejean & Matile-Ferrero 1996; Hanna *et al.*, unpubl. data), very little is known about its biology. Dejean & Matile-Ferrero (1996) reported that *A. tenella* exploits different species of homopterans living on the roots and the crown of diverse plants of the understory where workers capture all kind of prey both dead and alive, especially termites. However, this was not fully documented. The main objective of this study was to investigate *A. tenella* foraging activity and generate a more complete picture of its diet composition. This baseline information is important for developing management options against *S. vayssierei.*

MATERIAL AND METHODS

Study sites

Field studies were carried out from May to August 2006 at two localities in southern Cameroon; Awae II (03°54′30″N; 11°25′58″E) and Mengomo (02°34′37″N; 11°02′01″E) situated within the humid forest zone. Rainfall pattern is bimodal with a short wet season from mid-March to early July followed with a short dry season from July to the end of August, and the major wet season from September to mid-November is followed with a long dry season. Average annual rainfall is about 1692 mm in Awae II and 2500 mm in Mengomo. Mean air temperature ranges from 19.2 to 28.6 °C.

Daily foraging activity

In previous studies *A. tenella* nests were found in greater abundance in cassava fields than fallow and forest vegetation and workers were observed foraging mostly on the soil surface with no obvious sign of trails or paths resulting from digging (Fotso Kuate *et al.* 2006). Data were collected in two cassava fields (≈ 0.25 ha) at each locality. Ten plots of 1 m^2 were delineated in each field randomly. In each plot, the number of workers foraging on the soil surface was counted for five minutes every hour for 24 hours. Night counting was done using a 3 V lantern. During the first round of sampling in the wet season, soil temperature was taken every hour at 15 cm below the ground surface using a Barnant Thermocouple thermometer, model 600–1010 (temperature range –250 to 1372 °C). During the second round of sampling in the dry season, air temperature and relative humidity were taken using a Thermo-hygrometer (temperature range 0 to 50 °C; humidity range 2 to 98 %).

Diet composition

During the counting exercise, visible food items were collected from workers and preserved in 50 % alcohol in plastic vials for further identification. Workers carrying very small items may have escaped our attention, especially at night. Those carrying liquids were also difficult to distinguish and were not considered. These data were complemented with observations done during ecological surveys at various localities in southern Cameroon from April 2002 to August 2006 (Hanna *et al.*, unpubl. data), during which randomly selected known host plants of *S. vayssierei* were dug up and their roots system checked for the presence of both *S. vayssierei* and *A. tenella.* Foraging workers found with solid food items or tending hemiptera on plant parts above the ground were also recorded. A single plant or solid food item was considered as a sample unit (case or event). Solids items were collected as above. Hemipteran insects tended by *A. tenella* workers and their host plants were collected and identified. Insects were identified and voucher specimens were deposited in the Insect Museum of the International Institute of Tropical Agriculture, Cameroon Station.

Statistical analysis

At each locality, the mean number of workers counted in 20 plots from the two sites was considered to represent the foraging activity for a given hour. Mean number of workers counted from 07:00 to 18:00 and from 19:00 to 06:00 were considered as day and night foraging activities, respectively. Thus, 240 counts (20 × 12) were considered for the day and another 240 counts for the night. Day and night counts were kept separate while comparing wet and dry season results. Comparison of foraging activity levels between night and day, and wet and dry seasons were analysed using ANOVA. Percentages of solid foods were compared between night and day and between seasons by

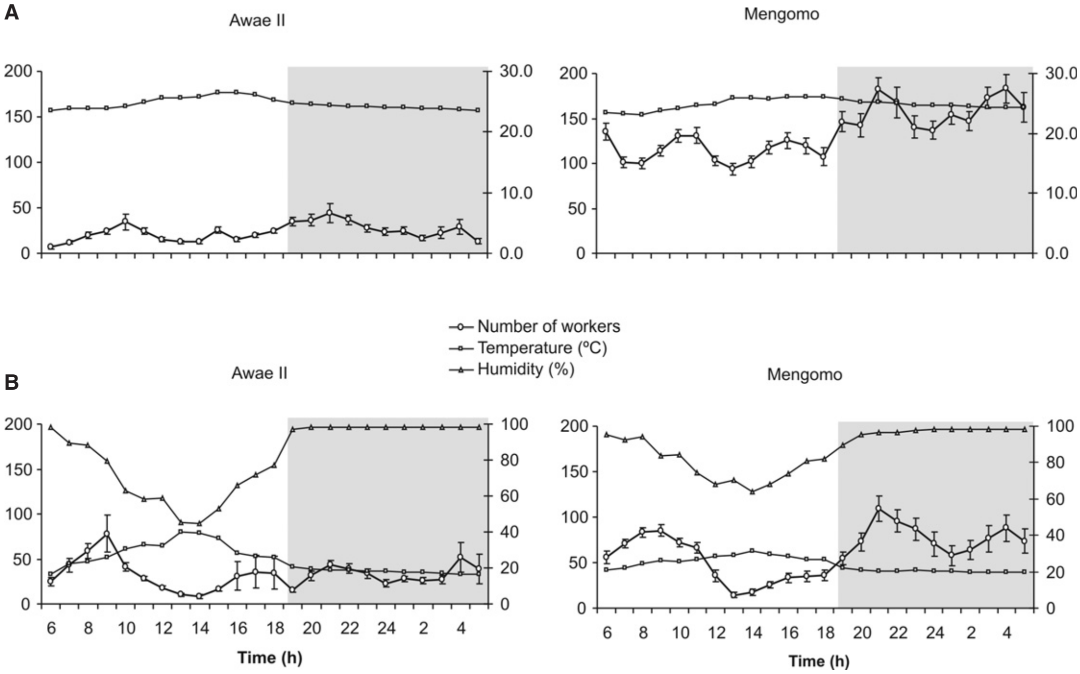

Fig. 1. Mean number of workers (± standard deviation) of *Anoplolepis tenella* recorded foraging daily at Awae II and Mengomo (southern Cameroon). Foraging activity was recorded on randomly chosen days during the short wet season (**A**) and the short dry season (**B**). Soil temperature and air humidity are also shown. Shaded area = night.

means of Fisher's exact test. Air or soil temperature and air relative humidity were correlated with ant activity using Pearson's correlation coefficient. Statistical analysis was performed using the Generalized Linear Model (GLM) of the SAS software version 9.1.

RESULTS

Daily foraging activity

The same pattern of foraging by *A. tenella* occurred during day and night in both Awae II and Mengomo in both seasons (Fig. 1), and showed two peaks of activity in each. The first diurnal peak was between 08:00 and 10:00 and the second between 15:00 and 17:00. Nocturnal peaks were recorded between 19:00 and 21:00 and 03:00 and 04:00 (Fig. 1). Foraging activity was not significantly correlated with soil temperature at either site (Table 1), but was positively correlated with air relative humidity and negatively correlated with air temperature at both sites (Table 1). More ants foraged on the ground during the wet than the dry season in both sites (Table 2). A maximum of 113.7 ± 4.1 (mean ± S.E.) workers/m^2 was recorded in Mengomo during the wet season (Table 2). A positive significant correlation was found between worker activity and the soil temperature during the rainy season at Awae II but not Mengomo, and between worker activity and air temperature at both sites in the dry season. Foraging activity was positively correlated with air relative humidity at both sites (Table 1). Except at Awae II during the dry season, more ants foraged at night than during the day (Table 2). The maximum mean number of 157.7 ± 4.1 (mean ± S.E.) workers per m^2 was recorded in Mengomo during the wet season (Table 2).

Composition of diet

The solid food items collected from workers (Table 3) consisted of live prey, mainly termites (*Nasutitermes latifrons*) (57.9 %) and earthworms (3.5 %), and dead animals (22.1 %). Arthropods represented 80.1 % of the items, including dead gynes of *A. tenella, Myrmicaria opaciventris* Emery, *Pheidole* sp., *Dorylus* sp. and *Tetraponera* sp. Animal parts, mostly insect wings and legs, were carried to the nest by one to three workers. Workers were recruited *en mass* to larger prey such as earth-

Table 1. Correlation between *Anoplolepis tenella* activity and air temperature, air humidity (in the dry season) and soil temperature (in the wet season). Activity is measured as the number of individual ants counted in a 1 m^2 quadrat in five minutes every hour at 20 randomly selected sites. Plot temperature and humidity was also measured. Average ant count per hour was correlated with associated average temperature and humidity. RH = relative humidity.

Localities	Season	Air temperature		RH		Soil temperature	
		Day	Night	Day	Night	Day	Night
Awae II	Dry	–0.58*	–0.45	0.63*	0.55*	–	–
Mengomo		–0.70*	–0.32	0.73*	0.39*	–	–
Awae II	Wet	–	–	–	–	–0.02	0.78*
Mengomo		–	–	–	–	–0.08	–0.24

*Statistically significant correlation.

worms and grasshoppers e.g. *Zonocerus variegatus* (L.). Plant materials (dry leaf particles) were carried by lone workers. Significantly more food items were retrieved during the day than at night ($\chi^2 = 54.2$, d.f. = 12, $P < 0.0001$), and also during the wet than the dry season ($\chi^2 = 47.5$, d.f. = 12, $P < 0.0001$). Unidentified solid and pasty substances were also observed (Table 2).

During ecological surveys, *A. tenella* workers were observed on 67 occasions (8 %, $n = 832$) carrying solid food items, including arthropod remains, but mostly gathering honeydew from various families of hemipterans (92 %, $n = 832$) attacking aerial or underground parts of various plants species, including economically important species (Table 4). *Stictococcus vayssierei* was the most frequently tended honeydew producer (98.5 %, $n = 754$), mainly on underground parts of root and tuber crops, where *A. tenella* built its nests. Tending activity of *A. tenella* workers on hemipterans above ground was noted on only 11 occasions (1.5 %, $n = 754$, Table 4) and they were seldom observed climbing on plants to tend extra-floral nectaries.

DISCUSSION

The foraging activity of *A. tenella* was continuous during the 24-hour period, with a daily pattern consisting of four peaks that were, interestingly, the same in both seasons and both localities. These results corroborate those of Abbott (2005) on the congeneric tramp species, *A. gracilipes,* on Christmas Island, which also maintained continu-

Table 2. Mean number of *Anoplolepis tenella* workers foraging in 1 m^2 per five minutes during the day and at night recorded in Awae II and Mengomo (southern Cameroon) during the short wet and short dry season of 2006. Mean numbers are compared between night and day, raining season and dry season using ANOVA. *F*-values and probabilities are included. *N* = total number of counting series; S.E. = standard error.

Locality	Season	*N*	Day Mean ± S.E.	Night Mean ± S.E.	*F* (1,48)	*P*
Awae II	Wet	240	18.9 ± 1.1	28.2 ± 1.8	20.9	<0.0001*
	Dry	240	32.9 ± 3.2	32.4 ± 2.4	0.02	0.89
Mengomo	Wet	240	113.9 ± 2.2	157.7 ± 4.1	97.1	<0.0001*
	Dry	240	48.4 ± 2.1	77.3 ± 3.8	47.9	<0.0001*

Comparison wet season *vs* dry season

Locality	Time	*F* (1,478)	*P*
Awae II	Day	17.9	<0.0001*
	Night	1.8	0.17
Mengomo	Day	470.6	<0.0001*
	Night	210.5	<0.0001*

*Statistically significant differences.

Table 3. List of solid food items collected by from *Anoplolepis tenella* workers. Observations were made in 960 plots (1 × 1 m) during four days and 24 hours every day in Awae II and Mengomo (southern Cameroon).

Food items		Wet		Dry		Total	
		n	%	*n*	%	*n*	%
Animal fragments	–	11.0	5.8	15.0	12.3	26.0	8.4
Annelids	Earthworms	9.0	4.8	2.0	1.6	11.0	3.5
Arthropods	Ants	6.0	3.2	13.0	10.7	19.0	6.1
	Caterpillars	0.0	0.0	1.0	0.8	1.0	0.3
	Cockroaches	3.0	1.6	0.0	0.0	3.0	1.0
	Crickets	17.0	9.0	3.0	2.5	20.0	6.4
	Grasshoppers	10.0	5.3	1.0	0.8	11.0	3.5
	Millipedes	0.0	0.0	13.0	10.7	13.0	4.2
	Nasutitermes latifrons	114.0	60.3	66.0	54.1	180.0	57.9
	Spiders	2.0	1.1	0.0	0.0	2.0	0.6
Plant matter	–	17.0	9.0	8.0	6.6	25.0	8.0
Total		189.0	100.0	122.0	100.0	311.0	100.0

ous activity even if no clear pattern was observed during a 24-hour period. In the Solomon Islands, *A. gracilipes* was also reported to be more active near dusk, when relative humidity rose and air temperature was still relatively high (Greenslade 1972). During the day, *A. tenella* activity was correlated negatively with air temperature and positively with relative humidity. As a consequence this species was more active during the night when weather parameters were more stable and more during the wet than the dry season. As in others ants, daily and seasonal variation in forag-

Table 4. List of hemipterans tended by *Anoplolepis tenella* workers and their host plants observed in southern Cameroon during ecological surveys from 2002 to 2006. Percentages are based on 754 cases of field observations. A single plant was considered as a sample unit (case).

Hemiptera families	Species	Host plant families	Species	Plant part*	
				A (%)	B (%)
Stictococcidae	*Stictococcus vayssierei*	Euphorbiaceae	*Manihot esculenta***	0.0	85.8
		Araceae	*Xanthosoma sagittifolium***	0.0	6.1
			*Colocasia esculenta***	0.0	1.3
		Papilionaceae	*Arachis hypogaea***	0.0	2.1
		Musaceae	*Musa* sp.**	0.0	0.3
		Commelinaceae	*Palisota hirsuta*	0.0	0.5
		Palmaceae	*Eleais guineensis***	0.0	0.3
		Asteraceae	*Chomolaena odorata*	0.0	0.5
		Costaceae	*Costus afer*	0.1	0.5
		Zingiberaceae	*Aframomum danielli*	0.0	0.8
		Cucurbitaceae	*Cucumis melo***	0.1	0.0
	Stictococcus sp.	Annonaceae	*Annona muricata***	0.1	0.0
	Parastictococcus sp.	Annonaceae	*Annona muricata***	0.1	0.0
Aphididae	*Aphis* sp.	Asteraceae	*Chomolaena odorata*	0.4	0.0
Membracidae	*Monocentrus* sp.	Tiliaceae	*Triumphetta cordifolia*	0.1	0.0
Pseudococcidae	*Saccharicoccus saccharis*	Gramineae	*Saccharum officinarum***	0.7	0.0
Total				1.7	98.3

*A = stems, leaves and fruits, B = roots and tubers.

**Economically important plant species.

ing activity were related both to temperature and moisture (Lévieux 1983; Torres 1984). Data presented here on *A. tenella* are very useful for management using bait, which would be selectively placed during period of high activity to reduce effects on non-target species. Increased foraging activity at night and during the wet season can be explained by the fact that *A. tenella* is a forest ant favouring sheltered sites (Dejean & Matile-Ferrero 1996). Expansion by *A. tenella* may be limited by moisture as are argentine ants in coastal California, which invade riparian areas but not adjacent drier upland habitat (Ward 1987; Holway 1998; Menke & Holway 2006). In fact, in tropical ecosystems, increases in humidity are often associated with increased insect abundance and activity. Increased ant activity in wet seasons and habitats may reflect colonies tracking food availability at reduced risk of desiccation (Kaspari & Weiser 2000). In the sympatric species, *Myrmicaria opaciventris,* in which honeydew collection and activities in trenches were also found to be continuous during the circadian cycle, hunting activity was most intense during the day in the wet season and did not vary during the dry season, when it was very low (Kenne & Dejean 1999). *Myrmicaria opaciventris* preferred open areas and fed on human wastes; *A. tenella* was seldom observed in this study.

Many studies of ant activity rhythms have been conducted at the entrance of the nest (Gordon 2002) or on trails or trenches (Lévieux 1983; Kenne & Dejean 1999), but as in *A. gracilipes* on Christmas Island, *A. tenella* rarely used observable trails (Fotso Kuate *et al.* 2006). Thus, a plot-based counting method was used and was more appropriate for the estimation of densities of ant foraging on the ground (Abbott 2005). Based on the highest mean number (157.7) of ants counted in 1 m^2 during this study, *A. tenella* density in cassava fields could reach a maximum of ≈1.6 million ants/ha, which is low compared to reported densities of *A. gracilipes* of 5 million ants/ha in the Seychelles (Haines & Haines 1978) and 20 million on Christmas Island (Abbott 2005), but is higher than that of *M. opaciventris,* which reached a density of 72 400 foraging individuals per hectare (Kenne & Dejean 1999).

Anoplolepis tenella, a ground-nesting ant species, has developed a close association with *S. vayssierei,* from which it harvests considerable amount of honeydew. Tending of other hemipteran species is rather opportunistic. *Myrmicaria opaciventris* was reported to exploit *S. vayssierei*, but less frequently and maintaining fewer individuals on cassava cuttings than *A. tenella* (Dejean & Matile Ferrero 1996). Since both *A. tenella* and *S. vayssierei* are native, one can speculate that they should have co-evolved with native plants and that the introduction of cassava and the establishment of fields after forest clearance offer additional resource opportunity for the associated insects. Much more research is needed to understand the relationship between *A. tenella* and *S. vayssierei,* especially the ant's mechanism to monopolize resources produced by *S. vayssierei*. Since success of many invasive ant species has been associated with the utilization of hemipteran honeydew (Helms & Vinson 2002), association with *S. vayssierei* might contribute to the numerical dominance of *A. tenella* in cassava fields.

Our data on diet are in line with those of Dejean & Matile-Ferrero (1996), who reported that *A. tenella* workers may forage on the ground, where they actively capture live termites and opportunistically feed on dead animals. The mechanism involved in predation by this stingless ant, however, is still to be elucidated. Predation may be by biting and the use of formic acid like formicine species. While termites are captured by individual workers, a mass recruitment strategy is used for large prey.

Colonization of new environments by invasive ant species is facilitated by several useful features, including unicoloniality, polygyny, omnivory and trophobiosis, continuous activity and mass recruitment (Holway *et al.* 2002). The data presented above indicated that in its native range, *A. tenella* is likely to have some of these features which allow it to dominate some areas disturbed by agriculture. Indeed, studies on *A. tenella* nest distribution and density indicated that they are more abundant in cassava fields than fallows and forests (Fotso Kuate *et al.* 2006), but the colony structure and composition of *A. tenella* is still to be determined. In South Africa, *A. custodiens* was also reported to have the ability to spread and dominate a variety of open-canopy subtropical habitats (Addison & Samways 2006).

Most research work to identify common characteristics of invasive species have been conducted in their introduced range rather than in their native range (see Kenne & Dejean 1999; Holway *et al.* 2002; Fournier *et al.* 2005; Addison & Samways

2006). Our data on invasive potential of *A. tenella* in its native range contribute to filling this information gap. Invasive potential in their native ranges was also demonstrated for *M. opaciventris* (Kenne & Dejean 1999) and *A. custodiens* (Addison & Samways 2006). Since invasive features are also found in *A. custodiens* (Addison & Samways 2006) and *A. gracilipes* (Abbott 2005), they probably occur throughout the genus.

Given the mutual benefits from close association between *A. tenella* and *S. vayssierei*, one strategy to reduce their population will be to disrupt their interaction. A disruption method targeting ants which are more active and responsible for the scale dispersal may be more efficient. Because it has fewer environmental effects, baiting seems to be an appropriate method for ant control (Haines & Haines 1979; Williams 1983; Steyn 1954). Amdro is one of the best known ant baits developed for control of the fire ant, *Solenopsis invicta* Buren, in the U.S.A. (Apperson *et al.* 1984; Williams, 1983) and tested in South Africa citrus against *Pheidole megacephala* (Fabricius) and *A. custodiens* (Steyn 1954; Samways 1985). We suggest that this bait be tested against *A. tenella* in southern Cameroon.

In conclusion, *A. tenella* forages day and night, captures live termites and earthworms and scavenges dead invertebrates using mass recruitment for large prey. This protein part of the diet is complementary to the important carbohydrate exudates obtained from the subterranean scale insect, *S. vayssierei*, with which it has developed a close association. Continuous foraging activity, omnivory and especially trophobiotic association with *S. vayssierei* are some factors that account for the numerical dominance of *A. tenella* in cassava fields.

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