



Impact of natural parasitism by two eucharitid wasps on a potential biocontrol agent ant in southeastern Mexico

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ABSTRACT

Eucharitids are specialized parasitoids of ants. The biology, life cycle and chemical ecology are known for a number of species, but the study of the impact of eucharitid wasps upon their ant hosts has been seldom addressed. Here, we determine the prevalence of the parasitism of two sympatric *Kapala* species upon a population of the neotropical ant *Ectatomma ruidum*, along a 12-month sampling period. Adult and immature parasitoids were present in the nests all year round, and several cases of superparasitism were observed. Parasitism varied strongly among the nests for any collecting date and among collecting dates, but the prevalence of *Kapala* parasitoids increased significantly during the rainy season, and the probability for a nest of being parasitized was positively correlated with colony size, particularly with cocoon number. At the population scale, more than 28% of all *E. ruidum* pupae produced during the ant reproductive and dispersal period (June) were infested. Our results are discussed from the point of view of the impact of these parasitoids on the colonies of *E. ruidum*, a potential biocontrol agent in coffee and cocoa plantations in southeastern Mexico.

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1. Introduction

Ants are among the most common predators of arthropod pests in various agroecosystems, and they have a marked impact on the terrestrial ecosystems in which they live (Kajak et al., 1972; Hölldobler and Wilson, 1990). Due to their stabilizing and/or regulating influence on pest insect populations, these predators are of particular interest for their potential in conservation biological control (Carroll and Risch, 1990; Way and Khoo, 1992). Their influence in tropical agroecosystems of economic importance (like coffee, cocoa, sugar cane, maize or mango) remains poorly studied, even though several species are known to be very common in these habitats and considered important in biological control (Perfecto, 1991; Ibarra-Núñez et al., 2001; Peng and Christian, 2006).

As an important food resource or due to the protection provided by their nests, social insect colonies constitute attractive targets for a large range of parasites (for a review see Wilson, 1971; Kistner, 1979, 1982; Hölldobler and Wilson, 1990). As a consequence, numerous arthropods have established facultative or obligatory symbiotic relationships with these colonies, exhibiting variable degrees of integration into the host society ranging from simple predation (the “synechtes” of Wasmann, 1890, 1894) to true

sympilic associations involving mutual benefits (highly integrated arthropods are fed and cared for as members of the colony). This is particularly well illustrated in the case of myrmecophiles, that is, arthropods associated in different ways with ants, which include a great diversity of Diptera, Hymenoptera, Coleoptera, Hemiptera, Thysanoptera and Strepsiptera (Hölldobler and Wilson, 1990; Passera and Aron, 2005).

Few groups of parasitoids have been able to adapt to ants as hosts, and only some dipteran, strepsipteran and hymenopteran species are true parasitoids of this taxon. Such species exhibit different kinds of relationships according to both the species and the stage of development of the parasitoid, ranging from simple endoparasitism as in strepsipterans (Kathirithamby and Hugues, 2002; Hugues et al., 2003) or ectoparasitism as in phorid flies (Feener and Brown, 1997) to temporal integration through chemical camouflage as in recently emerged eucharitid wasps (Vander Meer et al., 1989; Lachaud et al., 1998; Howard et al., 2001) or even to sophisticated symphily as in some other eucharitid (Wheeler, 1907; Mann, 1914; Wojcik, 1989) and diapiiid (Lachaud, 1981; Lachaud and Passera, 1982; Loíacono, 1987; Loíacono et al., 2000; Ramos-Lacau et al., 2007) wasps. Most ant parasitoids have gained interest from researchers due to their potential as biocontrol agents. In particular most species of phorid flies of the genus *Pseudacteon* (Calcaterra et al., 2005; Morrison and Porter, 2005) and some species of eucharitid wasps of the genus *Orasema* (Wojcik et al., 1987; Heraty et al., 1993; Heraty, 1994a) which are both parasitoids of fire ants in the New World.

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The family Eucharitidae *sensu stricto* (Hymenoptera: Chalcidoidea) is composed of three subfamilies (Oraseminae, Eucharitinae, and the Indo-Pacific Gollumiellinae) and is by far the largest and most diverse group of hymenopteran parasitoids associated with eusocial insects (Heraty, 2002; Heraty et al., 2004). All species of Eucharitidae for which the host is known are specialized parasitoids of immature stages of ants (Clausen, 1940a,b, 1941; Heraty, 1985, 2000), and the hosts of most genera are restricted to a few closely related genera of ants (Heraty, 1990, but see Pérez-Lachaud et al., 2006). Distributed worldwide, the family is most abundant and speciose in the tropics (Heraty, 2000). Fifty-three genera and more than 413 species are currently described (Heraty, 2002).

Eucharitids have a modified life cycle (Wheeler and Wheeler, 1937; Clausen, 1941; Heraty and Darling, 1984; Heraty, 1994b). Females oviposit away from ants, in or on plant tissue; the active, heavily sclerotized, first-instar larva (planidium) gains access to the host nest, presumably by phoresis, attaching to passing foraging ants or to insect prey later consumed by ants. Immatures develop as larval–pupal koinobionts: first-instars attach externally to ant larvae, begin feeding on prepupae and complete their development on the ant pupae (Clausen, 1940a, 1941; Johnson et al., 1986; Heraty, 1994b, 2000; Pérez-Lachaud et al., 2006). The complete life cycle has been described for a few species, but the biology inside the ant nest is poorly known, and, though the study of the potential impact of eucharitids on their ant hosts, at the population scale, has been addressed on a few occasions, the results are contrasting. Little or no control was reported for the temperate species *Pseudometagea schwarzii* (Ashmead) against populations of *Lasius neoniger* Emery (Ayre, 1962), and a possible potential for biological control of ant pests has been considered only for some *Orasema* species: *O. aenea* Gahan, *O. rapo* (Walker), and *O. xanthopus* (Cameron) parasitizing *Solenopsis invicta* Buren (Williams, 1980; Vander Meer et al., 1989; Wojcik, 1990; Heraty et al., 1993), *O. salebrosa* Heraty and *O. simplex* Heraty parasitizing *S. richteri* Forel (Heraty et al., 1993), and *O. minutissima* Howard parasitizing *Wasmannia auropunctata* Mayr (Mann, 1918; Heraty, 1994a). However, until now, a real study of the impact of eucharitids upon their ant host populations has been performed only for *O. xanthopus* and *O. minutissima* (Wojcik et al., 1987; Heraty et al., 1993; Heraty, 1994a).

Here, we document the presence of two sympatric *Kapala* species, *K. izapa* Carmichael and *K. iridicolor* (Cameron) and evaluate their prevalence and global impact on a population of the neotropical ectatommine ant *Ectatomma ruidum* Roger (Hymenoptera: Formicidae), over a 12-month period. Due to its predatory habits, *E. ruidum* has been considered a valuable potential biocontrol agent in various agroecosystems in Central and South America (Weber, 1946; Lachaud, 1990; Perfecto, 1991; Perfecto and Sediles, 1992; Lachaud et al., 1996; Ibarra-Núñez et al., 2001), but its effectiveness in biological control programs could be reduced due to interference by eucharitid wasps.

2. Materials and methods

2.1. Natural history

2.1.1. The parasitoids

Kapala izapa is a recently described species that is known only from *E. ruidum* in coffee and cocoa plantations in Chiapas, in the southern part of Mexico (Pérez-Lachaud et al., 2006). *Kapala iridicolor*, by contrast, attacks several species of ants: *E. ruidum*, *Gnampotogenys regularis* Mayr, *G. sulcata* (Fr. Smith), *G. striatula* Mayr (Formicidae: Ectatomminae) and *Pachycondyla stigma* (Fabricius) (Formicidae: Ponerinae) (Pérez-Lachaud et al., 2006). The biology and life history traits of both species are reported elsewhere (Pérez-Lachaud et al., 2006). Information on the chemical ecology

of ants and wasps is available for *Kapala izapa* (formerly referred to as *K. sulcifacies*) (Howard et al., 2001), but the host plants used by the females of this species remain unknown. *Kapala iridicolor* is known to oviposit on *Cordia macrostachya*, *C. cana* (Boraginaceae) and *Gossypium hirsutum* (Malvaceae) (Heraty and Woolley, 1993) and on *Melampodium divaricatum* (Asteraceae) (Pérez-Lachaud et al., 2006).

Adults of *K. iridicolor* may be distinguished from *K. izapa* individuals by having a smooth face, contrasting to a finely carinate face in *K. izapa*, and a mesonotum with low lateral profile (Heraty and Woolley, 1993), contrasting to a high profile of the mesonotum in *K. izapa*. *Kapala izapa* is also characterized by the abrupt elevation of the posterior margin of the scutellar disc above the scutellar spines (Pérez-Lachaud et al., 2006). Larval stages of both species follow the general morphology and behavior described for other eucharitids and cannot easily be distinguished from one another. As *K. iridicolor* and *K. izapa* attack *E. ruidum* both at the same site and at the same time, and because immatures cannot be properly assigned to a particular species, global parasitism rates for both parasitoids are reported in this work.

2.1.2. The host

Ectatomma ruidum is a diurnal earth-dwelling poneromorph ant that occurs in plantations and disturbed habitats as well as in damp forests, from sea level to an altitude of 1500–1600 m (Weber, 1946; Brown, 1958). Nests are composed of several chambers, the entrance being a simple hole in the soil. Widely distributed from southern Mexico to Brazil (Weber, 1946; Kugler and Brown, 1982), *E. ruidum* is a dominant species in various ecosystems ranging from forest zones (Kugler and Hincapié, 1983) to cultivated areas of economic importance, such as cocoa, coffee and maize plantations (Lachaud, 1990; Perfecto, 1991). The density of the nests may vary from 360 up to 11,200 nests/ha (Levings and Franks, 1982; Pratt, 1989; Breed et al., 1990; Lachaud, 1990; Schatz et al., 1998; Santamaría Velasco, 2007). In the study zone, colonies of *E. ruidum* are overdispersed and monodomous (Schatz and Lachaud, 2008) and may contain from one to several reproductive queens, some of which are microgynes (Lachaud et al., 1999b). Polygynous colonies represent up to 40% of the total population (Lachaud et al., 1999a), and the mean colony size was estimated at about 90 workers (range, 20–330 workers) (Lachaud et al., 1996).

Although mainly carnivorous, *E. ruidum* foragers commonly exploit extra-floral nectaries such as those of *Inga* trees and orchids (Weber, 1946; Jaffé et al., 1989; Passera et al., 1994). Individual foraging is usually performed during daylight (Lachaud et al., 1984; McCluskey, 1987; Pratt, 1989; Lachaud, 1990; Passera et al., 1994), but some nocturnal foraging has also been observed during the dry season (Jaffé et al., 1990; Lachaud, 1990), or as an adaptation to the exploitation of the orchid *Spathoglottis plicata* Blume in Guadeloupe, linked with the secretion cycle of its extra-floral nectaries, which exhibit a strong activity at sunset (Passera et al., 1994).

2.2. Sampling method

Between February 1997 and January 1998, a total of 215 nests of *E. ruidum* were collected from a population located in a coffee plantation of the Experimental Station INIFAP at Rosario Izapa, Tuxtla Chico Municipality, Chiapas, Mexico (14°58'25" N, 92°09'19" W, 430 m above sea level), where nest density had been estimated at 11,200 nests/ha just one year before the present study (Schatz et al., 1998; Schatz and Lachaud, 2008). The 20-year-old experimental coffee plot was shaded with *Inga* spp. trees. Some weed management was regularly done, but no agrochemicals were applied at any time during the collecting period. The weather of the

region is of the Am(w) type according to the classification of Köppen modified by Garcia (1981) and corresponds to a hot, humid climate with the rainy season occurring from May to November.

Due to logistical difficulties and constraints linked to the weather (heavy rains), no collection was performed during July, and only a single collection was performed for April–May, during the last week of April and the first week of May. For each of the ten collecting dates, 14–30 nests were completely excavated (during the dry season, especially in January, nests were located deeper up to two meters in hard soil, and fewer nests were excavated), and the numbers of queens, alate gynes, males, workers and cocoons per colony were recorded. Cocoons were kept in a climatized room ($28 \pm 2^\circ\text{C}$ and $75 \pm 5\%$ RH) for five days to wait for parasitoid emergence, and the number and sex of adult wasps emerged were also recorded. After this period, in order to determine both the exact number of parasitoids and parasitized ant pupae present in each colony and the variation of the rate of parasitism during the sampling period, all the remaining cocoons were carefully dissected under a stereomicroscope (Wild, $40\times$), and both the number and the developmental stage of any parasitoids (planidia, late larvae, pupae and pharate adults) were recorded. The sex ratio (proportion of males) for each sampling date was calculated taking into account both wasp pupae inside host cocoons (for which the sex could be asserted) and adult parasitoids that succeeded in emerging.

2.3. Statistical analysis

To test whether colony size and parameters associated with colony structure (monogynous, polygynous or queenless, number of sexual forms—gynes and males—and of cocoons) or with environmental conditions (mean precipitation and season—dry or rainy—) were associated with the probability for a nest of being parasitized, we conducted a binomial logistic regression analysis with occurrence of parasitism as the dependent variable (parasitized–unparasitized colonies) and the aforementioned variables as predictors. A separate regression was conducted for colony size alone. Data were analyzed using generalized linear modeling available in MINITAB v7.0 (Minitab, Inc.), with binomial response (parasitized–unparasitized colony) and a logistic link function. Data for “October” ($n = 17$ colonies) were not included in the analysis because all the colonies collected during that month were parasitized.

Data on superparasitism were analyzed with contingency tables. A two-way analysis of variance was used to analyze the mean number of cocoons per colony, with both collecting date (month) and parasitism condition (parasitized–unparasitized) as factors. Data are presented as means \pm SEM, unless stated.

3. Results

Of the 215 *E. ruidum* colonies collected, 12 did not contain cocoons or were considered incomplete (queenless and far too few brood present), and were not included in the analysis. Only one of these colonies contained a eucharitid wasp. For the remaining 203 colonies, the mean number of cocoons per nest for the whole collecting period was 32.0 ± 1.7 (range 1–134), with a peak occurring at the beginning of the rainy season, from late April to June (Table 1). A total of 791 eucharitids from planidia to teneral adults were obtained from 128 colonies that gave an average nest parasitism rate of 63.1% (proportion of *E. ruidum* colonies parasitized by *Kapala* spp.) during all sampling periods (Table 1).

Parasitized colonies were homogeneously distributed with respect to colony characteristics, with one exception. Parasitism occurred in 59.0–66.7% of the nests, without regard to presence/

absence of a queen, monogyny/polygyny, or presence/absence of microgynes in polygynous colonies (Table 2; contingency table, $\chi^2 = 2.79$, ns). In contrast, monogynous colonies with a microgyne experienced 87.5% parasitism (Table 2). However, the difference was not significant due to the very small number of colonies of this kind ($n = 8$).

The probability of a colony being parasitized was positively associated with its size, that is, the total number of adults (workers and sexuals) and pupae present (Logistic binary regression $\chi^2_{1} = 19.86$, $P < 0.0001$; Wald statistic for colony size: $W_1 = 16.44$, $P < 0.0001$). The mean size of parasitized colonies was 135.7 ± 5.5 ($n = 128$), while that of unparasitized colonies was 96.5 ± 6.8 ($n = 75$) (Fig. 1). The full model, including all the variables (Logistic binary regression $\chi^2_{13} = 64.47$, $P < 0.0001$), indicated that colony parasitism likelihood was positively associated with both the number of cocoons present in the nest (Wald statistic: $W_1 = 10.54$, $P < 0.001$) and the number of gynes ($W_1 = 4.36$, $P = 0.03$), but not with the number of queens nor males. Adding precipitation data or season (dry-rainy) did not change the model fit.

The mean number of cocoons in parasitized colonies was significantly different from the mean number of cocoons in unparasitized colonies (two-way ANOVA, $F_{1,167} = 37.54$, $P < 0.0001$). The month of collection also affected the mean number of cocoons (two-way ANOVA, $F_{8,167} = 2.83$, $P < 0.01$). However, there was no significant interaction between these two factors. Globally, the mean number of cocoons was 37.8 ± 2.1 in parasitized colonies ($n = 128$, October data included, Fig. 1), and 22.1 ± 2.5 in unparasitized colonies ($n = 75$).

Kapala individuals (both males and females) were encountered within the nests throughout the year (Table 1). On the basis of the 474 adults and pupae for which sex could be determined, the sex ratio was found always slightly biased to the males (global sex ratio at 0.58, Fig. 2), except in September when the sex ratio was 1:1. With the exception of December and January, when the number of collected eucharitids was extremely small, both sexes were commonly present together within the nests (at least in 48 out of the 97 colonies where the sex of the parasitoids could be determined). Both nest parasitism rate per sampling date and mean number of eucharitids present in parasitized nests fluctuated during the year according to the same pattern (Table 1 and Fig. 3). At the beginning of the dry season (November–December), parasitoids were dispersed among ant colonies: only 35–36.8% of the collected nests were parasitized, and the mean number of parasitoids per parasitized colony was small (4.1 ± 1.1 parasitoids per nest in November and only 1.1 ± 0.1 in December). At the height of the dry season, January, the prevalence of both *Kapala* species was at a minimum in the *E. ruidum* population as was the quantity of host pupae present within the colonies. At the onset of the rainy season, parasitism increased, and, from June to October 1997, eucharitids were spread out among the whole *E. ruidum* population with a nest parasitism rate often reaching 91–100% (Table 1). Parasitism was at its highest level in June, with a mean of 13.8 ± 2.9 parasitoids per parasitized nest (one individual nest contained up to 60 *Kapala* individuals, with half of the ant pupae present at that moment being parasitized).

In order to evaluate, at the population scale, the global impact of eucharitid parasitism on *E. ruidum* colony development (that is, the proportion of ant pupae destroyed by *Kapala*), a global rate of parasitism was calculated, for each collecting period, as the product of the nest parasitism rate and the proportion of parasitized pupae (Fig. 3). Over the whole year, an average of 7.2% host pupae were infested, but the impact was greater during the rainy season (12.1% on average between April–May and October), and greatest in June when more than 28% of all *E. ruidum* pupae produced were parasitized. Moreover, usually only one parasitoid emerged per host, but 19 pupae out of 266 parasitized during June were super-

Table 1
Prevalence of parasitism by *Kapala* spp. in *Ectatomma ruidum* colonies, incidence of superparasitism and number of parasitoids retrieved per collecting date

Sampling period	# Complete colonies	# Parasitized colonies	# Cocoons/nest (mean ± SEM)	Total # cocoons collected	# Parasitized pupae (%)	Superparasitism events		# <i>Kapala</i> Larval stages		Total # eucharitids	
						Double ^a	Triple ^b	Larval	Males		
February 1997	21	14 (66.7)	31.2 ± 4.7	655	61 (9.3)	2	—	19	19	25	63
March	19	12 (63.2)	27.9 ± 5.6	530	24 (4.5)	1	—	12	5	8	25
April–May	24	13 (54.2)	42.1 ± 5.1	1010	133 (13.2)	3	3	69	30	43	142
June	23	21 (91.3)	40.9 ± 5.9	940	266 (28.3)	14	5	71	98	121	290
August	30	22 (73.3)	26.8 ± 3.6	805	120 (14.9)	5	2	84	17	28	129
September	20	13 (65.0)	35.5 ± 7.5	711	24 (3.4)	1	—	9	8	8	25
October	17	17 (100)	31.2 ± 5.1	530	76 (14.3)	1	—	41	13	23	77
November	20	7 (35.0)	35.6 ± 4.9	712	27 (3.8)	2	—	6	5	18	29
December	19	7 (36.8)	20.7 ± 3.3	394	8 (2.0)	—	—	4	1	3	8
January 1998	10	2 (20.0)	21.2 ± 4.3	212	3 (1.4)	—	—	2	1	—	3
Total	203	128 (63.1)	32.0 ± 1.7	6499	742 (11.4)	29	10	317	197	277	791

^a Two parasitoids per host.

^b Three parasitoids per host.

parasitized, with two or three adult eucharitid wasps successfully emerging from a single host. The number of superparasitized pupae found in June accounted for 50% of all superparasitism events recorded during the whole sampling period (Table 1). However, the increase in superparasitism events in June was not significant (contingency table, $\chi^2 = 5.95$, ns) and appeared to depend only on the high number of parasitized pupae present in the nest during this month. Actually, the number of infested pupae was positively correlated with the number of pupae available in the colonies ($r^2 = 0.260$, $n = 200$, $P < 0.0001$; Fig. 4). Later in the rainy season, prevalence of parasitism and number of parasitoids per nest decreased, seemingly due to the twofold increase in precipitation recorded in September 1997 (750.6 mm against 349.7 mm during August), which negatively affected the ant host population as indicated by a decrease in the number of queens, workers and cocoons per colony (Fig. 1 and J.P.L., unpublished data).

4. Discussion

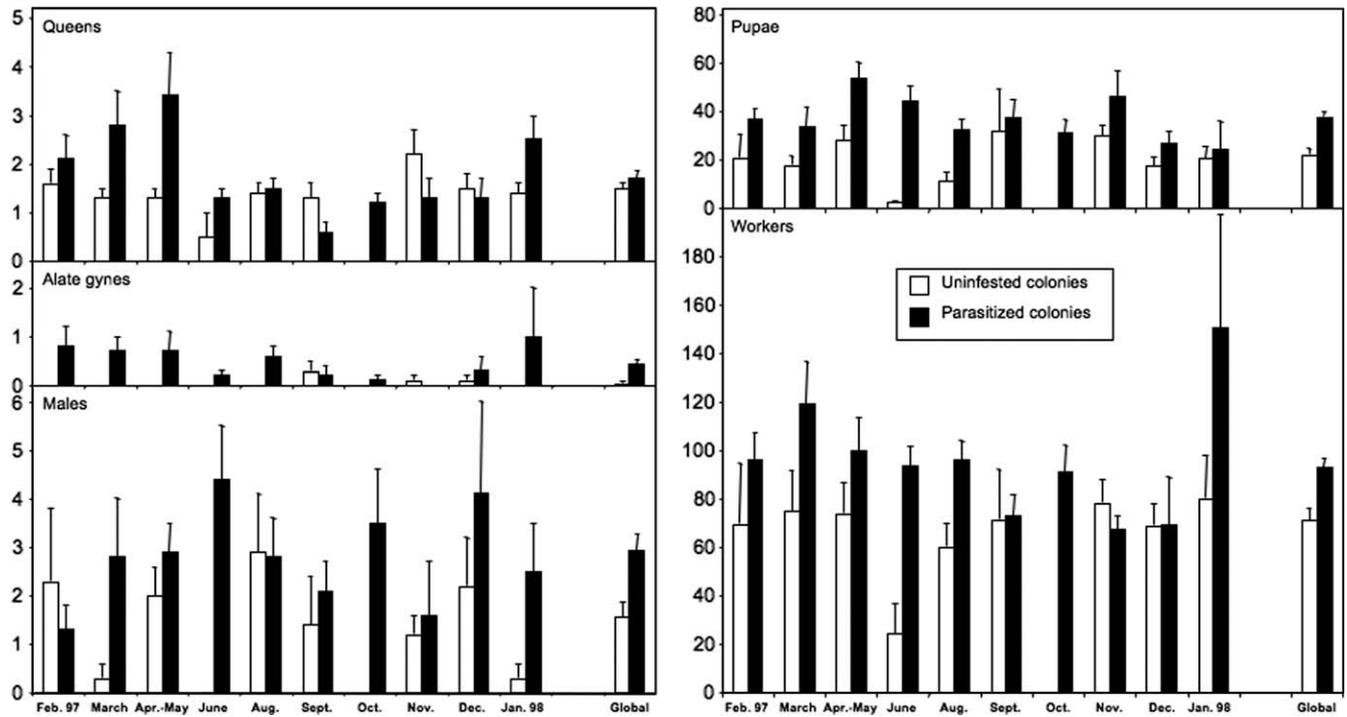
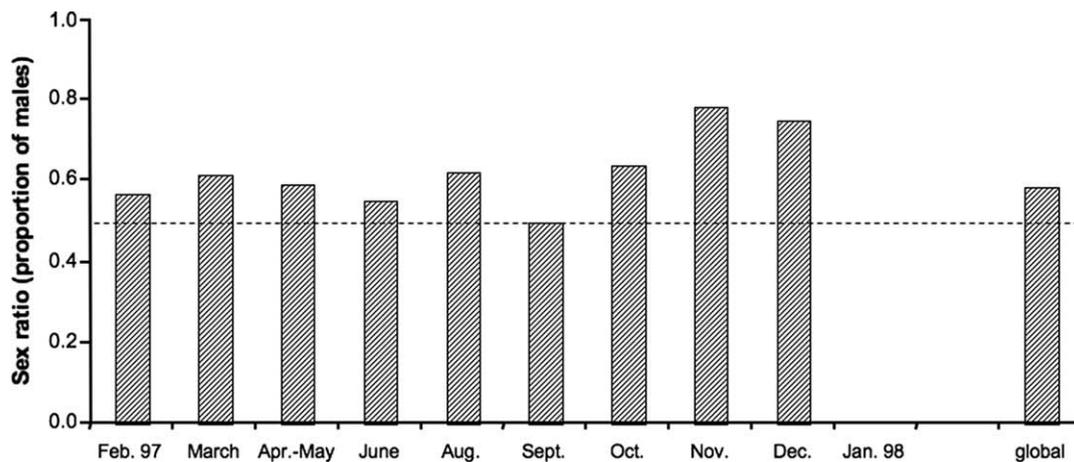
Percentage parasitism figures for a few eucharitid species are scattered in the literature, but data on population dynamics and impact on host populations are lacking. As stressed by Clausen (1941) and Ayre (1962), poor dispersal of both adult and planidium forms, as well as specificity for particular host plants (or plant structures) for oviposition, are among the factors thought to contribute to the seeming rarity of eucharitids and to the patchy distribution of their populations. For example, parasitism of larvae of the ant *Lasius neoniger* by *Pseudometagea schwarzii* was found by Ayre (1962) to reach between 80% and 90% in colonies located within an 8-m radius of the apparent center of infestation, but the levels of parasitism dropped with increasing distance (35% at 36 m, and 0% beyond 60 m), the maximum flight observed in *P. schwarzii* adults not having exceeded 3 m. Furthermore, infestation rates were highly variable as reported by Clausen (1923) for the parasitization of *Camponotus japonicus* Mayr by *Stilbula* (= *Schizaspidia*) *tenuicornis* (Ashmead), which reached a maximum of 47% one year, while declining to 16% the next year. Although parasitism in some instances might be temporarily and locally very high, the effective influence of eucharitid wasps on the population size of their host has been presumed to be small or even nil due to the lack of information.

Similarly to the case reported by Ayre (1962), data gathered in this study showed that parasitism of *E. ruidum* by *K. izapa* and *K. iridicolor* was localized. Though parasitoids appeared homogeneously scattered amongst the host population with respect to colony characteristics, some nests did escape from parasitoids while others were intensively infested (up to 100% of the pupae in some cases) in spite of the high density of nests per hectare in the study site. As proposed for *S. tenuicornis* and *P. schwarzii*, host plant distribution might be a much more limiting factor than host distribution or host abundance, and the foraging habits of ants might also affect the distribution of the parasitoids. Monopoly of certain foraging areas by some ant colonies and the resulting exclusion of ants from neighboring nests would both prevent other colonies from coming in contact with the planidia and favor continual reinfestations of the same nests (Clausen, 1941). Despite the very low aggression between neighboring colonies of *E. ruidum* (Breed et al., 1992; De Carli et al., 1998) and the extremely high density of its colonies (Schatz et al., 1998; Schatz and Lachaud, 2008), colony territoriality has been reported (Jaffé and Marquez, 1987; Breed et al., 1990; Schatz et al., 1997), and the resulting intraspecific competition between neighbors (De Carli et al., 1996; Jeral et al., 1997; Breed et al., 1999; Schatz and Lachaud, 2008) could be sufficient to explain the patchy distribution of *K. izapa* and *K. iridicolor* amongst their host population. Moreover, such a hypothesis is likely to be supported by the fact that, on average, parasitized colonies are larger than

Table 2

Distribution of parasitized host colonies according to colony characteristics: queenless, monogynous or polygynous, presence or absence of microgynes

	Total	Queenless colonies	Monogynous colonies		Polygynous colonies		Mixed
			Macrogynes	Microgynes	Macrogynes	Microgynes	
# Complete nests collected	203	23	97	8	30	6	39
# Parasitized nests	128	15	59	7	20	4	23
Proportion (%)	63.1	65.2	60.8	87.5	66.7	66.7	59.0

**Fig. 1.** Annual variation of the composition of the host colonies with (black bars) or without (white bars) parasitoids.**Fig. 2.** Annual variation of the secondary sex ratio of *Kapala* spp. (proportion of males). Dashed line indicates equilibrium.

uninfested ones. Large colonies of different ant species, such as *Pogonomyrmex barbatus* (Smith) (Gordon, 1992; Gordon and Kulig, 1996) or *S. invicta* (Tschinkel et al., 1995), have been reported to be more likely to overwhelm competing colonies and to extend their foraging area at the expense of those colonies, limiting in this way the exploitation of some resources by smaller colonies. However, despite this heterogeneity in the localization of the parasitism and the variations observed during the year in both the prevalence of

parasitism and the dispersion of parasitoids at the host population scale, the influence of *K. izapa* and *K. iridicolor* on *E. ruidum* populations was by no means insignificant, due to both the continuous presence and the level of global populational rate of parasitism recorded year round.

As our results showed, adults and larvae of both species were present within the host colonies throughout the year, and it is likely that multiple overlapping generations and mating occur year

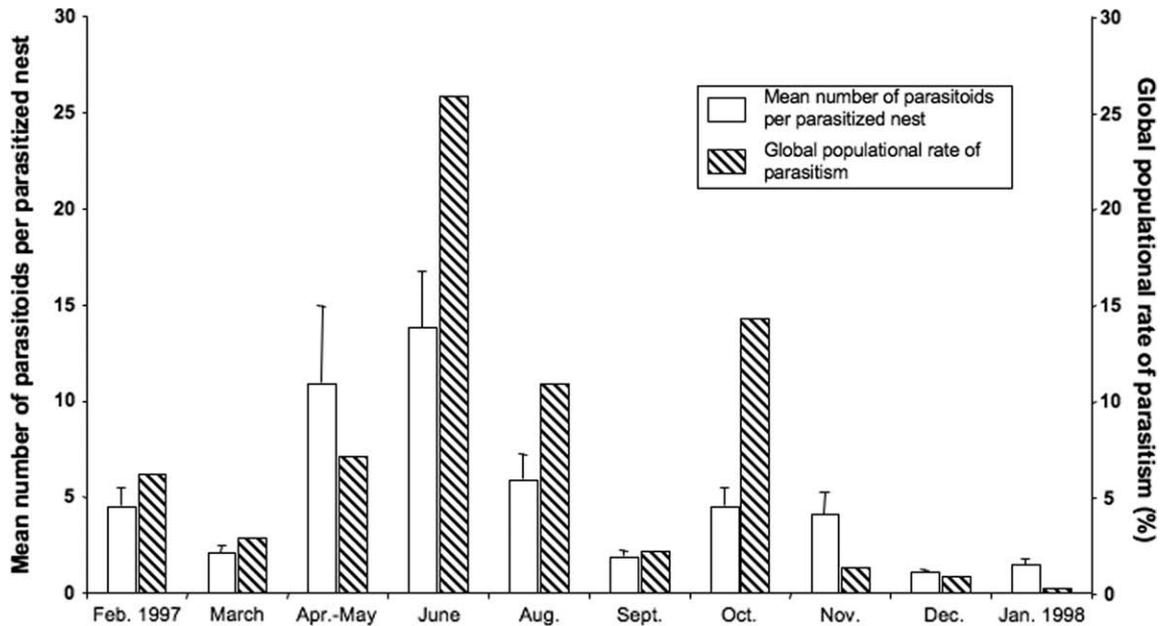


Fig. 3. Annual variation of the mean number of eucharitids (adults + immatures) present in infested *Ectatomma ruidum* nests (white bars) and of the global rate of parasitism (nest parasitism rate \times proportion of parasitized pupae) at the population scale (hatched bars).

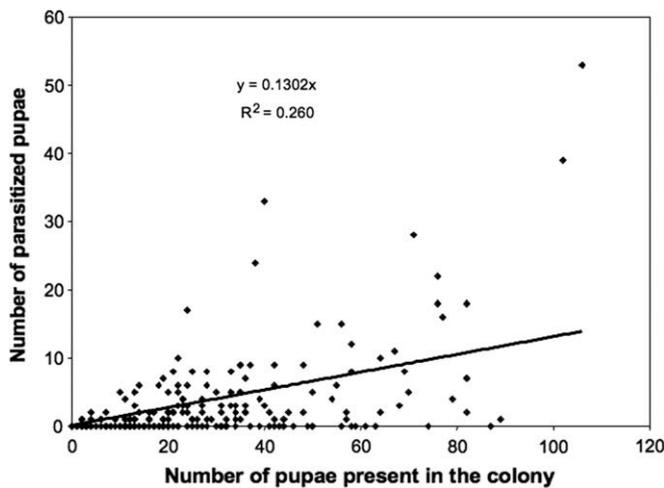


Fig. 4. Correlation between the number of pupae parasitized by *Kapala* spp. and the number of pupae available in 200 *E. ruidum* colonies.

round. The secondary sex ratio, evaluated inside host nests, was biased towards males, contrary to most species of parasitoids, whose secondary sex ratios are, in general, female biased (Quicke, 1997). Most eucharitid species reported in the literature have been collected using sweep nets and Malaise traps and, in such collections, males are more numerous than females, but this was considered an artifact due to males swarming at the entrance of ant nests for mating purposes (Heraty, 1995) and being more susceptible to being attracted by traps. Our data, however, ruled out this possibility and confirmed the relative predominance of males of *Kapala* over females. The sexual behavior of these parasitoids has not been observed, and nothing is known about the mating capacity of *Kapala* males. Females of *P. schwarzii* were reported by Ayre (1962) to accept multiple matings at emergence. However, this record is questionable considering the ability of *P. schwarzii* females to quickly escape from a harassing swarm of males after a first mating and then further being ignored while they fly to a nearby host plant and begin ovipositing (J.M. Heraty, personal communi-

cation). Like females of other short-lived parasitoid species, *Kapala* females emerge with a complete egg load, which can reach 4500 eggs in *K. iridicolor* (Pérez-Lachaud et al., 2006), and they begin oviposition soon after emergence, adhering to the haplodiploid sex-determination strategy common to all Hymenoptera. The high number of *Kapala* males present inside ant nests might be the consequence of a high oviposition pressure due to the limited lifespan of females along with an incomplete insemination of females at first mating, the sperm of a single male not being sufficient to fertilize all the eggs of a female. An alternative explanation could result from a differential mortality of the sexes during their development, to males' advantage.

More than the constant presence of *Kapala* individuals inside *E. ruidum* nests, the major argument for concluding that *K. izapa* and *K. iridicolor* actually impact their host population, remains that the populational rate of parasitism was relatively high throughout the year, especially during the rainy season. In fact, the mean level of parasitism depended essentially on the available number of host pupae present in the colonies, and the highest parasitism value occurred in June, when pupa production was at its height, with more than a quarter of all the pupae present in the population at that moment being destroyed. As is common in other parasitoids (Quicke, 1997), host size seemed to affect the number of *Kapala* parasitoids that can be produced per host since more than one parasitoid per host was frequent in June when numerous large, reproductive forms were produced by ants. Considering both that worker and reproductive forms of *E. ruidum* are parasitized (see Pérez-Lachaud et al., 2006), and that more than half of the annual production of sexuals occurs between May and June (J.P.L., unpublished data), such high levels of parasitism are likely to strongly affect colony growth.

Oraesema xanthopus is the only other species of eucharitid for which parasitism data (collected on an annual basis) demonstrated a real impact upon their ant host (Wojcik et al., 1987; Heraty et al., 1993). These wasps occurred in 18.5–67.5% of all colonies of *S. invicta* sampled in Brazil throughout a 30-month survey (33.2% of the 1585 nests), showing a consistent presence of all life stages during the year and an average number of 18.3 parasites per nest, with a clear increase of parasitism during the summer months. However,

even for *O. xanthopus*, the real mortality rate caused by eucharitids could not be assessed due to the lack of specific data concerning both the size of the ant host colonies (especially, the number of pupae actually present) and the density of these colonies in the field. In the case of *K. izapa* and *K. iridicolor* attacking *E. ruidum*, the global rate of parasitism we estimated reflects the actual impact of *Kapala* wasps on the potential growth of their host population. Therefore, *K. izapa* and *K. iridicolor* may be considered true indirect pests because of their negative impact on *E. ruidum* colony growth and their interference with the beneficial action of this ant.

Apart from the potential interest, already mentioned, in some eucharitid species as beneficial parasitoids of economically important pest ants, some other species have been reported as economic pests that cause injury to plant tissue (females oviposit in or on leaves), as is the case for *Orasema aenea* on olive leaves (Nicolini, 1950), *O. assectator* on tea leaves (Das, 1963; Kerrich, 1963), or *O. costaricensis* on young banana fingers (Tocchetto, 1942; Roberts, 1958). However, the extent of the actual damages on all these plants has not been further documented since the first reports, and the real pest status for the three *Orasema* species concerned is uncertain (Heraty, 1994a). The case, here documented, of *K. iridicolor* and *K. izapa* is quite different in that they constitute a measurably important limiting factor for *E. ruidum* populations, affecting the predatory impact of this biological agent against coffee and cocoa pests. Nevertheless, considering the extremely high nest densities recorded in the study zone (Schatz and Lachaud, 2008), the *E. ruidum* population did not appear to be seriously affected by such a high level of parasitism. The existence in this species of a complex reproductive strategy involving two distinct types of queens (microgynes and macrogynes), both of them involved in the reproduction and foundation of new colonies but with distinct dispersal capacities (Lachaud et al., 1999b), could be the evolutionary response of this ant species (see Sherman et al., 1988) to the strong parasitism exerted by eucharitids.

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