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SHORT COMMUNICATION

Teratocytes growth pattern reflects host suitability in a host–parasitoid assemblage

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Abstract. In some parasitoid species, the serosa membrane breaks apart at hatching and produces teratocyte cells that assume various functions (immunossupression, secretion and nutrition) mediating host–parasitoid relationships. Teratocyte growth pattern may thus reflect the host suitability for a parasitoid. The teratocyte growth pattern (increase in size and number of teratocytes as a function of time) is studied and used as an indirect measure of fitness to compare the development of the endoparasitoid *Dinocampus coccinellae* in a marginal host, the coccinellid *Harmonia axyridis*, and in a suitable host, *Coleomegilla maculata*. Indirect measures of fitness recorded in both host species confirm that *C. maculata* is a suitable host for *D. coccinellae* contrary to the marginal host *H. axyridis.* According to regression analysis, teratocyte numbers decrease linearly whereas teratocyte size increases linearly with time in the suitable host *C. maculata* (larvae or adults). In the marginal host, parasitism occurs only in the larval stage where a delay in the parasitoid larval development is observed. Increase in teratocyte size is also highly variable. The teratocyte growth pattern of the parasitoid in the marginal host does not follow the linear model found in the suitable host. Teratocyte growth pattern may be a useful criterion to evaluate host-suitability and host range of parasitoids.

Key words. Host suitability, marginal host, parasitoid nutrition, suitable host, teratocytes.

Introduction

For endoparasitoids, host characteristics directly influence the mother's fitness through offspring development. Females thus choose the hosts most likely to allow larval development and to optimize their fitness gain depending on internal and external parameters (van Alphen & Vet, 1986; Godfray, 1994). Nevertheless, parasitoid females can oviposit in marginal or unsuitable hosts in field and laboratory conditions (Heimpel *et al.*, 2003). A suitable host allows all or nearly all parasitoid immatures to develop into adults, whereas marginal hosts allow only a small proportion to develop and unsuitable hosts allow no parasitoid development. Host suitability thus depends on factors such as the host immune system, host toxins and host nutritional quality, which are often difficult to quantify (Vinson & Iwantsch, 1980; Strand & Pech, 1995; Lavine & Strand, 2002).

Teratocyte growth pattern could be a physiological factor reflecting host suitability at the same time as being relatively easy to quantify. In these families, when the egg hatches, the serosa membrane surrounding the embryo releases numerous spherical cells (i.e. teratocytes) in the haemolymph, with numbers ranging from 10 to 900 depending on the species (Dahlman, 1990). Teratocytes mediate host–parasitoid relationships through immunosuppression, secretion or nutrition (Dahlman, 1990; Vinson, 1990; Pennacchio *et al.*, 1994; Zhang *et al.*, 1997; Hotta *et al.*, 2001; Nakamatsu *et al.*, 2002; Rana *et al.*, 2002). In general, teratocytes absorb host nutrients and produce proteins that are either stocked inside the cells or released into the host haemolymph (Sluss & Leutenegger, 1968; Okuda & Kadono-Okuda, 1995; Nakamatsu *et al.*, 2002). The teratocyte diameter increases with time and their number decreases progressively when the parasitoid immature ingests them (Sluss & Leutenegger, 1968; Pennacchio *et al.*, 1994; Kadono-Okuda *et al.*, 1995; De Buron & Beckage, 1997;

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Zhang *et al.*, 1997; Alleyne *et al.*, 2001; Barratt & Sutherland, 2001; Hotta *et al.*, 2001).

Disrupted teratocyte growth pattern, either in the size and/or the number of teratocytes, has been observed in some host–parasitoid assemblages (Alleyne *et al.*, 2001; Barratt & Sutherland, 2001) or when immature parasitoids develop in low quality artificial media (Strand *et al.*, 1985). Low successful parasitism is linked to a lower number of teratocytes during the first days of parasitoid larval development (Alleyne *et al.*, 2001; Barratt & Sutherland, 2001). In the present study, it is hypothesized that the teratocyte growth pattern reflects host suitability for a parasitoid and that the number of teratocytes will be lower in a marginal compared with a suitable host. The braconid parasitoid *Dinocampus coccinellae* Schrank (Hymenoptera: Braconidae) and two hosts are used: the suitable host *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) and the marginal host *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). In the present study, total and successful parasitism is evaluated on each host, along with the developmental time, adult size and egg load as indirect measures of parasitoid fitness. Teratocyte growth pattern (size and number of teratocytes) is also evaluated in both host species.

Dinocampus coccinellae is a solitary endoparasitoid of coccinellids with a cosmopolitan distribution (Hodek & Honěk, 1996). Females lay eggs inside coccinellid adults or larvae; the immatures develop in the haemolymph of the host and emerge from the coccinellid adult to spin a cocoon between its legs (Balduf, 1926; Hodek & Honìk, 1996). *Dinocampus coccinellae* produces only females by thelytokous parthenogenesis (Balduf, 1926). Each parasitoid egg produces an average of 550 teratocytes, which gradually increase in size as they accumulate nutrients from host haemolymph during immature parasitoid development. The parasitoid larva feeds directly on these teratocytes, gradually reducing their number (Sluss & Leutenegger, 1968; Kadono-Okuda *et al.*, 1995). The role of *D. coccinellae* teratocytes appears to be mainly nutritional (Sluss & Leutenegger, 1968; Kadono-Okuda *et al.*, 1998; Gopalapillai *et al.*, 2005).

The marginal host *H. axyridis* is an exotic coccinellid introduced from Japan and ex-USSR in the U.S.A. throughout the 20th Century (Gordon, 1985; Tedders & Schaefer, 1994) and established in Canada in 1994 (Coderre *et al.*, 1995). In North America, *H. axyridis* has a similar ecology and shares habitats and food resource with *C. maculata,* a suitable host for *D. coccinellae* (LaMana & Miller, 1996; Musser & Shelton, 2003). Laboratory experiments showed that *D. coccinellae* attacks *H. axyridis* adults (Hoogendoorn & Heimpel, 2002; A. Firlej, unpublished data) but field and laboratory data report low levels of successful parasitism of *H. axyridis* adults by *D. coccinellae* in North America (Hoogendoorn & Heimpel, 2002; Firlej *et al.*, 2005). Even if *H. axyridis* is sympatric with *D. coccinellae* in Asia (Maeta, 1969), the degree of coevolution between *H. axyridis and D. coccinellae* remains unknown because the parasitoid native area is unclear (America or Europe) (Balduf, 1926).

Materials and methods

Insects

In summer 2002, the two hosts *C. maculata* and *H. axyridis* and the parasitoid *D. coccinellae* were collected from corn fields (*Zea maïs*) in Quebec, Canada (45°21'29'; 73°09'08'). The two coccinellids were reared on a meat-based artificial diet (Firlej *et al.*, 2006) with ground pollen and live aphids [*Acyrthosiphon pisum* (Harris)]. Field-collected adults were regularly added to the culture to maintain genetic variability. The strain of *D. coccinellae* originated from parasitized adults of *C. maculata*. Parasitoid adults were supplied with water and honey and reared on *C. maculata* adults: twice a week, 20 *C. maculata* adults were supplied to four *D. coccinellae* adults for parasitization and removed after 24 h. Thereafter, parasitized *C. maculata* adults were maintained in rearing boxes (Ziploc, 946 mL, Ziploc, S.C. Johnson & Sons. Inc., Brantford, Canada) until the development of parasitoid pupa. All insects were kept in growth chambers at 20 ± 2 °C with 60% relative humidity (RH) and under an LD 16 : 8 h photoperiod.

Indirect measures of Dinocampus coccinellae fitness in two hosts

Biological parameters of *D. coccinellae* were measured when reared in the two host species (*C. maculata* and *H. axyridis*) parasitized at two different stages (fourth instar and adult). Fourth-instar and adult coccinellids are both suitable stages for development of *D. coccinellae* (Obrycki *et al.*, 1985). A single *D. coccinellae* female, 1-week old, was placed in a Petri dish (diameter 5 cm; height 1 cm) where either one *H. axyridis* or one *C. maculata* host was offered until an insertion of the ovipositor was observed. Only one insertion of the ovipositor was allowed per host. All presumed parasitized hosts were kept individually in a Petri dish (diameter 5 cm; height 1 cm) with artificial diet, aphids (*A. pisum*) and lepidopteran eggs (*Ephestia kuehniella* Keller). The food was changed every 3 days and aphids every day until emergence of parasitoid adults. Hosts attacked from which no parasitoid emerged were dissected after 30 days to assess presence of *D. coccinellae* eggs or larvae. Under the experimental conditions, development of *D. coccinellae* takes an average of 21 days (Wright & Laing, 1978). The experiment was carried out at 24 ± 2 °C, 60% RH and under an LD 16 : 8 h photoperiod.

Dinocampus coccinellae egg-larval development time was calculated as the time between oviposition and emergence of a pupa from the host. The time between the emergence of the pupa and the emergence of *D. coccinellae* adult represented the pupal developmental time. Left hind tibia length and egg load (only mature eggs were counted) at emergence were measured on *D. coccinellae* adults. Successful parasitism by *D. coccinellae* was calculated as the percentage of *D. coccinellae* adults produced from the total number of hosts offered. Total parasitism by *D. coccinellae* was calculated as

the number of hosts from which *D. coccinellae* successfully emerged plus the number of hosts where eggs or dead larvae were found at dissection on the total number of hosts offered.

Egg-larval developmental time and tibia length of *D. coccinellae* females were compared between hosts and stages using a one-way analysis of variance followed by a post-hoc comparison with a Tukey–Kramer test when required (Sokal & Rholf, 1981). Because assumptions of residual normality and equality of variances were not met even after data transformation, pupal and total developmental time and egg-load of *D. coccinellae* females were compared between hosts and stages using a nonparametric Kruskal–Wallis test. When post-hoc comparisons were required, Wilcoxon nonparametric test were used with error rates corrected at $\alpha = 0.0169$ according to Scherrer (1984). Total and successful parasitism were compared between hosts and stages with the *G*-test (Sokal & Rholf, 1981) and error rates were corrected at $\alpha = 0.0169$ in post-hoc comparisons according to Scherrer (1984). Analyses were carried out using the software JMPin (SAS Institute Inc., Cary, North Carolina).

Teratocytes growth pattern

To assess teratocytes growth pattern (size and number), one adult (7 days old) or one fourth instar of each host species was offered for parasitization to one *D. coccinellae* female (2–12 days old) as described above. Starting 5 days after parasitization, corresponding to the time of egg hatch (Obrycki *et al.*, 1985), three to six adults of each host species were dissected daily. At this time, hosts parasitized during the fourth instar had moulted into adults. The *D. coccinellae* larvae were measured from the tip of the head to the end of the abdomen with microscope (magnification: × 200) or stereomicroscope (magnification: × 32 to × 50) depending of their size. The immature third- and fourth-instar parasitoids could not be distinguished. Teratocyte numbers were assessed by washing a host with saline solution and pipetting the diluted haemolymph onto a slide where the number of teratocytes was counted under a stereomicroscope (magnification: × 8 to × 32). The diameter of 30 randomly selected teratocytes was measured with the help of a microscope (magnification: × 200 to × 600) connected to the image analysis software Image Pro (Media Cybernetics Inc., Sylver Spring, Maryland).

Linear regression analysis was used to study the relationship between *D. coccinellae* larval growth and the time postparasitization (PROC REG procedure) for each host species and stage parasitized (Sokal & Rholf, 1981). Kadono-Okuda *et al.* (1995) observed that, in *C. septempunctata* adults, the *D. coccinellae* teratocytes number decreased linearly and teratocytes diameter increased linearly with time after parasitization. Therefore, linear regression analysis was used to study the relationship between the diameter and number of teratocytes and time postparasitization (PROC REG procedure). Slopes and intercepts of each regression curve were compared with a PROC REG procedure. Analyses were carried out using the software SAS (SAS Institute Inc.).

Results and discussion

Measures of Dinocampus coccinellae fitness in two hosts

No pupae of *D. coccinellae* formed and no eggs or larvae were found after dissection when *H. axyridis* adults were used as hosts. *Dinocampus coccinellae* parameters (Table 1) were therefore statistically compared only between *C. maculata* larvae and adults and between *C. maculata* larvae and *H. axyridis* larvae. Total and successful parasitism by *D. coccinellae* were significantly influenced by the type of host offered ($G = 12.22$; d.f. $= 2$; $P = 0.002$ and $G = 21.48$; d.f. $= 2$; $P < 0.001$, respectively). No differences in total and successful parasitism between larvae and adults of *C. maculata* parasitized by *D. coccinellae* were observed (total parasitism: $G = 0.11$; d.f. $= 1$; $P = 0.738$; successful parasitism: $G = 0.69$; d.f. $= 1$; $P = 0.407$). *Harmonia axyridis* larvae were significantly less parasitized by *D. coccinellae* and adult emergence was lower than in *C. maculata* larvae (total parasitism: $G = 7.95$; d.f. $= 1$; $P = 0.005$; successful parasitism: $G = 19.17$; d.f. $= 1$; $P < 0.001$).

The egg-larval and the total development time of *D. coccinellae* were longer in *H. axyridis* larvae than in

Table 1. *Dinocampus coccinellae* biological parameters after parasitization of fourth instar and adult of *Coleomegilla maculata* and *Harmonia axyridis.*

	Host species and stage parasitized			
	Coleomegilla maculata		*Harmonia axyridis*	
	Fourth instar	Adult	Fourth instar	Adult
Total parasitism (%)*	58.3[a]	62.2[a]	28.6[b]	0
Successful parasitism (%)*	58.3[a]	48.6[a]	12.2[b]	0
Developmental time (days ± SE)				
Egg-larval†	17.2 ± 1.3[b]	15.4 ± 0.9[c]	19.7 ± 2.2[a]	–
Pupal‡	7.1 ± 0.6[b]	7.9 ± 0.5[a]	8.2 ± 0.5[a]	–
Total‡	24.3 ± 1.2[b]	23.4 ± 0.8[b]	28.0 ± 2.0[a]	–
Dinocampus coccinellae tibia length (mm ± SE)†	1.26 ± 0.05[a]	1.29 ± 0.07[a]	1.32 ± 0.07[a]	–
Dinocampus coccinellae egg load (nb ± SE)‡	154 ± 34[a]	184 ± 41[a]	158 ± 37[a]	–

Means with different superscript letters in the same row differ significantly at $\alpha = 0.05$ (*chi-square test, †Tukey–Kramer) and at $\alpha = 0.017$ (‡Wilcoxon test).

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C. maculata larvae (egg-larval: $P < 0.05$; total: $Z = 3.07$; d.f. = 1; $P = 0.002$) or *C. maculata* adults (egg-larval: $P < 0.05$; total: $Z = 3.13$; d.f. = 1; $P = 0.002$). *Dinocampus coccinellae* spent more time in pupal stage when issued from *H. axyridis* larvae and *C. maculata* adults than from *C. maculata* larvae ($Z = 2.77$; d.f. = 1; $P = 0.006$; $Z = 3.75$; d.f. = 1; $P = 0.002$). *Dinocampus coccinellae* offspring parameters (tibia length and egg load) did not differ significantly with the host offered (tibia length: $F = 2.15$; d.f. = 2; $P = 0.129$; egg load: $\chi^2 = 4.61$; d.f. = 1; $P = 0.01$).

Lower successful parasitism and delay in developmental time are observed in marginal hosts compared with suitable ones. The important difference between the total and successful parasitism in *H. axyridis* is due to the *D. coccinellae* immature mortality (43%). Because *D. coccinellae* teratocytes have a nutritive role (Sluss & Leutenegger, 1968; Kadono-Okuda *et al.*, 1998; Gopalapillai *et al.*, 2005), their absence or low number in *H. axyridis* may result in insufficient food for the parasitoid larval growth and could explain both the lower successful parasitism and the developmental delay. A similar observation was made with *Aphidius ervi* (Hymenoptera: Braconidae) parasitizing a clone of the aphid *A. pisum* (Li *et al.*, 2002) where a complete absence of successful parasitoid development is linked to a complete absence of teratocytes in the host haemolymph. Despite the observation of females *D. coccinellae* attacking *H. axyridis* adults, no parasitoid develops in these adults. Neither eggs nor larvae of *D. coccinellae* were found in *H. axyridis* adults even 1 month after a contact, confirming previous observation by Hoogendoorn & Heimpel (2002).

Teratocyte growth pattern

Dinocampus coccinellae larval size increased linearly along time postparasitization in *C. maculata* and *H. axyridis* whatever the developmental stage offered (Table 2; Fig. 1). Lower r^2 were obtained when *D. coccinellae* larvae were in *C. maculata* adults ($r^2 = 0.23$) and *H. axyridis* larvae ($r^2 = 0.29$) than in *C. maculata* larvae ($r^2 = 0.59$) (Table 2). Slopes and intercepts were not significantly different between regression lines ($P > 0.05$). The diameter of teratocytes increased linearly with time in *C. maculata* larvae and adults and in *H. axyridis* larvae (Table 2; Fig. 2) but r^2 was lower in the latter ($r^2 = 0.16$) (Table 2). Slopes and intercepts were not significantly different between lines ($P > 0.05$). At egg hatching, an average 514 teratocytes were found in *C. maculata* when parasitized at adult stage, 432 teratocytes when parasitized at larval stage and 177 teratocytes in *H. axyridis* when parasitized at larval stage. Teratocytes numbers decreased linearly with time in both *C. maculata* adults and larvae (Table 2; Fig. 3). Slopes and intercepts did not differ significantly ($P > 0.05$). Teratocyte number did not evolve linearly in function of the time postparasitization in *H. axyridis* larvae (Table 2; Fig. 3).

The linear increase in size and linear decrease in number of teratocytes observed in *C. maculata* is indicative of a suitable host for *D. coccinellae*. The correlations observed for these factors in *C. maculata* are similar to that observed in the suitable host *Coccinella septempuncata brucki* (Kadono-Okuda *et al.*, 1995). In this latter host species, the teratocyte diameter increases from 40 to 500 μm at the end of the parasitoid development in response to a polyploidization and the accumulation of proteins inside the cell (Kadono-Okuda *et al.*, 1995; Kadono-Okuda *et al.*, 1998). The teratocyte number also decreases progressively after ingestion by *D. coccinellae* larvae during their development (Kadono-Okuda *et al.*, 1995). Decreasing teratocyte number could also be due to apoptosis events observed at the final phase of the parasitoid immature development in other studies (Volkoff & Colazza, 1992; De Buron & Beckage, 1997).

The prediction that the number of teratocytes should be lower in marginal hosts compared with suitable hosts is supported by the results obtained in the present study. Most *H. axyridis* larvae that contain a parasitoid larva are devoid of teratocytes. Similarly, in *Cotesia* and *Microctonus* parasitoid species, a low number of teratocytes is observed during the first days of parasitoid larval development in hosts considered less suitable for offspring development (Alleyne *et al.*, 2001; Barratt & Sutherland, 2001). Strand *et al.* (1985) suggested that a decreasing enzymatic activity could cause the serosa membrane to cleave into fewer teratocytes in low

Table 2. Linear regression analysis parameters of *Dinocampus coccinellae* larval size, teratocyte number and teratocyte diameter evolution in function of time postparasitization.

	$y = ax + b$	F	P	r^2
Larval size				
Fourth instar *Coleomegilla maculata*	$y = 242.08x + 304.29$	61.68	< 0.001	0.59
Adult *Coleomegilla maculata*	$y = 234.10x + 300.09$	11.74	0.002	0.23
Fourth instar *Harmonia axyridis*	$y = 215.91x - 191.37$	21.01	< 0.001	0.29
Teratocyte number				
Fourth instar *Coleomegilla maculata*	$y = -42.82x + 785.87$	37.70	< 0.001	0.51
Adult *Coleomegilla maculata*	$y = -42.94x + 739.90$	26.10	< 0.001	0.40
Fourth instar *Harmonia axyridis*	–	1.76	0.191	–
Teratocyte diameter				
Fourth instar *Coleomegilla maculata*	$y = 26.23x - 47.15$	91.36	< 0.001	0.71
Adult *Coleomegilla maculata*	$y = 24.64x - 32.96$	30.97	< 0.001	0.49
Fourth instar *Harmonia axyridis*	$y = 36.50x - 162.36$	4.95	0.035	0.16

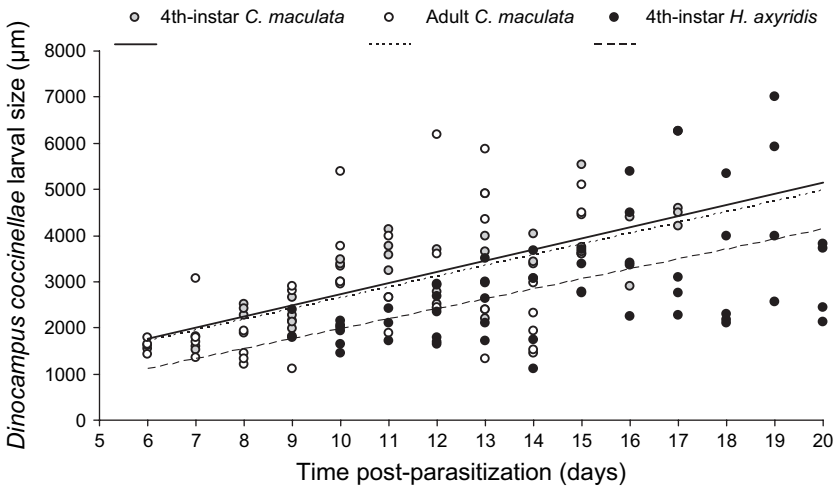

Fig. 1. *Dinocampus coccinellae* larval size (µm) in suitable host *Coleomegilla maculata* and marginal host *Harmonia axyridis* in function of the time postparasitization (days).

quality media. Fewer mononucleate teratocytes and more polynucleate teratocytes were observed. Further experiments should aim to study nucleation of teratocytes in *H. axyridis* to establish the proportion of polynucleate teratocytes. Whereas *D. coccinellae* teratocytes can reach 500 µm in suitable hosts (Sluss, 1968; Kadono-Okuda *et al.*, 1995), teratocytes ranging from 600 to 900 µm are observed when *H. axyridis* larvae are parasitized. A similar pattern of excessive growth of teratocytes is also observed in marginal hosts (Alleyne *et al.*, 2001) or when teratocytes are reared in suboptimal artificial media (Strand *et al.*, 1985). An excessive endopolyploidization, which usually occurs in teratocytes (Strand & Wong, 1991), or larger growth in a larger host could comprise possible mechanisms to explain this excessive teratocyte growth in *H. axyridis*.

As predicted, the teratocyte growth pattern is different in marginal vs. suitable hosts: the number of teratocytes is higher in the suitable host *C. maculata* compared with the marginal host *H. axyridis* whose adult stage is completely unsuitable for egg-larval *D. coccinellae* development. Attacking the marginal host is costly for the parasitoid female because either she wastes handling time if no egg is deposited or she wastes an egg if oviposition occurs. Even when parasitizing *H. axyridis* larvae, the high immature mortality and the delayed development time represent a cost even if the surviving parasitoid has a similar fitness (size and egg load) to those developing in *C. maculata* larvae. Those results should be interpreted with caution because of the low number of replicates obtained from successful parasitism in the marginal host larvae. The fact that *D. coccinellae* attacked both larvae and adults of *H. axyridis* could favour the suitable host *C. maculata* because the parasitoid wasted time and eggs doing so (Hoogendoorn & Heimpel, 2002; Heimpel *et al.*, 2003). On other hand, the ability of part of the parasitoid population to develop in a marginal host could provide selective advantage to a generalist when the suitable host abundance declines in the environment.

Teratocyte growth patterns differ between hosts of different suitability. Because the teratocytes of *D. coccinellae* do not develop normally in the marginal host, the immature of the

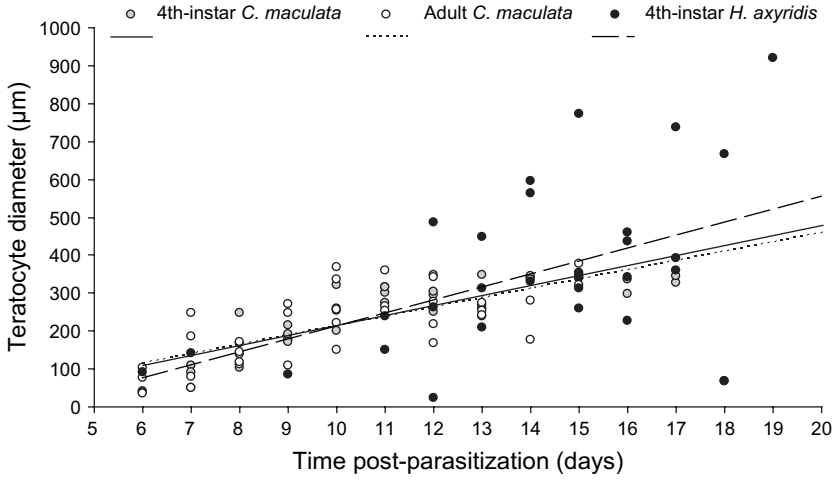

Fig. 2. *Dinocampus coccinellae* teratocyte diameter (µm) in suitable host *Coleomegilla maculata* and marginal host *Harmonia axyridis* in function of the time postparasitization (days).

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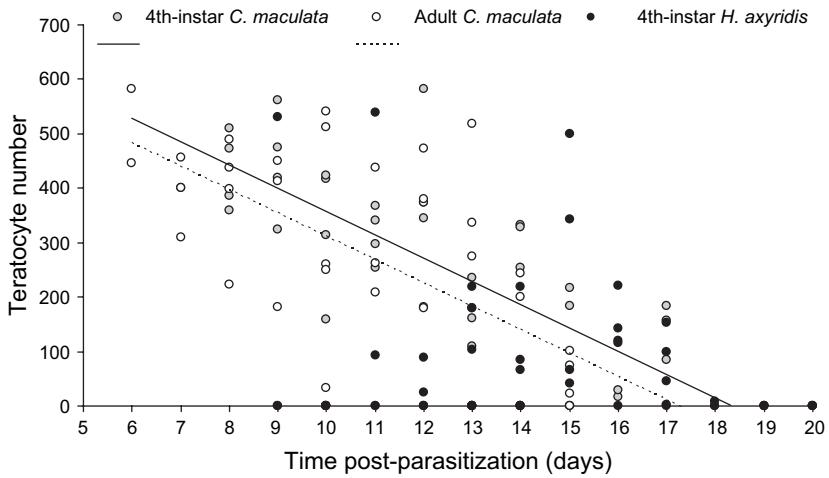

Fig. 3. *Dinocampus coccinellae* teratocyte number in suitable host *Coleomegilla maculata* and marginal host *Harmonia axyridis* in function of the time postparasitization (days).

parasitoid either fails to develop or develops more slowly. It is proposed that quantifying the teratocyte growth pattern could provide a suitable index of the physiological suitability of other coccinellid hosts belonging to *D. coccinellae* host range (approximately 40 coccinellids species). Such an index would provide cues to understand the limitation of a parasitoid host range and would also predict the performance of parasitoids on novel hosts after a biological control introduction.

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