

Costs of secondary parasitism in the facultative hyperparasitoid

***Pachycrepoideus dubius*: does host size matter?**

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Abstract - Although hyperparasitism frequently occur in parasitic insects, many aspects of this strategy remain unknown. We investigated possible fitness costs of hyperparasitism as influenced by host size. Our study was conducted with the facultative hyperparasitoid *Pachycrepoideus dubius* Ashmead (Hymenoptera: Pteromalidae), which parasitizes host species differing greatly in size. We compared some fitness traits (level of successful parasitism, development time, sex ratio and offspring size) of *P. dubius* developing on large secondary / primary (*Delia radicum* L. (Diptera: Anthomyiidae)/ *Trybliographa rapae* Westwood (Hymenoptera: Figitidae)) or small secondary / primary host species (*Drosophila melanogaster* L. / *Asobara tabida* Nees (Hymenoptera: Braconidae)). In no-choice and choice experiments, *P. dubius* was able to develop on different stages of *T. rapae* (L2 (endophagous), L4 (ectophagous), and pupae) but that it preferred to parasitize unparasitized *D. radicum* pupae over pupae parasitized by *T. rapae*. Furthermore, in *P. dubius*, hyperparasitism was associated with fitness costs (lower level of successful parasitism, smaller adult size) and these costs were greater on the smallest host complex. We hypothesize that the size of *D. melanogaster* pupae parasitized by *A. tabida* may be close to the suboptimal host size for *P. dubius* beneath which the costs of hyperparasitism make this strategy nonadaptive. Hyperparasitism in terms of trade-offs between host quality and abundance of competitors is discussed.

Key words - *Pachycrepoideus dubius*, Hymenoptera, Pteromalidae, *Delia radicum*, *Trybliographa rapae*, *Drosophila melanogaster*, *Asobara tabida*, facultative hyperparasitism, fitness, host size, host quality.

INTRODUCTION

Hyperparasitism is one of the most complex interactions between animals (Sullivan, 1987, 1988). Hyperparasitoids develop on or inside other parasitoids, called primary hosts, while hosts of primary parasitoids (often phytophagous insects) are named secondary hosts (Sullivan, 1987, 1988). This parasitic strategy is widespread in insects, especially in the Hymenoptera (Gordh, 1981). The majority of hyperparasitoids are ectoparasitoids, and attack the larval or the pupal stage of their primary hosts (Gordh, 1981). Two main types of hyperparasitism can be distinguished: obligatory and facultative hyperparasitism. An obligatory hyperparasitoid develops exclusively on primary parasitoids, whereas a facultative hyperparasitoid can develop on either the primary parasitoid or its host (Sullivan, 1987). Although hyperparasitism occurs frequently in animal communities, many aspects of this parasitic strategy, such as life history, evolution of facultative hyperparasitism, and consequences of hyperparasitism on community ecology, remain unknown (Brodeur, 2000).

In the present paper we aimed at better understanding the evolution of facultative hyperparasitism by studying potential costs associated with this strategy. Facultative hyperparasitism is common in many families of Hymenoptera where it seems more frequent than obligatory hyperparasitism (Brodeur, 2000). Facultative hyperparasitism may represent an evolutionary transition between primary parasitism and obligatory hyperparasitism, and studying this strategy could help understanding the shift of trophic levels (Brodeur, 2000). According to Godfray (1994), competition for hosts may have been the most significant factor in the evolution of primary parasitism towards facultative hyperparasitism. Indeed, facultative hyperparasitism can be very advantageous for competing parasitoids because it provides access to additional host resources. However, the quality of such host resources for the developing offspring may differ in terms of type of host (phytophagous vs entomophagous) and in terms of host size (loss in biomass because of energy required to convert phytophagous-biomass into primary parasitoid-biomass – van Alphen & Thunnissen, 1983). Therefore, fitness costs may be associated with such a parasitic strategy. Moreover, the extent of these costs may be strongly influenced by the initial size of the phytophagous secondary

host. Herein, we addressed fitness costs of hyperparasitism and the influence of the size of the secondary host on these costs.

Our study was conducted with the facultative hyperparasitoid, *Pachycrepoideus dubius* Ashmead (Hymenoptera: Pteromalidae), a solitary idiobiont ectoparasitoid distributed worldwide (Crandell, 1939). It is a generalist known to parasitize the pupal stages of a variety of cyclorrhaphous flies (Nostvik, 1954). *Pachycrepoideus dubius* has also been recorded as an ectophagous hyperparasitoid of a few species of parasitoids such as *Leptopilina heterotoma* Thomson (Cynipidae) and *Asobara tabida* Nees (Braconidae), parasitizing *Drosophila melanogaster* (van Alphen & Thunnissen, 1983). In our laboratory, *P. dubius* is reared on pupae of the cabbage root fly *Delia radicum* L. (Diptera: Anthomyiidae), and was also observed parasitizing *Trybliographa rapae* Westwood (Hymenoptera: Figitidae), a specialist larval parasitoid of *D. radicum*. In spite of this observation, the hyperparasitism level and success of *P. dubius* on *T. rapae*, which development comprises both an endophagous and an ectophagous stage, remains unknown.

In this study, we first questioned the occurrence of hyperparasitism in the newly recorded host complex, *D. radicum* / *T. rapae*. For that purpose, we evaluated the ability of *P. dubius* to hyperparasitize *D. radicum* pupae infested by different development stages of the primary parasitoid, *T. rapae*, in no-choice experiments, and we evaluated the preference of *P. dubius* between unparasitized *D. radicum* pupae and pupae parasitized by *T. rapae* in choice experiments.

Second, we investigated possible fitness costs of hyperparasitism and the influence of host size on such costs. To evaluate these costs, we compared levels of successful parasitism, development time, sex ratio and offspring size of *P. dubius* developing as primary parasitoid or hyperparasitoid on large (*D. radicum* / *T. rapae*) or small secondary / primary host species (*D. melanogaster* / *A. tabida*). Studying the cost of hyperparasitism necessarily involves the use of different species. Therefore, to confirm our results, we also studied these life history traits on different size hosts of a single species: *D. radicum*.

MATERIALS AND METHODS

Insects

The secondary host. The *D. radicum* strain originated from pupae collected from Crucifera fields (Le Rheu, Brittany, France) in 1994. It was reared in a climate room ($20 \pm 2^\circ\text{C}$, 60 ± 10

% r.h., L16:D8) on rutabaga (*Brassica napus* L.) roots. Preliminary experiments (Grandgirard, unpubl.) showed that maximal infestation levels of *D. radicum* by *P. dubius* were obtained with pupae aged 5-10 days after pupation. Therefore in all our experiments, we used 7-day-old *D. radicum* pupae. The size of the pupae used in all the experiments is reported in Table 1. The *D. melanogaster* strain was collected in Ste Foy-les-Lyon (France) in 1991. The flies were provided by G. Doury (Amiens, France), where they were reared on an artificial diet (David, 1959) under laboratory conditions described by Monconduit & Prévost (1994). In our laboratory, they were maintained at 25 ± 2 °C (60 ± 10 % r.h., L16:D8). The pupae (≈ 3 mm in length, table 1) were used in our experiments six days after hatching.

The primary host. *Trybliographa rapae* was reared on *D. radicum* as described by Neveu et al. (1996). The strain also originated from *D. radicum* pupae collected from Crucifera fields (Le Rheu, Brittany, France) in 1994 and was refreshed yearly. It was reared in a climate room (20 ± 2 °C, 60 ± 10 % r.h., L16:D8). It is a koinobiont endoparasitoid with an endophagous and an ectophagous stage: the first and the second instar larvae develop inside the host, while the third and fourth instar develop outside the host but within the puparium (Wishart & Monteith, 1954). Three *T. rapae* development stages were used as primary hosts in our experiments: endophagous larvae (second stage, 14 days old after parasitism, ≈ 0.7 mm in length), ectophagous larvae (fourth-instar, 24 days old, ≈ 3 mm in length), and pupae (40 days old, ≈ 3.5 mm in length). The *A. tabida* strain was collected in Ste Foy-les-Lyon (France) in 1991. It was provided by G. Doury (Amiens, France) where it was reared as described by Monconduit & Prévost (1994) on its habitual host, *D. melanogaster*. *Drosophila melanogaster* pupae parasitized by the ectophagous stage of *A. tabida* (≈ 1.5 mm in length, 12 days old) were used in our experiments. Parasitized pupae were maintained at 25 ± 2 °C (60 ± 10 % r.h., L16:D8) in our laboratory.

The hyperparasitoid. The *P. dubius* strain was provided by R. Allemand (Villeurbanne, France). *Pachycrepoideus dubius* was reared on *D. radicum* pupae in a climate room (25 ± 2 °C, 60 ± 10 % r.h., L16:D8). Adults were maintained in plexiglas cages (25×25×25 cm) with two openings (\varnothing : 6 cm) on the sides covered with mesh screen. Fresh droplets of honey and a humidified piece of cotton were provided regularly. A petri dish filled with fine sand containing about 100 *D. radicum* pupae was placed in the cage for parasitism. Pupae were

changed three times a week. Parasitized pupae were stored in petri dishes in the climate room until emergence of *P. dubius*, and new adults were introduced into the rearing cage.

Experiments

All experiments were conducted in a climate room (25 ± 2 °C, 60 ± 10 % r.h., L16:D8). The experiments always started in the morning which is the time of highest activity in *P. dubius* females (Crandell, 1939). The females used were between 18 and 39 h-old and of medium size (≈ 2 mm in length). They were mated and naive (no previous oviposition experience).

Occurrence of hyperparasitism in the newly recorded host complex, D. radicum / T. rapae

No-choice experiments. One *P. dubius* female was placed in a petri dish (\emptyset : 8 cm, h: 2.5 cm) with water and honey and five *D. radicum* pupae for 24 h. Pupae were glued to the bottom of the petri dish with UHU Patafix®. The pupae were either unparasitized or parasitized by one of the three development stages of *T. rapae*. This experiment was repeated between 23 and 27 times for each type of host tested, the different treatments were combined randomly. The pupae were dissected to determine levels of parasitism and superparasitism. Leaving the female during 24 h with five hosts increases the probability that all hosts will be attacked, therefore, superparasitism levels were used to distinguish between different strategies in *P. dubius* confronted with unparasitized or parasitized hosts.

Choice experiments. One *P. dubius* female was placed for 8 h in a small petri dish (\emptyset : 3 cm, h: 1 cm) with four unparasitized *D. radicum* pupae and four *D. radicum* pupae parasitized by *T. rapae* at the ectophagous stage. The ectophagous stage of *T. rapae* was chosen because it is probably the easiest stage to detect for *P. dubius* females, since it is a mobile stage (in contrast to *D. radicum* or *T. rapae* pupae) and since at the end of that stage the entire *D. radicum* pupae will be consumed. The pupae were arranged in a circle (\emptyset : 2.5 cm) alternating unparasitized and parasitized pupae. This experiment was repeated 30 times. After females were removed, pupae were dissected and the number and distribution of eggs were recorded.

Costs of hyperparasitism and influence of host size. As in the first experiment, one *P. dubius* female was placed in a petri dish (\varnothing : 8 cm, h: 2.5 cm) for 24 h with water, honey and five pupae. The pupae were *D. radicum* or *D. melanogaster* pupae either unparasitized or parasitized by the ectophagous stage of *T. rapae* or *A. tabida*. Following parasitism by *P. dubius*, the pupae were individually isolated in gelatin capsules and placed in a climate room (25 ± 2 °C, 60 ± 10 % r.h., L16:D8) until emergence. Emerging adults were frozen ($- 18$ °C) on the day of emergence to be preserved before different measurements were performed. The variables used to evaluate fitness were: level of successful parasitism (% emerging adults), development time (recorded daily), secondary sex ratio (percentage of males emerged) and size (total body length : from top of head to tip of abdomen).

This experiment was carried out on: 1) unparasitized *D. radicum* pupae and *D. radicum* pupae parasitized by *T. rapae* at the ectophagous stage (30 replicates for each host type), 2) large *D. radicum* pupae (≈ 6.3 mm in average) and small *D. radicum* pupae (≈ 5.0 mm in average) (24 replicates for each size), and 3) unparasitized *D. melanogaster* pupae and *D. melanogaster* pupae parasitized by *A. tabida* at the ectophagous stage (16 replicates for each host type). See Table 1 for sizes of pupae used in this experiment.

Statistical analysis

The effect of host types on: percentages of parasitism, percentages of superparasitism, percentages of successful parasitism, and sex ratio (% males) was analyzed with an ANOVA. As the number of pupae proposed was not the same in each replicate, the effect of host types on the percentages of parasitism, percentages of superparasitism, percentages of successful parasitism, and sex ratio was analyzed with an ANOVA using binomial errors and number of proposed pupae as sample size. ANOVA analysis were conducted using GLIM 3.77 (Royal Statistical Society of London, 1985). We verified that there was no overdispersion in the data using appropriate tests (χ^2 or F; Crawley, 1993). Unpaired t tests were used to compare development times and sizes of offspring among the different host types tested.

RESULTS

Occurrence of hyperparasitism in the newly recorded host complex, D. radicum / T. rapae

No-choice experiments. The number of females that did not oviposit on any host was not significantly different for any host types tested ($\chi^2 = 2.19$, 3 df, $P > 0.05$) (table 2). Therefore, only ovipositing females were taken into consideration to calculate parasitism and superparasitism levels. All host types offered were parasitized by *P. dubius*. Parasitism levels (expressed as the number of parasitized pupae relative to the total number of pupae offered) ranged between 81.0 and 90.8% and did not differ significantly among host types ($\chi^2 = 4.72$, 3df, $P > 0.05$) (Table 2). However, superparasitism levels (expressed as the number of pupae bearing more than one egg relative to the number of parasitized pupae) differed significantly among host types ($\chi^2 = 16.35$, 3 df, $P < 0.001$), they were twice as high on unparasitized pupae than on pupae parasitized by *T. rapae* (Table 2).

Choice experiments. When *P. dubius* females were given a choice between unparasitized and parasitized *D. radicum* pupae, they significantly preferred to parasitize unparasitized pupae ($\chi^2 = 6.25$, 1 df, $P < 0.05$) (Table 3). Superparasitism levels remained low and were higher on unparasitized than on parasitized pupae ($\chi^2 = 4.36$, 1 df, $P < 0.05$).

Costs of hyperparasitism and influence of host size

Delia radicum / Trybliographa rapae host complex. Successful parasitism was calculated as the number of *P. dubius* adults emerging relative to the total number of pupae exposed to the parasitoid. Only replicates in which at least one *P. dubius* emerged were used in the calculations for all experiments. The level of successful parasitism was high on unparasitized (84.1%) and on parasitized *D. radicum* pupae (80.7%) and no significant difference was found between the two host types ($F_{1,54} = 0.13$, $P > 0.05$) (Fig. 1A).

Development time on unparasitized and parasitized *D. radicum* pupae did not differ significantly ($t = 0.51$, $P > 0.05$). The mean development time of *P. dubius* was close to 23 days (Fig. 1B). There was no significant difference between the percentage of males emerging from unparasitized or parasitized *D. radicum* pupae ($\chi^2 = 0.911$, 1 df, $P > 0.05$) (Fig. 1C). The sex ratio did not differ significantly from a 1:1 distribution ($\chi^2 = 3.71$, 1 df, $P > 0.05$).

Individuals developing on parasitized pupae (2.08 mm) were significantly smaller than individuals developing on unparasitized pupae (2.22 mm) ($t = -6.21$, $P < 0.001$) (Fig. 1D).

Large and small unparasitized D. radicum pupae. The level of successful parasitism was high (around 80%) and did not differ significantly between the two host sizes ($F_{1,37} = 0.38$, $P > 0.05$) (Fig. 2A). The development time of *P. dubius* averaged 25 days and did not differ significantly between the two host sizes tested ($t = -1.85$, $P > 0.05$) (Fig. 2B).

The sex ratio did not differ significantly between the two host sizes ($\chi^2 = 0.79$, 1 df, $p > 0.05$) and did not differ significantly from a 1:1 distribution ($\chi^2 = 0.02$, 1 df, $P > 0.05$) (Fig. 2C). The emerging adults were significantly smaller on small pupae (2.14 mm) than on large pupae (2.22 mm) ($t = 3.26$, $P > 0.001$) (Fig. 2D).

Drosophila melanogaster / Asobara tabida host complex. The level of successful parasitism significantly differed between the two host types ($\chi^2 = 12.89$, 1 df, $P < 0.001$), it was lower on parasitized (45.3%) than on unparasitized *D. melanogaster* pupae (78.8%) (Fig. 3A). The development time was significantly longer on parasitized (18.7 days) than on unparasitized *D. melanogaster* pupae (17.8 days) ($t = -2.55$, $P < 0.05$) (Fig. 3B).

The sex ratio differed significantly between the two host types ($\chi^2 = 7.17$, 1 df, $P < 0.01$). It did not differ significantly from a 1:1 distribution on unparasitized pupae (51.2% of males), ($\chi^2 = 0.02$, 1 df, $P > 0.05$) and was male-biased on parasitized pupae (83.3%) ($\chi^2 = 8.75$, 1 df, $P < 0.01$). Only four females of *P. dubius* emerged from parasitized pupae (Fig. 3C). Individuals developing on parasitized pupae (1.43 mm) were significantly smaller than individuals developing on unparasitized pupae (1.80 mm) ($t = 8.24$, $P < 0.001$) (Fig. 3D).

DISCUSSION

According to Godfray (1994), competition for hosts is the most important factor in the evolution of primary parasitism towards facultative hyperparasitism. In pupal parasitoids, this evolution is likely to be a result of competition with larval parasitoids. In an environment with strong interspecific competition, larval parasitoids have an important competitive advantage over pupal parasitoids since they have access to hosts before pupal parasitoids. Therefore when there is a strong competition with larval parasitoids, it may be advantageous for pupal

parasitoids, like *P. dubius*, to become facultative hyperparasitoid. Indeed this strategy provides access to additional host resources and, as a result of hyperparasitism, leads to a reduction of competition in the next generation. However, as we stated in the introduction, costs may be associated with this strategy since the quality of primary hosts for developing offspring may be inferior to that of secondary hosts.

We studied the occurrence of hyperparasitism behaviour in *P. dubius* in the newly recorded host complex, *D. radicum* / *T. rapae*. In the no-choice experiments, we showed that *P. dubius* females accepted at equal rates both unparasitized *D. radicum* pupae and *D. radicum* pupae that were already parasitized by the larval parasitoid *T. rapae* at the three development stages tested (endophagous larvae, ectophagous larvae, and pupae). This result suggests that when *P. dubius* is in an environment where competition with this larval parasitoid is very strong, it will be able to parasitize the majority of already parasitized hosts regardless of the stage of the developing primary parasitoid.

Nevertheless, high levels of superparasitism on unparasitized *D. radicum* pupae could indicate a preference for healthy pupae. The results obtained in the choice experiments confirm this preference since they show that *P. dubius* females oviposit preferentially in healthy *D. radicum* pupae rather than in pupae parasitized by *T. rapae*. These results suggest that when competing larval parasitoids are not very abundant, *P. dubius* females will oviposit preferentially in healthy pupae. This behaviour appears to be adaptive, because females choose the hosts ensuring the highest fitness to their progeny. Indeed, our results show that hyperparasitoid development is costly, and that the extent of the costs are influenced by host size.

Preference for unparasitized *D. radicum* pupae versus pupae parasitized by *T. rapae* may be due to the perception of differences in the quality of the two host types, in terms of total amount and kind of resources available. However, the influence of artificial selection or preimaginal conditioning can not be excluded since *P. dubius* has been reared on unparasitized *D. radicum* pupae in our laboratory for the last three years. Oviposition preferences for hosts they had been reared on has been shown in other facultative hyperparasitoids (Kfir et al., 1993).

In the *D. radicum* / *T. rapae* complex, a large size host-complex for *P. dubius*, the fitness costs of hyperparasitism appeared moderate; levels of successful parasitism,

development time, and sex ratio of the offspring were not significantly different than when *P. dubius* parasitize *D. radicum*. One difference was that individuals developing as hyperparasitoids were smaller than individuals developing as primary parasitoids. Adult size, however, plays a major role in individual fitness, since in many parasitoids species it can be correlated with survival and mating success of parasitoids (Godfray, 1994; Nicol & Mackauer, 1999; Ueno, 1999; van dem Assem et al., 1989). In *P. dubius*, it has been shown that large males win more often the competition for mating than small males (M. Goubault, M. plantegenest, D. poinsot, L. Krespi, A.M. Cortesero, unpubl.). The causal link between female size and other components of female fitness remains to be tested in *P. dubius*.

Host quality is generally considered to depend on species, development stage, size, and parasitism status of the host (Godfray, 1994). *Delia radicum* and *T. rapae* are different species which differ in development stage and size. Host size may play a major role in the quality difference between primary and secondary hosts, since in idiobionts such as *P. dubius*, host size is a key factor of female fitness because resources available to the immature stages are fixed (Otto & Mackauer, 1998). The results obtained with large and small *D. radicum* pupae tend to confirm this hypothesis: when *P. dubius* developed on small pupae the same results as with pupae parasitized by *T. rapae* were obtained (a decrease in size of the adults but no difference in successful parasitism, development time, and sex ratio).

Pachycrepoideus dubius is a generalist parasitoid which has been recorded on hosts differing greatly in size. *Pachycrepoideus dubius* has been found, for example, on *Calliphora* spp. which pupae can reach 14 mm, but also on *D. melanogaster* which pupae do not exceed 3 mm (Perrier, 1963; Rueda & Axtell, 1985). We hypothesized that costs of hyperparasitism may be more important on a smaller host complex such as *D. melanogaster* and its usual parasitoid, *A. tabida*. Indeed, the size of this complex is very small and may be close to the size beneath which hyperparasitism becomes lethal for *P. dubius*.

Our results tend to confirm this hypothesis since development of *P. dubius* as a hyperparasitoid on the *D. melanogaster* / *A. tabida* complex affected all fitness variables measured. Compared to development on unparasitized *D. melanogaster* pupae, the level of successful parasitism was halved, development time was longer, the sex ratio was strongly male biased, and adult size was much smaller. Moreover, half of the parasitized pupae exposed to the parasitoid gave no emergence at all (neither *P. dubius* nor *A. tabida*), whereas such a mortality was never observed on *D. radicum* parasitized pupae.

These results indicate that a female *P. dubius* may gain less fitness from

hyperparasitism in the *D. melanogaster* / *A. tabida* host complex than in the *D. radicum* / *T. rapae* host complex. These two complexes only differed in quality by host species and size. Indeed, only hosts previously unparasitized by *P. dubius* were used in the experiments and both species of primary hosts used were at the same stage of development. In our study, there appears to be a relationship between pupal size of the hosts and fitness of females using these hosts (*D. radicum* unparasitized > *D. radicum* parasitized > *D. melanogaster* unparasitized > *D. melanogaster* parasitized), therefore the fitness costs associated with hyperparasitism seem to depend on the size on the host-parasitoid complex. The size of *D. melanogaster* pupae parasitized by *A. tabida* may be close to the suboptimal host size for *P. dubius* beneath which the costs of hyperparasitism make this strategy nonadaptive. Although host size is likely to have a strong influence on the fitness costs associated with hyperparasitism in *P. dubius*, the influence of host species cannot be completely ruled out and additional experiments using large and small *D. radicum* pupae parasitized by *T. rapae* would be necessary.

Although some fitness costs are involved with facultative hyperparasitism, this strategy allows *P. dubius* to adapt to variations the quality of its environment. Indeed, if *P. dubius* is in an environment with few competing larval parasitoids, it will often meet healthy hosts. Based on our results, we can assume that, under these conditions, it will be able to parasitize the majority of these hosts and will produce presumably high fitness offspring. On the other hand, when competing larval parasitoids are abundant in the environment, *P. dubius* will often meet parasitized hosts. In this case, parasitism levels may remain high, but offspring fitness will decrease. We have shown that in the case of particularly small hosts, the costs associated with hyperparasitism could be very important. However, this strategy remains adaptive because it is better to have the ability to oviposit, even in a poor quality host, than to die with unlaidd eggs. Therefore, in natural conditions, *P. dubius* populations could be maintained regardless of the abundance of larval competitors in the foraging environment of the females.

Facultative hyperparasitism, which enables *P. dubius* to adapt to a varying environment and especially to population fluctuations of its hosts, appears to be a very advantageous strategy for this parasitoid. *Pachycrepoideus dubius* has been described in many areas of the world (North America, South America, West Indies, Africa, Europe, etc., Rueda & Axtell, 1985) and such a hyperparasitic strategy could be in part responsible for its cosmopolitan distribution.

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Tables and figures

Table 1 - Mean (\pm SE) size (length in mm) of the host pupae (*Delia radicum* and *Drosophila melanogaster*) used in all the experiments

	<i>D. radicum</i> pupae (mean size \pm SE)	n pupae	<i>D. melanogaster</i> pupae (mean size \pm SE)	n pupae
Unparasitized	5.41 \pm 0.02	189	3.04 \pm 0.03	40
Parasitized by:				
- <i>Trybliographa rapae</i>	4.97 \pm 0.02	396		
- <i>Asobara tabida</i>			2.48 \pm 0.03	36
Large unparasitized	6.29 \pm 0.02	107		
Small unparasitized	5.09 \pm 0.04	121		

Table 2 - Percentage of *Pachycrepoides dubius* females not ovipositing on any host and levels of parasitism and superparasitism of different host types by *P. dubius* in 24 h no-choice experiments. The hosts used were either unparasitized *Delia radicum* pupae (unpara) or *D. radicum* pupae parasitized by *Trybliographa rapae* at different development stages : endophagous (endo), ectophagous (ecto) or pupal (pupal)

	% females not ovipositing on any host	n females	% parasitism (mean \pm SE)	n pupae	% superparasitism (mean \pm SE)	n pupae
unpara	22.2a	27	90.8 \pm 0.1a	98	43.8 \pm 0.3a	89
endo	8.7a	23	82.7 \pm 0.3a	98	21.0 \pm 0.2b	81
ecto	13.0a	23	81.0 \pm 0.3a	100	23.5 \pm 0.3b	81
pupal	20.8a	24	86.7 \pm 0.2a	90	24.4 \pm 0.3b	78

Values in the same column followed by different letters are significantly different at $P < 0.05$ (ANOVA using binomial errors and number of proposed pupae as sample size followed by χ^2).

Table 3 - Levels of parasitism and superparasitism by *Pachycrepoideus dubius* when given a choice (for eight hours) between four unparasitized *Delia radicum* pupae (unpara) and four *D. radicum* pupae parasitized by *T. rapae* at the ectophagous larval stage (para)

	% parasitism (mean \pm SE)	% superparasitism (mean \pm SE)
unpara	84.5 \pm 0.2a	14.9 \pm 0.1a
para	70.1 \pm 0.2b	6.7 \pm 0.1b
n females	27	13

Values in the same column followed by different letters are significantly different at $P < 0.05$ (ANOVA using binomial errors and number of proposed pupae as sample size followed by χ^2).

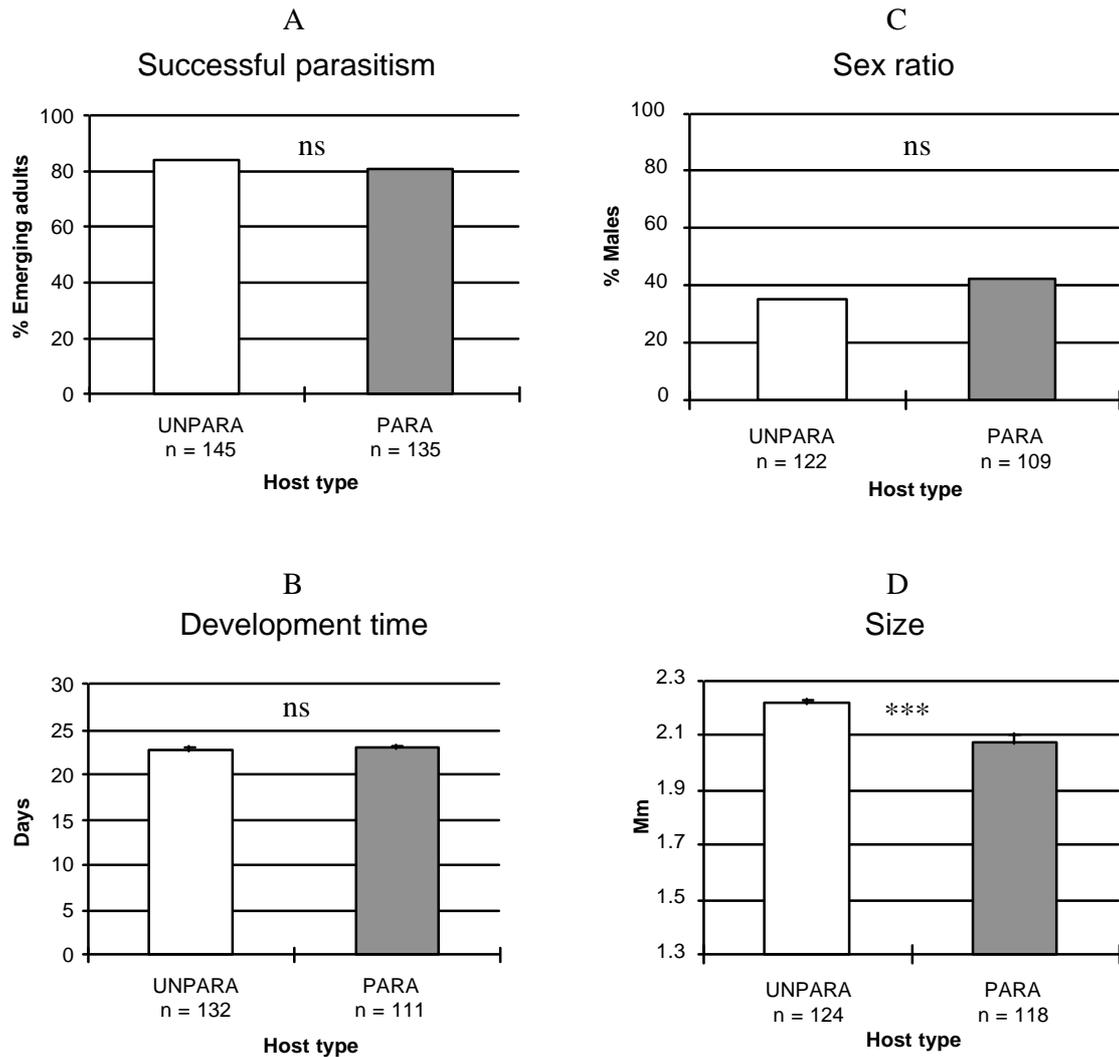


Figure 1 - Level of successful parasitism (A), development time (B), sex ratio (C), and size (D) of *Pachycrepoideus dubius* developing on unparasitized *Delia radicum* pupae (UNPARA) or on *D. radicum* pupae parasitized by *Trybliographa rapae* (PARA). [Proportions (\pm SE) were analyzed with an ANOVA using binomial errors and number of proposed pupae as sample size followed by appropriate test (χ^2 or F) (ANOVA analysis were conducted using GLIM 3.77) (A, C) and means (\pm SE) by t tests (B, D). *** : P < 0.001, ns : not significant. n = number of *P. dubius*].

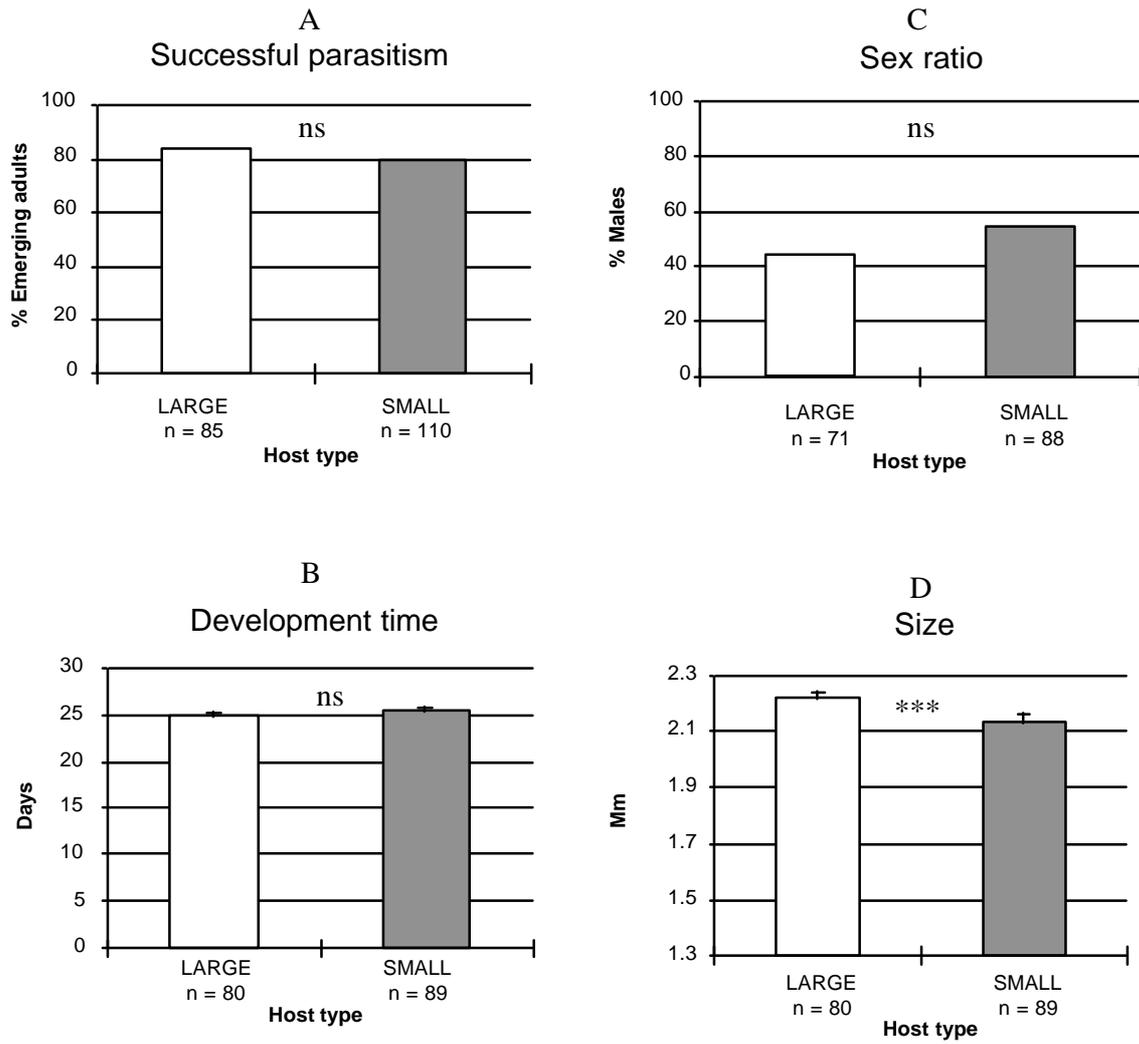


Figure 2 - Level of successful parasitism (A), development time (B), sex ratio (C), and size (D) of *Pachycrepoideus dubius* developing on large or small *Delia radicum* pupae. See legend in Fig. 1.

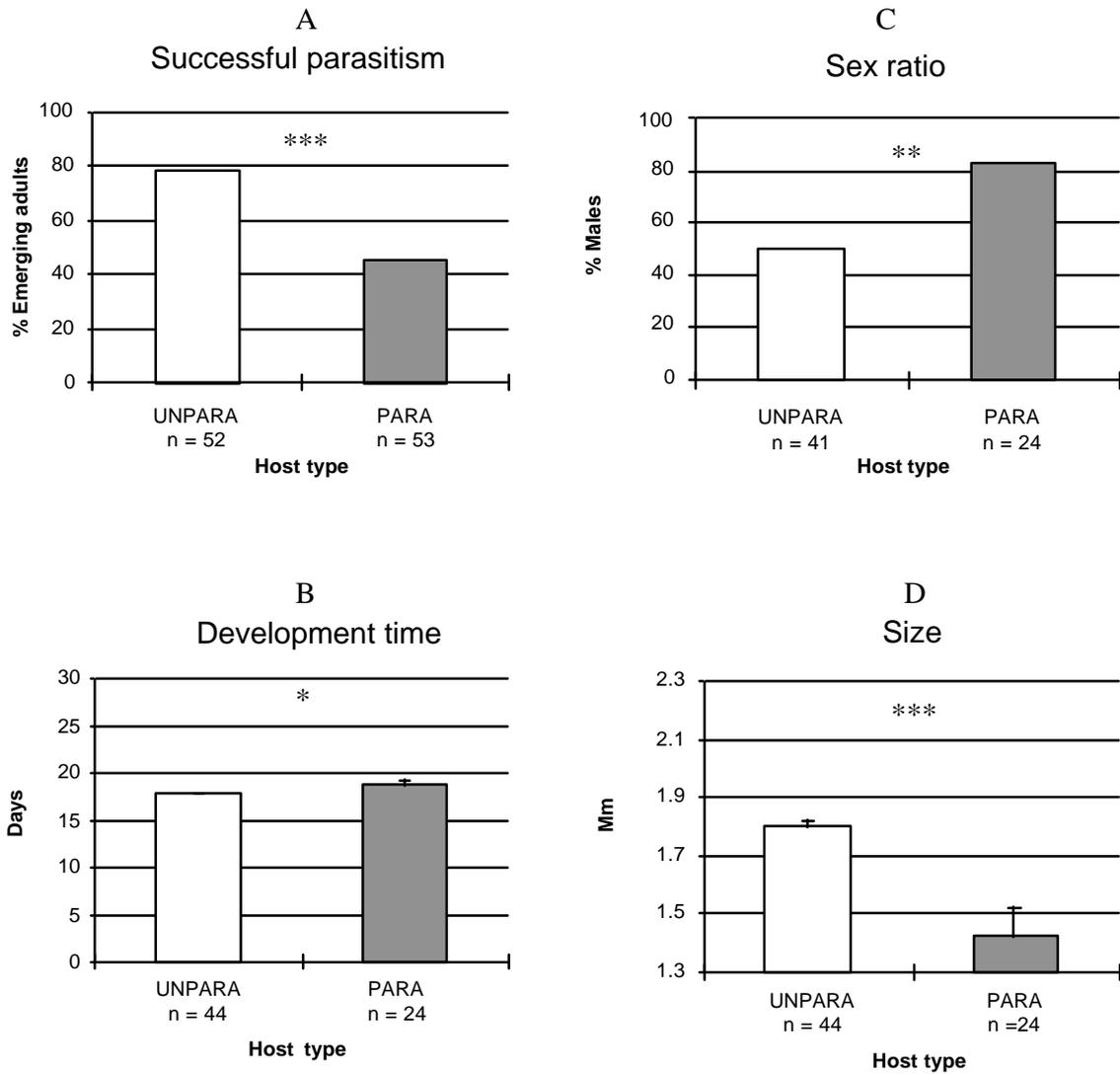


Figure 3 - Level of successful parasitism (A), development time (B), sex ratio (C), and size (D) of *Pachycrepoideus dubius* developing on unparasitized *Drosophila melanogaster* pupae (UNPARA) or on *D. melanogaster* pupae parasitized by *Asobara tabida* (PARA). See legend in Fig. 1.