

# Influence of a bimodal emergence strategy of a Dipteran host on life-history traits of its main parasitoids

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**Abstract.** 1. Among a great diversity of other strategies, insects have evolved polymodal emergence patterns that can increase survival in the face of annual variations in environmental conditions. *Delia radicum* L. (Diptera: Anthomyiidae) is a polyvoltine pest that attacks several cultivated cruciferous species. At the time of emergence, most populations show a polymodal emergence of type A (i.e. all individuals that enter diapause in the same year terminate diapause the following growing season, and exhibit a bimodal emergence curve). This results in the occurrence of two sympatric phenotypes, early and late, which differ by the timing of adult emergence in both diapausing and non-diapausing generations.

2. In Brittany, *D. radicum* pupae can be heavily parasitised by three parasitoids, *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae), *Aleochara bipustulata* L., and *Trybliographa rapae* (Hymenoptera: Eucoilidae). As in all parasitoids species, the successful development of both *Aleochara* species and *T. rapae* larvae depends mainly on the amount and quality of the food provided by the host.

3. The relationship between early and late host phenotype and (i) the parasitism efficiency, (ii) emergence patterns, and (iii) host selection behaviour were investigated for the three parasitoid species.

4. Depending on parasitoid species and their different parasitism and development mode, the results reveal that host phenotype can influence (i) survival and development time in *T. rapae*, and (ii) survival in *Aleochara* species. *Aleochara* larvae did not appear to discriminate between early and late host pupae on the basis of phenotype, but rather selected them according to their developmental stage. Furthermore, it was discovered that the same phenological strategy occurred in *T. rapae* and in *D. radicum*. However, for *D. radicum* the results indicate that such a strategy has a cost as the longer development time of late host pupae results in a longer period of time favourable for parasitism.

**Key words.** *Delia radicum*, emergence pattern, life-history traits, parasitoids.

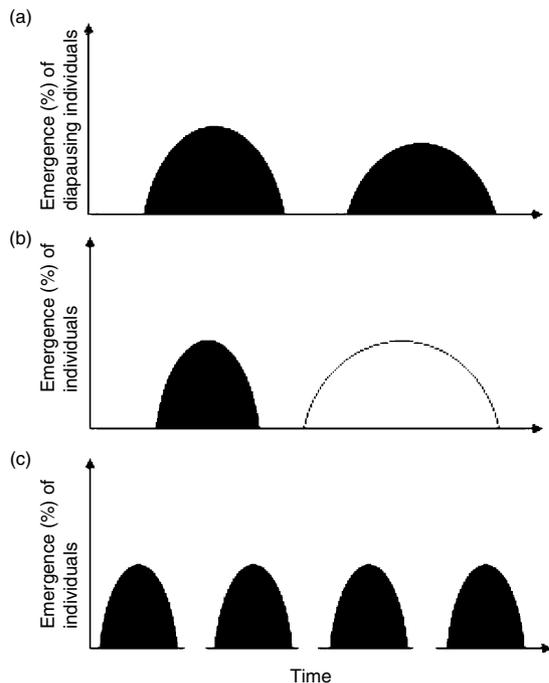
## Introduction

Among insects, life cycles usually involve four main phases: reproduction, growth and development, dormancy, and movement and migration. The seasonal timing of each of these phases is adapted, in part, to circumvent unfavourable physical factors and, in part, to synchronise activity with

favourable physical conditions and seasonally available, biotic requisites such as food, mates, oviposition sites, and periods free from natural enemies (Tauber & Tauber, 1978). Among a great diversity of other strategies, insects have developed polymodal emergence that can increase survival facing the annual variations of environmental conditions. Such a strategy has evolved essentially in Lepidopteran and Dipteran species, but also in some Hymenopteran and Odonata species (Bradshaw, 1973; Waldbauer, 1978; Finch & Collier, 1983; Hagen & Lederhouse, 1985; Goulson, 1993; Biron *et al.*, 2002, 2003). According to

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Waldbauer (1978) and Tauber *et al.* (1986), it can be divided in three major types (Fig. 1). In type A (Fig. 1a), all individuals that enter diapause in the same year terminate diapause the following growing season, and exhibit a bimodal emergence curve. In type B (Fig. 1b), the modes of the polymodal emergence curve represent individuals that belong to different year classes. In type C (Fig. 1c), the emergence of a year class extends over two or more years, resulting in two or more modes that are separated by intervals of 1 year (Waldbauer, 1978). Some Dipteran and Lepidopteran pest species of economic importance show the polymodal emergence of type A (Biron *et al.*, 2002, 2003). Among them is the cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae), a polyvoltine pest that attacks several cultivated and wild cruciferous species in the temperate zone (35–68°N) (CAB, 1989). *Delia radicum* overwinters as a pupa and in the spring most of the populations show a type A polymodal emergence pattern (Finch & Collier, 1983; Finch *et al.*, 1986; Walgenbach *et al.*, 1993). Two sympatric phenotypes, early and late, are observed in *D. radicum* populations, which differ by the timing of adult emergence in both diapausing and non-diapausing generations (Waldbauer & Sternburg, 1986; Collier *et al.*, 1989). The criterion for differentiating both phenotypes is emergence in less than 20 days for the early phenotype and in more than 30 days for the late phenotype at  $19 \pm 1^\circ\text{C}$  (Collier *et al.*, 1989; Walgenbach *et al.*, 1993). Like other species showing a polymodal emergence, the expression of early and late phenotypes of *D. radicum* is controlled genetically (Goulson, 1993; Biron, 1998; Biron *et al.*, 1998, 2002). Both phenotypes result in different



**Fig. 1.** Phenological patterns observed for polymodal emergence in insects: (a) type A, (b) type B, and (c) type C. The graphs have different time scales.

development times at the pupal stage, which is three times longer for late pupae than for early ones (Biron *et al.*, 2002). Moreover, a significant maternal effect is observed on the mortality of eggs (Biron *et al.*, 1999).

In Brittany (western France), *D. radicum* pupae can be heavily parasitised by three parasitoid species: *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae), *Aleochara bipustulata* L. and *Trybliographa rapae* West. (Hymenoptera: Eucilidae) (Lahmer, 1982; Brunel & Fournet, 1996). Both *Aleochara* species parasitise *D. radicum* at the pupal stage. The first-instar larva locates and penetrates inside the host puparia, and then develops as an ectoparasitoid of the host pupa. *Trybliographa rapae*, on the other hand, is a koinobiont parasitoid of *D. radicum* larvae (Wishart & Monteith, 1954). The larva first develops as an endoparasitoid until the pupal stage of *D. radicum* and then becomes an ectoparasitoid and feeds on the fly remains.

Late *D. radicum* pupae take longer to develop than early ones and successful development of parasitoid larvae depends strongly on the quality of food provided by the host (see reviews by Godfray, 1994; Jervis & Copland, 1996; Strand, 2000). Therefore, it is hypothesised that the phenotype of *D. radicum* could seriously influence life-history traits such as survival and development time of its parasitoids. Previous results tend to confirm this hypothesis as the *D. radicum* phenotype significantly affects survival and development time of *A. bilineata* larvae (Langlet, 1997).

Thus, the main objective of this study was to determine whether the host phenotype should be considered as a new component of host quality for *D. radicum* parasitoids. This question was addressed by studying the influence of early or late host phenotypes on the parasitism efficiency and emergence patterns of two of the three major parasitoids of *D. radicum* in Brittany: *A. bipustulata* L. and *T. rapae* West. The influence of the host phenotype on the host selection behaviour of the two pupal parasitoids of *D. radicum* – *A. bilineata* and *A. bipustulata* – was also investigated.

## Materials and methods

### Insect rearing

Colonies of *D. radicum*, *A. bilineata*, and *A. bipustulata* were established using field-collected cabbage root fly pupae from La Rimbaudais, France. Rearing procedures were based on Fournet *et al.* (2001). Early and late populations of *D. radicum* were selected using backcrosses over six and four generations respectively. *Trybliographa rapae* were reared according to the method of Neveu *et al.* (1996). All insect colonies were maintained at  $19 \pm 1^\circ\text{C}$ , 65% r.h., and a LD 16:8 h cycle.

### Experimental set-up

All *D. radicum* puparia used in the experiments were medium-sized (between 5.5 and 6.2 mm) as host size can significantly affect development time and host selection behaviour in *Aleochara* species (Fournet, 2000).

In all parasitisation experiments using *A. bipustulata* larvae, newly formed *D. radicum* puparia of both phenotypes (early and late) were placed in a 35-ml cup (Solo cup, Chicago, U.S.A. P100) on 2 ml of sand moistened with 1 ml of distilled water. The puparia were then covered with 2 ml of moist sand (2 ml of sand + 1 ml of distilled water). In experiments in which a single puparium was required, the puparium was placed in the centre of the cup. When two puparia were needed, puparia were placed at 5 mm from the cup wall and oriented in the axis of the cup radius. *Aleochara bipustulata* larvae were individually released on a piece of damp filter paper deposited on the sand at the centre of the cup. Larvae that did not immediately crawl into the sand were replaced to avoid any bias in parasitisation success as a result of manipulation injury. Cups were capped and kept in complete darkness under the same climatic conditions as described above.

*Experiments – acceptance, survival rate, development time, and emergence pattern of Aleochara bipustulata and Trybliographa rapae*

For *A. bipustulata*, the influence of the host phenotype was evaluated in a no-choice experiment, by introducing one newly emerged larva (< 8 h) into a cup where one puparium was buried in the sand. Puparia were examined after a period of 96 h, and the number of penetrated host pupae was recorded. Penetrated puparia were buried in the sand again, until the emergence of *Aleochara* adults. Ten larvae of *A. bipustulata* were tested for each phenotype and the experiment was replicated 30 times.

For *T. rapae*, the influence of the host phenotype was evaluated by introducing (during 72 h) one mated *T. rapae* female (48–72 h old) into a plastic cup containing water and honey as food source and a piece of turnip (between 35 and 40 g) infested with *D. radicum* larvae. Forty *D. radicum* eggs were deposited on the turnip piece 16 days before the introduction of *T. rapae* females (i.e. day 0). The eclosion rate of *D. radicum* eggs was examined after a period of 8 days and the number of available larvae was recorded. *Delia radicum* pupae were extracted from the sand 21 days after the start of the experiment and then put in a plastic cup on moist sand until the emergence of *D. radicum* and *T. rapae* adults.

Survival rate was measured as the proportion of adults emerging from parasitised pupae. Development time was calculated as the time to adult emergence from the start of the experiment for *A. bipustulata* and from the day of introduction of females for *T. rapae*. Newly emerged flies, *T. rapae* and *A. bipustulata* adults were counted every other day to establish the emergence patterns. *Trybliographa rapae* adults were sexed just after emergence by observation of the length of their antennae (males have longer antennae).

*Statistical analysis*

The influence of the host phenotype (early or late) on the survival rate of *T. rapae* and *A. bipustulata* was evaluated

with ANOVA using binomial errors and number of emerged pupae as the sample size. For both species, the influence of host phenotype on development time was evaluated with ANOVA. ANOVA analyses were conducted using GLIM 3.77 (Royal Statistical Society of London, 1985). It was verified that there was no overdispersion in the data by using appropriate tests (Crawley, 1993). The distributions of *A. bipustulata* emergence and the distributions of *T. rapae* males and females were compared between both host phenotypes with a Fisher exact test (SAS Institute, 1988).

*Host phenotype selection behaviour of Aleochara bilineata and Aleochara bipustulata host-seeking larva*

The host selection behaviour was evaluated in a choice experiment by introducing one newly emerged *Aleochara* (*A. bilineata* or *A. bipustulata*) larva in a cup where two puparia of both phenotypes were buried in the sand. To evaluate the influence of host age on selection behaviour, each replicate was composed of three cups which were infested at a determined age of the host pupae: 0 days, 8 days, and 14 days. Puparia were examined after a period of 96 h, and the number of puparia of each phenotype penetrated by the larvae was recorded. Penetrated puparia were buried in the sand again until they emerged as adults. The experiment was replicated 30 times for each species.

The proportions of larvae entering the two offered hosts were compared with the null expectation of 0.5:0.5 using a  $\chi^2$  test for both host ages and species. The effect of the host age on the choice of the larva was determined using a Fisher exact test (SAS Institute, 1988).

**Results**

*Acceptance, survival rate, development time, and emergence pattern of Aleochara bipustulata and Trybliographa rapae in early or late Delia radicum host puparia*

The acceptance rate of *A. bipustulata* was not influenced by the host phenotype, while survival was significantly lower in early host puparia (Table 1). Development time (Table 1) and emergence pattern (Fisher exact test,  $P = 0.347$ ) were not influenced by the host pupae phenotype. Emergence pattern of *A. bipustulata* adults consisted of only one peak (Fig. 2). The spread of the emergence peak was 23 days when reared on early *D. radicum* pupae and 24 days when reared on late *D. radicum* pupae.

For *T. rapae* there was a strong influence of host phenotype on survival rate and development time (Table 1). Regardless of the host pupae phenotype, the emergence pattern of *T. rapae* adults showed two peaks corresponding to a bimodal emergence of type A with a group of early emergers and a group of late emergers (Fig. 3). The spread of the first peak, corresponding to early emerging *T. rapae* adults, was 21 days when reared on the early *D. radicum* phenotype and 24 days when reared on the late *D. radicum* phenotype (Fig. 3).

**Table 1.** Influence of the host phenotype on acceptance, survival, and development time of *Aleochara bipustulata* and *Trybliographa rapae*. For *A. bipustulata*, survival rate was measured as the proportion of adults emerging from penetrated pupae. For *T. rapae* survival rate was measured as the proportion of *T. rapae* adults from emerged pupae.

	Host phenotype		Test	d.f.	p
	Early	Late			
<i>Aleochara bipustulata</i>					
Acceptance (%)	78.73 ± 6.09	81.3 ± 5.56	$\chi^2 = 0.83$	1	0.362
Survival (%)	62 ± 4.26	72.54 ± 6.70	$\chi^2 = 5.65$	1	0.017
Mean development time (days)	31.68 ± 0.85	30.95 ± 0.78	$t = 1.87$	323	0.062
<i>Trybliographa rapae</i>					
Survival (%)	40.49 ± 9.43	71.77 ± 10.64	$\chi^2 = 59.08$	1	$1.514 \times 10^{-14}$
Mean development time (days)	46.63 ± 1.61	55.81 ± 1.87	$t = 7.21$	495	$2.106 \times 10^{-12}$

The spread of the second peak, corresponding to late emerging *T. rapae* adults, was 37 days with both *D. radicum* phenotypes (Fig. 3). For both host phenotypes, early or late, emergence patterns of males were significantly different than those of females (Fisher exact test,  $P < 0.0001$ ).

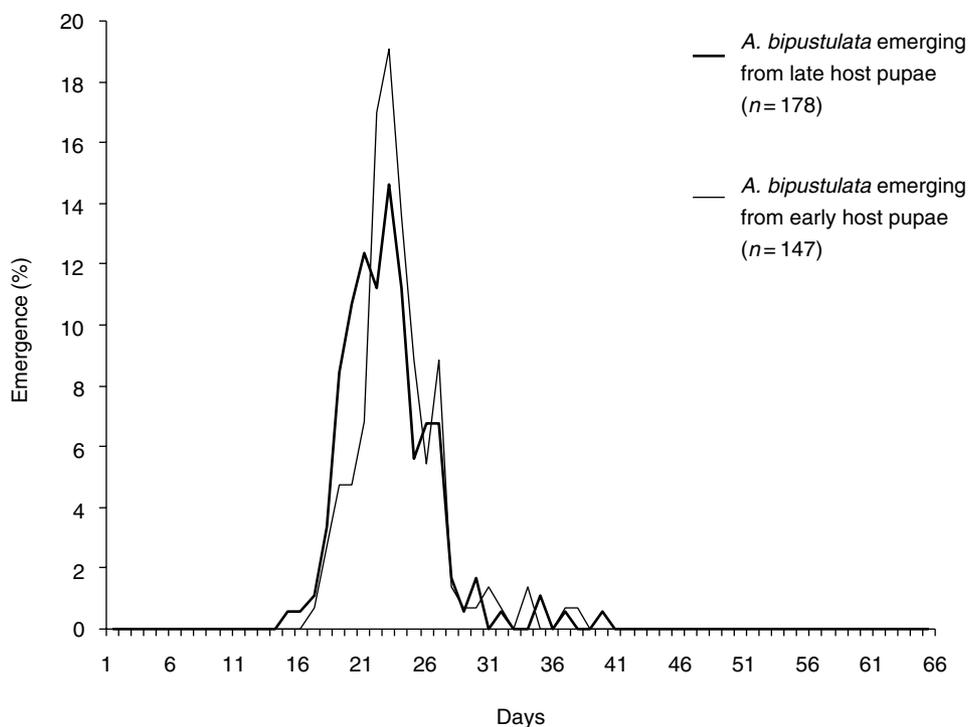
#### Host phenotype selection behaviour of *Aleochara bilineata* and *Aleochara bipustulata* host-seeking larvae

The host selection behaviour of the larvae was clearly influenced by the age of the host pupae for both *Aleochara* species (Fisher exact test, *A. bilineata*:  $P = 0.012$ ; *A. bipustulata*:  $P = 0.041$ ) (Fig. 4). For 0- and 8-day-old pupae, *A. bilineata* and *A. bipustulata* larvae showed no host phenotype

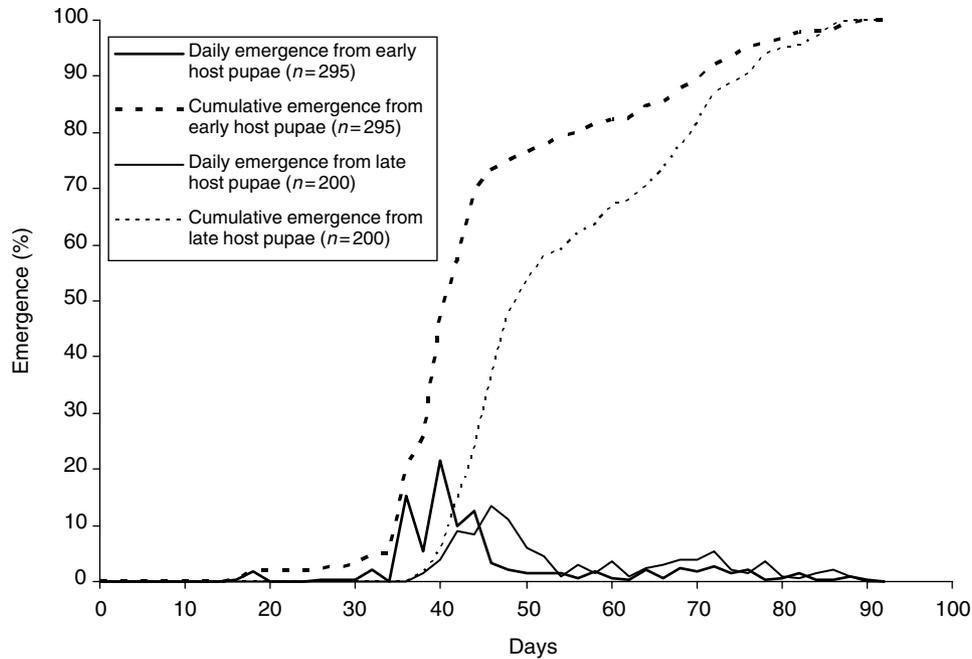
preference ( $\chi^2_1 = 0.18$  and  $\chi^2_1 = 0.14$  respectively at day 0; and  $\chi^2_1 = 0.33$  and  $\chi^2_1 = 0$  respectively at day 8; both  $P > 0.05$ ). However for 14-day-old pupae, larvae of both species penetrated significantly more often in late host pupae ( $\chi^2_1 = 14.44$  and  $\chi^2_1 = 8.895$  respectively, for *A. bilineata* and *A. bipustulata*; both  $P < 0.001$ ).

#### Discussion

In the first set of experiments we investigated how the host phenotype, early or late, influenced survival and development time of *A. bipustulata* and *T. rapae* larvae. The host phenotype did not affect the parasitisation rate or development time of *A. bipustulata* larvae. The same



**Fig. 2.** Emergence pattern of *Aleochara bipustulata* adults reared on early and late *Delia radicum* pupae at 19 °C, 65% r.h. and LD 16:8 h cycle.



**Fig. 3.** Emergence pattern and cumulative emergence curves of *Trybliographa rapae* adults reared on early and late *Delia radicum* pupae at 19°C, 65% r.h. and 16: 8 h LD cycle.

parasitism level was obtained by Langlet (1997) for *A. bilineata*. In *T. rapae*, however, development time was longer in late host pupae than in early ones. Also, survival of *A. bipustulata* and *T. rapae* larvae was affected by the phenotype of the host pupa. For these two species, survival was significantly higher in late host pupae than in early ones. The reverse tendency was shown for *A. bilineata* larvae, which had a higher survival rate in early *D. radicum* host pupa (Langlet, 1997).

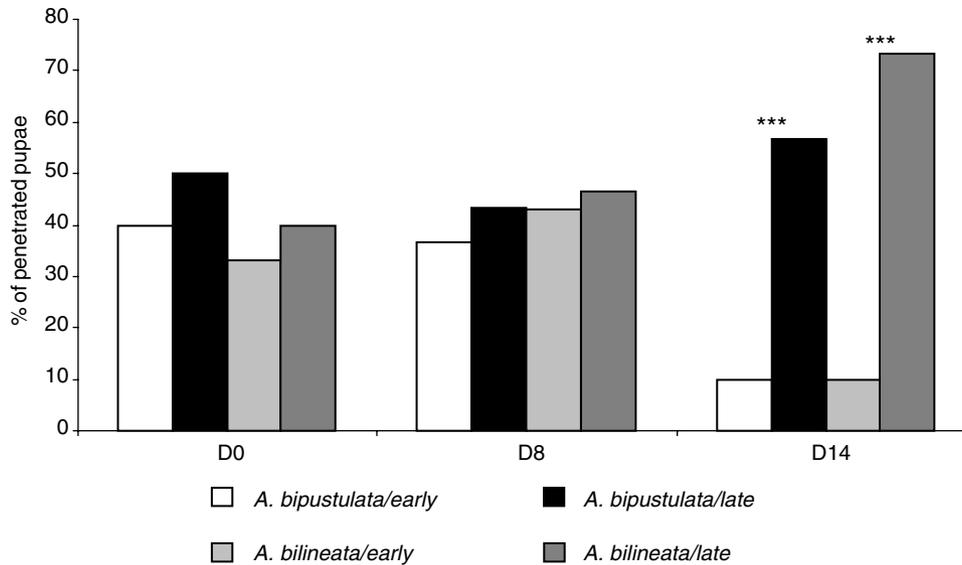
As early and late *D. radicum* host pupae differ in their growth rate (Biron *et al.*, 2002), differences in development time for *T. rapae* may be due to adaptations to the pupal growth rate at the moment of destructive feeding. As early host pupae develop faster, they provide the necessary amount of food needed for the successful development of the parasitoid larva and the optimisation of its size. Consequently, the larva begins its destructive feeding on the host tissues earlier and, therefore, development proceeds faster than in late host pupa. Such a mechanism does not occur in both *Aleochara* species that parasitise the host at its exponential growth (i.e. the pupal stage). For these species, development time is influenced by host size only, as it often takes less time to consume small hosts than large ones (Godfray, 1994).

Among the three parasitoid species, survival was not affected by host phenotype in the same proportion. One functional explanation may be that both host and parasitoid development have to be well synchronised to ensure successful development. Indeed, host development is associated with important physiological changes (especially from the beginning of the nymphal stage to the

adult stage just before emergence) that can strongly modify the nutritional quality of the host for the parasitoid larva and thus affect its successful development. For *T. rapae* and *A. bipustulata*, development of early hosts probably proceeds too fast compared with parasitoid larvae requirements (in term of quality and quantity of food) and ensures a lower survival rate than in late host pupae. In contrast, *A. bilineata* larvae, which need less time to develop than both other parasitoid species (Brunel *et al.*, 1999; Fournet *et al.*, 2000), encountered a high development success in early and furthermore in late host pupae.

Given the influence of the host phenotype on the successful development of the parasitoid, the question arises whether or not host-seeking larvae of *Aleochara* species are able to discriminate between early and late host pupae. Hence, host preference in larvae given a choice between one early and one late host puparia was investigated.

In choice experiments, host-seeking larvae of *A. bilineata* and *A. bipustulata* showed no host preference when the host was 0–8 days old, but strongly preferred late hosts when puparia were 14 days old. As larvae preferred late host puparia when they were 14 days old but showed no host phenotype preference when host puparia were 0–8 days old, they did not appear to discriminate between such hosts directly on the basis of phenotype but rather selected them according to their developmental stage. If there were no apparent differences between early and late host puparia at 0 and 8 days, there were strong differences at 14 days. As late host pupae take three times longer to develop (Biron *et al.*, 2002), they were still at the pupal stage at 14 days while early ones were at the pharate adult stage just before



**Fig. 4.** Host phenotype preference (% of penetrated pupae) relating to the age of host pupae of first-instar larvae of *Aleochara bilineata* and *Aleochara bipustulata* when one early and one late *Delia radicum* pupae were offered simultaneously. ( $\chi^2$  test). D0, day 0; D8, day 8; D14, day 14. \*\*\* $P < 0.001$ .

emergence. Host-seeking larvae probably avoid parasitising hosts that have finished their development. As a consequence, the longer pupal development of the late emerging phenotype results in a longer period of time favourable for parasitisation by *Aleochara* larvae in the field and thus in a higher vulnerability of this biotype. The results reveal that host development stage, like host size, host species, and host parasitisation status (see Fournet, 2000 for a review) is a key factor in the host selection behaviour of Coleopteran parasitoids.

In the last part of this study, it was determined if the host phenotype had an influence on parasitoid emergence pattern. The host phenotype affects the emergence pattern of neither *T. rapae* nor *A. bipustulata* (nor *A. bilineata* according to Langlet, 1997). In both *Aleochara* species, adults emerged in only one peak; however, independently of the host phenotype, *T. rapae* adults emerged in two peaks. This second result was more surprising and showed that polymodal emergence also occurs in hymenopteran parasitoid species. Indeed, polymodal emergence of type A has been observed in four insect orders, Hymenoptera, Diptera, Lepidoptera, and Odonata, but only in holometabolous and phytophagous species (Corbet, 1963; Biron *et al.*, 2002, 2003). In *D. radicum*, such an emergence type gives some evolutionary advantages by optimising the resource use by the presence of adult flies over a longer period of time during the season and ensuring that a sizeable proportion of larvae enter diapause before overwintering. As for phytophagous species, one functional explanation for a polymodal emergence in *T. rapae* may be the avoidance of detrimental breeding conditions, especially competition with other parasitoid species. In Brittany, *T. rapae* competes strongly with both *Aleochara* species for the parasitisation

of *D. radicum*; however, *T. rapae* seems to be a poor competitor as both *Aleochara* species can parasitise and develop successfully in puparia already parasitised by *T. rapae* (Reader & Jones, 1990; Fournet *et al.*, 2000). Thus, delaying emergence in a second peak could increase the probability that *T. rapae* larvae can complete their development at a time when *Aleochara* first-instar larvae are not active in the soil.

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