Effect of expected offspring survival probability on host selection in a solitary parasitoid

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Abstract

Optimal Foraging Theory predicts that parasitoid females should optimize their host selection to maximize their lifetime fitness gain and parasitize the most profitable hosts. In particular, in solitary parasitoids, females should avoid superparasitism, at least when sufficient unparasitized hosts are available. However, when unparasitized hosts are scarce, they should prefer, among already parasitized hosts, those that provide the best survival probability to their progeny, which depends on the age and the developmental stage of the first parasitoid.

To test this hypothesis in a solitary ectoparasitoid, *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae), we first assessed the survival probability of a second parasitoid according to the time elapsed since initial parasitism. We then analyzed the female selection behavior in patches containing a mixture of hosts parasitized over various time intervals.

Our results showed that the older the opponent larva was, the lower the survival probability of the second parasitoid was. However, when the first individual had reached the prepupal stage, both individuals could complete their development. At this stage, the survival probability of the second parasitoid was surprisingly high but such individuals were reduced in size.

Our study also showed that host acceptance by females was strongly correlated with the survival probability of their progeny when the first parasitoid was from 0 to less than 10 days-old. When the first parasitoid had reached the prepupal stage, females usually rejected these hosts, although the survival probability of the offspring was quite high. This discordance between female host selection behavior and progeny survival probability is discussed.

Introduction

Parasitoid females should adapt their oviposition behavior in relation to the profitability of the hosts that they encounter (Charnov & Skinner, 1985). In solitary species, females should especially avoid superparasitism, as much as possible, to enhance their fitness, since the survival probability of a second parasitoid is generally strongly reduced. Such an avoidance of parasitized hosts requires the ability to distinguish parasitized from unparasitized hosts (i.e., host discrimination) (van Alphen & Nell, 1982). However, superparasitism can become advantageous under certain circumstances (van Alphen & Visser, 1990; Visser

et al., 1992a,b; Godfray, 1994; Sirot & Krivan, 1997). In situations where superparasitism is adaptive, the ability to choose from parasitized hosts those that offer the best survival probability to the progeny could be an advantageous trait. This probability frequently depends on the age (i.e., the developmental stage) of the first parasitoid present in or on the host (Mackauer, 1990; Tillman & Powell, 1992; Ueno, 1999; Islam & Copland, 2000). Thus, the ability to use cues that are correlated with the time elapsed since the first parasitism could provide parasitoids with a strong selective advantage by allowing them to select their hosts more efficiently.

In solitary parasitoids, only one individual can emerge per host: competitors are eliminated during their development (van Lenteren, 1981). Various mechanisms can be involved in the elimination of competitors. These mechanisms have

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mainly been studied in endoparasitoids. They can be classified into two basic categories: physical combat (i.e., fights between larvae) and physiological suppression [i.e., starvation, anoxia, hemolymph changes due to the defensive reaction of the host in response to the first parasitism or the effect of products such as toxins or cytolytic enzymes secreted by the first larva, teratocytes, or ovipositing females (see Vinson & Hegazi, 1998 for a review)] (Salt, 1961; Mackauer, 1990; Marris & Casperd, 1996; Mayhew & van Alphen, 1999). Although this question has rarely been investigated in ectoparasitoids, it seems that the main mechanism of elimination in these species is physical attack by first-instar larvae (Wylie, 1971; Wai & Fujii, 1990). These larvae are generally able to kill older larvae, their success rate decreasing with the size (i.e., the developmental stage) of the opponent.

Pachycrepoideus vindemmiae Rondani (Hymenoptera: Pteromalidae) is a solitary parasitoid parasitizing the pupae of many cyclorrhaphous dipteran species (Crandell, 1939; Nøstvik, 1954). In this ectoparasitoid species, eggs are deposited on the nymphs but inside the puparium. Its first-instar larvae are assumed to be able to kill adverse eggs and older larvae (Crandell, 1939). Indeed, contrary to the other instar larvae that are fixed on the host to feed upon its tissue, newly hatched first-instar larvae actively explore the surface of the host, searching for potential competitors in order to kill them with their well-developed mandibles (Crandell, 1939). Using this species, we tested the following hypotheses with respect to the survival probability of supernumerary larvae: (1) if two eggs are laid simultaneously, each eclosing larva has a 50% chance to win the competition, (2) the survival probability of the second egg is strongly reduced when the first parasitoid has reached the first instar, (3) after the first parasitoid has reached the second instar, the survival probability of the second egg increases because the combative first instar is expected to kill older instars, and finally (4) the survival probability of the second parasitoid is expected to decrease when the competitor becomes older, since an older larva is also a bigger one and a bigger opponent is usually more difficult to kill.

Offspring survival probability is expected to influence female host selection. Theoretical models predict that the optimal decision rule of females should be a zero-one rule (either never or always accept hosts of a given value in a given environmental context for a female in a given physiological state) (Janssen, 1989; Mangel, 1989; van Alphen & Visser, 1990; Rosenheim, 1999). Thus, *P. vindemmiae* females, placed in the same conditions and having a similar experience, are expected to always accept parasitized hosts which ensure some threshold survival probability to a second parasitoid and always reject all other hosts. When

facing hosts parasitized over different time intervals, and according to the expected survival probability of supernumerary larvae, females should always lay on the most profitable hosts and avoid the less profitable ones. As very recently parasitized hosts (containing eggs) and hosts containing second instar larvae (i.e., small non-fighting larvae) seem to be more profitable than hosts containing first instar (i.e., fighting larvae) or old larvae (i.e., big larvae), it can be expected that females preferentially accept the first two host types rather than the others.

Although many theoretical studies have dealt with host acceptance in relation to host quality (Hughes, 1979; Iwasa et al., 1984; Charnov & Stephens, 1988; Janssen, 1989), experimental studies with simultaneous direct measurement of host quality and host acceptance remain scarce and few empirical studies have attempted to test existing models (Godfray, 1994). Herein, we carried out two experiments in order to simultaneously assess: (1) the quality of already parasitized hosts in relation with the time elapsed since initial parasitism (this quality was estimated by the probability that the second egg will result in an adult parasitoid and a measure of fitness of this adult), and (2) host selection by females confronted with hosts of different quality.

Materials and methods

Rearing

The host, *Delia radicum* L. (Diptera: Anthomyiidae), originated from pupae collected in cabbage fields (*Brassica oleracea* L.) (Brassicaceae) (Le Rheu, Brittany, France) in 1994. It was reared on rutabaga roots (*Brassica napus* L.) in a climate-controlled room ($20 \pm 2\,°C$; $60 \pm 10\%$ r.h.; L16:D8) according to the technique described in Neveu et al. (1996).

Pachycrepoideus vindemmiae females are able to discriminate parasitized hosts from healthy ones (Nell & van Lenteren, 1982) on the basis of external cues (M. Goubault, L. Krespi, G. Boivin, D. Poinsot, J.P. Nénon & A.M. Cortesero, unpubl.). Superparasitism is nevertheless observed, at least in laboratory conditions (Crandell, 1939, M. Goubault, L. Krespi, G. Boivin, D. Poinsot, J.P. Nénon & A.M. Cortesero, unpubl.).

Two strains of *P. vindemmiae* differing in eye color were used. The *P. vindemmiae* black-eyed strain was collected in 2000 (Rennes, Brittany, France) and was reared on the pupae of *D. radicum* in a climate-controlled room ($25 \pm 1\,°C$; $60 \pm 10\%$ r.h.; L16:D8). Adults were supplied with honey, water, and about 150 host pupae which were replaced three times a week. Parasitized pupae were stored in Petri dishes in the same climatic room until emergence of the adults. A recessive mutation appeared spontaneously

in the black-eyed strain, allowing us to select a red-eyed strain, which was then reared separately under similar conditions.

Experimental procedures

Survival probability of competing offspring. Unmated females (n = 20) were allowed to oviposit on *D. radicum* pupae (n = 20) for 4 h. Our tests were only performed on male parasitoid larvae to avoid the effect of a time interval between ovipositions being hidden by the potential effect of sexual asymmetry of larval competition ability (van Baaren et al., 1999). Groups of black-eyed and red-eyed females oviposited separately. Parasitized pupae were then dissected and the eggs present on the pupae (but inside the puparium) were carefully picked up with a needlepoint. Previously unparasitized hosts were artificially 'parasitized' by inserting these eggs through a crack previously made with the needlepoint in the puparium. Unparasitized hosts were 4–6-day-old *D. radicum* pupae, since preliminary studies showed that on older pupae host development resulted in a high larval mortality. In cases where the hosts were naturally parasitized by females, the females seem to have an action on the hosts (e.g., venom injection) which stopped or refrained their development and thus favored immature parasitoid survival. The survival probability of individuals coming from artificially parasitized hosts (done on 4–6-day-old-pupae) was similar to that of individuals coming from naturally parasitized hosts (done on 7–9-day-old pupae). Two eggs were deposited on each unparasitized host (one from each strain). The second deposited egg was laid at varying time intervals after the first. Nine time intervals between successive ovipositions were tested: 0 (less than 4 h separated the two ovipositions), 1, 2, 3, 5, 7, 10, 15, and 18 days. According to these time intervals, the developmental stage of the first parasitoid was expected to be a young egg, an old egg, a first-instar larva, a second-instar larva, a third-instar larva, a fifth-instar larva, a prepupa, a pupa, or a pre-emerging adult, respectively. To control for strain effects, both orders of oviposition were tested (i.e., eggs from black-eyed female first and eggs from red-eyed female second and vice versa). Replicates were around 50 for each time interval and each order, except for the time interval of 0 day, where 160 observations were performed. The number of emerging adults and their eye color were recorded. The size of the individuals obtained was evaluated by measuring the width of their head.

To assess the probability of a parasitoid of either strain achieving its development in the absence of a competitor, a single egg was deposited on 49 unparasitized hosts for the black-eyed strain and on 48 for the red-eyed strain.

Host selection by females. In order to test the ability of the females to use cues that are correlated with time elapsed since first parasitism, a group of 10 hosts consisting of two hosts of five types was offered to one female (n = 24) in a Petri dish (Ø = 2.8 cm, 1.3 cm). These five types of hosts were parasitized less than 4 h (0 day), 1, 2, 5, and 10 days before. Hosts that had been naturally parasitized by black-eyed females were used to avoid potential host rejection due the host manipulation that has to be done for artificial egg insertion. Pupae were 7–9 days old at the time of parasitism, since previous experiments showed that this age range corresponded to the maximal infestation levels of *D. radicum* by *P. vindemmiae* in the laboratory (Grandjirard et al., 2002). The females used for the tests were from the black-eyed strain. They were 24 h old and fed with honey. In order to have females mated and experienced, they were individually placed, prior to testing, in the presence of one male and five unparasitized *D. radicum* pupae for 13 h. The females were then placed in an empty Petri dish for 30 min. By dissection of the pupae, we found that 90% of the females submitted to such conditions were mated and had at least one oviposition experience. During tests, the behavior of each female was recorded over 2 h, and acceptance of the different types of hosts were recorded. When ovipositions were observed, host pupae were dissected to check for egg presence and to confirm the developmental stage of the first parasitoid.

Statistical analysis

Probability of survival and host acceptance were analyzed with a generalized linear model (GLIM), assuming a logit link and a binomial distribution (McCullagh & Nelder, 1989). For survival probability, the variables introduced into the model were the strain and the age difference between the eggs. For host acceptance probability, the variables introduced into the model were the time interval between ovipositions, the female identity, and the total number of hosts encountered by each female during the course of the experiment. Analyses were carried out using SAS Software (Version 3.04, SAS Institute Inc.) with the GENMOD procedure. Pair-wise comparisons of frequencies were performed with χ^2 tests. The sizes of the individuals were compared with ANOVA and Fisher's PLSD.

Results

Survival probability of competing offspring

The survival probability of the two immatures present on the hosts in relation to the age difference between them was first analyzed globally with the GLIM program. This analysis showed that the survival probability of the first

Table 1 Survival probabilities of individuals from both strains (black = black-eyed strain; red = red-eyed strain) and proportion of hosts from which at least one individual emerges in relation with the time interval between ovipositions

	Single oviposition	Time interval between ovipositions (in days)								
		0	1	2	3	5	7	10	15	18
1st individual survival										
Black	0.61	0.50	0.37	0.38	0.42	0.54	0.66	0.64	0.71	0.55
Red	0.73	0.30	0.54	0.47	0.41	0.72	0.68	0.40	0.65	0.81
2nd individual survival										
Black	–	0.50	0.22	0.17	0.26	0.04	0.00	$0.23 + 0.12$[a]	$0.06 + 0.29$[a]	$0.04 + 0.40$[a]
Red	–	0.30	0.35	0.29	0.20	0.12	0.02	$0.08 + 0.36$[a]	$0.02 + 0.35$[a]	$0.07 + 0.36$[a]
Proportion of hosts from which at least one individual emerges[b]										
Black (then Red)	0.61	0.80	0.73	0.67	0.63	0.66	0.68	0.72	0.73	0.62
Red (then Black)	0.73		0.75	0.65	0.67	0.76	0.68	0.63	0.71	0.85

[a]The second individual emerged from a host where the first individual had already completed its development.
[b]Corresponds to the proportion of hosts from which at least one individual emerged, whatever its eye color. When time interval is 0 day, there is a single group of data and thus only one result.

parasitoid was dependent on the time interval between ovipositions ($\chi^2 = 40.74$, d.f. = 7, P < 0.0001), but not on the strain ($\chi^2 = 2.25$, d.f. = 1, P = 0.13) (Table 1). Similarly, the survival probability of the second parasitoid was dependent on the delay between the two ovipositions ($\chi^2 = 98.37$, d.f. = 7, P < 0.0001) but not on the strain ($\chi^2 = 3.00$, d.f. = 1, P = 0.08) (Table 1). The interaction between strain and time interval had no significant effect on the survival probability of the second parasitoid ($\chi^2 = 6.55$, d.f. = 7, P = 0.48) but had a significant effect on the survival probability of the first parasitoid ($\chi^2 = 19.30$, d.f. = 7, P = 0.007). This was mainly due to an excess in survival probability of the red strains for time intervals of 1, 5, and 18 days and to an excess in survival probability of the black strain for a time interval of 10 days. The survival probabilities of the two strains when reared alone (i.e., only one egg per host) were not significantly different ($\chi^2 = 1.50$, d.f. = 1, P = 0.22) and were $67.0 \pm 4.8\%$ when the data from the two strains were pooled (Table 1).

The emergence probability (i.e., the proportion of pupae from which at least one parasitoid emerged) was constant (Table 1). It was $69.2 \pm 1.4\%$ when the data from the two strains were pooled and was independent of the age difference between the two parasitoids (GLIM, $\chi^2 = 16.50$, d.f. = 17, P = 0.49). Thus, in all situations (i.e., for every time interval between ovipositions and in both orders of oviposition), no parasitoid emerged from approximately one-third of the pupae.

From the 160 pupae on which two eggs of both strains had been simultaneously deposited, 77 adults of the black-eyed strain were obtained and 47 adults of the red-eyed strain. Double emergences were never observed. The competition between the two strains was not perfectly

symmetric: the survival of the black-eyed strain individuals was higher than of the red-eyed strain ($\chi^2 = 11.85$, d.f. = 1, P < 0.001). However, results from the global analysis showed that the advantage of the black-eyed strain disappeared as soon as the ages between the two parasitoids differed.

When the age difference between the eggs was greater than or equal to 10 days, the survival probability of the first parasitoid was not affected when compared to its survival when reared alone ($\chi^2 = 0.56$, d.f. = 1, P = 0.45). Conversely, the survival probability of the second parasitoid was significantly reduced from 0.67 to 0.40 ($\chi^2 = 22.0$, d.f. = 1, $P = 2.7 \times 10^{-6}$). Whereas no double emergence was observed when the age difference between the parasitoid offsprings introduced on the host was shorter than 8 days; they accounted for about 44% of all emergences when the interval was equal to 10 days or more. For these time intervals (i.e., 10, 15, and 18 days), 79% of the second parasitoids that survived emerged from hosts that had already permitted the development of a first parasitoid. These results suggest the existence of a critical stage after which both individuals have a better chance of completing their development.

We developed a model that summarizes our results and also allows the description and estimation of the parameters that influence the survival probability of immatures.

The survival probability should conform to the following model:

$$P_s = P_{su} \cdot [P_c(d) \cdot (1 - P_{crit}(d)) + P_2 P_{crit}(d)] \qquad (1)$$

where P_s is the probability of survival of each individual, either the first or the second: it depends on the time interval between ovipositions, d (by convention, d < 0 for

the first developing parasitoid and d > 0 for the second), P_{su} is the probability of the pupa being suitable, $P_c(d)$ is the probability of winning the competition when the interval between ovipositions is d and the competitor has not reached the critical stage, $P_{crit}(d)$ is the probability that the competitor has reached the critical stage d days after oviposition, and P_2 is the factor of reduction in survival probability due to the presence of a competitor having reached the critical stage.

Equation 1 shows that survival probability is the product of the basic probability of survival P_{su} (in the absence of competition not all ovipositions lead to an emergence) multiplied by the probability of surviving the competition. If the competitor has not yet reached the critical stage [which happens with a probability $1 - P_{crit}(d)$], the probability of survival depends on its age $P_c(d)$ and decreases with it. If the competitor has reached the critical stage (which happens with probability $P_{crit}(d)$), the probability of survival is reduced by a constant factor P_2, that could simply account for a reduction of the host quality caused by resource sharing.

The canonical links Logit (McCullagh & Nelder, 1989) functions were chosen for $P_c(d)$ and $P_{crit}(d)$:

$$\ln\left(\frac{P_c}{1-P_c}\right) = a \cdot d \text{ and } \ln\left(\frac{P_{crit}}{1-P_{crit}}\right) b \cdot (d-c)$$

where a, b, and c are unknown parameters.

The adequacy of the model was checked, and estimates of its parameters were obtained by fitting it to the data. This was carried out by maximizing the likelihood of the observations with the function 'solver' of Microsoft Excel 97 (Microsoft Office 97 for Windows, Microsoft Corporation). The variances of the estimates were estimated by the diagonal elements of the inverse of the negative of the information matrix (Jones et al., 1991). Calculations were performed with Maple V Release 4 (Waterloo Maple Software). As no difference in survival between the two strains was found, the data from both strains were pooled to compare the survival probability of the first and second individuals according to the time interval between ovipositions.

The estimates of the different parameters (and their standard error) were $P_{su} = 0.68$ (0.018), $P_2 = 0.59$ (0.045), a = −0.36 (0.037), b = 7.9 (100) and c = 8.8 (19). As indicated by the large standard error of their estimates, the precision of the estimation of the parameters b and c was very low. This resulted from an abrupt switch in the survival probability of the second parasitoid when the first was between 7 and 10 days old. However, except for the case of d = 10, the observed survival probabilities appeared to be adequately predicted by the model, and this confirmed
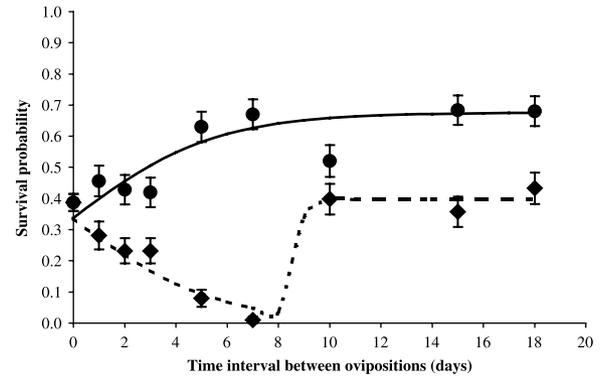
Figure 1 Survival probability observed (first individual: circles, second individual: diamonds) and predicted by the model (Eqn 1) (first individual: solid line, second individual: dotted line) as a function of the time interval between the two ovipositions.

that the data were consistent with our modeling hypotheses (Figure 1). The parameter c provided an estimation of 8.8 days for the age at which 50% of the individuals had reached the critical stage. The critical stage thus corresponded to the prepupal stage. The estimate of P_{su} (0.68) was very similar to the value observed for an individual reared alone (0.67) or when there were two individuals developing on the same host (0.69), confirming that the competition neither decreased nor increased the global value of the host.

Concerning the size of emerging parasitoids, it appeared that the second individuals from double emergences were significantly smaller than first individuals from double emergences or individuals from single emergences. The average head width of the second individuals from double emergences was 0.57 ± 0.04 mm vs. 0.63 ± 0.02 mm for the others (F = 104.11; d.f. = 2; P < 0.001).

Host selection

The probability of oviposition at first encounter was significantly dependent on host status (Figure 2) (i.e., the age of the first parasitoid) ($\chi^2 = 41.60$, d.f. = 1, P < 0.001) but not on the female identity ($\chi^2 = 19.70$, d.f. = 23, P = 0.66) or on the total number of hosts she encountered during the full experiment ($\chi^2 = 0.58$, d.f. = 1, P = 0.45). These last two results suggest that the effect of female experience was negligible when compared to the effect of host status.

The following model was fitted to the data (Figure 2):

$$\ln\left(\frac{P_o}{1-P_o}\right) = f \cdot d + g \tag{2}$$

where P_o is the probability of oviposition, d is the delay since the first oviposition, and f, g are parameters.
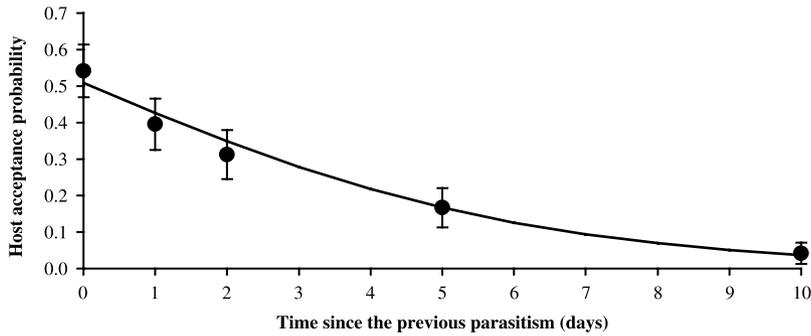
Figure 2 Proportion of hosts accepted for oviposition at first encounter by the second female as a function of the time elapsed since oviposition by the first female. Circles: observations. Solid line: predictions of the model (Eqn 2).

Estimates of f and g were obtained by maximizing the likelihood with the function 'solver' of Microsoft Excel 97 and were, respectively, −0.33 (0.06) and 0.03 (0.21). Numbers within brackets are the standard errors of the estimates and were calculated using the same method as for Eqn 1.

Relationship between the oviposition probability and the survival probability of the offspring

Equations 1 and 2 allowed us to relate the oviposition probability of females to the survival probability of their offspring, according to the age of the competitor. For delays between ovipositions ranging from 0 to 8 days (i.e., the critical stage), the simulated oviposition probability appeared to increase almost linearly with survival probability (Figure 3).

Discussion

In situations of superparasitism, the age and developmental stage of the first immature parasitoid present on or in a host influence the fitness of the second parasitizing female (Mackauer, 1990; Tillman & Powell, 1992; Marris & Casperd, 1996; Ueno, 1999; Islam & Copland, 2000),
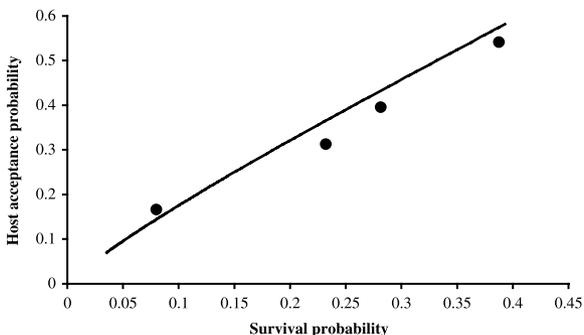
Figure 3 Relationship between the probability that a female will accept a parasitized host and the probability of survival of its offspring when the time between two ovipositions ranges from 0 to 8 days. Circles: observations. Solid line: predictions of the model (Eqns 1 and 2).

especially in solitary species. This should favor evolution of the ability to assess the age of the competitor on a parasitized host. The results we obtained indicate that *P. vindemmiae* has actually evolved such a discriminating ability.

The outcome of larval competition has been evaluated using two strains that were easily distinguishable by their eye color. When two eggs were laid simultaneously, the probability of winning the competition was not symmetric: black-eyed parasitoids won more often than mutant red-eyed parasitoids. However, the global analysis showed that the advantage of the black-eyed strain disappeared when the time interval between ovipositions was equal to 1 day or more. This superiority, which was observed when the eggs of both strains were laid simultaneously, could be explained by a slightly earlier hatching in the black-eyed strain. The hatching time difference between both strains seemed to be short (shorter than 1 day, as after 1 day between ovipositions, no strain effect was found).

When the delay between ovipositions was greater than 1 day, the survival probability of the second parasitoid decreased progressively down to almost 0 when the first parasitoid had reached the fifth larval instar (i.e., 7 days after oviposition). Thus, whereas the first-instar larvae were expected to kill their competitors (Crandell, 1939), the strong reduction of survival probability of the second parasitoid expected when the first had reached the first instar was not observed. Therefore, our results invalidate the hypothesis that the elimination of competitors in situations of superparasitism is mainly due to the first larval instar, as shown in other solitary ectoparasitoids (Wylie, 1971; Wai & Fujii, 1990). Moreover, a second individual could survive and win the competition in 30% of the cases when it was laid after the first parasitoid reached the first instar. Moreover, first-instar larvae did not often seem to be able to kill later-instar larvae. Thus, contrary to our predictions, the survival probability of the second individual of *P. vindemmiae* did not increase again after the first parasitoid had reached the second instar, but regularly decreased as the age of the opponent increased and was

close to 0 when the first individual had reached the fifth larval instar. In fact, the greater the size difference between the larvae, the higher the probability of the bigger one (i.e., the first installed parasitoid) winning the competition. Finally, when the first parasitoid had reached a critical stage which corresponded to the beginning of the prepupal stage [8.8 days after oviposition according to our model (Eqn 1)], both individuals succeeded in completing their development and double emergences were frequently observed (about 44% of the emergences were double). Considering these results, the broadly accepted status as solitary parasitoid of *P. vindemmiae* (Crandell, 1939; Nøstvik, 1954; van Alphen & Thunissen, 1983; Phillips, 1993) can be questioned. *Pachycrepoideus vindemmiae* could be intermediate between strictly solitary and gregarious species, similar to *Aphaereta genevensis* (Mayhew & van Alphen, 1999). Moreover, competitors seem to be eliminated through direct interactions. Indeed, double emergences indicate that (1) resources available in *D. radicum* pupae were sufficient to feed two male larvae (even if the second had a smaller size); (2) competition occurred during larval stages but stopped as soon as the first parasitoid reached the prepupal stage. Therefore, starvation, which was observed in some other ectoparasitoid species (Wylie, 1971; Wai & Fujii, 1990), is not the main method of competitor elimination on *D. radicum*. Actually, additional behavioral observations (M. Goubault, unpubl.) of larvae competing for hosts, not presented here, have revealed that all larval stages were able to eliminate conspecifics by fighting with their mandibles and that older larvae usually won against younger ones. Physical attacks resulted in the appearance of melanized wound marks on the opponent's tegument and often ended in cannibalism.

These results have been obtained by studying only male larvae in order to avoid the effect of time between ovipositions on larval competition being hidden by a potential sexual asymmetry of larval competition ability (van Baaren et al., 1999). Nevertheless, results could be quite different for female larvae. Indeed, as *P. vindemmiae* females are bigger than males (Crandell, 1939), *D. radicum* pupa may not offer enough nutrients for two developing females, and double emergences of females could be rare. This point remains to be studied.

Host selection experiments showed that, contrary to some other solitary parasitoid species (Hofsvang, 1988; Visser et al., 1992a,b), when *P. vindemmiae* females had the choice between hosts parasitized at different time intervals, they preferred those recently parasitized. This suggests that *P. vindemmiae* females are either able to detect the variation in the host quality according to the age of the first parasitoid, or that their host discrimination capacity increases with time elapsed since first parasitism. The exact cues that allowed the females to discriminate between the different host types remain unknown. Indeed, as females were confronted with naturally parasitized hosts, they had access to cues coming from individuals in development on the host, as well as potential marks left by the first ovipositing females, to evaluate the time elapsed since the first oviposition. Nevertheless, whatever the cues involved, when the hosts were parasitized for less than 8.8 days (i.e., when the first individual was still at a larval stage), the probability of host acceptance was strongly correlated with larval survival, as had previously been found in *Asobara tabida* (van Alphen & Janssen, 1982) and *Leptopilina clavipes* (Driessen et al., 1991). However, this complex behavior is unexpected as models generally predict that the females should switch from host rejection to host acceptance when host quality exceeds some threshold value (Janssen, 1989; van Alphen & Visser, 1990; Rosenheim, 1999). Even if these predictions are applicable to all variations of host quality, they were mainly made for situations where only two categories of hosts are considered (parasitized vs. unparasitized) and in that case, the models predict a zero-one rule (parasitized hosts always accepted or always rejected) (Janssen, 1989; van Alphen & Visser, 1990). Therefore, an apparent discrepancy exists between model expectations that predict a zero-one rule and observations that reveal partial preferences (Sirot & Krivan, 1997). Various explanations have been proposed to account for this discrepancy. First, it could be attributed to some imperfection in host discrimination (Rechten et al., 1983). It could also be an artifact observed at the population level: the zero-one rule is followed by each individual but with a switching threshold which varies among individuals (Stephens, 1985; Mangel, 1989). These variations could result from basic individual differences (genetical) or from different physiological states. Finally, Sirot & Krivan (1997) have shown that partial superparasitism could evolve when host-parasitoid dynamics are taken into account as a means of stabilizing the dynamics. However, it is not clear why selection should favor behavior that leads to a global equilibrium of the system. The first two explanations appear realistic and highly relevant. However, our results do not support them since, first, we did not observe any clear tendency to switch from rejection to acceptance but a regular and very progressive change in acceptance probability when host quality varies. Second, our observations were carried out under standardized controlled conditions and the females did not show an significant inter-individual variability in host acceptance probability, which suggests a low genetic variability at this level. Finally, our results, that could be explained by a simple model (Eqn 2), added to those obtained by previous authors, suggest that partial

preferences could rather be the rule than the exception and could then be adaptive. The possibility of partial preference adaptiveness was theoretically shown by Sirot & Bernstein (1997).

Although *P. vindemmiae* females choose hosts that offered the best survival probability to their offspring among hosts from 0 to less than 8.8 days, this is not true after that time interval. Indeed, whereas hosts parasitized for more than 8.8 days (i.e., when the first individual has reached the prepupal stage) provided a high survival probability to offspring (about 40%) (especially thanks to double emergences), *P. vindemmiae* females rarely accepted such hosts (only about 4% of these hosts were accepted). This surprising discordance between female choice and progeny survival probability could be related to differences in the physical traits of the host puparium related to its age. However, females that have the choice between unparasitized pupae of different ages do not display any preference for pupae of a particular age (Metzger, 2003). This discordance could also be due to the fact that parasitism status may be more efficiently estimated on hosts containing old parasitoid larvae (i.e., parasitized for a long time) than on hosts containing parasitoid eggs (i.e., recently parasitized). Thus, hosts parasitized for more than 8.8 days may be rejected more often only because the probability that females recognize them as parasitized is higher. Another more adaptive explanation of the discordance could be related to a fitness reduction in offspring developing on hosts parasitized for more than 8.8 days. Indeed, individuals emerging from hosts that had already supported the development of a first parasitoid were on average 10% smaller than the first ones. Even if size is not a sufficient parameter to precisely evaluate the fitness of individuals (Roitberg et al., 2001), fitness and size are usually strongly correlated. Additional experiments that we conducted in *P. vindemmiae* showed that in choice situations, bigger males were more successful than smaller ones in mating with females. Therefore, even if their offspring had a good survival probability in hosts parasitized for more than 8.8 days, females could reject them in a choice situation and prefer alternative hosts that provided fewer but fitter offspring.

Our results show that foraging females are not only able to choose hosts that maximize their fitness, as predicted by Optimal Foraging Theory (Charnov & Skinner, 1985), but that they can also very precisely adjust their host selection to the potential offspring fitness on these hosts. Indeed, the results we obtained indicate that host profitability does not only involve the survival probability of the offspring but also that the potential fitness of these offspring may play a crucial role and influence host selection by female parasitoids.

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